1 **Recent Urban Development Reduces Bee Abundance and Diversity**

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Abstract

Wild bee communities persist in cities despite major disruption of nesting and food resources by urban development. Bee diversity and abundance is key for urban agriculture and maintenance of plant diversity, and assessing what aspects of cities enhance bee populations will promote our capacity to retain and provision bee habitat. Here, we assessed how variation in land cover and neighborhood development history affected bee communities in the midwestern US urban landscape of Madison, Wisconsin. We sampled bee communities across 38 sites with relatively high (> 55%) or low (< 30%) levels of impervious surface, and assessed effects of land use and neighborhood development history on bee abundance and species richness. We show abundance and richness of bees was lower in recently developed neighborhoods, with particularly strong negative effects on soil nesting bees. Soil nesting bees and bee community richness decreased as cover of impervious surface increased, but above ground nesting bees were minimally impacted. Bee community similarity varied spatially and based on dissimilar local land cover, only for soil nesting bees, and the overall bee community. Impervious surface limited bee abundance and diversity, but new neighborhoods were associated with greater negative effects. We suggest that enhancing the structural diversity of new neighborhoods in urban ecosystems may imitate the structural benefits of older neighborhoods for bee populations.

Keywords: Urban ecosystems, bee community, habitat guilds, habitat filtering, impervious surface, development history

Declarations:

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34   Conflict of interest: The authors declare they have no conflict of interest

35   Availability of data and material: Bees are submitted to the University of Wisconsin-Madison

36   insect museum.

37   Code availability: https://github.com/verawp

38   Author contributions: VWP designed study, performed analysis and drafted manuscript, JSB and

39   DWC participated in manuscript writing. All authors gave final approval for publication.

40   Compliance with ethical standards

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45 **Introduction**

46   Urban development is rapidly transforming the Earth's surface. Impervious surfaces and

47 fragmented patches of vegetation that typify urban ecosystems threaten species diversity (Rebele

48 1994). In urban ecosystems, ecological communities are also exposed to loss of food and nesting

49 resources, despite cultivated gardens adding diversity (Rebele 1994, Rosenzweig 2003). Urban

50 habitat fragmentation often leads to the loss of plants and associated pollinators, especially plants

51 reliant on animal pollination (Biesmejer et al. 2006; Theodorou et al. 2020). However, organisms

52 differ in their sensitivity to urbanization, and certain pollinators thrive in urban ecosystems

53 despite high disturbance. More research is thus needed to assess relationships between ecological

54 community structure and land use in urban landscapes to protect biodiversity and ecosystem

55 services in ecosystems supporting most of the human population (Daily et al. 1997).

56   Native bees promote diversity of urban ecosystems by pollinating native, ornamental, and

57 agricultural plants across seasons (Hoehn 2008, Garibaldi 2013). As urban development expands,

58 urban agriculture is growing, emphasizing the need to maintain urban pollinators to produce food

59 where people live (Hodgson et al. 2011). Habitat simplification and high density of honey bee

60 apiaries in urban systems can negatively affect wild bees (Gonzales et al. 2013, Martins et al.

61 2013; Renner et al. 2021), but high bee diversity has also been observed in cities like New York

62 and Chicago, US (McFrederick and LeBuhn 2006; Matteson et al. 2008; Fetridge et al. 2008).

63 This shows urban land can provide diverse floral resources, especially when gardens provide

64 flowers for a longer duration than other ecosystems (Goddard et al 2010, Threlfall et al. 2015).

65 Urbanization may have different impacts on bees with different ecology, however.

66   Within urban ecosystems, variation in pollinator nesting strategy may predict sensitivity of

67   species to the high levels of disturbance in urban systems. In many cases, below-ground nesting

68   cavity bees are expected to be more affected by urbanization than bees that nest aboveground

69   given the prevalence of impervious surfaces (Larsen 2005, Cane et al. 2006; Jha and Kremen

70   2013). For example, many bees excavate or construct their own nesting cavities using mud,

71   wood or pithy stems, or dig cavities in the soil, and these habitats are often less available in

72   urban compared to natural or rural landscapes. However, man-made structures can in some cases

73   supplement nesting habitat, by providing stone walls, wooden structures, and various other

74   cavities, as well as bare ground and loosened soil. By investigating what aspects of land cover

75   and land use underlie trends in species filtering, we can increase our capacity to restore the

76   resources that are lost along with associated taxa.

77   Here we assessed effects of land cover and neighborhood development on the urban bee

78   communities associated with the growing urban cityscape of Madison, Wisconsin, United States.

