

1 **Pollinator habitat plantings benefit wild, native bees, but do not necessarily favor rare**  
2 **species**

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## 21 **ABSTRACT**

22 1. Installing pollinator habitat is a ubiquitous conservation tool, but little is known about which  
23 pollinator taxa require support, or which benefit from habitat installations.

24 2. We studied the response of rare and common bees to pollinator habitat enhancement. We used  
25 independent regional datasets to designate bee species as common or rare based on their rank  
26 according to one of three metrics: a) site occurrence frequency, b) local relative abundance, and  
27 c) geographic range size. We asked whether the abundance or richness of rare and common bees  
28 were greater in pollinator habitat, relative to old-field controls. Because we used an arbitrary,  
29 quantile-based cutoff to categorize species rarity, we conducted sensitivity analysis and  
30 controlled for rarity classification errors with a null model. With this null model, we determined  
31 whether rare and/or common species responded to pollinator habitat disproportionately,  
32 compared to the expectation for ‘typical’ bee species.

33 3. We found that the number of individuals and of species designated as rare based on local  
34 relative abundance was greater in pollinator habitat enhancements. The number of individuals  
35 from bee species designated as rare based on site occurrence was lower in pollinator habitat  
36 enhancements, but the number of species was not clearly different between habitat types. We  
37 did not find a clear positive nor negative effect of habitat enhancement for species designated  
38 rare based on geographic range size. For all three rarity metrics, common species increased in  
39 abundance and richness in pollinator habitat relative to controls. Null models indicated that in  
40 most cases, neither rare nor common species disproportionately benefited from pollinator habitat.

41 4. *Synthesis and Applications:* Our results suggest that pollinator habitat can lead to an increase  
42 in the abundance and richness of bees, including species that are rare and that are common.  
43 However, rare species appeared to respond differently than typical species, and depending on  
44 how species were classified as rare, could display muted or even negative responses to habitat  
45 enhancement. Targeting rare species with specific floral resources or unique habitat types may  
46 lead to better outcomes for rare and threatened species.

47

## 48 **1 | INTRODUCTION**

49 Habitat restoration is increasingly an important tool for conserving biodiversity (Hobbs  
50 2007; Brudvig 2017). Currently, considerable government funding goes into restoring habitat for  
51 pollinators (Garbach & Long 2017). The primary method by which land managers restore habitat  
52 is the planting of wildflowers to provide resources such as pollen and nectar (Tonietto & Larkin  
53 2018). For wild, native bee communities, the lack of floral resources is likely one of the main  
54 limiting factors (Roulston & Goodell 2011) and has been linked to declines in native bee health  
55 and abundance as well as species extinction (Carvell *et al.* 2006; Williams *et al.* 2012; Ollerton  
56 *et al.* 2014; Crone & Williams 2016). Increasing floral cover and diversity increases the overall  
57 diversity and abundance of bee pollinators (Blaauw & Isaacs 2014; Kleijn *et al.* 2015; Scheper *et*  
58 *al.* 2015; Williams *et al.* 2015; Tonietto & Larkin 2018; Albrecht *et al.* 2020).

59 Rare species comprise the bulk of biodiversity (McGill *et al.* 2007), and are often at  
60 greater risk of extirpation (Lande 1988; Manne *et al.* 1999; Payne & Finnegan 2007; Harnik *et*  
61 *al.* 2012). Conservation practices are often implemented to protect or benefit rare species *per se*  
62 (Hallett *et al.* 2013). However, few studies have specifically examined whether particular groups  
63 of pollinator species benefit from pollinator plantings (but see Pywell *et al.* 2012; Scheper *et al.*  
64 2015; Sutter *et al.* 2017). There are reasons to expect that pollinator plantings both would, and  
65 would not, benefit rare species. On the one hand, such plantings could have a disproportionately  
66 positive effect on rare species if they contained specific resources that are limiting to those rare  
67 species in the wider landscape (Gibbs *et al.* 2008; Swarts & Dixon 2009). On the other hand,  
68 pollinator plantings in a degraded landscape might benefit only species that persist in these  
69 landscapes, and are thus resilient to anthropogenic change and likely not of greatest conservation  
70 concern (Kleijn *et al.* 2015). Lastly, restored pollinator plantings may similarly benefit both rare  
71 and common species. In this case, changing plant seed mixes to increase flower species preferred  
72 by rare bees may lead to better conservation outcomes for all species (Sutter *et al.* 2017;  
73 MacLeod *et al.* 2020).

