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10 TITLE:

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

13
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20 ABSTRACT

21 1. Large flower plantings are often used to combat negative effects of habitat loss on pollinators,
22 but whether these floral additions are effective at smaller scales remains unclear, particularly in
23 urban settings.

24 2. To test the effectiveness of small-scale floral additions on enhancing urban bee populations, as
25 well as their impact from one year to the next, different quantities of potted sweet alyssum
26 (*Lobularia maritima*) flowers were placed across sites in Ann Arbor, Michigan for two
27 consecutive years and the resulting Halictid bee visitors were monitored.

28 3. Overall we found the number of flowers added at the local level was significantly and
29 positively correlated with small Halictid bee abundance and species density in an urban
30 landscape. At smaller flower quantities dynamics were clearly linear, where incremental

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31 increases in number of flowers showed significant increases in bee abundance and species
32 density. At larger quantities of floral additions, however, dynamics were nonlinear in that
33 incremental increases in flower quantity had no effect on bee abundance and highly variable
34 effects on bee species density.

35 4. When comparing the change in small Halictid bee abundance and species density from one
36 year to the next, we found a significant increase in bee species density in the second year of
37 small-scale floral additions, but no significant difference in bee abundance.

38 5. *Synthesis and applications.* Our results show that small flower plantings can have positive
39 effects on small bee communities in urban systems even over a short period of time, and
40 therefore confirm that encouraging citizens to plant flowers can be an effective conservation
41 strategy for certain urban pollinator populations. In addition, our finding that smaller flower
42 plantings may have higher impacts on small pollinators than larger plantings suggests resource
43 managers interested in pollinator conservation should consider spreading multiple, smaller floral
44 plantings across the urban landscape, rather than pooling all resources into one large flower
45 patch.

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KEYWORDS

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

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51

INTRODUCTION

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

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

79 Although the link between floral resources and bees is clear, the contexts in which floral
80 additions effectively increase bee abundance and diversity are less clear, particularly for urban
81 landscapes. Urban gardens can provide bees with both floral and nesting resources (Pawelek *et*
82 *al.* 2009; Matteson & Langellotto 2010; Garbuzov & Ratnieks 2014), and given the trend toward
83 increasing urbanization, urban gardens could become an important tool for pollinator
84 conservation (Goddard, Dougill & Benton 2010). The impact of floral additions on pollinators
85 has been well-studied in agricultural contexts—where the impact is generally positive (Haaland,
86 Naisbit & Bersier 2011; *but see* Wood, Holland & Goulson 2015)—but fewer studies have been
87 conducted in cities, where the scales of floral additions are smaller and overall trends aren’t
88 clear. Two studies, for example, found clear increases in pollinators in an urban areas as a result
89 of floral additions in one main flower-rich garden (Pawelek *et al.* 2009; Garbuzov & Ratnieks
90 2014). In contrast, an experiment that placed patches of native flowers within existing urban
91 community gardens (Matteson & Langellotto 2011a), and two experiments that planted floral

92 patches of varying sizes in urban sites found no significant differences in pollinator visitation
93 (Yurlina 1998; per unit area, Garbuzov, Madsen & Ratnieks 2015).

94 Several factors that are difficult to control may have contributed to the differences seen
95 across studies. First is the issue of independent samples. Some studies place experimental floral
96 patches within short distances of each other (e.g. flower patches planted 2m apart, or 30–50m
97 apart), which may inadvertently act as one large patch of flowers to pollinators not limited by
98 such distances (Garbuzov, Madsen & Ratnieks 2015; Yurlina 1998). Second is the issue of
99 landscape context for both floral and nesting resources. If floral additions are placed in areas
100 already well-populated with flowers, such as community gardens, the effects of floral additions
101 may be negligible (Matteson & Langellotto 2011a). At the same time, if the amount of nesting
102 resources available throughout a landscape is limited, pollinators limited by distance will remain
103 unable to reach floral additions no matter their size (Matteson & Langellotto 2011a). Related to
104 the second issue of landscape context is the third issue of potentially saturating relationships.
105 There is no reason to expect that the relationship between floral additions and pollinator
106 communities is linear, where pollinators increase proportionally to the increase in floral quantity.
107 Instead, it is possible that a saturating relationship exists, where after a saturation point is
108 reached additional floral resources have little to no impact on pollinators (Feldman 2006;
109 Ebeling *et al.* 2008). If this is the case, floral additions will only be beneficial to pollinators until
110 this saturation point is reached, potentially explaining why some studies (Pawelek *et al.* 2009,
111 Garbuzov & Ratnieks 2014, Blackmore & Goulson 2014) find floral additions to be effective
112 (systems before saturation point of flowers) while other studies do not (Matteson & Langellotto
113 2011a) (systems after saturation point).