79   Our study tested three main hypotheses. First, we predicted that property development would

80   increase the amount of impervious surface area, disturbing bee habitat and reducing abundance

81   and species richness of bee communities. In particular, we expected stronger effects of property

82   development on below-ground cavity nesting bees that require already excavated cavity spaces,

83   often underground. Second, we predicted that bee community composition would be more

84   dissimilar with greater geographic distance across the city, especially for small soil-nesting bees

85   with limited dispersal capacity. Third, we predicted that property development would decrease

86   similarity in the composition of bee communities. By assessing effects of land cover, property

87   development, and spatial scale on species richness and species composition of bee communities,

88   our study contributes to the empirical foundations of pollination ecology as it relates to

89   conservation and restoration efforts in urban ecosystems.

90

91   **Materials and methods**

92   **Study area and sampling design**

93   Madison, Wisconsin is an urban state capital surrounded by agricultural land in one of the

94   fastest growing counties in the US. The primary transition type occurring in the Madison area for

95   the past century is the conversion of agricultural to urban land around the city edge (Wegener

96   2001; Carpenter et al. 2007; Riera et al. 2001). The dominant urban area is typified by mixed

97   residential and commercial zones with small forest patches and city parks. The 123 km^2 central

98   urban zone of Madison includes 46 km^2 (37%) of impervious surface, 30 km^2 (24%) of vegetated

99   space, with the remaining landscape covered by lakes. The city receives semi-frequent rain and

100   severe thunderstorms throughout the summer months that supports abundant flowering prairie

101   plants in city parks or where native grasslands have been conserved or restored around the city.

102   Flower-visiting insects were sampled across Madison using a spatially stratified survey to

103   account for changing regional species pools. To select sites, a grid of 2.5   2.5km squares was

104   laid across Madison and cells dominated by lake or agriculture were excluded, leaving 19 cells

105   dominated by high-density residential and urban land (Fig. 1). In each of these cells we used a

106   paired design and selected two sites characterized by either (1) high (> 55%) or (2) low (< 30%)

107   impervious surface area within the surrounding 200 m based on a lower resolution classified land

108   cover surface (USDA-NASS 2013). Within each cell, paired sites with high or low impervious

109   surface area were separated by at least 400 m. These 38 sites were selected in a stratified-random

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110   manner, and permission from property owners (identified from a city database) was requested

111   until appropriate locations were identified. Sample sites included primarily residential properties,

112   as well as commercial properties, urban storm water management areas, and city parks.

113

114   **Bee community sampling**

115   Bees were sampled six times between early June and late August 2013. Pan traps were

116   distributed every two weeks during clear, sunny days when bees were foraging. All traps were

117   distributed across the same evening to early morning period (after 17:00-dark and before dawn-

118   8:00), and collected 4 d later. Six bee traps were placed at least 5 m apart within a 40 m area in

119   each site, with two dark blue, two canary yellow, and two white; bees were also trapped in 0.5 L

120   pan traps suspended 20 cm or 2.5 m from the ground to match the height of flowering vegetation.

121   Bees were identified to species using the discover life online key and a comprehensive

122   dichotomous key available for *Lasioglossum* (Ascher & Pickering 2013; Gibbs 2011).

123   We classified bee taxa as soil-nesting, below-ground cavity-nesting, and above-ground

124   nesting bees, based on available observations. The below ground cavity-nesting bees included 7

125   species of bumble bees (*Apidae: Bombus*). Above-ground nesting bees included small carpenter

126   bees (*Ceratina spp.*), yellow faced bees (*Hylaeus spp.*), carder, mason, and leafcutter bees

127   (*Megachilidae*), and two sweat bees that nest in decaying wood, *Lasioglossum cressonii*

128   (Mitchell 1960) and *L. oblongum* (Sakagami & Michener 1962). Above-ground nesting bees

129   included 22 species. The rest of the bees were classified as soil nesting bees, which included 69

130   species across several groups: (i) long-horned bees (Tribe Eucerini), (ii) mining bees (Andrena

7

131   spp.), (iii) green bees, (iv) all of the other sweat bees, and (v) any others were classified as soil

132   nesting bees, although natural history observation of many species could not be located.