74 An important first step in assessing the impact of habitats on rare species is to define  
75 which species are, in fact, rare. Rarity can be defined using multiple metrics, including local  
76 abundance, site occurrence frequency across a larger area, and/or geographic range size  
77 (Rabinowitz 1981; Gaston 1994). Species categorized as rare based on different metrics may be  
78 sensitive to different ecological processes. Species with low local abundance are prone to local  
79 extinction via stochastic demographic processes (Lande 1988). Site occurrence frequency can  
80 predict extinction risk (Payne & Finnegan 2007; Harnik *et al.* 2012) because species that are  
81 found at fewer sites are less likely to recolonize following disturbance (Fagan *et al.* 2002).  
82 Further, species that are only at a few sites may be habitat specialists and at risk if those  
83 particular habitats are lost (Rabinowitz 1981). A third metric, geographic range size, is an  
84 important predictor of extinction in the fossil record (Kiessling & Aberhan 2007; Payne *et al.*  
85 2011). Species with small ranges may be especially worthy of conservation action because  
86 populations may be less able to escape more local- or regional-scale disturbances such land-use  
87 change (Manne *et al.* 1999; Manne & Pimm 2001).

88 Here, we test whether pollinator habitat installations, created through wildflower  
89 plantings developed for pollinators (herein pollinator planting) generally, benefit rare and/or  
90 common species of native bees. We sampled native bees in a paired study design, in which each  
91 pollinator planting 'treatment' was compared to a nearby semi-natural old field 'control'. Old

92 fields provide a realistic control habitat type because in our study region, they are the early  
93 successional habitat that regenerates without any intervention. They also provide a conservative  
94 control for assessing the effect of pollinator plantings, because they are one of the best habitats  
95 for wild bees in the region of this study (Mandelik *et al.* 2012). To compare bee communities  
96 between pollinator plantings and controls, we collected all species of wild, native bees at 16 pairs  
97 of sites over five years. Because there are no comprehensive assessments (such as Red Lists) of  
98 bee rarity for North America, we categorized species as regionally rare or common based on  
99 large, independent datasets. We asked two questions: 1) Do pollinator habitat plantings benefit  
100 rare and/or common bees? 2) Do pollinator habitat plantings benefits accrue disproportionately  
101 to either rare or common bee species? We answered these questions categorizing species as rare  
102 or common based on one of three metrics: a) local relative abundance, b) site occurrence  
103 frequency, and c) geographic range size

104

## 105 **2 | METHODS**

### 106 **2.1 Study Design and Data Collection.**

107 This study took place from 2011 to 2015 in New Jersey and eastern Pennsylvania, USA  
108 (Fig. 1). We selected a total of 16 pollinator plantings that were separated by at least 4.5km. All  
109 habitats were installed by private landowners following United States Department of Agriculture  
110 National Resource Conservation Service guidelines for pollinator habitat. We used a paired  
111 design and at each pollinator planting chose a nearby old field as a control plot. Old-field control  
112 plots were located between 200-800m from the pollinator planting, which allowed us to  
113 minimize the spatial variation in native bee communities and landscape context between the  
114 habitat and controls. Hereafter, we refer to a pollinator planting and its paired old-field control  
115 together as a site.

116 To determine bee use of pollinator planting and old-field controls, we sampled bees along  
117 40 m transects. In any given site- by- year combination, we sampled either 2 or 4 transects,  
118 always with the same number of transects and equal effort at both the treatment and control plots  
119 within a site. We walked along each transect and collected all wild, native bees visiting flowers  
120 within 1m of each side of the transect. Transects were sampled for 10 minutes each, with the  
121 timer stopped to process specimens. Each transect was sampled once in the morning and once in  
122 the afternoon. To minimize variation due to weather, we sampled bees in dry, warm (>14C), and  
123 still conditions (winds below 3.5 m/s). To minimize observer bias, each collector completed the  
124 same number of transects in the pollinator restoration and old-field control each day. Sites were  
125 sampled approximately once a month from June through September for a total of four rounds per  
126 year. Sites were sampled for 1-4 years. This resulted in a total of over 293 hours of net  
127 collecting, not including time to process specimens.