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

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

121 While we are unable to control all factors in our field experiment, we attempt to account for
122 issues of independent samples, landscape context, and potential non-linearity by: selecting sites

123 separated by distances larger than the foraging range of target pollinators (addressing the issue of
124 independent samples), placing our floral additions adjacent to parking lots—a space where floral
125 and nesting resource availability should be uniformly low—but still documenting landscape floral
126 and nesting resource levels to account for potential effects (addressing the issue of landscape
127 context), and focusing our experiment on small pollinators, in the hopes of providing a full
128 gradient of floral resources—from too little to too much (to explore the possibility of a non-linear
129 or saturating relationship). Over two summers, we manipulated floral resources across urban and
130 suburban areas in Ann Arbor, in southeastern Michigan, U.S.A., and monitored the local small
131 Halictid bee response.

132 133 MATERIALS AND METHODS

134 *Sampling Locations*

135 This study was conducted in the summer of 2015 and 2016 at 16 sites in Ann Arbor,
136 Michigan, U.S.A. (**Fig.1, Table S1** in Supporting Information). In an effort to make sites more
137 comparable within a heterogeneous urban landscape, all selected sites bordered paved parking
138 lots, which provide little to no floral and nesting resources for bees. Sites were distanced more
139 than 200 m apart (mean 819 m; range 235 m - 3,182 m) to minimize interactions between small
140 Halictid bee populations, which are estimated to have foraging ranges no greater than 200 m
141 (*pers. comm.* Jason Gibbs, Greenleaf *et al.* 2007). Further details on site selection can be found
142 in **Appendix S1** in Supporting Information.

143 144 *Flower Treatments*

145 The number of white sweet alyssum flowers (*Lobularia maritima*, Easter Bonnet
146 Lemonade variety clones from C. Raker & Sons Inc., Litchfield, MI, USA) was manipulated
147 across the landscape to test effects on small bee communities. Sweet alyssum is a perennial plant
148 introduced to North America from the Mediterranean, and can bloom from late spring to mid-fall
149 (Picó & Retana 2001; gardening.cornell.edu). Sweet alyssum was chosen because of its common
150 use in landscaping, long flowering period and small flower size, which attracts mostly small
151 pollinators such as Halictid bees, especially in the genus *Lasioglossum* (Bosch, Retana & Cerda
152 1997). Our field observations and past studies confirm that sweet alyssum flowers provide nectar
153 resources (Davis *et al.* 1998), but we were unable to observe or find information on bees also

154 utilizing sweet alyssum pollen. We wanted our flower choice to target *Lasioglossum* bees
155 because of the diversity of *Lasioglossum* species found in urban areas; targeting this genus
156 ensured we would be able to examine both bee richness and abundance as a response to floral
157 additions. Restricting the study to small pollinators increased the likelihood of our experiment
158 simulating the full spectrum of nectar required by the observed pollinator community—from
159 potentially not enough nectar to more than enough—assuming their small body size translates to
160 ingesting a few microliters of nectar per day. Focusing on small pollinators also increased the
161 likelihood of sampling independent communities across our sites, given that small pollinators are
162 assumed to have smaller foraging distances (Greenleaf *et al.* 2007).

163 Ten pots of soil (Sun Gro Horticulture Professional Growing Mix, Agawam, MA, USA;
164 NSI Blow Molded Container Pots, 11” wide, A.M. Leonard, amleo.com) were placed at each
165 site in a 2 by 5 pot configuration, with either 0, 3, 6, or all 10 pots filled with white sweet
166 alyssum flowers. Sites that had pots with 0 sweet alyssum flowers in 2015 (our control) were
167 changed to have 1 pot of sweet alyssum flowers in 2016, because after establishing that 0 pots
168 lead to 0 bees in 2015, we wanted to understand how floral quantities even smaller than 3 pots of
169 flowers affected Halictid bees. There were four replicates of each treatment: four sites had 10
170 pots filled with sweet alyssum flowers, four sites had 6 pots, four sites had 3, and the remaining
171 four sites had 0 or 1 pot filled with flowers. The number of soil-containing pots was kept
172 constant across all sites to keep potential added nesting habitat equal across all treatments, as
173 *Lasioglossum* spp. can be ground-nesting and have been shown to nest in potted plants (Tonietto
174 *et al.* 2011). This minimized the possibility of confounding the effect of floral additions with the
175 effect of nesting resource additions. However, since pots of sweet alyssum were discarded at the
176 end of 2015 and replaced with new pots of flowers for the summer of 2016, any nests created in
177 pots in 2015 did not influence the small bee abundance or richness observed in 2016. Each
178 flower pot was watered with Blumat watering probes (Blumat 23308 Bottle Adapter for
179 Automatic Plant Watering, Austria, amazon.com) attached to 1.5L clear plastic bottles.

