

Experimental small-scale flower patches increase species density but not abundance of small urban bees

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Abstract

1. Large flower plantings are often used to combat negative effects of habitat loss on pollinators, but whether these floral additions are effective at smaller scales remains unclear, particularly in urban settings.
2. To test the effectiveness of small-scale floral additions on enhancing urban bee populations, as well as their impact from 1 year to the next, different quantities of potted sweet alyssum (*Lobularia maritima*) flowers were placed across sites in Ann Arbor, Michigan for two consecutive years and the resulting Halictid bee visitors were monitored.
3. Overall, we found the number of flowers added at the local level was significantly and positively correlated with small Halictid bee abundance and species density in an urban landscape. At smaller flower quantities, dynamics were clearly linear, where incremental increases in number of flowers showed significant increases in bee abundance and species density. At larger quantities of floral additions, however, dynamics were nonlinear in that incremental increases in flower quantity had no effect on bee abundance and highly variable effects on bee species density.
4. When comparing the change in small Halictid bee abundance and species density from 1 year to the next, we found a significant increase in bee species density in the second year of small-scale floral additions, but no significant difference in bee abundance.
5. *Synthesis and applications.* Our results show that small flower plantings can have positive effects on small bee communities in urban systems even over a short period of time and therefore confirm that encouraging citizens to plant flowers can be an effective conservation strategy for certain urban pollinator populations. In addition, our finding that smaller flower plantings may have higher impacts on small pollinators than larger plantings suggests resource managers interested in pollinator conservation should consider spreading multiple, smaller floral plantings across the urban landscape, rather than pooling all resources into one large flower patch.

KEYWORDS

bee, biodiversity, flowers, *Lasioglossum ephialtum*, *Lobularia maritima*, patch size, planting size, pollinator, sweet alyssum, urban

1 | INTRODUCTION

Wild bees are an important group of pollinators that appear to be in decline (Koh et al., 2016; Ollerton, Erenler, Edwards, & Crockett, 2014). Given their vital role as pollinators of many wildflowers and crops (Klein et al., 2007; Ollerton, Winfree, & Tarrant, 2011), declines in wild bees could have cascading effects on both ecosystem function and crop yields (Allen-Wardell et al., 1998; Kearns & Inouye, 1997; Vanbergen, 2013). Bee declines have been attributed to various factors including pesticides, invasive parasites, pathogens and habitat loss (Goulson, Nicholls, Botías, & Rotheray, 2015); in this study, we focus on habitat loss and the efforts to reverse its negative effects through the planting of additional flowers. Habitat loss, often the result of agricultural expansion, intensification and urbanization, reduces the floral and nesting resources that bees rely on (Goulson et al., 2015).

There is strong evidence that floral resource availability regulates wild bee populations (Roulston & Goodell, 2011), and increasing floral resource availability has therefore become a focus of pollinator conservation efforts. Floral resources are vital for bee survival—providing both nectar and pollen (Frankie & Thorp, 2009)—and numerous studies confirm the positive link between floral resource availability and bee abundance, richness and diversity (Roulston & Goodell, 2011; Winfree, Bartomeus, & Cariveau, 2011). As a result, many U.S. federal agencies and non-profits recommend increasing floral resource to promote pollinator conservation. The U.S. Department of Transportation's Federal Highway Administration recently released roadside management guidelines encouraging the protection of native vegetation and adjusted mowing frequencies along roadsides to benefit pollinators (Hopwood, Black, & Fleury, 2015). In addition, in response to former President Obama's Executive Strategy to "Promote the Health of Honey Bees and Other Pollinators," an initiative known as the Million Pollinator Garden Challenge was launched to incentivize the spread of pollinator flower habitats across the nation (millionpollinatorgardens.org). Non-profits such as the Pollinator Partnership and the Xerces Society for Insect Conservation stress the importance of both floral and nesting resources and encourage planting pollinator-friendly flowers in gardens and on agricultural lands (<http://pollinator.org/guides>, <http://xerces.org/providing-wildflowers-for-pollinators/>).

Although the link between floral resources and bees is clear, the contexts in which floral additions effectively increase bee abundance and diversity are less clear, particularly for urban landscapes. Urban gardens can provide bees with both floral and nesting resources (Garbuzov & Ratnieks, 2014; Matteson & Langellotto, 2010; Pawelek, Frankie, Thorp, & Przybylski, 2009), and given the trend towards increasing urbanization, urban gardens could become an important tool for pollinator conservation (Goddard, Dougill, & Benton, 2010). The impact of floral additions on pollinators has been well studied in agricultural contexts—where the impact is generally positive (Haaland, Naisbit, & Bersier, 2011; *but see* Wood, Holland, & Goulson, 2015)—but fewer studies have been conducted in cities, where the scales of floral additions are smaller and overall trends are not clear. Two studies, for example, found clear increases in pollinators in an urban area

as a result of floral additions in one main flower-rich garden (Garbuzov & Ratnieks, 2014; Pawelek et al., 2009). In contrast, an experiment that placed patches of native flowers within existing urban community gardens (Matteson & Langellotto, 2011) and two experiments that planted floral patches of varying sizes in urban sites found no significant differences in pollinator visitation (Yurlina, 1998; per unit area, Garbuzov, Madsen, & Ratnieks, 2015).

