

1 **Bees use anthropogenic habitats despite strong natural habitat**

2 **preferences**

3 Miguel Á. Collado^{1,2}, Daniel Sol^{2,3}, Ignasi Bartomeus¹

5 Miguel Á. Collado <https://orcid.org/0000-0002-4216-317X>

6 D. Sol <https://orcid.org/0000-0001-6346-6949>

7

8 I. Bartomeus <https://orcid.org/0000-0001-7893-4389>

10 ¹ Estación Biológica de Doñana (EBD-CSIC), Avd. Americo Vesputio 26, 41092 Sevilla, Spain

11 ² CREAF, Cerdanyola del Vallès, Catalonia 08193, Spain

12 ³ CSIC, Cerdanyola del Vallès, Catalonia 08193, Spain

13

14 xmiguelangelcolladox@gmail.com

15 d.sol@creaf.uab.cat

16 nacho.bartomeus@gmail.com

17

18 Correspondence author information:

19 Miguel Ángel Collado Aliaño

20 e-mail: xmiguelangelcolladox@gmail.com

21 telephone number: +34 692 77 57 74

22

23 **ABSTRACT**

24 Habitat loss and alteration is widely considered one of the main drivers of the current loss of
25 pollinator diversity. Unfortunately, we still lack a comprehensive analysis of habitat importance,
26 use and preference for major groups of pollinators. Here, we address this gap analysing a large
27 dataset of 15,762 bee specimens (more than 400 species) across northeast USA. We found that
28 natural habitats sustain the highest bee diversity, with many species strongly depending on such
29 habitats. By characterizing habitat use and preference for the 45 most abundant species, we also
30 show that many bee species can use human-altered habitats despite exhibiting strong and clear
31 preferences for forested habitats. However, only a few species appear to do well when the habitat
32 has been drastically modified. We conclude that although altered environments may harbor a
33 substantial number of species, preserving natural areas is still essential to guarantee the
34 conservation of bee biodiversity.

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36 **Keywords:** Habitat importance, Habitat preference, Habitat use, Landscape, Pollinators, Evergreen forests, Urban,
37 Apoidea, Beta diversity.

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53 INTRODUCTION

54 Pollinators are considered to be of conservation concern worldwide (Goulson et al. 2015). As more than 80% of plants
55 are pollinated by animals (Ollerton et al. 2011), including 75% of crops species (Klein et al. 2007), the extinction of
56 pollinator species is expected to have far-reaching impact on ecosystem functioning and human well-being. For
57 example, in Europe, more than 20% of bees assessed by the IUCN are threatened (Nieto et al. 2014), and in North
58 America there is evidence that the populations of many bee species have drastically declined (Cameron et al. 2011;
59 Bartomeus et al. 2013).

60
61 While the current loss of pollinators may have a variety of causes, habitat loss and alteration is widely assumed to be
62 one of the main drivers (Winfree et al. 2011). The conversion of natural habitats into urban and agricultural systems is
63 often drastic and rapid (Frishkoff et al. 2014). Therefore, it is expected that the tolerance limits of many species are
64 exceeded, putting them at risk of extinction. Currently, over 40% of Earth's terrestrial surface has already been
65 modified by humans (Ellis et al. 2010) and the surface is expected to continue increasing in the next decades (Tilman et
66 al. 2001).

67
68 Although human-induced changes in the habitat are expected to have a negative impact on some pollinator species
69 (Winfree et al. 2011), they can also offer ecological opportunities to other species (McFrederick and LeBuhn 2005,
70 Matteson et al. 2008). Pollinators are highly mobile animals, and some are capable of using multiple habitat types
71 (Kremen et al. 2002). For example, some bee species nest in forested habitats while foraging in agricultural habitats
72 (Klein et al. 2003), and some even use highly transformed environments such as those altered by urbanisation and
73 intensive agriculture (Saure 1996, Baldock et al. 2015). If human modified habitats create new opportunities for some
74 pollinators, this may reduce the impact of habitat loss and alteration on pollinator communities and associated
75 ecosystem services (Kremen et al. 2002).

76
77 To anticipate the consequences of land use change on pollinator communities, we therefore need to assess the extent to
78 which different species are able to persist in intensively human-modified environments. This will inform us about the
79 sensitivity of species to habitat alteration and will help to identify habitats of conservation importance for protection
80 plans, but unfortunately, we still lack a comprehensive analysis of habitat importance, use and preference for major
81 groups of pollinators. A major obstacle has been the paucity of large-scale datasets on species-habitat associations. In
82 bees, for example, habitat suitability has only been modelled indirectly based on expert knowledge (Lonsdorf et al.
83 2009, Koh et al. 2015)

84

85 In the present study, we use a comprehensive dataset from an extensive monitoring program for bees in the northeast
86 and midwest US to directly estimate habitat use and preference across the entire region. Previous work has established
87 that bee community composition may be strikingly different among habitats (Brosi et al. 2007). For example, in
88 agricultural areas pollinator communities are typically dominated by common species and have few rare or threatened
89 species (Kleijn et al. 2015). Our first goal was to extend this work to ask how bee composition differs among natural
90 and human altered habitats at a regional scale. We assessed habitat importance for bee pollinators, both in terms of
91 species diversity and number of habitat specialists, using data for 15,762 individual bees from 433 species recorded
92 over 15 years. As pollinators are mobile species and the surrounding landscape often determines the presence of a
93 species in the focal habitat (Kremen et al. 2002). we also investigated the effect of the surrounding landscape on
94 determining bee responses.