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

184

185 *Pollinator Measurements*

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

195

196 *Surrounding landscape floral and nesting measurements*

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

207 The amount of suitable nesting habitat in the landscape was estimated within 120m of
208 each site. This scale was selected to match the extent of area covered by floral surveys, and
209 because of its relevance to the smaller scale at which small Halictid bees observed are assumed
210 to operate (Greenleaf *et al.* 2007). Within each 120m radius, a grid of 2.5m cells was created
211 atop an aerial image base layer in ArcMap software (ESRI 2011. ArcGIS Desktop: Release 10.
212 Redlands, CA: Environmental Systems Research Institute). Presence of nesting resources was
213 recorded for each cell in the field. The nesting resources considered in each cell included: bare
214 soil exposed to light for at least part of the day, dead wood, slope (recorded as presence of an
215 inclined surface), rock ‘mulch’ (aggregations of rocks greater than approximately 1 cm), and

216 areas of herbaceous plants. Dead wood and slope were considered because both have been cited
217 as factors in nesting preferences for certain Halictid bees (Sakagami & Michener 1962). Rock
218 ‘mulch’ was considered because of a study finding *Halictus rubicundus* bees preferred to nest in
219 areas between landscaped pebbles rather than bare dirt (Cane 2015). To calculate each site’s
220 nesting habitat availability, each cell marked with the presence of nesting resources was given a
221 value of 1 per nesting resource available (with a few exceptions, see **Appendix S1**), and values
222 were summed across all cells within the grid.

223

224 *Analysis*

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

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

238 Both research questions 1. and 2. were answered using a generalized additive model with
239 the mgcv package in R. A generalized additive model is very similar to a general linear model or
240 generalized linear model, but can incorporate nonlinear forms of predictor variables (Clark
241 2016); making it ideal for our research question, where we question the linear assumptions of the
242 flower predictor variable. In each generalized additive model, either *bee abundance* or *species*
243 *density* was chosen as the response variable, *number of sweet alyssum flowers* as the nonlinear
244 predictor, *landscape nesting availability*, *landscape floral availability*, *time (hh:mm) of*
245 *sampling*, *month* and *year* as linear predictors, and *site* as a random variable. Since all three
246 measures of *landscape floral availability* (total landscape floral area, floral area of small flowers,

247 and floral richness) were highly correlated, three separate models were run, each including one
248 of the *landscape floral availability* measures, and the model with the lowest AIC value was
249 selected.

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

261 For research question 2 we focused on the effect of the *year* predictor variable in the
262 generalized additive model, to determine whether there was a significant change in bee
263 abundance or species density from 2015 to 2016, given the effect of the remaining predictor
264 variables. In addition, we re-ran each generalized additive model using the same predictor and
265 response variables, but excluding data from the four ‘control’ sites (which had 0 and 1 pots of
266 flowers in 2015 and 2016, respectively) in case the change in number of flower pots biased
267 trends seen between years. We found no differences in yearly trends from original models using
268 the full data set, and therefore proceeded with original models’ results.

269

270

RESULTS

271 *Overall bee community and sweet alyssum flower trends*

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

276 Despite planting the same quantities of sweet alyssum flowers each year at each site, the
277 summer of 2016 was unusually warmer and we observed increased sweet alyssum mortality. In

278 2015 the mean number of sweet alyssum flowers estimated across sites was $10,479 \pm 14,661$ s.d.,
279 while in 2016 the mean number was $4,666 \pm 5,178$ (*paired t-test*, $t = 3.125$, $p = 0.003$).