Several factors that are difficult to control may have contributed to the differences seen across studies. First is the issue of independent samples. Some studies place experimental floral patches within short distances of each other (e.g. flower patches planted 2 m apart, or 30–50 m apart), which may inadvertently act as one large patch of flowers to pollinators not limited by such distances (Garbuzov et al., 2015; Yurlina, 1998). Second is the issue of landscape context for both floral and nesting resources. If floral additions are placed in areas already well populated with flowers, such as community gardens, the effects of floral additions may be negligible (Matteson & Langellotto, 2011). At the same time, if the amount of nesting resources available throughout a landscape is limited, pollinators limited by distance will remain unable to reach floral additions no matter their size (Matteson & Langellotto, 2011). Related to the second issue of landscape context is the third issue of potentially saturating relationships. There is no reason to expect that the relationship between floral additions and pollinator communities is linear, where pollinators increase proportionally to the increase in floral quantity. Instead, it is possible that a saturating relationship exists, where after a saturation point is reached additional floral resources have little to no impact on pollinators (Ebeling, Klein, Schumacher, Weisser, & Tschardtke, 2008; Feldman, 2006). If this is the case, floral additions will only be beneficial to pollinators until this saturation point is reached, potentially explaining why some studies (Blackmore & Goulson, 2014; Garbuzov & Ratnieks, 2014; Pawelek et al., 2009) find floral additions to be effective (systems before saturation point of flowers), while other studies do not (Matteson & Langellotto, 2011) (systems after saturation point).

Our study seeks to understand whether different sizes of small, local floral additions affect small Halictid bee communities, and tries to control for the aforementioned confounding factors. Our research questions are as follows:

1. Does the number of flowers added at the local level affect small Halictid bee abundance and species density, and what is the shape of this relationship (e.g. linear or saturating)?
2. Do flower additions at the local level affect small Halictid bee abundance and species density over a temporal scale (i.e. from one year to the next)?

While we are unable to control all factors in our field experiment, we attempt to account for issues of independent samples, landscape context and potential nonlinearity by: selecting sites separated by distances larger than the foraging range of target pollinators (addressing the issue of independent samples), placing our floral additions adjacent to parking lots—a space where floral and nesting resource availability should