128 All bees were pinned, labeled, and identified to species or species complex (Table S1).  
129 To identify bees to species, we used the following taxonomic revisions (Mitchell 1960; LaBerge  
130 1961; Mitchell 1962; LaBerge 1967; Ribble 1968; LaBerge 1971, 1973; LaBerge and Ribble  
131 1975; LaBerge 1977; Bouseman and LaBerge 1979; LaBerge 1980, 1986; McGinley 1986;  
132 LaBerge 1987; Laverty and Harder 1988; LaBerge 1989; Coelho 2004; Gibbs 2011; Rehan and  
133 Sheffield 2011; Gibbs et al. 2013) and keys available online (Arduser 2016; Larkin et al. 2016).  
134 With the exception of the three most common bumble bee species (*Bombus impatiens*, *B.*

135 *bimaculatus*, and *B. griseocollis*), and the carpenter bee *Xylocopa virginica*, for which only  
136 voucher specimens were kept, all specimens are stored in the Winfree Lab at Rutgers University  
137 in New Brunswick, NJ USA. This dataset is hereafter referred to as the pollinator planting  
138 dataset and is distinct from the independent datasets used for determining rarity, described  
139 below.

140

## 141 **2.2 Determining Rarity**

142 Using independent datasets, we categorized species as rare or common based on three  
143 metrics: local relative abundance, site occurrence frequency, and geographic range size. Species  
144 were rare or common depending on whether they were in the lowest or highest quartile (Gaston  
145 1994). Descriptions of the datasets and which datasets were used for each rarity metric follow  
146 below.

147

### 148 **2.2.1 | Local Relative Abundance**

149 To determine whether a species was rare or common in terms of local relative abundance  
150 and site occurrence, we compiled a large dataset of bee specimens collected in the states of New  
151 Jersey, Pennsylvania, and New York, USA. The specimens came from six studies, conducted by  
152 members of the Winfree research group, in which bees were collected using pan traps or hand  
153 nets between 2003 and 2016 (Table S2). In all of these studies, collectors did not target particular  
154 species or species groups, and collection took place irrespective of abundance; therefore, we  
155 assumed that specimen records from these datasets, on average, reflect actual bee abundances at  
156 sites in our region, and use these records to compute relative local abundance within sites.

157 We filtered records to generate rarity designations for our study region using the  
158 following criteria. First, to evaluate rarity within the same region as the pollinator plantings, we  
159 drew a rectangle where each edge was 100km from the nearest site in each cardinal direction.  
160 Second, we filtered records for phenology, and used only records collected within two weeks of  
161 the year from the start and end of the collection events of our restoration study. This could mean  
162 that in our filtered dataset, bee species that are common either outside of our spatial scale or in a  
163 different season may be classified as rare. Third, we removed exotic species (1.4% of all  
164 individual records and <5% of species across the 6 reference data sets). Our study focused  
165 exclusively on native species for a number of reasons. First, both the abundance and site  
166 occurrence frequencies of exotic species are likely driven by unique factors such as human-  
167 mediated colonization events and time since invasion. Second, as many of our specimens from  
168 the independent datasets come from historic collections, exotic species are likely  
169 underrepresented. Finally, we were most interested in characterizing native species; exotic  
170 species are rarely the target of conservation efforts.

171 We then calculated local relative abundance as follows: First, to avoid artifacts related to  
172 small sample sizes, we removed all records from sites at which fewer than 10 total specimens  
173 had been collected. Second, we calculated relative abundance for each species at each location.  
174 Abundances for each species at each locality were summed across years and sample rounds.  
175 Third, for each species, we calculated mean local relative abundance across sites by summing the  
176 relative abundances at all sites at which a species was present, and dividing this sum by the  
177 number of sites at which that species was detected. Thus, when a species was not recorded at a

178 site, that site was not included in the local relative abundance calculation for that species; this  
179 exclusion of zeros was done to make our measure of relative abundance distinct from site  
180 occupancy (below). Finally, there were 10 species (represented by 47 specimens) that were  
181 collected in the pollinator plantings dataset but were not recorded at the sites used to calculate  
182 relative abundance. These species were removed from the analysis for local relative abundance.  
183 In total, the data used to calculate local abundance consisted of 52,885 specimens and 294  
184 species. Collections took place at 261 different locations (Fig. 1).