95
96 The assessment of habitat importance can provide important insight into their sensitivity to environmental change.
97 However, the association of a species with a particular habitat does not necessarily indicate that the species is doing
98 well in that habitat, instead, it may simply indicate that it is the only habitat that is available. To better assess species
99 sensitivities, it is necessary to assess habitat preferences, defined as the tendency of a species to be non-randomly
100 associated with certain environments (Rice 1984). Therefore, the second goal of our study was to investigate such
101 species-habitat associations. We used null models to assess habitat preference and avoidance for 45 bee species with a
102 sufficiently large sample of occurrences (species with ≥ 100 independent records). We then characterized their
103 sensitivity to human altered habitats by estimating the extent to which the species occurs in highly-modified
104 environments or, instead, use multiple habitats that buffer them against destruction of their preferred habitat.

105

106 **MATERIAL AND METHODS**

107 **Sampling design**

108 Bees were intensively sampled from 2000 to 2015 by USGS Native Bee Inventory and Monitoring Laboratory, their
109 collaborators, and volunteers using pan traps, (~75%) and hand netting (~25%). As the sampling was designed to
110 maximize the area covered, not to repeat areas within a season or along years, different locations were selected in each
111 sampling point. Yet, all habitats were sampled enough to cover the entire phenology and with similar monitoring
112 techniques (Figure S1, Table S1). Although sampling was carried out over a larger region, we restricted our analyses to
113 samples taken from the area with the highest sampling effort, covering latitude 35.01 S to 42.79 N and longitude -87.54
114 W to -69.97 E (Fig. 1).

115

116 After capture, each specimen was identified to species level by expert taxonomists and the coordinates of the collection
117 site were recorded using GPS. Unidentified individuals or extremely rare species (i.e. those collected only once) were
118 removed from the dataset. Overall, we retained 31,505 individuals, which represent a 66% of the original data. To
119 ensure the independence of the collection events, we excluded from analysis specimens belonging to the same species
120 when collected at the same locality during the same day. After this last filtering, the final dataset comprised 15,762
121 individuals from 433 species collected from 1,452 different sites, all of which were used in subsequent analysis. All
122 specimens were vouchered at USGS Native Bee Inventory and Monitoring Laboratory.

123

124 For each georeferenced sampling site, we extracted habitat information using the National Land Cover Database
125 (NLCD) raster layer (Homer *et al.* 2015) with the R packages *raster*, *rgdal* and *stringr* (Bivand, Keitt T, and
126 Rowlingson 2014, Wickham 2015, Hijmans 2015). The 14 habitats considered for this study are described in Table 1.
127 We first extracted the habitat type from the focal point based on the precise coordinates. To take into account the
128 surrounding landscape, we also extracted the habitat composition in a buffer of 1,000 m radius around each focal point;
129 1,000 m is the maximum distance that most bees under 4 mm of intertegular span can forage (Greenleaf et al. 2007).
130 While our dataset spans 15 different years, information on land cover was only available for 2001, 2006 and 2011. To
131 account for this, bees sampled before 2005 were assigned to habitats based on information from the 2001 layer (28.11
132 % of our data), those sampled between 2006-2010 were assigned to the 2006 layer (42.32%) and for the rest (2011-
133 2015) we used the 2011 layer (29.57%). To estimate availability of each habitat in our study region, we divided all the
134 pixels of the habitat by the total pixels of the entire study area (Fig. S2 in Supporting information).

135

136 **Data analysis**

137 **Habitat importance**

138 We first evaluated the importance of different habitats for bee species using the number of species detected in each
139 habitat (i.e., species richness). Although species richness is a traditional index of habitat importance (Chao and Jost
140 2012), it treats all species as equal, which may not be optimal for conservation purposes. For instance, a habitat may
141 have high species richness but primarily sustain common species that are widely present elsewhere, whereas another
142 habitat with equal or lower species richness could mostly support rare species that are highly dependent on this
143 particular habitat. Thus, we used in addition to species richness, a metric of habitat strength, as a way of weighting for
144 the species depending on particular habitats (see below).

145

146 Habitat strength was calculated using a metric derived from network analysis. The strength of a node (i.e., a single

147 element from a network, in this case the focal habitat) in a bipartite interaction network of species per habitats is defined
148 as the sum of the dependencies of nodes corresponding to the other level in the bipartite network (in this case, the bee
149 pollinator species) linked to that habitat (Bascompte et al. 2006). The dependence of a bee pollinator on a given habitat
150 is calculated as its proportional use of this habitat relative to the other habitats and ranges from zero to one. For
151 example, if a species node has a dependence value near one on a habitat node, we conclude that species depends strictly
152 on that habitat. However, if the dependence is close to zero, the species does not depend on that single habitat and
153 instead, uses other habitats.