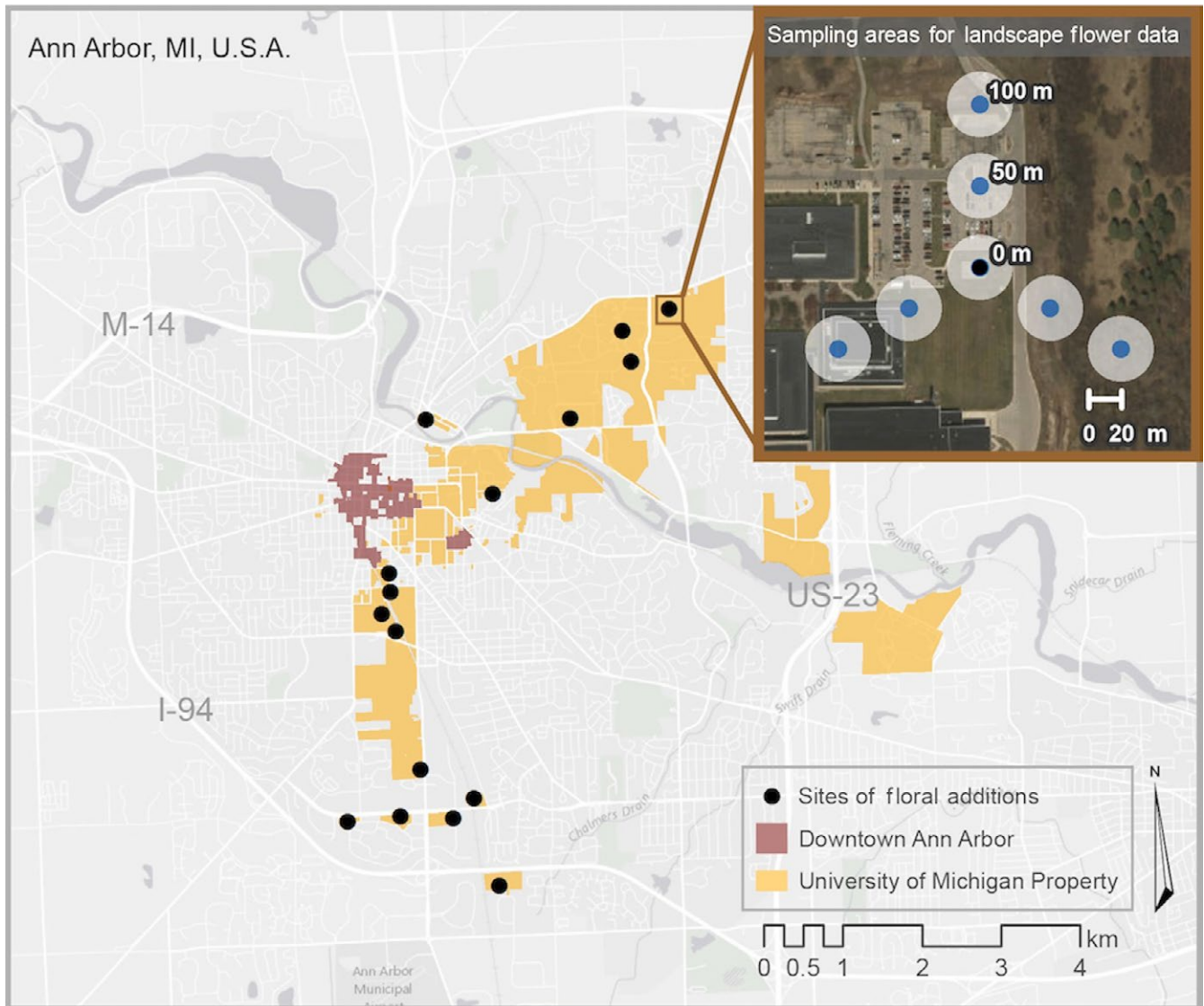


FIGURE 1 Locations of sites where floral additions were placed within Ann Arbor, Michigan. Inset map shows one sampling site in detail, where potted sweet alyssum flowers were placed in the centre (black dot) and landscape flower resource data were taken within 20 m (white circle areas) of sampling points spaced 50 m (blue dots) along three 100 m transects from the centre. Source of base layer: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

be uniformly low—but still documenting landscape floral and nesting resource levels to account for potential effects (addressing the issue of landscape context), and focusing our experiment on small pollinators, in the hopes of providing a full gradient of floral resources—from too little to too much (to explore the possibility of a nonlinear or saturating relationship). Over two summers, we manipulated floral resources across urban and suburban areas in Ann Arbor, in south-eastern Michigan, U.S.A., and monitored the local small Halictid bee response.

2 | MATERIALS AND METHODS

2.1 | Sampling locations

This study was conducted in the summer of 2015 and 2016 at 16 sites in Ann Arbor, Michigan, U.S.A. (Figure 1, Table S1 in

Supporting Information). In an effort to make sites more comparable within a heterogeneous urban landscape, all selected sites bordered paved parking lots, which provide little to no floral and nesting resources for bees. Sites were distanced more than 200 m apart (mean 819 m; range 235–3,182 m) to minimize interactions between small Halictid bee populations, which are estimated to have foraging ranges no greater than 200 m (*pers. comm.* Jason Gibbs, Greenleaf, Williams, Winfree, & Kremen, 2007). Further details on site selection can be found in Appendix S1 in Supporting Information.

2.2 | Flower treatments

The number of white sweet alyssum flowers (*Lobularia maritima*, Easter Bonnet Lemonade variety clones from C. Raker & Sons Inc.,

Litchfield, MI, USA) was manipulated across the landscape to test effects on small bee communities. Sweet alyssum is a perennial plant introduced to North America from the Mediterranean and can bloom from late spring to mid-fall (Picó & Retana, 2001; gardening.cornell.edu). Sweet alyssum was chosen because of its common use in landscaping, long flowering period and small flower size, which attracts mostly small pollinators such as Halictid bees, especially in the genus *Lasioglossum* (Bosch, Retana, & Cerda, 1997). Our field observations and past studies confirm that sweet alyssum flowers provide nectar resources (Davis, Pylatuik, Paradis, & Low, 1998), but we were unable to observe or find information on bees also utilizing sweet alyssum pollen. We wanted our flower choice to target *Lasioglossum* bees because of the diversity of *Lasioglossum* species found in urban areas; targeting this genus ensured we would be able to examine both bee richness and abundance as a response to floral additions. Restricting the study to small pollinators increased the likelihood of our experiment simulating the full spectrum of nectar required by the observed pollinator community—from potentially not enough nectar to more than enough—assuming their small body size translates to ingesting a few microlitres of nectar per day. Focusing on small pollinators also increased the likelihood of sampling independent communities across our sites, given that small pollinators are assumed to have smaller foraging distances (Greenleaf et al., 2007).

Ten pots of soil (Sun Gro Horticulture Professional Growing Mix, Agawam, MA, USA; NSI Blow Molded Container Pots, 11" wide, A.M. Leonard, amleo.com) were placed at each site in a two by five pot configuration, with either 0, 3, 6 or all 10 pots filled with white sweet alyssum flowers. Sites that had pots with zero sweet alyssum flowers in 2015 (our control) were changed to have one pot of sweet alyssum flowers in 2016, because after establishing that zero pot lead to zero bees in 2015, we wanted to understand how floral quantities even smaller than three pots of flowers affected Halictid bees. There were four replicates of each treatment: four sites had 10 pots filled with sweet alyssum flowers, four sites had six pots, four sites had three, and the remaining four sites had zero or one pot filled with flowers. The number of soil-containing pots was kept constant across all sites to keep potential added nesting habitat equal across all treatments, as *Lasioglossum* spp. can be ground-nesting and have been shown to nest in potted plants (Tonietto, Fant, Ascher, Ellis, & Larkin, 2011). This minimized the possibility of confounding the effect of floral additions with the effect of nesting resource additions. However, as pots of sweet alyssum were discarded at the end of 2015 and replaced with new pots of flowers for the summer of 2016, any nests created in pots in 2015 did not influence the small bee abundance or richness observed in 2016. Each flower pot was watered with Blumat watering probes (Blumat 23308 Bottle Adapter for Automatic Plant Watering, Austria, amazon.com) attached to 1.5-L clear plastic bottles.