133

134   **Measuring land cover and neighborhood development around study sites**

135   Six-inch resolution digital aerial images were used to classify impervious surfaces such as

136   roads, parking lots, and structures. Unsupervised classification was initiated with 30 classes that

137   were clumped into land cover types. The impervious surface layer from this classification was

138   added to the City of Madison building footprint and road layer to recover impervious surface

139   obscured by tree canopy. Natural vegetation was identified visually within 1000 m of each site

140   and included open canopy, perennial grasses and forbs in greenways, parks, or transportation

141   corridors. Closed canopy forest was also digitized around sites. Each land cover variable was

142   measured as a percent of the landscape, then variables were standardized with a mean of zero

143   and standard deviation of 1 for comparison in analyses. The three land cover types were also

144   consolidated in a distance matrix at each scale. To characterize neighborhood development

145   history, publicly accessible tax assessment data was obtained and property development year was

146   extracted for parcels located within a 200 m radius of each site, from which we extracted an area-

147   weighted average development year for each site. A Bray-Curtis distance matrix was constructed

148   to contrast sites based on the variability of the area-weighted average, median development year,

149   and most recent property development year within the 200m buffer.

150

151   **Data analysis**

152   Individual-based rarefaction curves were constructed for each site using the 'vegan' R package,

153   and rarefaction-based species richness estimates were compared to observed richness (Oksanen

154   et al. 2018). Rarefied richness did not reach an asymptote, so raw abundance and richness values

155   were used as sampling effort was standardized (Fig. 2). We used linear regression models to test

156   whether land cover and neighborhood development (median property development year) affected

157   bee species richness (α-diversity); separate analyses were conducted for the overall community

158   and three bee guilds. All variables were scaled to a mean of 0 and standard deviation of 1 and top

159   models were selected using stepwise AIC model selection using the 'MASS' R package (Ripley

160   et al. 2018). For purposes of comparison we discuss "old" neighborhoods as those with a median

161   development year prior to 1960 and "new" neighborhoods as those with a median development

162   year after 1960. Bee abundance and richness seemed to drop off after this time point, reflecting a

163   qualitative difference rather than a gradual, linear decline. The Moran's I test was used to check

164   for spatial autocorrelation in model fit for each full and final models, applied using the 'car' R

165   package (Fox et al. 2018).

166   We used multiple regression on distance matrices (MRM) to assess effects of the various

167   explanatory variables on bee community composition at the landscape scale (β-diversity), which

168   was implemented through the R package 'ecodist' (Legendre and Legendre 1998; Goslee and

169   Urban 2017). This allowed us to capture the various multifaceted explanatory variables reflecting

170   heterogeneity of land cover and land use history. MRMs measure the effect magnitude of each

171   explanatory distance matrix using a non-parametric framework and pseudo *t*-tests are used to

172   assess significance of explanatory variables (Goslee and Urban 2017).

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174 **Results**

175   We captured 1331 bees at the 38 sites. Across families, 31% were Apidae, 3% Andrenidae,

176 55% Halictidae, 8% Megachilidae, and 3% Collitidae. Sites were surrounded by 0 to 43% natural

177 vegetation (Mean = 10.3; SD = 9.1) and 0 to 28% forest (Mean = 5.0; SD = 6.3) with median

178 property development varying between 1920 and 2003 (Mean = 1947; SD = 22). All full bee

179 community and soil nesting bee community analyses were performed across all sites (n = 38).

180 Above ground nesting bee and below ground cavity nesting bee analyses were performed across

181 sites where bees from the nesting guild were present, 32 and 17 sites, respectively.

182

183 **Effects of recent property development on bee abundance and diversity**

184   The average bee abundance decreased from 41.7 to 20.8 (t = -2.77, df = 25.98, P = 0.01),

185 and average species richness from 17.4 to 11.3 (t = -2.76, df = 24.16, P = 0.01), in pre-1960

186 compared to post-1960 median development year neighborhoods (Fig. 3). This was driven

187 mainly by decreases in soil-nesting bees, which decreased in abundance from 28.7 to 13.6 bees,

188 and 11.3 to 7.6 species, from old (n = 29) to new (n = 9) neighborhoods. The abundance and

189 richness of above-ground nesting bees, and below-ground cavity nesting bees, were similarly

190 abundant and rich in old and new neighborhoods (P > 0.24 for all four metrics). In multiple

191 variate linear regression models including development and land cover variables, a negative

192 influence of recent property development was the strongest predictor of overall bee and soil

193 nesting bee species richness, and the term was included with the negative influence of

194 impervious surface in top models (Tables 1, 2).