154
155 To calculate richness and strength for each habitat, we first rarefied each habitat to equalize sampling effort to that of
156 the least sampled habitat. To this purpose, we first calculated the coverage value (the percentage of the total species
157 diversity) for each habitat and then rarefied to the number of individuals necessary for equal coverage of all habitats
158 (Hsieh et al. 2012). The common coverage value used was 0.60, meaning that 60% of species richness from each habitat
159 was sampled to calculate richness and strength. Coverage was calculated using the “iNEXT” package (Hsieh et al.
160 2012). By using the same coverage for every habitat we avoided that the most sampled habitats were over-represented.
161 However, the total richness at the regional scale (i.e., gamma-diversity) is likely to depend on the area covered by each
162 habitat, independent of the number of samples for each habitat, so we show the proportion of each land cover type (Fig.
163 S2) to aid interpretation of gamma-diversity values.

164
165 Finally, we assessed beta-diversity among and within habitats to identify the habitats that are complementary in species
166 composition and determine the degree of species turnover within habitats across space (Whittaker 1960). Among habitat
167 beta-diversity was calculated using Sørensen beta-diversity dissimilarity index across all pairs of habitats (Sørensen
168 1948, Fig. 2). Habitats were then grouped according to their similarity using a hierarchical cluster analysis. Within
169 habitat beta-diversity was calculated as the slope of the species-samples accumulation curves for each habitat. This
170 metric represents the rate at which new species appear within that habitat as sample size increases (see Fig. 2). The
171 species-samples relationship was almost linear and hence we did not log-transformed the data (Baselga and Orme, 2012
172 log-transforming the data using natural logarithms produced similar results).

173
174 As bees are mobile organisms that likely depend on adjacent habitats in the landscape, we repeated the above analyses
175 at a landscape scale. We classified landscapes at a 1,000 m radius surrounding each sampling site into discrete groups
176 using a k-mean algorithm. The total number of groups (k) was determined using “the elbow method”, where k is the
177 number of clusters beyond which additional clusters no longer improve the model (k = 20, Fig. S3) so 20 types of
178 landscapes were made. These 20 landscape categories range from mainly forested landscapes, to heterogeneous

179 landscapes that include agriculture and forested areas (Table S2).

180

181 **Habitat use and preference**

182 Disentangling habitat use and preference of individual species requires a large sample size for each species studied, thus
183 we only used species that had > 100 independent collection events (n = 45 species). We considered a habitat to be used
184 by a species when at least one individual of that species was sampled in that habitat. To normalize for differences in the
185 number of species occurrences, we did 100 rarefaction events and extracted the means of the number of habitats used by
186 each species.

187

188 We defined habitat preferences as the non-random association of a species with certain habitats. Therefore, a species
189 was considered to exhibit habitat preference if it was sampled in a habitat more frequently than expected by chance.
190 Species preferences can be confounded with species distributions if their geographic range only covers some of all
191 available habitats. For example, species distributed only in the northern part of the sampling area may appear to prefer
192 evergreen forests simply because this habitat is more common there. However, this limitation was negligible in our
193 study because the geographic range of the species studied covered the entire study area, implying that all sites could
194 have been potentially occupied by any species if habitat choice was completely random. We compared a habitat-species
195 matrix (i.e., the “observed” matrix) to 1,000 null matrices (i.e., the “expected” matrices). These expected matrices were
196 created by means of the function “nullmodel” contained in the “bipartite” package (Dormann et al. 2009). This function
197 generates random bipartite tables maintaining the sum of rows and columns using Patefield's algorithm, so the
198 proportional abundance of species and habitats is maintained, but their associations are re-shuffled. We considered that
199 a species exhibited preference for a particular habitat if it was more abundant than the 0.95 quantile of expected
200 abundances. Species less abundant than the 0.05 quantile were considered to avoid that habitat (Sol et al. 2014).

201

202 For the sake of clarity, we present in the results section habitat preferences grouped by three main habitat types: 1)
203 urban: developed, high intensity and medium intensity; 2) crops and semi-natural areas: cultivated crops,
204 herbaceous/hay/pasture, developed, low intensity and open space; and 3) forested: deciduous forest, evergreen forest
205 and mixed forest, see Fig. 2 for details. Detailed preferences for each species in each habitat can be found in Table S3.

206

207 **RESULTS**

208 **Habitat importance**

209 Our estimates of species richness and strength for each habitat were positively correlated (Fig. 3, Table S3). Despite co-

210 varying positively, the strength values allowed us to differentiate the quality of habitats with similar richness values. For
211 example, except for evergreen forest, which was the habitat with the greatest rarefied species richness (107.7), all
212 rarefied richness values for the three other forested habitats were very similar (range = 91.0 to 91.2 species). Yet, the
213 strength values for these habitats varied substantially, being lowest in mixed forest (22.46), intermediated in woody
214 wetlands (24.56) and highest deciduous forest (25.80). This is because the strength value for a habitat does not only
215 increases with species richness but also when the species are highly dependent on this particular habitat (Fig. S4).

216

217 Human-modified habitats sustained a considerable fraction of the regional pool of bee species, however they had lower
218 species richness and strength than less altered and more natural habitats (Fig. 3). However, this loss was in part
219 compensated by the presence of many non-indigenous species. From the 29 exotic bee species we recorded, 22 were
220 collected in urban areas. This is remarkable as only 5% of the sampling area was composed of urban habitat. Exotic
221 species depending on urban habitat were thus contributing to the high habitat strength values reported in urban areas.