280

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

283 In the best-fit generalized additive model, the number of sweet alyssum flowers
284 significantly affected both overall bee abundance ($F(3.214, 3.915) = 3.188$, $p = 0.019$) and bee
285 species density ($F(7.733, 8.522) = 5.347$, $p < 0.001$; **Fig. 3, Table 1**). Upon visual inspection of
286 each model's trend lines, neither showed a clean and perfectly distinct saturating function;
287 however, both models appeared to follow a similar pattern, where at low floral densities the bee
288 response showed a positive and linear trend, yet at mid-range and higher floral densities, bee
289 response showed more flat or variable trends. We therefore identified the point of transition–
290 between linear increase and lack of clear, linear increase—for each model as 11,000 sweet
291 alyssum flowers for bee abundance and 4,000 for bee species density (**Fig. 3**). For both bee
292 abundance and bee species density, we found a significant linear positive relationship before the
293 point of transition (abundance, 3.985 ± 1.481 s.e., $t = 2.692$, $p = 0.009$; species density, $4.266 \pm$
294 1.306 s.e., $t = 3.265$, $p = 0.002$), and no significant relationship with sweet alyssum flowers was
295 found after the point of transition (abundance, 0.436 ± 0.760 s.e., $t = 0.574$, $p = 0.577$; species
296 density, 0.007 ± 0.175 s.e., $t = 0.041$, $p = 0.967$).

297

298 2. *Do flower additions at the local level affect small Halictid bee abundance and species density*
299 *over a temporal scale, i.e. from one year to the next?*

300 In the generalized additive model, for bee abundance there was not a significant effect of
301 year (-0.775 ± 0.956 , $t = -0.81$, $p = 0.421$), but for bee species density, there was a significant
302 effect of year (0.636 ± 0.316 , $t = 2.01$, $p = 0.049$; **Fig. 4, Table 1**).

303

304 *Additional findings*

305 A few of the additional predictor variables included in our models also produced notable
306 results. For bee abundance, the variation between sites was significant (**Table 1**). This may be
307 explained by one site with particularly high bee abundance values (site RH in **Figure S2** in
308 Supporting Information), and the four sites with 0 or 1 pot of sweet alyssum flowers that had

309 consistently low bee abundances (sites ARB, NC53, OSEH, and WT in **Table S1**). For species
310 density, both time (hh:mm) of sampling and month were significant effects. Time showed a
311 slightly negative effect, meaning slightly fewer bees were collected later in afternoon, as
312 compared to the morning. Sampling month had the expected significant effect for bee
313 abundance, in that more bees were collected in the warmer months of July and August as
314 compared to June. We also verified that for both bee abundance and bee species density, neither
315 floral or nesting resources at the landscape level were significant effects (**Table 1, Figure S1** in
316 Supporting Information).

317

318

319

DISCUSSION

320

321 Overall our results are encouraging for urban planners and conservationists interested in
322 green infrastructure, demonstrating that even over short time scales (one year), small-scale floral
323 additions can make effective contributions to small, urban bee conservation. To summarize our
324 findings, our analysis of the relationship between floral additions and small Halictid bees showed
325 suggestive signals of a saturating relationship, with significant linear increases at smaller scales
326 of floral additions, but not at larger scales. From one year to the next, small-scale urban floral
327 additions significantly increased Halictid bee density but did not have a significant effect on
328 Halictid bee abundance. Neither of the landscape-level measures of nesting or floral resources
329 significantly correlated to bee responses.

329

330 *Lasioglossum ephialtum* dominated the bee community visiting sweet alyssum flowers in
331 Ann Arbor, Michigan; they are small-bodied ground-nesters native to North America and are
332 expected to be primitively eusocial (Gibbs *et al.* 2012), but as with many native bees, little has
333 been documented on their behaviour, life history, and preferred habitats. Only recently described
334 (Gibbs 2010), it is commonly found in urban areas—even on green roofs (MacIvor *et al.* 2015)

334

335 Our results on the functional relationship between floral additions and Halictid bees
336 suggest the relationship is nuanced, but has important implications for decisions on effective
337 patch sizes for pollinator conservation. Past studies have explored similar questions of saturating
338 relationships between floral resources and pollinators, with varying results. One study, for
339 example, tested whether flat, linear, saturating, or sigmoidal models best fit the relationship
340 between plant density and pollinator visits, and found pollinator visits were best explained with a

340 saturating function model (Feldman 2006). In Matteson’s study of bees in New York City
341 gardens, however, he found a linear–not saturating–relationship between garden floral area and
342 bee richness (Matteson 2007). Yet, another experimental study done near Jena, Germany, found
343 bee species richness followed a saturation curve with blossom cover, while bee abundance
344 increased linearly (Ebeling *et al.* 2008). We found evidence of direct linear increases in bee
345 abundance and species density at smaller ranges of floral additions, but less of a linear and more
346 of a variable response at higher ranges of floral additions. In other words, in the context of our
347 field experiment with small Halictid bees, adding 3,000 sweet alyssum flowers showed more
348 significant effects on bee species density than adding 1,000 sweet alyssum flowers, but at the
349 higher end of the scale, adding 15,000 sweet alyssum flowers attracted roughly the same species
350 density as 40,000 flowers. Our result suggests that, at least for small bees in urban landscapes,
351 there is a semblance of a saturating relationship where additions of independently spaced,
352 smaller patches of flowers may have greater overall impacts than planting one large patch of
353 flowers.