195

Effects of surrounding land cover on bee species diversity

In addition to effects of neighborhood development, the proportion of impervious surface also reduced the species richness (α-diversity) of the overall bee community, soil-nesting bees, and above-ground nesting bees (Tables 1, 2). The negative influence of impervious surface on the overall richness of bee species and soil-nesting bees were each about half the magnitude of the property development effect in the scaled regression model. For the overall bee community, the regression model indicates a 2.9 factor decrease in bee species richness per 23% increase in the proportion of impervious surface. The below-ground cavity-nesting bee species richness was negatively associated with surrounding forest cover with a 1.0 factor decrease in bumble bee species with each 12% increase in surrounding forest cover.

Variation in bee community composition across the study extent

The final multiple regression on distance matrix model (MRM) for the full bee community composition included only the land cover effect ($P = 0.03$) (Table 3). For the soil nesting bee community, there was a clear influence of geographic distance on community dissimilarity ($P = 0.040$) and a land cover effect ($P = 0.04$) (Table 3). The below-ground cavity nesting community composition included a weakly significant influence of geographic distance ($P = 0.07$) (Table 3). And there were no observed effects of geographic distance or land cover on the above-ground bees (Table 3). None of the bee community final models included significant effects of property development on community composition (Table 3).

Discussion

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218   Bees from each nesting guild were observed throughout the City of Madison at both low

219   and high impervious surface sites. This result suggests that in general, bees are able to use small

220   patches of habitat within the most urbanized landscapes of the city (Theodorou 2016; Hall et al.

221   2016, Daniels et al. 2020). Our observation of an association between impervious surface and

222   reduced bee community richness, especially for soil nesting bees, reflected patterns reminiscent

223   of a 60-year study in Brazil, which documented an increase of impervious surface and decrease

224   in soil bee nests, abundance, and declines of species richness and phylogenetic diversity (Pereira

225   et al. 2020). The negative influence of impervious surface on soil-nesting bees, above-ground

226   cavity-nesting bees, and the entire bee community, may stem from a loss of exposed soil used for

227   nesting habitat, and associated decreases in flowering forbs that bees use as a food resource.

228   Our finding that more recently developed neighborhoods exhibited lower bee abundance

229   and diversity was not based on our initial expectations of mechanistic associations between land

230   cover transformation and bee habitat provisioning. A negative influence of recent development

231   was observed for the full bee community and soil-nesting bees. While this negative effect may be

232   due to disturbance and soil compaction, we also observed a reduction of structural complexity in

233   recently developed neighborhoods surrounded by more grass lawn and less gardens that may

234   provision diverse types of bee habitat. More established neighborhoods more frequently offered

235   more complex built habitat including rock walls and gardens rather than simple lawn land cover.

236   While we expected that below-ground cavity nesting bees would be the most impacted by

237   urbanization and impervious surface, we did not observe that result. Bumble bees that comprised

238   this nesting habitat guild can forage long distances, and other studies have observed bumble bee

239   foraging presence to be strongly influenced by floral resources (Turo et al. 2019, Reeher et al.

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240   2020, Cohen et al. 2020) In fact, greater urban cover can sometimes increase the abundance of

241   urban bumble bees in urban gardens, and promote higher in-garden foraging, alongside plant

242   richness as another contributing factor (O'Connell et al. 2020). Another study of urban bumble

243   bees in the American Midwest found that bumble bee abundance and richness were unaffected

244   by the amount of impervious surface across several cities (Reeher et al. 2020).

245   While geographic distance did not explain the dissimilarity of the full bee community, it

246   contributed to the dissimilarity in soil-nesting and below-ground cavity-nesting bee community

247   composition. This confirmed our hypothesis that generally smaller, soil-nesting bee communities

248   would vary more across the urban study extent. Past studies have confirmed that bee foraging

249   distances are correlated with body size, contributing to patchy distributions of small bee species

250   (Steffan-Dewenter et al. 2002; McKinney 2008). A recent study of pollinators around cotton

251   farms in Texas found no geographic pattern of isolation by distance for bees, but these patterns

252   were observed for beetles and other more movement limited insect taxa (Cusser et al. 2018).

253   Urbanization can also filter bee community composition, with some evidence that urban

254   bee communities are more homogenous subsets of nearby rural bee communities (Banaszak-

255   Cibicka 2020). In the models for the species composition of the full bee community as well as

256   each nesting habitat guild, property development did not appear to filter the species composition.

257   Surrounding land cover did affect the full bee and soil-nesting bee community dissimilarity.

258   While the influence of land cover significantly influenced the dissimilarity of species

259   assemblages, these factors did not explain much of the variation overall. High species richness

260   of bees was observed across the city, as well as patchy distributions of rare species.