### 185 **2.2.2 | Site Occurrence Frequency**

186 To assess rarity based on site occurrence frequency, we used the same dataset used for local  
187 relative abundance (see above), supplemented by a previously published dataset compiled from  
188 species records from nine museums (Bartomeus *et al.* 2013). This dataset includes over 11,000  
189 collection events, spanning 139 years (1870-2010). The data set is filtered to use only one record  
190 (individual bee) per species per collection event to reduce biases that might be present in  
191 museum collections. Specifically, collectors were unlikely to collect each species proportional to  
192 its relative abundance. Thus, we use this data set for the occupancy analysis but not the  
193 abundance analysis (above). For use in the occurrence analysis, we standardized the abundance  
194 dataset to presence-absence form also (i.e., retained only one individual of each species per site-  
195 date). We filtered the museum dataset for phenology, spatial extent and native status in the same  
196 manner as the abundance dataset. After filtering and combining, the occurrence data set included  
197 59,918 individual records of 384 species across 992 different locations (Fig. 1). To determine  
198 site occurrence frequency, we counted the number of sites at which each species was collected.  
199 Finally, we collected five species (represented by 35 specimens) in the pollinator habitat dataset  
200 but that were not recorded at all in the site occurrence dataset. We categorized these species as  
201 rare based on site occupancy.

202

### 203 **2.2.3 | Geographic Range Size**

204 To assess geographic range size, we used the methods from a study completed by some  
205 of the present coauthors (Harrison *et al.* 2017). This study used recorded state records from the  
206 Discover Life AMNH\_BEES database (Ascher & Pickering 2019). A minimum bounding  
207 polygon was then calculated to contain the centroids of each state in which each species was  
208 present. For details see (Harrison *et al.* 2017).

209

## 210 **2.3 | Quantile Designation of Rare and Common Species:**

211 For *local relative abundance*, 74 species in the regional dataset were designated as rare  
212 (local relative abundance = <0.81%) and 73 species as common (local relative abundance =  
213 >3.7%). For *site occurrence frequency*, there was an unequal number of species in some quartiles  
214 due to ties. Ties for the first and second quartiles and the third and fourth quartile were placed in  
215 the first and fourth quartile respectively. There were 105 species designated as rare (< 4 sites)  
216 and 94 as common (>26 sites). For *geographic range size* we designated 96 species as rare and  
217 96 as common. A table of all species and their rarity classifications can be found in Table S1.

218

## 219 **2.4 Data Analysis**



#### 220 **2.4.1 | Do pollinator habitat restorations benefit rare and or common bees?**

221 We designated each species collected in the pollinator restoration dataset as rare or  
222 common (or neither, constituting those between the 25th-75th percentiles) for each of the three  
223 rarity metrics. For each pollinator planting and old-field control at each site, we then summed  
224 (across all years and sampling rounds) the number of individuals (hereafter, “abundance”) and  
225 species (hereafter, “richness”) of rare and common bees. To determine how pollinator planting  
226 affected the richness or abundance of rare, and separately, common bees, we fit generalized  
227 linear models with either richness or abundance of either rare or common bees, according to one  
228 of the three metrics, as the response variable. As predictors in each model, we incorporated  
229 treatment (pollinator planting or old-field control) as a fixed effect. Additionally, because we  
230 used a paired study design, with one wildflower planting and one control at each site, we  
231 included site as a random effect. We fit generalized linear mixed-effects models for each  
232 response variable with a negative binomial error structure using the function *glmer\_nb* from the  
233 R package “lme4” (Bates *et al.* 2015). Model assumptions were checked using the DHARMA  
234 package (Hartig 2020). This analysis was conducted using R 4.0.5 (R Core Team 2021).

235

#### 236 **2.4.2 | Do pollinator habitat restoration benefits accrue disproportionately to either rare or** 237 **common bee species?**

238 The models described above test for increases in the abundance or richness of a specified  
239 group of species (e.g. those that have smaller geographic ranges), regardless of how other species  
240 respond. If managers believe that rare species are especially vulnerable to global change, it may  
241 be strategic to focus management actions that benefit these species. We generated a null model to  
242 test whether the species we designated as rare, or those we designated as common, especially  
243 benefit from habitat enhancement, or whether they respond about as strongly as expected, given  
244 that the response group consists of about one quarter of the species in our study region.