222

223 The composition of bee species also exhibited remarkable differences across habitats. Cluster analysis on beta-diversity
224 values classified species composition in three main habitat groups: forested habitats (forest), high and medium intensity
225 developed habitats (urban), and crops, pasture and semi-natural habitats (crops and semi-natural) (Fig. 2). The beta-
226 diversity within habitats, which describes the rate at which diversity increases when adding new sampling events, also
227 differed across habitats (Fig. 2). The higher value was observed in evergreen forests, which may explain its high overall
228 species; the lower value instead found in deciduous forests, indicating a high resemblance in species composition across
229 space.

230

231 The results at the landscape level highly resembled those at the habitat level. Landscapes dominated by forests had the
232 highest species richness and strength (Fig. 3b, groups 14, 4, 10, 12, 13), even when mixed with crops (groups 5, 9, 17).
233 Coastal areas (6) had also high levels of richness and strength, yet these values diminished again when the proportion of
234 crops and/or pastures increased (1, 3). When crops were the dominant habitat (8), instead, the values of species richness
235 and strength were significantly lower. Finally, urban landscapes (11,19) had low importance than other habitats in terms
236 of species richness, yet their strength values were unexpectedly high because of the presence of urban exploiters (i.e.,
237 specialists in developed habitats; Table S2 and Table S3).

238

239 **Habitat use and preference**

240 The 45 most common bee species were recorded using most habitats, but 33 out of 45 showed a strong preference for a
241 single habitat (Table S3). After grouping habitats in three main categories (see justification in the methods), 23 out of

242 45 showed preferences for single groups. Fourteen species preferred natural forested habitats, six preferred urban
243 habitats and three preferred agricultural habitats (Table 2).

244

245 Importantly, species that exhibited a preference for forests also showed a tendency to avoid urban habitats. Thus, 13 of
246 the 14 species that preferred forested habitats avoided urban habitats (Table 2). The only exception was *Lasioglossum*
247 *imitatum*, who had preference for forested habitats but also presented a high preference for urban habitats (Table 2).

248 Perhaps unexpectedly, some degree of habitat specialization was also detected among urban dwellers (Table 2): seven
249 out of 11 that preferred some type of urbanized environment avoided crops, pastures and forests (Table S3). From all
250 the studied species, the most generalist was the managed bee *Apis mellifera*, which exhibited no preference or
251 avoidance for any habitat.

252

253 **DISCUSSION**

254 Four main conclusions can be drawn from our comprehensive analysis of bee species across northeast USA. First,
255 although no habitat appeared to be completely inhospitable to bee pollinators, many species showed a strong preference
256 for natural habitats while consistently avoiding human-modified habitats. Second, the dominant habitat within the
257 landscape was the strongest determinant of species diversity and, contrary to previous studies (Steffan-Dewenter and
258 Tschamtkke 1999), heterogeneity only had moderate buffer effects on diversity. Third, and as a consequence of the two
259 previous findings, human-altered environments supported significantly less diversity of species (and had less strength)
260 than the surrounding natural environments. Finally, the loss of biodiversity in human-altered environments could have
261 been higher had not been partially compensated by the addition of human commensals and some exotic species

262

263 Natural habitats were the most suitable for bees regarding both importance (richness and strength) and the number of
264 species that preferred them. Evergreen forests in particular exhibited the highest habitat importance in the region,
265 despite harbouring very few habitat specialists. Evergreen forests are widespread in the region and the associated bee
266 species have high spatial beta-diversity, meaning that bee composition largely varies between different evergreen forest
267 sites. These forests comprise flower rich areas like the coastal Pine Barrens that are fragmented and crossed by right of
268 way infrastructures, which can increase their attractiveness for bees (Hill and Bartomeus 2016). Hence, the evergreen
269 forests of our study area may not be representative of more northern evergreen forests. In contrast, bee communities
270 associated with deciduous forests and other natural habitats had lower beta-diversity and lower overall species richness.
271 However, they sustained a large number of habitat specialists, a possibility already advanced in previous studies (Burkle
272 et al. 2013).

273

274 As specialised adaptations to particular habitats may limit the success of bee species in other habitats, it is unsurprising
275 that the majority of forest specialist species avoid urban habitats and/or crops and pastures. There is therefore a
276 possibility that many of these species may become extinct, at least locally, if forested habitats disappear from the
277 landscape (Burkle et al. 2013).

278
279 Much of the current risk of species loss comes from the replacement of natural forests by crops and pastures, the most
280 frequent alteration of natural habitats (Newbold et al. 2015). Crops and pastures exhibit a significantly low species
281 richness and strength values compared to natural forests (Newbold et al. 2015). Thus, while some species used crops
282 and pastures opportunistically, very few became specialized to exploit them (see also Kleijn et al. 2015). Moreover,
283 within habitat beta-diversity for agricultural habitats was low, reinforcing the view that these habitats sustain a limited
284 set of common habitat generalists. Cropping systems are however highly heterogeneous, ranging from cereal
285 monocultures to diverse flowering cropping systems (Donald 2004) implying that the impact may vary depending on
286 the intensity of the alterations. Although our dataset do not allow for finer scale analyses separating the effects of
287 different crops, current evidence suggests that most modern crop managing practices (i.e., herbicide and insecticide
288 application) are likely to negatively impact on bee populations (Goulson et al. 2015, Woodcock et al. 2016).