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261   Research documenting responses of bee communities to urbanization is on the rise, but a

262 recent meta-analysis only discovered three published studies assessing the relationships between

263 bee traits and urbanization (Buchholz and Egerer 2020). As urbanization processes continue to

264 transform landscapes around the world, improving our understanding of habitat provisioning and

265 ecosystem services in urban ecosystems is of great importance. Globally, urban bee research is

266 heavily biased towards cities in developed countries with temperate climates (Silva et al. 2021).

267 Improving the targeted nature of urban pollinator research and accomplishing this research in

268 diverse urban landscapes will bolster our capacity to integrate habitat that supplies pollination

269 services and biodiversity to cityscapes around the world.

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423

424   **Figure 1.** Map of urban bee community sampling sites selected in a spatially stratified design

425   across the City of Madison, (a) surrounded by 200m buffers, filled with impervious land cover

426   and (b) overlaid on kriged property development year surface.

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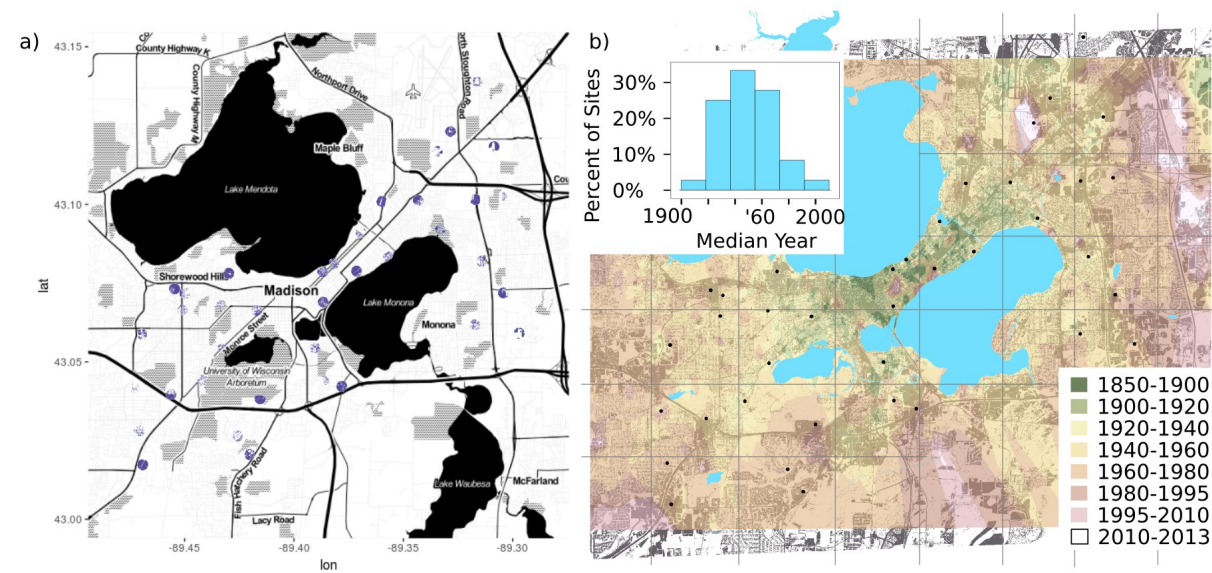
429 **Figure 2**. Species accumulation curves for overall site species richness with site numbers.
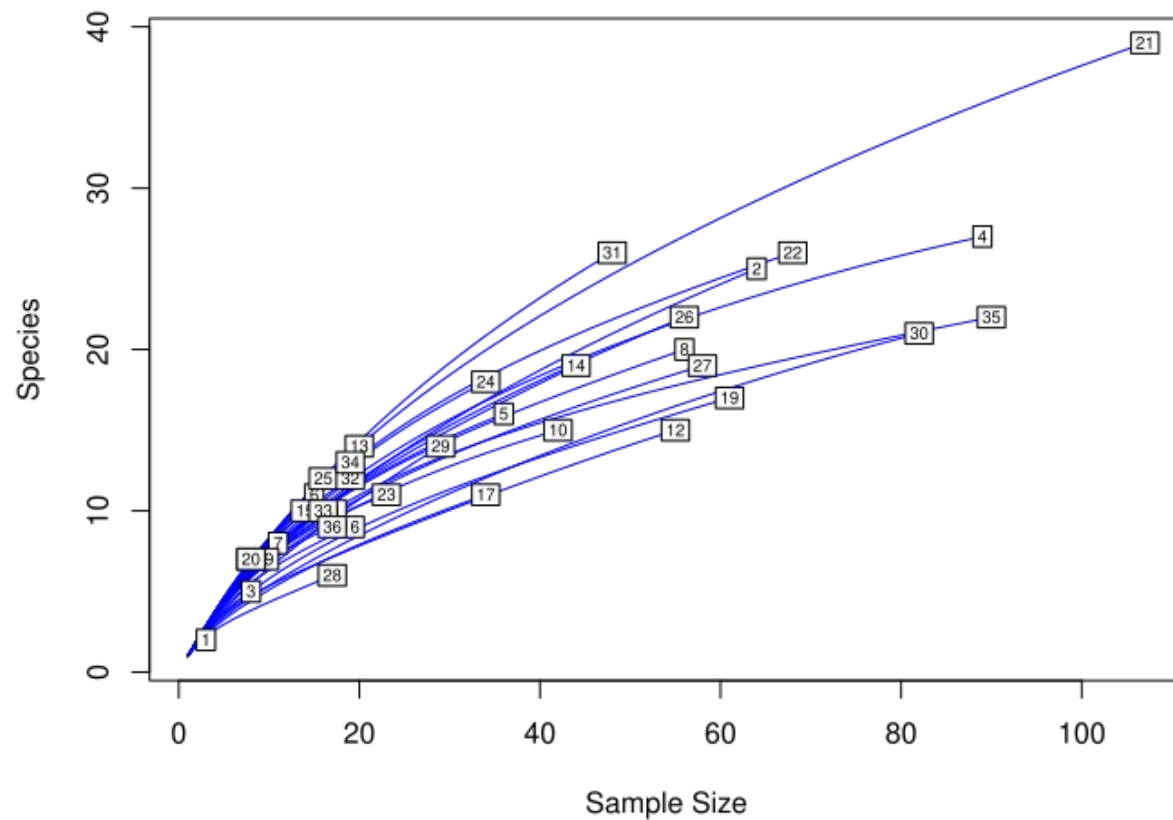
431   **Figure 3.** Average bee abundance and species richness for older neighborhoods and recently