245 In each iteration of our null model, we designate a random subset of species as rare or  
246 common, where the number of rare and common species in the null group is the same as the  
247 number of rare and common species in the empirical data. We used our observations of these  
248 species in the pollinator habitats and old-field controls, and refit the models for each rarity  
249 criterion (i.e. for each group of [null] “rare” or [null] “common” species) and each response (i.e.  
250 richness or abundance). We then compared the model estimates for the effect of habitat  
251 enhancement for the species group from 9,999 iterations of each null model to the model  
252 estimate for our observed data. In short, this null model tells us how strongly any randomly-  
253 chosen fraction (up to ~25%, depending on overlap between regional rarity and occurrence in the  
254 restoration dataset) of our species responds to habitat enhancement, providing scope to test  
255 whether rare species respond especially strongly to habitat enhancements. There are at least two  
256 reasons that we could fail to find a clear difference between the empirical model coefficients and  
257 those from the null models. The first of these is biological: the factors leading species to be  
258 regionally rare or common may not be strongly correlated to the factors that predispose species  
259 to respond strongly to habitat enhancement. The second of these is more related to classification  
260 accuracy: Even if *truly* regionally rare and common bee species respond differently to habitat  
261 enhancement than typical species do, we may have misclassified species as rare or, less likely, as  
262 common, obscuring the link between rarity/commonness and the propensity to benefit from  
263 habitat enhancement (Harrison *et al.* 2017). This null model analysis entailed generating nearly

264 120,000 mixed-effects models, and therefore, we did not complete model validation for the null  
265 datasets.

266 We consider a group to clearly exhibit a stronger or weaker than expected response to  
267 pollinator habitat restoration (e.g., abundance in pollinator planting vs. abundance in control)  
268 when empirical model estimates are above 97.5% or below 2.5% of the null model results. This  
269 analysis was conducted using R 3.4.1 (R Core Team 2017).

### 270 **2.4.3 | Testing sensitivity of quartiles**

271 To test whether our results were sensitive to the quantile threshold for what constitutes rarity (or  
272 commonness), we re-ran our analyses and the null model for 10 additional thresholds, ranging  
273 from the 20th to the 30th percentile. This analysis was conducted using R 3.4.1 (R Core Team  
274 2017).

275

## 276 **3 | Results**

277 In the pollinator restoration dataset, we collected a total of 10,809 individual bees of 157  
278 native species or species complexes. Of these, 195 specimens (37 species) were designated as  
279 locally rare and 8,642 specimens (39 species) as locally common, based on the relative  
280 abundance data set. Based on the site occurrence dataset, 65 specimens (14 species) were  
281 designated as rare and 9,977 specimens of (77 species) were designated as common. For the  
282 geographic range size metric, 316 specimens (34 species) were rare and 4081 specimens (40  
283 species) were common.

284

### 285 **3.1 | Do pollinator habitat restorations benefit rare and/ or common bees?**

286 Species defined as rare based on local relative abundance had higher abundance and  
287 richness? in the pollinator plantings compared to old-field controls by factors of nearly 3 and 2  
288 (Table 1; Fig. 2A). Species categorized as rare based on low site occurrence frequency did not  
289 exhibit a clear difference in the number species collected; however, the abundance of these rare  
290 bees was reduced by 50% reduction in treatment versus controls (Table 1, Fig. 2B). Species  
291 categorized as rare based on small geographic range size were not clearly more abundant or  
292 species rich in pollinator plantings (Table 1, Fig. 2C). Regardless as to how we defined  
293 commonness, we collected both more species and individuals from common bee species in  
294 pollinator restorations compared to controls (Table 1, Fig. 3).

295

### 296 **3.2 | Do pollinator habitat restorations lead to a disproportionate benefit for 297 either the rare or the common bees?**

298 For almost all species rarity criteria and response types (richness or abundance), we  
299 found no difference between the response of the species designated as rare, and results for a null  
300 model that randomly chose an equally-sized group of species (Fig. 4). There was one exception:  
301 habitat enhancements supported 54% lower abundance of bee species designated as rare based  
302 on regional site occupancy (Fig. 4e,  $p < 0.01$ ). Similarly, for bee species designated as common



303 (for all commonness criteria) richness and abundance responses to habitat enhancement were not  
304 different than expected for a random group of species (Fig. 5).

305

### 306 **3.3 | Testing sensitivity of quartiles**

307 The quantile sensitivity analysis mostly did not reveal qualitative differences in the  
308 results (Table S3). However, as the quantile thresholds for rarity/commonness got larger (and  
309 thus more inclusive), model coefficients tended towards the average for all species.