289
290 While the conversion of natural habitats to cities is not so widespread as the replacement by crops and pastures
291 (Newbold et al. 2015), urbanisation is currently considered one of the most rapid and drastic alterations of natural
292 ecosystems. In line with previous studies (Chapin 1997, Sol et al. 2014), urbanised habitats harboured substantially
293 fewer species than the surrounding natural habitats. The persistence of bee populations in urban habitats may be limited
294 for resource availability. Food resources are often dominated by exotic or ornamental species (Ellis et al. 2012), which
295 few bee species are able to exploit (Bartomeus et al. 2016). However, urban habitats also offer resource opportunities
296 for some species. For example, *P. bombiformis* specializes in exploiting plants from the *Hibiscus* genus, a popular
297 ornamental plant. New opportunities may also emerge for hole nesting bees in the form of human made constructions
298 (Cane et al. 2007). As natural enemies are often scarcer in cities (Sorace and Gustin 2009), these “urban exploiters”
299 may proliferate despite their little opportunity to adapt to the new environments. Likewise, we show that non-
300 indigenous species, proliferate in urbanised environments, being most of the exotic bees collected only in urban areas.
301 Although the presence of urban exploiters and non-indigenous species importantly contributed to increase species
302 richness in urbanised environments, their diversity was low and hence did not fully compensate for the loss of diversity
303 associated with urban avoiders (see also Sol et al. 2017).

304
305 Past work suggests that while undisturbed habitats are essential to preserve biodiversity, habitats that have experienced

306 low intensity alterations may still help buffer against extreme diversity loss (Frishkoff et al. 2014, Sol et al. 2017). Our
307 results provide some support to this view, showing that species loss was not as accentuated in moderately modified
308 habitats (Table 2). For example large gardens within cities provide diverse food resources for pollinators, harbouring a
309 higher bee diversity and abundance than city centres. In fact, in Berlin, half of the total German bee fauna was recorded
310 inside the city (Saure, 1996) and in San Francisco, USA, higher mean abundances of *Bombus spp* were found in urban
311 gardens compared with natural parks beyond the city boundaries (McFrederick and LeBuhn 2006). Likewise, some
312 flowering crop fields provide good foraging opportunities for generalist bee species (Magrath et al. 2017), despite low
313 plant diversity and short bloom periods (Donald 2004).

314
315 Although the analyses of single focal habitats are essential to establish habitat importance and assess the sensitivity of
316 species to habitat alterations, species diversity typically depends on the mosaic of habitats present in a region (Steffan-
317 Dewenter and Tschamtkke 1999). We expected that species able to use multiple habitats would be less vulnerable to
318 habitat modification than species with specific habitat requirements. However, at the landscape level, our results show
319 that the dominant habitat within the landscape was the strongest determinant of species diversity and that heterogeneous
320 landscapes only had intermediate diversity levels. This is exemplified by the finding that forested habitats intermixed
321 with human-modified habitats had lower species diversity than fully forested habitats.

322
323 Altogether, our results provide clear evidence that the loss and alteration of natural habitats caused by human activities
324 leads to many “losers” and a few “winners”. Albeit the specific bee-habitat associations vary as a function of the
325 intensity of the alterations and may change in other geographical regions, the pattern we observe might be general
326 (Palma et al. 2017). Admittedly, our estimations of species sensitivity to habitat alterations are conservative, as these
327 analyses were restricted to common species and hence some habitat specialists may have been missed. However, the
328 analyses using the strength index, which did include rare species, consistently showed that the species dependency on a
329 given habitat decreased with the degree of habitat modification (Fig 3). Regardless of any potential bias in the species
330 for which we can assess its preference, our analyses show that the loss of bee diversity could have been higher had not
331 been partially compensated by the colonisation of native opportunists and exotic species (see also Sol et al. 2017).
332 Moreover, the new species may differ from those they replace in functional traits, particularly those that provide
333 environmental tolerance such as life history, body size, multivoltinism and dietary generalism (see Kitahara and Fujii
334 1994, Bartomeus et al. 2013; Sol et al. 2014; Scheper et al. 2014), and hence probably play different roles in the
335 ecosystem (Bartomeus et al. 2017). As the loss of functional diversity may affect ecosystem functioning and reduce the
336 long-term sustainability of ecosystem services, identifying these functional traits represent an important avenue of
337 future research.

338

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447 field conditions. - J. Appl. Ecol. 53(5), 1358–1362.
- 448

449 **FIGURES AND TABLES**



451 **Figure 1.** Map of the sampling area. It covers the area from 35.01 S to 42.79 N and -87.54 W to
452 -69.97 E, northeast USA. This area was selected as it represents a large but homogeneous region.