As sweet alyssum flower vitality varied across sites throughout the season and between years, an estimate of the actual number of sweet alyssum flowers available was calculated each instance pollinators were sampled. For further details, including how this estimate was calculated, see Appendix S1.

2.3 | Pollinator measurements

Pollinators were sampled at each site for 15-min intervals once a month from June to August each year. Each month pollinators from all sites were sampled on the same day and by the same collector between 10 a.m. and 6 p.m., when bees were observed to be most active. Data were collected on mostly sunny or partly sunny days, with a few observations on mostly cloudy days. One limitation of the study design was the non-randomized sequence of site observations due to travel and time constraints; we therefore recorded sampling times (hh:mm) for each site. To sample pollinators, all insects entering the perimeter of pots were collected using a 1-gal Ziploc bag. Bee specimens were identified to species by Jason Gibbs. All specimens—bees and non-bees—are stored in the Insect Division of University of Michigan's Museum of Zoology.

2.4 | Surrounding landscape floral and nesting measurements

Floral surveys of the surrounding landscape were conducted within a day of pollinator sampling to measure surrounding floral resource availability. At each site, three 100-m transects were extended, starting from the centre of the sweet alyssum flower pot location and extending in either a north, south-east or south-west direction. At the 0-m, 50-m and 100-m points on each transect, the area within a 20-m radius of each point was surveyed for flowers (Figure 1, inset). To survey flowers, the number of flower morphospecies (richness) and the proportion of space covered by flowers (abundance) were estimated. The proportion of space covered by flowers within the 20-m area was quantified in increments of 5% at the lower range of floral cover (where the majority of the data fell) and then 25% increments at the higher range. For specific details, see Appendix S1.

The amount of suitable nesting habitat in the landscape was estimated within 120 m of each site. This scale was selected to match the extent of area covered by floral surveys and because of its relevance to the smaller scale at which small Halictid bees observed are assumed to operate (Greenleaf et al., 2007). Within each 120-m radius, a grid of 2.5 m cells was created atop an aerial image base layer in ArcMap software (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). The presence of nesting resources was recorded for each cell in the field. The nesting resources considered in each cell included: bare soil exposed to light for at least part of the day, dead wood, slope (recorded as presence of an inclined surface), rock "mulch" (aggregations of rocks greater than approximately 1 cm) and areas of herbaceous plants. Dead wood and slope were considered because both have been cited as factors in nesting preferences for certain Halictid bees (Sakagami & Michener, 1962). Rock "mulch" was considered because of a study finding *Halictus rubicundus* bees preferred to nest in areas between landscaped pebbles rather than bare dirt (Cane, 2015). To calculate each site's nesting habitat availability, each cell marked with the presence of nesting resources was given a value of 1 per nesting resource available (with a

few exceptions, see Appendix S1), and values were summed across all cells within the grid.

2.5 | Analysis

In our analyses, we treated small Halictid *bee abundance* and *bee species density* (number of species found across equal unit areas, see Gotelli & Colwell, 2011) as our response variables, and *number of sweet alyssum flowers*, *landscape nesting availability*, *landscape floral availability*, *time (hh:mm) of sampling*, *month* and *year* as predictor variables. *Site* was included as a random effect. Neither bee richness nor bee diversity rarefaction curves were constructed because most sites had fewer than 20 individuals per sample and therefore did not meet minimum requirements for rarefaction analysis (N. Gotelli, pers. comm.).

For exploratory analysis, we first plotted each response variable against each predictor variable and ran simple regressions to test for correlated predictor variables. We then used a paired *t* test in *R* (R Core Team, 2015) to compare *sweet alyssum flowers* between years. One data point proved to be an extreme outlier in number of sweet alyssum flowers and heavily skewed subsequent models (causing a third of trend line to be based on one data point) and was therefore excluded from subsequent analyses.

Both research questions 1 and 2 were answered using a generalized additive model with the *mgcv* package in *R*. A generalized additive model is very similar to a general linear model or generalized linear model, but can incorporate nonlinear forms of predictor variables (Clark, 2016), making it ideal for our research question, where we question the linear assumptions of the flower predictor variable.

In each generalized additive model, either *bee abundance* or *species density* was chosen as the response variable, *number of sweet alyssum flowers* as the nonlinear predictor, *landscape nesting availability*, *landscape floral availability*, *time (hh:mm) of sampling*, *month* and *year* as linear predictors and *site* as a random variable. As all three measures of *landscape floral availability* (total landscape floral area, floral area of small flowers and floral richness) were highly correlated, three separate models were run, each including one of the *landscape floral availability* measures, and the model with the lowest AIC value was selected.