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

371 showed significant changes in wild bee visits during the third year of sampling (Blaauw & Isaacs
372 2014a).

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

389 The main implications of our results are that 1) small scale flower plantings in urban
390 areas can be effective in attracting small Halictid bees, even over short time periods, and that 2)
391 for targeted pollinator species or groups, there may be optimal ranges of flower addition sizes
392 that maximize pollinator response. These results contradict previous findings suggesting that
393 only larger areas of floral plantings are effective in increasing pollinator diversity (Blaauw &
394 Isaacs 2014b), and suggest instead that actions taken in smaller areas—e.g. at the individual scale
395 of an urban home garden—can be effective. A study examining pollinator services throughout the
396 city of Chicago reported a similar result, finding that when models simulated increased flower
397 plantings by residents in their home gardens, pollination services significantly increased
398 throughout the city (Davis *et al.* 2017). A study in Chicago, IL, documented the benefits of
399 individual flower gardens in urban areas, finding that more densely populated neighbourhoods
400 had a greater diversity of flowering plants, which correlated to increased bee abundance,
401 richness, and visitation (Lowenstein *et al.* 2014). We recommend that urban natural resource

402 managers focus on spreading multiple, smaller flower plantings out across urban landscapes,
403 rather than concentrating resources into one large floral patch.

404 While our results are encouraging, they are most relevant to small Halictids in temperate
405 urban areas. Pollinator species in this region, however, include more than just Halictid bees and
406 can be active from late-April to October (Wilson & Carril 2016). To reach the full suite of
407 pollinators, floral additions must include a diversity of flower species and nesting habitats that
408 match the range of pollinator preferences throughout the pollinator community's active season.
409 The urban pollinator ecology field would therefore benefit from similar additional studies with
410 different species with different natural history traits, varying floral species with earlier or later
411 blooming periods, and studies focused on longer temporal dynamics.

412 413 AUTHORS' CONTRIBUTIONS

414 MCMS conceived the idea and design of the study; MCMS and JM collected the data;
415 MCMS analysed the data, and JM and IP contributed to analysis interpretations; MCMS and JM
416 drafted the article; MCMS, JM and IP revised the article and gave final approval for publication.

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424 Analytics Research, Maria-Teresa Simao and our anonymous reviewers.