432   developed neighborhoods with median property development year in the surrounding 200m

433   landscape sector before or after 1960.

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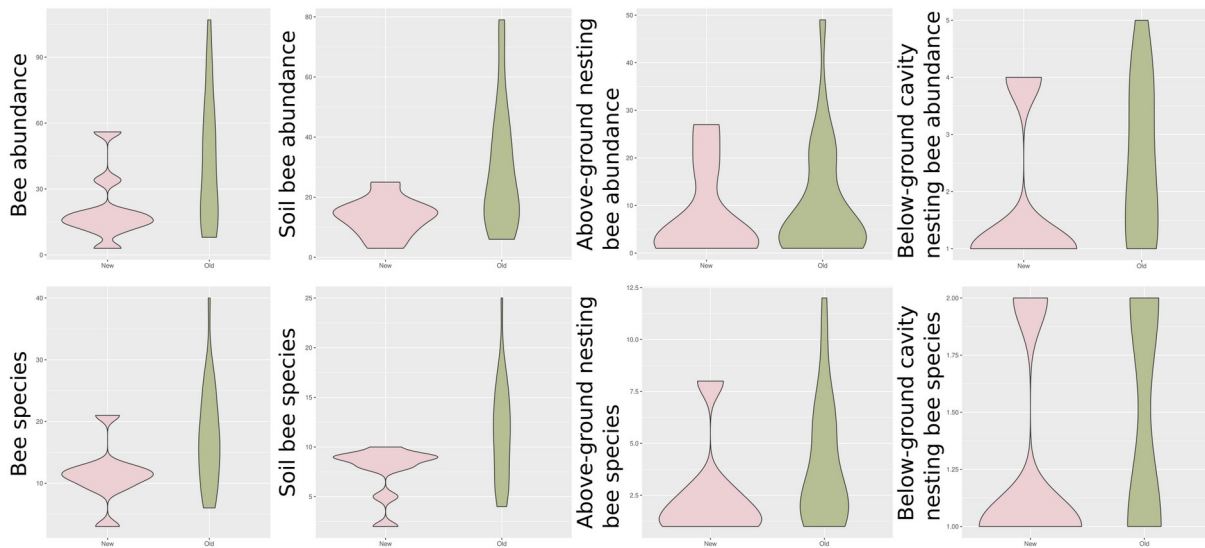
439 **Table 1.** Results of top AICc-selected multiple linear regression models for species richness of a.

440 the full bee community, b. soil-nesting bees, c. cavity-nesting bees, and d. above-ground bees.