310

## 311 **4 | Discussion**

312

### 313 **4.1 | Rare bee species exhibit atypical responses to habitat enhancements**

314 Pollinator plantings, in general, increase the overall abundance and richness of wild,  
315 native bees (reviewed in Tonietto & Larkin 2018; & Nicholson *et al.* 2020). We found that  
316 common bee species and, depending on the criteria for designation, rare bee species had higher  
317 abundance and species richness in wildflower plantings as compared to old-field controls. Our  
318 results partially support other studies that found pollinator plantings benefit wild bees, including  
319 rare and common species (Pywell *et al.* 2012; Scheper *et al.* 2015). For example, in the EU,  
320 Scheper *et al.* (2015) found that all bee species, including those designated as rare by the IUCN,  
321 increased in floral strips. Pollinator plantings likely benefit both rare and common species when  
322 both groups overlap in the species of flowers they prefer, and these floral species are included in  
323 the plantings (Macleod *et al.* 2020). As common species are among the most important crop  
324 pollinators (Winfree *et al.* 2015), pollinator plantings that benefit them (even if they do not also  
325 support rare species effectively) could have positive impacts on crop pollination (Blaauw &  
326 Isaacs 2014; but see Nicholson *et al.* 2020; Lowe *et al.* 2021). However, depending on how bee  
327 species were categorized as rare, and which response variable we tracked, pollinator plantings  
328 failed to benefit all rare bees. In particular, bee species categorized as rare based on regional site  
329 occurrence frequency had lower abundance in pollinator plantings as compared to old-field  
330 controls. Overall, this indicates that, although pollinator plantings in general can have benefits  
331 for biodiversity and ecosystem services, these two goals are not always met simultaneously  
332 (Nicholson *et al.* 2020; Lowe *et al.* 2021), and not all species benefit from this conservation  
333 action (Senapathi *et al.* 2015).

334 The effect of pollinator plantings on rare species depended on rarity criteria. Bee species  
335 designated as rare based on local relative abundance were more abundant and species rich in  
336 pollinator plantings. Even if a species has low local abundance, it may still benefit from  
337 pollinator plantings if it occurs frequently across the landscape. This echoes findings elsewhere  
338 that benefits of pollinator habitat enhancement are greatest in landscapes regions with  
339 intermediate cover of natural and seminatural habitat, and are therefore likely to contain source  
340 populations able to exploit additional resources (Grab *et al.* 2020; Griffin *et al.* 2021;  
341 McCullough *et al.* 2021, but see Lane *et al.* 2020).

342 Conversely, species that do not commonly occur across a region may be unlikely to  
343 benefit from pollinator plantings for two reasons. First, a number of rare bees are specialists and  
344 collect pollen from a limited suite of plants. These species may be common when their host

345 species is present. Wildflower seed mixes used in pollinator plantings are only a small subset of  
346 native plants within a region, inevitably fail to include important floral hosts. For example, at  
347 one site, we caught seven *Trachusa dorsalis* (Megachilidae; Lepeletier 1841) in an old-field  
348 control. This species had not been recorded in New Jersey or Pennsylvania (states where this  
349 study occurred) for over 100 years (Ascher & Pickering 2019). *Trachusa dorsalis* specializes on  
350 plants in the genus *Strophostyles* (Fabaceae), a genus not planted in the pollinator habitats we  
351 sampled. Second, plantings are not targeted towards specific habitat types that may support rare  
352 bees (Harrison *et al.* 2018). In our dataset, specialist bee species are likely to be categorized as  
353 rare based on site occurrence frequency (assuming the resource on which they specialize is  
354 heterogeneously available across the region), and potentially by approximate range size (if the  
355 resource on which they specialize is also geographically restricted). We found that bee species  
356 with low regional site occupancy showed much less of an abundance response to habitat  
357 installation than we would expect for a random group of species, in line with our expectation that  
358 pollinator plantings may not benefit uncommon specialist species with atypical resource  
359 requirements. This finding echoes suggestions elsewhere (e.g. Macleod *et al.* 2020) that species-  
360 specific management actions may be necessary if rare species conservation is an objective of  
361 restoration efforts.

362

## 363 4.2 | Limitations

364 One limitation of our study is that the plantings we studied did not contain early-  
365 blooming spring plants - a common problem in pollinator plantings (Wood *et al.* 2018).  
366 Therefore, we were not able to assess whether pollinator plantings with spring plant species  
367 might benefit spring bees. This may be particularly important in our region, as a number of early  
368 spring species are known to be rare (Harrison *et al.* 2017).