For research question 1, we focused on the effect of the nonlinear predictor *number of sweet alyssum flowers* and observed the shape of the modelled curve. If the *number of sweet alyssum flowers* proved to be a significant predictor variable in the generalized additive model and the resulting trend line showed semblance of a saturating relationship, we tested for further evidence of a positive saturating relationship by first identifying a potential saturation point—or point of transition from linear to nonlinear relationship—in the trend line, and second testing for a linear relationship before and after the perceived saturation point with a linear mixed model. To better scale variables within the linear mixed model, values of sweet alyssum flowers were divided by 10,000. If the linear mixed model was significant before the saturation point but not after, we interpreted this as further support—although not complete confirmation—of a saturating relationship.

For research question 2, we focused on the effect of the *year* predictor variable in the generalized additive model, to determine whether there was a significant change in bee abundance or species density from 2015 to 2016, given the effect of the remaining predictor

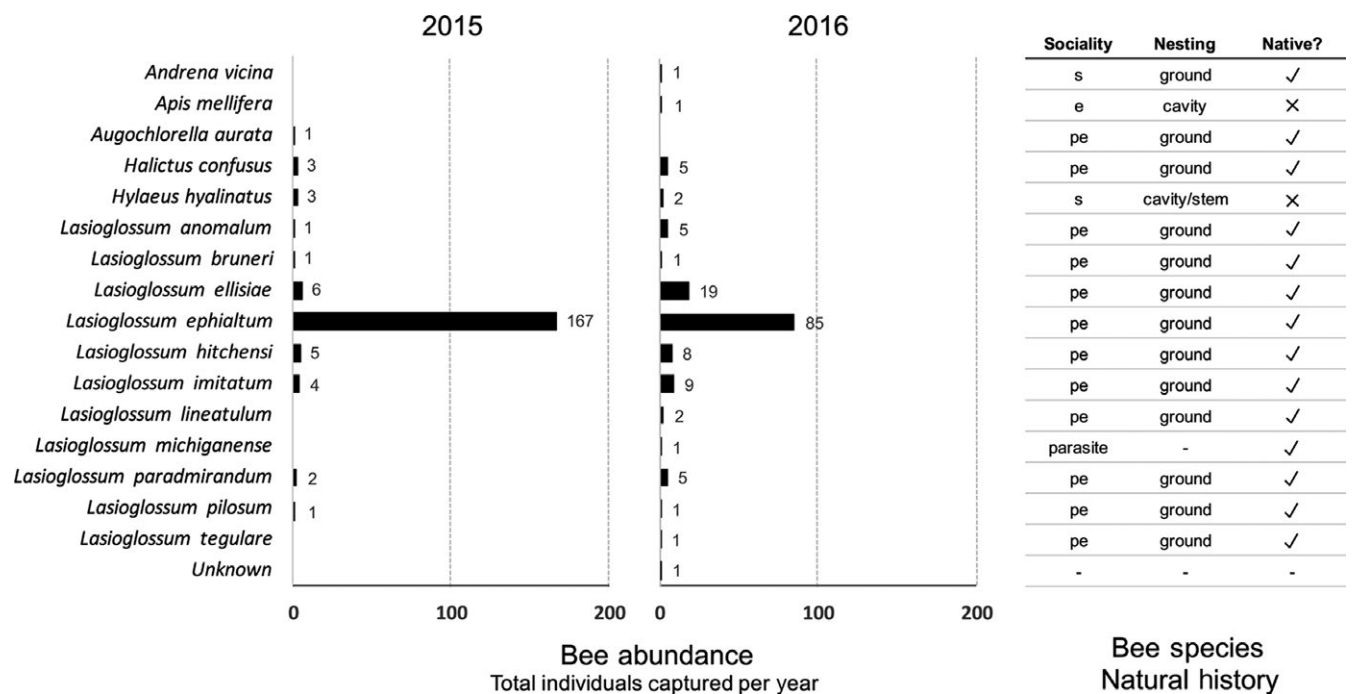


FIGURE 2 Total bee abundance found across sites in 2015 and 2016 with associated natural history of each species. *Lasioglossum ephialtum* dominated the bee community captured each year, although other species saw slight increases from 2015 to 2016. Most bees captured are considered native in Michigan and are ground-nesters, and one parasitic species was found. In bee species natural history descriptions, “s” refers to solitary, “e” to eusocial and “pe” to primitively eusocial

variables. In addition, we reran each generalized additive model using the same predictor and response variables, but excluding data from the four “control” sites (which had zero pot and one pot of flowers in 2015 and 2016, respectively) in case the change in number of flower pots biased trends seen between years. We found no differences in yearly trends from original models using the full dataset and therefore proceeded with original models’ results.

3 | RESULTS

3.1 | Overall bee community and sweet alyssum flower trends

In 2015, 194 bees were collected and identified to 11 unique species. In 2016, 147 bees were collected and identified to 15 unique species (Figure 2). In both years, the dominant species was *Lasioglossum ephialtum*, comprising 86% of all bees captured in 2015 and 58% in 2016 (Figure 2). Most bees collected were ground-nesters and native (Figure 2).