441

442

Table 1. Best AICc-selected multivariate linear regression models

Full bee community					
Variable	Estimate	Std Error	P	Model adj R^2	P
Intercept	16.355	1.312	>0.001	0.217	0.007
Develop	-5.554	2.631	0.042		
Imp200	-2.880	1.140	0.017		
Soil nesting bee community					
Variable	Estimate	Std Error	P	Model adj R^2	P
Intercept	0.460	0.817	>0.001	0.197	0.010
Develop	-3.387	1.638	0.047		
Imp200	-1.667	0.710	0.025		
Above ground nesting bee community					
Variable	Estimate	Std Error	P	Model adj R^2	P
Intercept	3.630	0.492	>0.001	0.0954	0.0475
Imp200	-1.029	0.500	0.048		
Below ground cavity nesting bee community					
Variable	Estimate	Std Error	P	Model adj R^2	P
Intercept	0.460	0.294	0.131	0.426	0.002
For1000	-0.357	0.494	0.477		
For200	-1.022	0.392	0.015		

26

443 **Table 2.** Model average coefficients for the 95% confidence model set of AICc-selected multiple

444 linear regression models for species richness of a. the full bee community, b. soil-nesting bees, c.

445 cavity-nesting bees, and d. above-ground bees.

Table 2. 95% confidence model set average coefficients for species richness multiple variate linear regressions

Full bee community								
Variable	Intercept	Forest (1km)	Nat Veg (1km)	Imp (1km)	Forest (200m)	Nat Veg (200m)	Imp (200m)	Development
Model Avg Coef	15.997	0.250	-0.061	0.029	-0.27	-0.798	-3.049	-5.725
Sum of Weights		0.250	0.190	0.180	0.25	0.22	0.89	0.72
Soil nesting bee community								
Variable	Intercept	Forest (1km)	Nat Veg (1km)	Imp (1km)	Forest (200m)	Nat Veg (200m)	Imp (200m)	Development
Model Avg Coef	11.134	0.807	0.329	-0.131	-0.327	-0.457	-1.724	-3.608
Sum of Weights		0.290	0.200	0.180	0.21	0.22	0.82	0.73
Above ground bee community								
Variable	Intercept	Forest (1km)	Nat Veg (1km)	Imp (1km)	Forest (200m)	Nat Veg (200m)	Imp (200m)	Development
Model Avg Coef	3.695	-0.169	-0.641	-0.054	-0.009	-0.337	-0.679	-0.316
Sum of Weights		0.180	0.360	0.180	0.18	0.22	0.67	0.27
Below ground cavity bee community								
Variable	Intercept	Forest (1km)	Nat Veg (1km)	Imp (1km)	Forest (200m)	Nat Veg (200m)	Imp (200m)	Development
Model Avg Coef	1.434	-0.129	0.092	-0.027	0.368	0.081	-0.092	-0.017
Sum of Weights		0.520	0.170	0.200	0.51	0.15	0.14	0.12

447

27

448   **Table 3.** Multiple regression on distance matrices to assess the influence of geographic distance,

449   neighborhood development, and land cover on the full bee community, soil-nesting bees, above-

450   ground nesting bees, and d. below-ground cavity nesting bees.

451

Table 3. Multiple regression on distance matrices to investigate bee community beta-diversity

Full bee community					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	5.55×10^{-1}	0.81	2.78	0.02	0.007
Geographic distance	1.03×10^{-6}	0.28			
Neighborhood development	8.61×10^{-4}	0.18			
Land cover (200m)	-1.83×10^{-4}	0.04 *			
Land cover (1000m)	1.53×10^{-4}	0.43			
Full bee community – Final model					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	0.570	0.030	9.690	0.02	0.09
Land cover (200m)	-1.86×10^{-4}	0.03 *			
Soil nesting bee community					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	4.92×10^{-1}	1.000	4.160	0.030	0.020
Geographic distance	2.16×10^{-6}	0.04 *			
Neighborhood development	7.51×10^{-4}	0.260			
Land cover (200m)	-1.70×10^{-4}	0.04 *			
Land cover (1000m)	-1.26×10^{-4}	0.500			
Soil nesting bee community – Final model					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	4.91×10^{-1}	0.97	7.390	0.020	0.010
Geographic distance	-1.70×10^{-4}	0.04 *			
Land cover (200m)	2.18×10^{-6}	0.04 *			
Above ground nesting bee community					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	8.13×10^{-1}	0.110	1.590	0.01	0.36
Geographic distance	-1.84×10^{-6}	0.210			
Neighborhood development	1.65×10^{-4}	0.480			
Land cover (200m)	3.33×10^{-4}	0.680			
Land cover (1000m)	-3.71×10^{-4}	0.170			
Above ground nesting bee community – Final model					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	7.69×10^{-1}	0.270	2.130	0	0.14
Land cover (1000m)	-4.00×10^{-4}	0.140			
Below ground cavity nesting bee community					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	3.76×10^{-1}	0.95	5.810	0.070	0.040
Geographic distance	5.07	0.08 .			
Neighborhood development	-2.55	0.63			
Land cover (200m)	-4.30×10^{-4}	0.92			
Land cover (1000m)	-3.60×10^{-3}	0.6			
Below ground cavity nesting bee community – Final model					
Variable	Regression Coefficients	P	F-value	Model R^2	P
Intercept	3.72×10^{-1}	0.96	3.810	0.030	0.070
Land cover (1000m)	5.23×10^{-6}	0.07 .			