453

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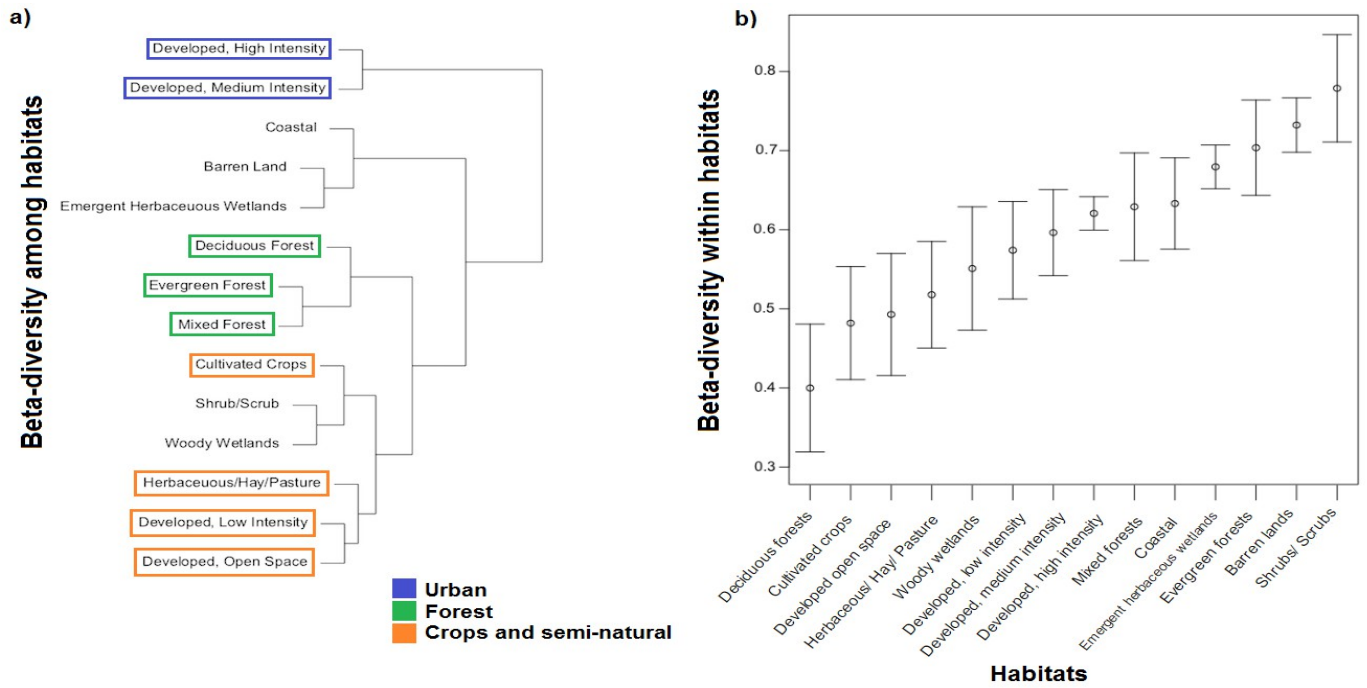
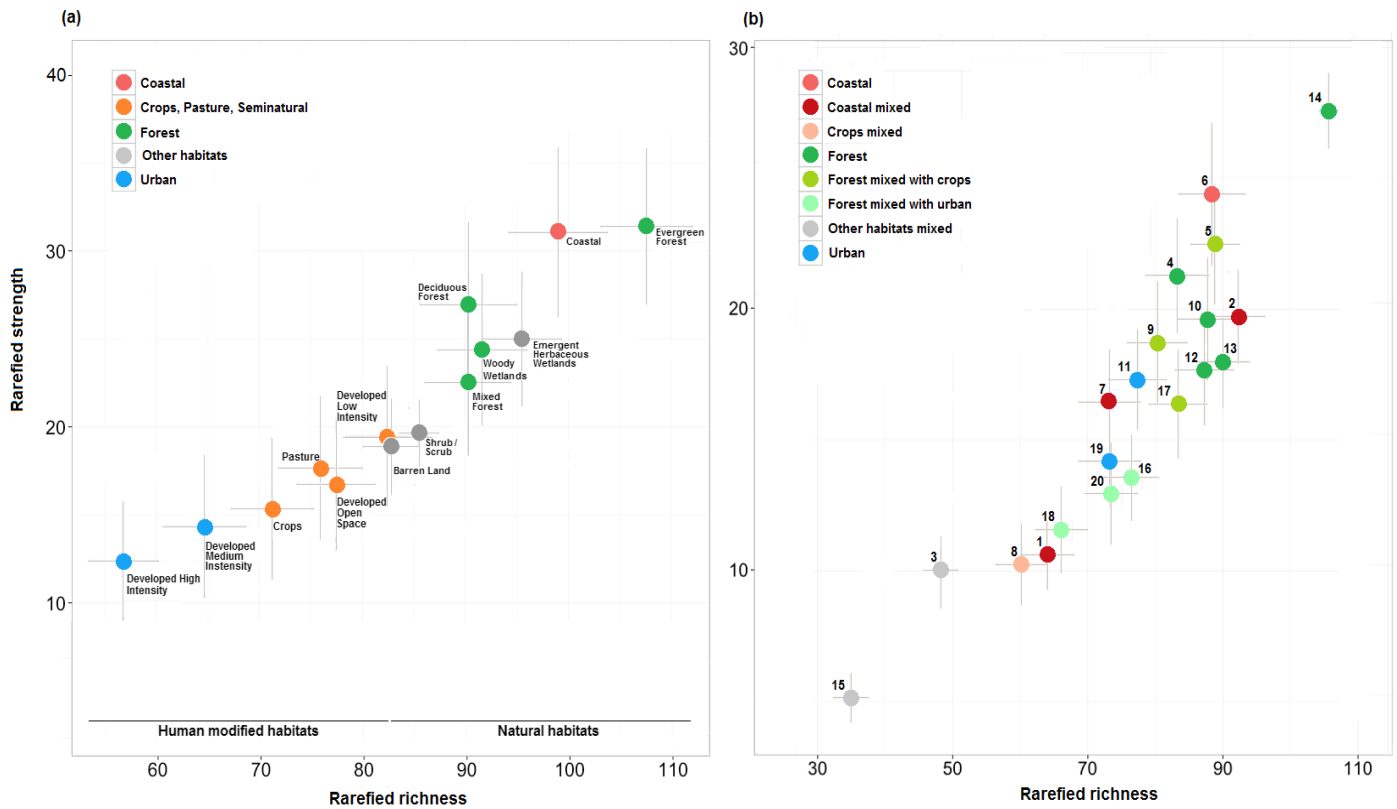