Despite planting the same quantities of sweet alyssum flowers each year at each site, the summer of 2016 was unusually warmer and we observed increased sweet alyssum mortality. In 2015, the mean number of sweet alyssum flowers estimated across sites was $10,479 \pm 14,661$ s.d., while in 2016, the mean number was $4,666 \pm 5,178$ (paired *t* test, $t = 3.125$ $p = .003$).

1. Does the number of flowers added at the local level affect small Halictid bee abundance and species density, and what is the shape of this relationship, for example, linear or saturating?

In the best-fit generalized additive model, the number of sweet alyssum flowers significantly affected both overall bee abundance ($F(3.214, 3.915) = 3.188$, $p = .019$) and bee species density ($F(7.733, 8.522) = 5.347$, $p < .001$; Figure 3, Table 1). Upon visual inspection of each model’s trend lines, neither showed a clean and perfectly distinct saturating function; however, both models appeared to follow a similar pattern, where at low floral densities, the bee response showed a positive and linear trend, yet at mid-range and higher floral densities, bee response showed more flat or variable trends. We therefore identified the point of transition—between linear increase and lack of clear, linear increase—for each model as 11,000 sweet alyssum flowers for bee abundance and 4,000 for bee species density (Figure 3). For both bee abundance and bee species density, we found a significant linear positive relationship before the point of transition (abundance, 3.985 ± 1.481 SE, $t = 2.692$, $p = .009$; species density, 4.266 ± 1.306 SE, $t = 3.265$, $p = .002$), and no significant relationship with sweet alyssum flowers was found after the point of transition (abundance, 0.436 ± 0.760 SE, $t = 0.574$, $p = .577$; species density, 0.007 ± 0.175 SE, $t = 0.041$, $p = .967$).

2. Do flower additions at the local level affect small Halictid bee abundance and species density over a temporal scale, that is, from 1 year to the next?

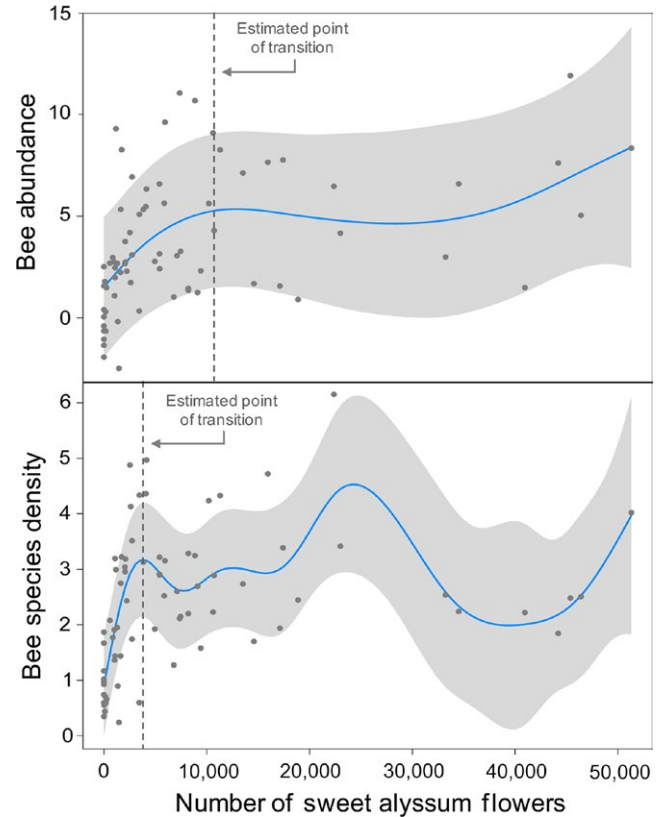


FIGURE 3 Partial residual plots of generalized additive model results, showing the fitted trend line in the relationship between flowering sweet alyssum quantity on bee abundance (top) and bee species density (bottom). Graphs do not show raw data, but instead show data given other independent variables in the data. Visually estimated points of transition between linear and nonlinear portion of the trend line are also shown

In the generalized additive model, for bee abundance, there was not a significant effect of year (-0.775 ± 0.956 , $t = -0.81$, $p = .421$), but for bee species density, there was a significant effect of year (0.636 ± 0.316 , $t = 2.01$, $p = .049$; Figure 4, Table 1).