28

452   Supplemental Table 1

453

454   <u>Bee species</u>
455   *Agapostemon sericeus*
456   *Agapostemon virescens*
457   *Andrena bisalicis*
458   *Andrena crataegi*
459   *Andrena erythronii*
460   *Andrena milwaukensis*
461   *Andrena nasonii*
462   *Andrena nigrae*
463   *Andrena nuda*
464   *Andrena phaceliae*
465   *Andrena wellesleyana*
466   *Anthidium maculifrons*
467   *Anthidium manicatum*
468   *Anthidium oblongatum*
469   *Apis mellifera*
470   *Augochlora pura*
471   *Augochlorella aurata*
472   *Augochlorella persimilis*
473   *Augochlorella sp*
474   *Augochloropsis fulgada*
475   *Bombus affinis*
476   *Bombus bimaculatus*
477   *Bombus fervidus*
478   *Bombus griseocollis*
479   *Bombus impatience*
480   *Bombus rufosphinctus*
481   *Bombus sandersoni*
482   *Ceratina calcarata*
483   *Ceratina dupla*
484   *Ceratina mikmaqi*
485   *Ceratina strenua*
486   *Coelioxys spp*
487   *Colletes spp*
488   *Eucera atriventris*
489   *Florilegus condiginus*
490   *Halictus confusus*
491   *Halictus ligatus*
492   *Halictus parallelus*
493   *Halictus rubicundus*
494   *Hylaeus affinus*
495   *Hylaeus annulatus*

496   *Hylaeus floridanus*
497   *Hylaeus mesillae*
498   *Hylaeus rudbeckiae*
499   *Lasioglossum albepenne*
500   *Lasioglossum anomalum*
501   *Lasioglossum atwoodi*
502   *Lasioglossum atwoodii*
503   *Lasioglossum bruneri*
504   *Lasioglossum cattelae*
505   *Lasioglossum coreopsis*
506   *Lasioglossum corerulevum*
507   *Lasioglossum coriaceum*
508   *Lasioglossum cressoni*
509   *Lasioglossum divergens*
510   *Lasioglossum egregium*
511   *Lasioglossum hartii*
512   *Lasioglossum illinosese*
513   *Lasioglossum imatatum*
514   *Lasioglossum leucozonium*
515   *Lasioglossum lineatulum*
516   *Lasioglossum michiganense*
517   *Lasioglossum nigrovirde*
518   *Lasioglossum nymphacorum*
519   *Lasioglossum obscurum*
520   *Lasioglossum paraforbesii*
521   *Lasioglossum pilosum*
522   *Lasioglossum pruinosum*
523   *Lasioglossum spp*
524   *Lasioglossum tegulare*
525   *Lasioglossum timothyi*
526   *Lasioglossum versans*
527   *Lasioglossum weems*
528   *Lasioglossum weemsi*
529   *Lasioglossum zephyrum*
530   *Lasioglossum zonulum*
531   *Megachile inimica*
532   *Megachile latimanus*
533   *Megachile melanophoea*
534   *Megachile mendica*
535   *Megachile relativa*
536   *Melissodes agilis*
537   *Melissodes bimaculatus*
538   *Melissodes boltonae*
539   *Melissodes comunis*

540   *Melissodes dentiventris*
541   *Melissodes druriellus*
542   *Melissodes rustica*
543   *Melissodes tinctus*
544   *Melissodes trinodis*
545   *Nomada affabilis*
546   *Nomada articulata*
547   *Nomada cressoni*
548   *Nomada illinoensis pygmaea*
549   *Osmia sp.*
550   *Sphecodes sp.*
551   *Stelis louisae*
552   *Stelis nitida*
553