425 426 DATA ACCESSIBILITY

427 Data are available from the Dryad Digital Repository. DOI: 10.5061/dryad.393n5 (Simao *et al.*
428 2017).

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546

547 TABLES

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

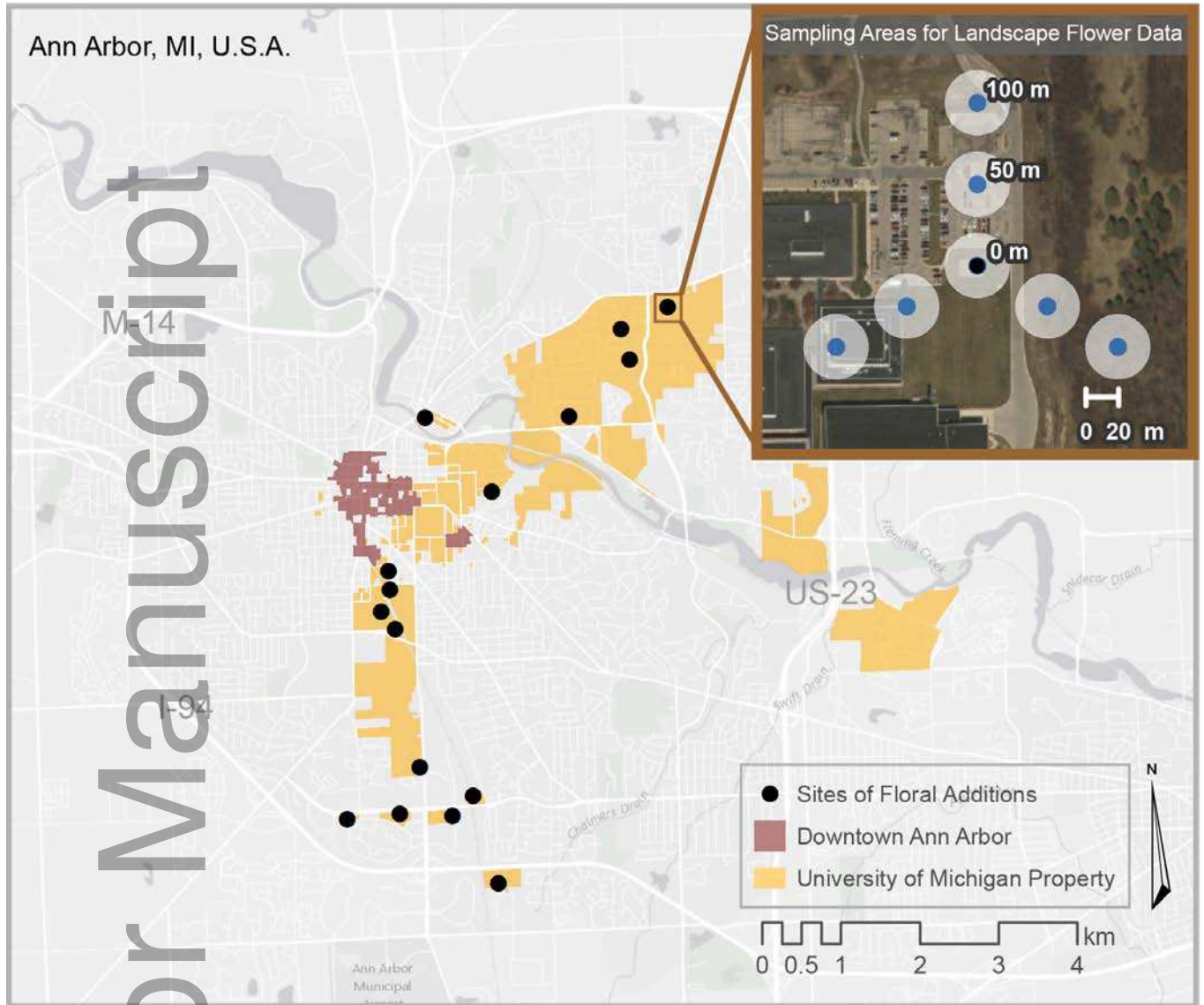
Response variable	Predictor variables	Estimate	Std.Error	t	p-value
Bee abundance	(Intercept)	1567.000	1927.000	0.813	0.420
	Landscape nesting availability	-0.004	0.007	-0.589	0.558
	Landscape floral area	-0.001	0.001	-0.979	0.332

Time (hh:mm) of sampling	-0.020	0.018	-1.118	0.268
Month (July)	0.844	1.147	0.736	0.465
Month (August)	2.296	1.329	1.728	0.090
Year	-0.775	0.956	-0.811	0.421
Nonlinear Predictor variables	edf	Ref.df	F	p-value
Number of sweet alyssum				
flowers	3.214	3.915	3.188	0.019*
Site, <i>random effect</i>	8.584	14	1.846	0.001*

Response variable	Predictor variables	Estimate	Std.Error	t	p-value
Bee species density	(Intercept)	-1281.000	637.700	-2.008	0.049*
	Landscape nesting availability	<0.001	0.002	0.103	0.918
	Landscape floral area of small flowers	<0.001	<0.001	-0.895	0.374
	Time (hh:mm) of sampling	-0.014	0.006	-2.437	0.018*
	Month (July)	1.142	0.395	2.896	0.005*
	Month (August)	1.500	0.444	3.378	0.001*
	Year	0.636	0.316	2.011	0.049*
	Nonlinear Predictor variables	edf	Ref.df	F	p-value
	Number of sweet alyssum				
	flowers	7.733	8.522	5.347	<0.001*
Site, <i>random effect</i>	3.125	14	0.33	0.144	

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FIGURES



556

557 **Figure 1.** Locations of sites where floral additions were placed within Ann Arbor, Michigan.

558 Inset map shows one sampling site in detail, where potted sweet alyssum flowers were placed in

559 the centre (black dot) and landscape flower resource data were taken within 20 m (white circle