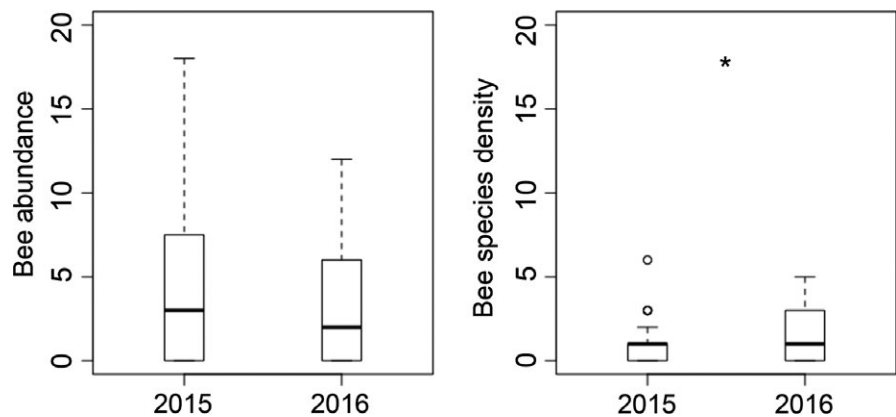
3.2 | Additional findings

A few of the additional predictor variables included in our models also produced notable results. For bee abundance, the variation between sites was significant (Table 1). This may be explained by one site with particularly high bee abundance values (site RH in Figure S2 in Supporting Information), and the four sites with zero pot or one pot of sweet alyssum flowers that had consistently low bee abundances (sites ARB, NC53, OSEH and WT in Table S1). For species density, both time (hh:mm) of sampling and month were significant effects. Time showed a slightly negative effect, meaning slightly fewer bees were collected later in afternoon, as compared to the morning. Sampling month had the expected significant effect for bee abundance, in that more bees were collected in the warmer months of July and August as compared to June. We also verified that for both bee abundance and bee species

TABLE 1 Results of the two generalized additive models used to analyse trends in bee abundance and bee species density. Each model included the same linear predictor variables (landscape nesting availability, landscape floral availability, time of sampling, month, year), one nonlinear predictor variables (number of sweet alyssum flowers) and one random effect (site). A * indicates a significant effect

Response variable	Predictor variables	Estimate	SE	t	p-value
Bee abundance	(Intercept)	1567.000	1927.000	0.813	.420
	Landscape nesting availability	-0.004	0.007	-0.589	.558
	Landscape floral area	-0.001	0.001	-0.979	.332
	Time (hh:mm) of sampling	-0.020	0.018	-1.118	.268
	Month (July)	0.844	1.147	0.736	.465
	Month (August)	2.296	1.329	1.728	.090
	Year	-0.775	0.956	-0.811	.421
	Nonlinear Predictor variables	edf	Ref.df	F	p-value
	Number of sweet alyssum flowers	3.214	3.915	3.188	.019*
	Site, random effect	8.584	14	1.846	.001*
Response variable	Predictor variables	Estimate	SE	t	p-value
Bee species density	(Intercept)	-1281.000	637.700	-2.008	.049*
	Landscape nesting availability	<0.001	0.002	0.103	.918
	Landscape floral area of small flowers	<0.001	<0.001	-0.895	.374
	Time (hh:mm) of sampling	-0.014	0.006	-2.437	.018*
	Month (July)	1.142	0.395	2.896	.005*
	Month (August)	1.500	0.444	3.378	.001*
	Year	0.636	0.316	2.011	.049*
	Nonlinear Predictor variables	edf	Ref.df	F	p-value
	Number of sweet alyssum flowers	7.733	8.522	5.347	<.001*
	Site, random effect	3.125	14	0.33	.144

FIGURE 4 Differences in small bee abundance and species density between years. Abundance did not differ significantly between years, but bee species density significantly increased (as indicated by the *)



density, neither floral or nesting resources at the landscape level were significant effects (Table 1, Figure S1 in Supporting Information).

4 | DISCUSSION

Overall, our results are encouraging for urban planners and conservationists interested in green infrastructure, demonstrating that even over short time-scales (1 year), small-scale floral additions can make effective contributions to small, urban bee conservation. To

summarize our findings, our analysis of the relationship between floral additions and small Halictid bees showed suggestive signals of a saturating relationship, with significant linear increases at smaller scales of floral additions, but not at larger scales. From 1 year to the next, small-scale urban floral additions significantly increased Halictid bee density but did not have a significant effect on Halictid bee abundance. Neither of the landscape-level measures of nesting or floral resources significantly correlated to bee responses.

Lasioglossum ephialtum dominated the bee community visiting sweet alyssum flowers in Ann Arbor, Michigan; they are small-bodied

ground-nesters native to North America and are expected to be primitively eusocial (Gibbs, Brady, Kanda, & Danforth, 2012), but as with many native bees, little has been documented on their behaviour, life history and preferred habitats. Only recently described (Gibbs, 2010), it is commonly found in urban areas—even on green roofs (Maclvor, Ruttan, & Salehi, 2015).