369 A more general limitation is the inherent problems with categorizing species as rare in the  
370 first place. Here we use a number of metrics and employ a quantile method to characterize  
371 species rarity (Gaston 1994). This method has a number of important advantages: it is  
372 straightforward, has a clear cut-off, and easily incorporates new data. One potential drawback is  
373 the need to make an arbitrary decision about which quantile value to use for rarity designation  
374 (Gaston 1994). Here we show that our results were robust to choice of quantile. However, there  
375 are other important considerations when using this approach. For example, sampling biases (e.g.  
376 in habitat type) in the reference datasets means the quantitative rankings might still not reflect  
377 wider patterns of abundance and occurrence in nature.

378 We faced both misclassification risks and statistical limitations inherent to studying rare  
379 species. Due to limited monitoring efforts for wild bees, it is not clear which species in our  
380 region are truly rare, and classification errors are likely (Harrison *et al.* 2017). First, in defining  
381 rarity, we chose to focus on records collected within a few hundred kilometers of our study sites,  
382 and within a few weeks of the year of our sampling period, and thus consider species to be rare  
383 even if they are common elsewhere or in other seasons. Second, due to limited data coverage, it  
384 is likely that our rarity categorizations conflated rarity types: species with low abundance (for  
385 example, specialized kleptoparasitic bees) could be mistakenly categorized as low occupancy  
386 even if they are widespread in our study region, or species with strong habitat specialization or  
387 low relative abundance over a large range could have erroneously small range-size estimates.  
388 Furthermore, binary rarity classifications based on arbitrary thresholds (and for regional metrics,

389 arbitrary spatial scale) are likely to miss more biologically relevant definitions of rarity (Gaston  
390 1994; Inger *et al.* 2015; Reed *et al.* 2020; Balbuena *et al.* 2021). Additionally, because they are  
391 rare, any study of rare species is likely to face issues of statistical power and related concerns,  
392 such as type-S and type-M errors (Gelman & Carlin 2014). In part, we were able to defend  
393 against these issues with sensitivity analysis and our null model simulation. Yet, even as  
394 qualitative patterns were robust to changing rarity thresholds, and null-model simulations, in  
395 some cases, indicated that differing responses from rare species were not expected simply as a  
396 result of classifying some species as rare and others as not rare, we urge caution in generalizing  
397 our findings. Overall, our results demonstrate heterogeneity in response to habitat enhancements  
398 at the species level, and many species are, of course, rare. Diverse taxonomic and functional  
399 groups are unlikely to respond uniformly to conservation actions, and more targeted conservation  
400 goals and strategies may be easier to assess and fine-tune.

401

### 402 **4.3 | Conclusions and Management Implications**

403 Currently, plant species used in pollinator plantings are chosen because of cost,  
404 availability, or whether the seed mix attracts high pollinator species richness or abundance  
405 (Harmon-Threatt & Hendrix 2015; M’Gonigle *et al.* 2017; Williams & Lonsdorf 2018).  
406 However, it may be that current pollinator plantings primarily benefit species that already persist  
407 within anthropogenic landscapes (Senapathi *et al.* 2015). If land managers aim to conserve rare  
408 bees, they may need to incorporate plants not traditionally used in pollinator habitat plantings  
409 (MacLeod *et al.* 2020).

410 Although they were the focus of our study, it is not necessarily the case that rare species  
411 *should be* the target when designing and implementing pollinator plantings. While conservation  
412 biology has focused on rarity, temporal trends (population decline, habitat loss, and range  
413 contraction) may better predict extinction risk (Collen *et al.* 2016) – of course, these trends are  
414 difficult to detect in rarely sampled species, such as many we have studied here. At the same  
415 time, common species are also of critical conservation concern. In Europe, common bird species  
416 are experiencing declines while less abundant species are increasing (Inger *et al.* 2015). Further,  
417 common species may also have large effects on ecosystem function (Gaston 2011; Kleijn *et al.*  
418 2015; Genung *et al.* 2018). More important than whether current practices benefit rare species,  
419 ensuring overlap between conservation approaches and their likely impact on *particular* species  
420 of concern may produce the best conservation outcomes, as disparate responses to habitat  
421 alterations should be expected across diverse taxonomic groups.

422

423 Author Contributions: RW, MR, and DPC designed the study. DPC, MR, MG, and TH collected  
424 the data. DPC wrote the manuscript with considerable input from MR. All authors contributed to  
425 writing and conceptual development. MR and DPC analyzed the data. RW oversaw writing and  
426 analysis. JG identified native bee specimens.