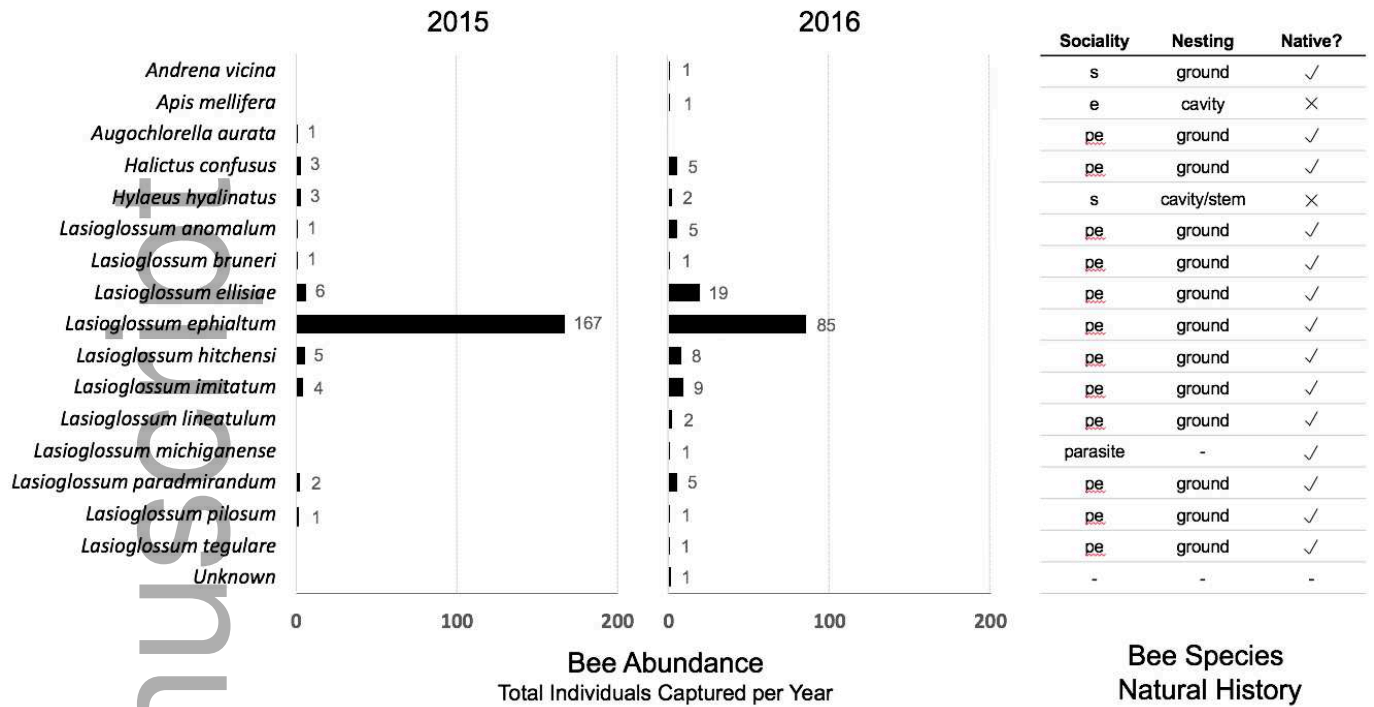
560 areas) of sampling points spaced 50 m (blue dots) along three 100 m transects from the centre.

561 Source of base layer: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and

562 the GIS user community.