Our results on the functional relationship between floral additions and Halictid bees suggest the relationship is nuanced, but has important implications for decisions on effective patch sizes for pollinator conservation. Past studies have explored similar questions of saturating relationships between floral resources and pollinators, with varying results. One study, for example, tested whether flat, linear, saturating or sigmoidal models best fit the relationship between plant density and pollinator visits and found pollinator visits were best explained with a saturating function model (Feldman, 2006). In Matteson's study of bees in New York City gardens, however, he found a linear—not saturating—relationship between garden floral area and bee richness (Matteson, 2007). Yet, another experimental study carried out near Jena, Germany, found bee species richness followed a saturation curve with blossom cover, while bee abundance increased linearly (Ebeling et al., 2008). We found evidence of direct linear increases in bee abundance and species density at smaller ranges of floral additions, but less of a linear and more of a variable response at higher ranges of floral additions. In other words, in the context of our field experiment with small Halictid bees, adding 3,000 sweet alyssum flowers showed more significant effects on bee species density than adding 1,000 sweet alyssum flowers, but at the higher end of the scale, adding 15,000 sweet alyssum flowers attracted roughly the same species density as 40,000 flowers. Our result suggests that, at least for small bees in urban landscapes, there is a semblance of a saturating relationship where additions of independently spaced, smaller patches of flowers may have greater overall impacts than planting one large patch of flowers.

In the second year of floral additions, we found no significant change in bee abundance from the previous year. This finding contradicts the widely accepted direct relationship between floral resources and bee communities (Roulston & Goodell, 2011), but matches some previous studies where floral additions had no significant impact on bee visitation (Matteson & Langellotto, 2011; Yurlina, 1998). These past studies suggested the lack of impact might have stemmed from floral additions that were either too close together or too small in size, or that other limiting factors such as nesting availability were not addressed. Our study made an effort to address these factors by explicitly spreading sites out beyond the foraging range of target pollinators, providing a range of thousands of flowers and incorporating both nesting and floral landscape resources data into our models. We believe the lack of impact found in our study was associated with problems in flower mortality in the second year, where roughly half of the flowers placed across sites died in 2016. Ann Arbor—like much of the U.S.A.—experienced “much above average” temperatures from June to August of 2016 (NOAA, 2016). Sweet alyssum flowers prefer cooler summer temperatures, and the above-average heat aligned with increased mortality of sweet alyssum flowers in the second year. Extending this type of study across larger time-scales would reduce

the impact of unique years, or at least allow more confidence in the patterns that emerge over time. Floral additions placed next to blueberry fields; for instance, only showed significant changes in wild bee visits during the third year of sampling (Blaauw & Isaacs, 2014a).

Despite collecting 24% fewer bees in 2016, we were surprised to find a significant increase in bee richness between years. In 2016, we collected five new bee species, in addition to nearly all of the species seen the previous year. Although little is known about the behaviour and preferences of many of the species collected here, we assume the patterns seen here are rooted in the distribution of each species across the landscape. Species seen in both years of sampling may have already been established in nests within flying range of our floral additions; if newly emerged reproductive females of those species exhibit preferences to nest near or in their natal nest, we assume the existence of adequate floral resources in the landscape—especially supplemented by our floral additions—would encourage them to remain within range of our sites. The species newly collected in 2016 however—with the exception of *Apis mellifera*, whose distribution is likely more influenced by human activity—may have originated in nests slightly outside the foraging range distance of our floral additions, but upon emerging in the spring may have wound up nesting and reproducing at a location within range of our floral additions. Knowledge of the nesting behaviour and distribution of these bees remains a gap in the literature, but is vital information if we are to understand the mechanisms behind bee dynamics across urban landscapes.

The main implications of our results are that (1) small-scale flower plantings in urban areas can be effective in attracting small Halictid bees, even over short time periods, and that (2) for targeted pollinator species or groups, there may be optimal ranges of flower addition sizes that maximize pollinator response. These results contradict previous findings suggesting that only larger areas of floral plantings are effective in increasing pollinator diversity (Blaauw & Isaacs, 2014b), and suggest instead that actions taken in smaller areas—for example at the individual scale of an urban home garden—can be effective. A study examining pollinator services throughout the city of Chicago reported a similar result, finding that when models simulated increased flower plantings by residents in their home gardens, pollination services significantly increased throughout the city (Davis et al., 2017). A study in Chicago, IL, documented the benefits of individual flower gardens in urban areas, finding that more densely populated neighbourhoods had a greater diversity of flowering plants, which correlated to increased bee abundance, richness and visitation (Lowenstein, Matteson, Xiao, Silva, & Minor, 2014). We recommend that urban natural resource managers focus on spreading multiple, smaller flower plantings out across urban landscapes, rather than concentrating resources into one large floral patch.

While our results are encouraging, they are most relevant to small Halictids in temperate urban areas. Pollinator species in this region, however, include more than just Halictid bees and can be active from late-April to October (Wilson & Carril, 2016). To reach the full suite of pollinators, floral additions must include a diversity of flower species and nesting habitats that match the range of pollinator preferences

throughout the pollinator community's active season. The urban pollinator ecology field would therefore benefit from similar additional studies with different species with different natural history traits, varying floral species with earlier or later blooming periods, and studies focused on longer temporal dynamics.

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AUTHORS' CONTRIBUTIONS

M.-C.M.S. conceived the idea and design of the study; M.-C.M.S. and J.M. collected the data; M.-C.M.S. analysed the data, and J.M. and I.P. contributed to analysis interpretations; M.-C.M.S. and J.M. drafted the article; M.-C.M.S., J.M. and I.P. revised the article and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.393n5> (Simao, Matthijs, & Perfecto, 2018).

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