Figure 2. Beta-diversity analysis results: a) using the beta-diversity values among habitat types (Sørensen beta-diversity dissimilarity matrix). We grouped the 14 habitats according to their similarity in community composition. Groups of habitats used for the preference analysis are highlighted. b) Estimated beta-diversity and standard deviation within habitats, calculated as the slopes of the species-sample accumulation curves for each habitat, as an indicator of the rate new species for that habitat appear with increasing sample size. Larger values indicate more rapid gain of new species with increased sample size.

456



457 **Figure 3.** Importance of each analyzed habitat. We defined importance as a function of both
458 strength and richness. Both metrics are correlated, but give different information (see text for
459 details). Each point represents the mean of 100 rarefied strength and richness values for each
460 habitat. Bars are the standard deviation across 100 runs for both strength and richness. a)
461 Shows habitat importance results considering only the habitat where bees were found. While
462 human modified habitats are less important than the natural habitats, they still sustain a
463 substantial amount of pollinator species. b) Shows habitat importance considering landscape
464 composition where species were collected. Similar landscapes were grouped by color; detailed
465 composition of each landscape can be found in Table S1.

466

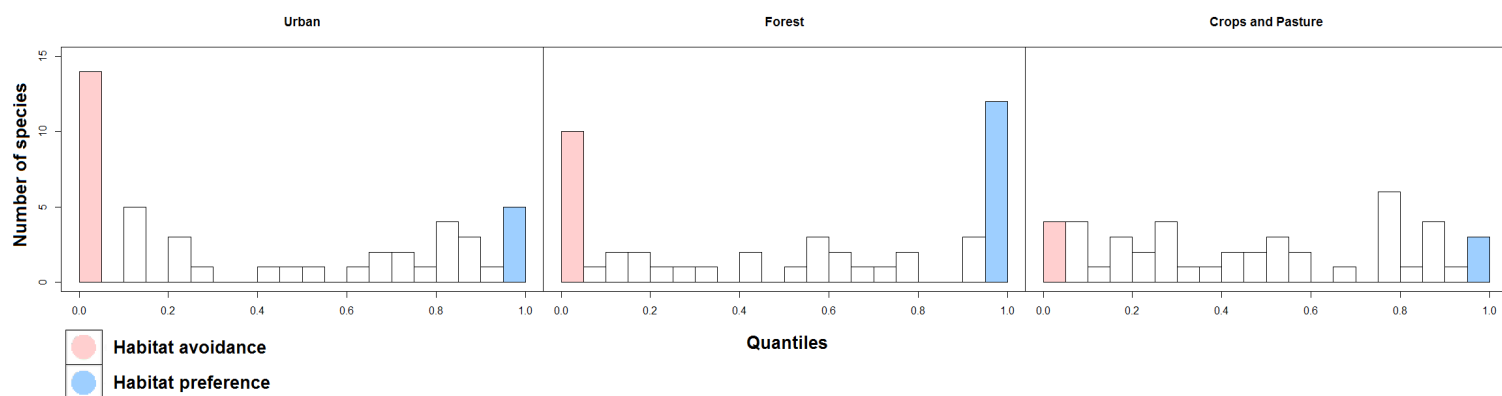


Figure 4. The distribution of species habitat preferences from Table 4. Red bars are the number of species avoiding that habitat, and blue bars are the number of species preferring that habitat. Urban habitats have both avoiders (14 of 45) and exploiters (6 of 45). Forests also have avoiders (10 of 45) but have a higher proportion of exploiters (14 of 45). Crops and pasture are more equally distributed, with few species preferring or avoiding them.

468 **Table 1.** Description of the habitats used to assess importance, use and preference for bee pollinator
 469 species, as they are defined and contained in the National Land Cover Database 2011, which is a
 470 modified version of the Anderson Land Cover Classification System (J. R. Anderson et al 1976).