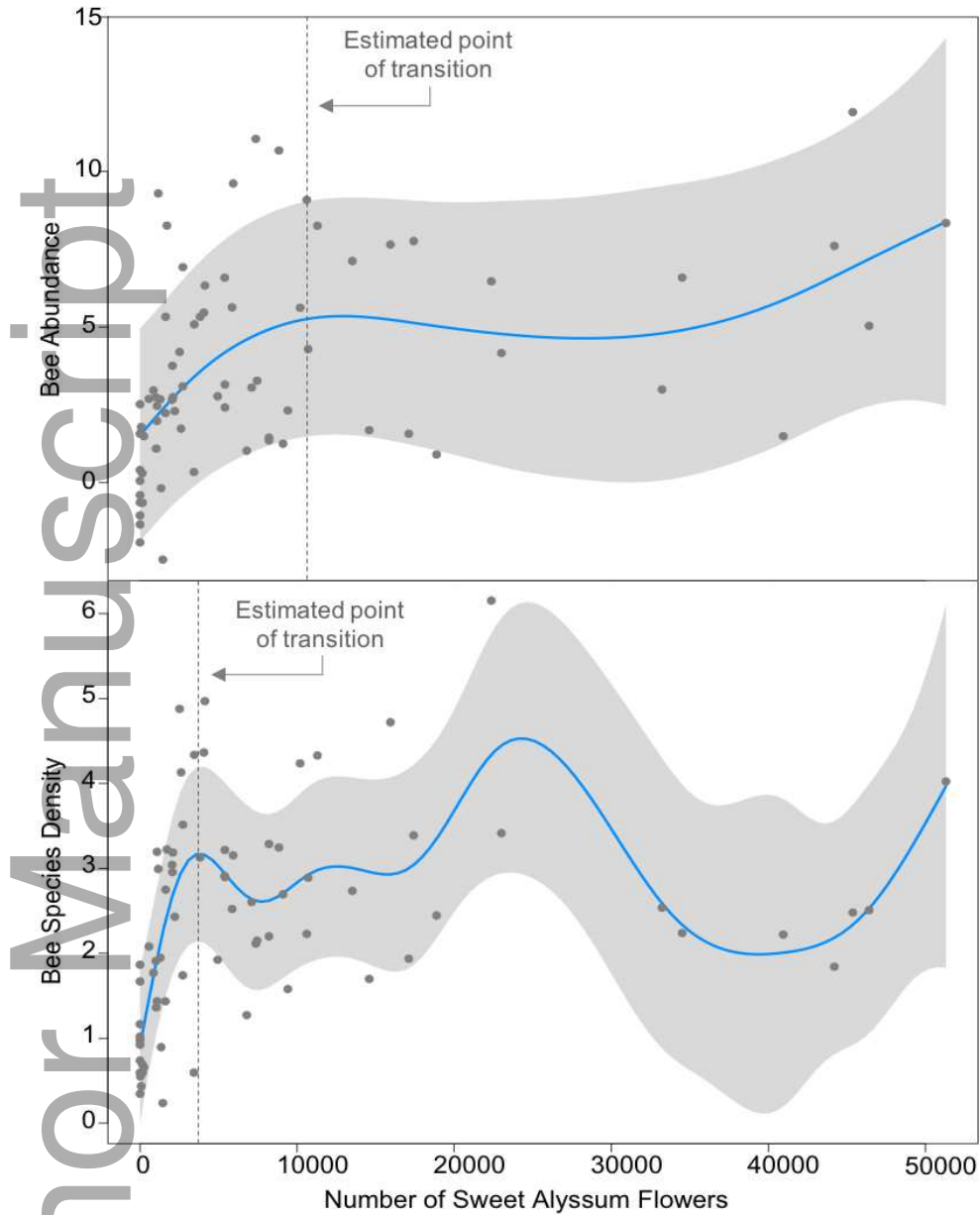
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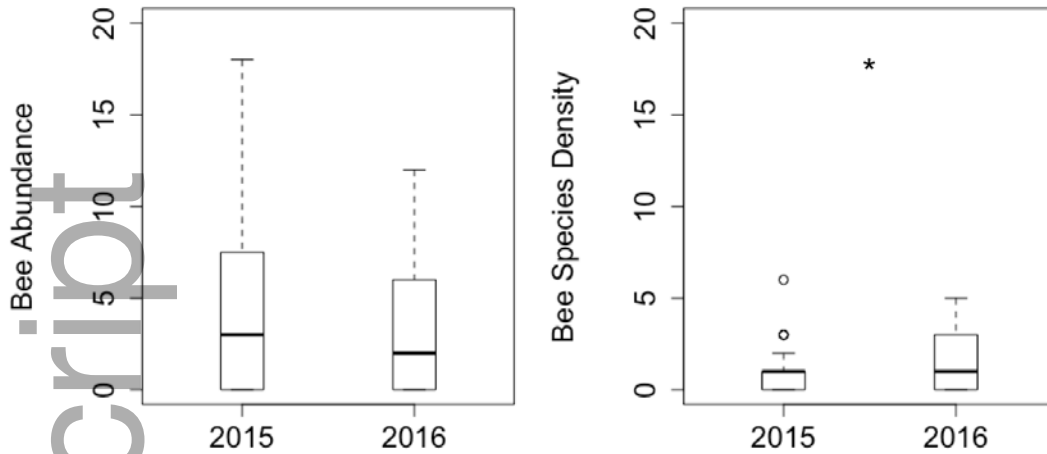
Figure 2. Total bee abundance found across sites in 2015 and 2016 with associated natural history of each species. *Lasioglossum ephialtum* dominated the bee community captured each year, although other species saw slight increases from 2015 to 2016. Most bees captured are considered native in Michigan 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.



576

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

582



583
 584 **Figure 4.** Differences in small bee abundance and species density between years. Abundance did
 585 not differ significantly between years, but bee species density significantly increased.
 586

587 **SUPPORTING INFORMATION**

588 Additional supporting information can be found in online version of this article.

589 **Table S1.** Flower treatments and geographic coordinates of sampling sites.

590 **Appendix S1.** Details on study site selection, landscape floral, and landscape nesting
 591 measurements

592 **Figure S1.** Frequency distributions of floral and nesting resources at the landscape level.

593 **Figure S2.** Variation in bee abundance and species density across sites