Habitat	Description
Barren Land	Areas of bedrock, desert pavement, scarps, talus, slides, volcanic material, glacial debris, sand dunes, strip mines, gravel pits and other accumulations of earthen material. Generally, vegetation accounts for less than 15% of total cover.
Coastal	Areas next to open water, generally with less than 25% cover of vegetation or soil.
Cultivated Crops	Areas used for the production of annual crops, such as corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards. Crop vegetation accounts for greater than 20% of total vegetation. This class also includes all land being actively tilled.
Deciduous Forest	Areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change
Developed: Low Intensity	Areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20–49% of total cover. These areas most commonly include single-family housing units.
Developed: Medium Intensity	Areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50–79% of the total cover. These areas most commonly include single-family housing units.
Developed: High Intensity	Highly developed areas where people reside or work in high numbers. Examples include apartment complexes, row houses, and commercial/industrial. Impervious surfaces account for 80–100% of the total cover.
Developed: Open Space	Areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for less than 20% of total cover. These areas most commonly include large-lot single-family housing units, parks, golf courses, and vegetation planted in developed settings for recreation, erosion control, or aesthetic purposes.
Emergent Herbaceous Wetlands	Areas where perennial herbaceous vegetation accounts for greater than 80% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.
Evergreen Forest	Areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.
Herbaceous/Hay/Pasture*	Areas of grasses, legumes, or grass–legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle, also containing areas dominated by graminoid or herbaceous vegetation. Pasture/hay vegetation accounts for greater than 20% of total vegetation.
Mixed Forest	Areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. Neither deciduous nor evergreen species are greater than 75% of total tree cover.
Shrub/Scrub	Areas dominated by shrubs less than 5 m tall with shrub canopy typically greater than 20% of total vegetation. This class includes true shrubs, young trees in an early successional stage or trees stunted from environmental conditions.
Woody Wetlands	Areas where forest or shrub-land vegetation accounts for greater than 20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.

471

472 *Herbaceous and Hay/Pasture are classified as two different habitats in NLCD. We merged them
473 because herbaceous areas in our sampling region are always for livestock (Koh et al 2015).

474

Table 2. Species habitat preference or avoidance. The first column indicates the number of rarefied habitats used for each species listed, the other three columns show for every habitat (see Fig. 4 for habitat grouping) the habitat preference (> 0.95 , marked in blue) or avoidance (> 0.05 , marked in red), calculated as the probability of having a higher or lower observed abundance than expected under the null model.

Species	Habitats used	Pasture and Crops	Forests	Urban
<i>Agapostemon virescens</i>	12.47	0.66	0.1	0.89
<i>Andrena carlini</i>	11.38	0.43	0.78	0.01
<i>Andrena cressonii</i>	12.41	0.53	0.61	0.02
<i>Andrena erigeniae</i>	11.43	0.1	1	0.01
<i>Andrena nasonii</i>	12.32	0.09	0.99	0.03
<i>Andrena perplexa</i>	10.82	0.94	0.51	0.01
<i>Andrena violae</i>	11.85	0.39	0.92	0.01
<i>Apis mellifera</i>	12.46	0.5	0.61	0.69
<i>Augochlora pura</i>	11.34	0.29	0.96	0.21
<i>Augochlorella aurata</i>	12.3	0.05	0.75	0.5
<i>Bombus bimaculatus</i>	12.04	0.05	0.99	0.04
<i>Bombus fervidus</i>	12.93	0.87	0.03	0.73
<i>Bombus griseocollis</i>	12.28	0.19	0.43	0.82
<i>Calliopsis andreniformis</i>	12.68	0.76	0.14	1
<i>Ceratina calcarata/dupla/mikmaqi*</i>	12.53	0.53	0.24	0.27
<i>Ceratina strenua</i>	12.06	0.99	0.02	0.73
<i>Halictus confusus</i>	12.2	0.52	0.6	0.99
<i>Halictus ligatus/poeyi</i>	12.42	0.09	0.26	0.95
<i>Halictus rubicundus</i>	11.64	0.78	0.18	0.67
<i>Hylaeus affinis/modestus</i>	12.38	0.3	0.95	0.41
<i>Lasioglossum bruneri</i>	11.81	0.87	0	0.96
<i>Lasioglossum callidum</i>	12.35	0.99	0.01	0.11
<i>Lasioglossum coriaceum</i>	12.52	0	1	0.02
<i>Lasioglossum cressonii</i>	11.9	0.01	1	0.04
<i>Lasioglossum hitchensi</i>	12.13	0.88	0.17	0.55
<i>Lasioglossum illinoense</i>	11.59	0.79	0.77	0.89
<i>Lasioglossum imitatum</i>	12.18	0.11	0.99	0.9
<i>Lasioglossum near_admirandum</i>	11.29	0.85	0.44	0.83
<i>Lasioglossum oblongum</i>	12.33	0.34	0.01	0.15
<i>Lasioglossum pectorale</i>	11.59	0.58	0.11	0.15
<i>Lasioglossum pilosum</i>	12.59	0.79	0	0.99
<i>Lasioglossum tegulare</i>	12.51	0.76	0.01	0.25
<i>Lasioglossum versatum</i>	11.96	0.5	0.7	0.25
<i>Megachile brevis</i>	12	0.89	0.01	0.63
<i>Megachile mendica</i>	11.9	0.08	0.34	0.81
<i>Melissodes bimaculata</i>	11.94	1	0	0.84
<i>Nomada bidentate_group</i>	12.52	0.42	0.98	0.02
<i>Nomada pygmaea</i>	11.65	0.21	0.96	0
<i>Osmia atriventris</i>	10.27	0.18	0.98	0

<i>Osmia bucephala</i>	11.94	0.29	1	0.11
<i>Osmia georgica</i>	12.93	0.22	0.95	0.12
<i>Osmia pumila</i>	12.45	0.19	0.97	0.02
<i>Osmia taurus</i>	11.64	0.57	0.59	0.01
<i>Ptilothrix bombiformis</i>	11.53	0.78	0	0.99
<i>Xylocopa virginica</i>	11.65	0.28	0.6	0.79

475

476 * This group of species was merged because they are morphologically similar and very difficult to

477 separate by classic taxonomy.