427

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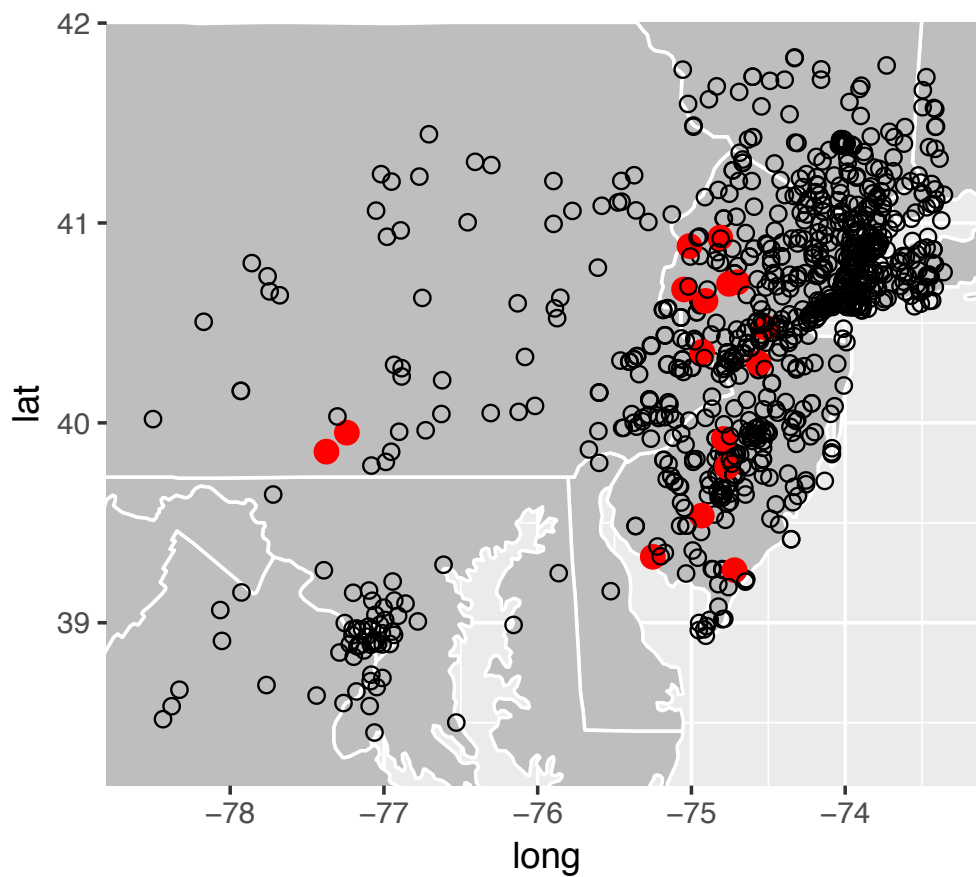


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583 Table 1. Model output of comparison between pollinator plantings and paired old-field controls  
 584 for all three rarity metrics. Proportion change is exponentiated model output of change in  
 585 pollinator planting treatments compared to old-field controls. Bold and asterisks represent significant  
 586 difference between pollinator planting and old field controls at  $p < 0.05$ .

	Relative Abundance			Site Occurrence Frequency			Geographic R	
	Proportion Increase	Confidence Interval	p-value	Proportion Increase	Confidence Interval	p-value	Proportion Increase	Confidence Interval
<b>Rare Species</b>								
Richness	<b>1.95</b>	<b>1.14 – 3.33</b>	<b>0.014*</b>	1.5	0.55 – 4.09	0.428	1.64	0.97 –
Abundance	<b>2.93</b>	<b>1.31 – 6.55</b>	<b>0.009*</b>	<b>0.46</b>	<b>0.24 – 0.88</b>	<b>0.019*</b>	1.6	0.70 –
<b>Common Species</b>								
Richness	<b>1.34</b>	<b>1.11 – 1.62</b>	<b>0.002*</b>	<b>1.42</b>	<b>1.22 – 1.64</b>	<b>&lt;0.001*</b>	<b>1.43</b>	<b>1.17 –</b>
Abundance	<b>2.78</b>	<b>1.77 – 4.39</b>	<b>&lt;0.001*</b>	<b>2.67</b>	<b>1.72 – 4.14</b>	<b>&lt;0.001*</b>	<b>3</b>	<b>1.72 –</b>

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Figure 1. Map of wildflower plantings (solid red circles) and locations of specimen records from independent regional dataset (open black circles).

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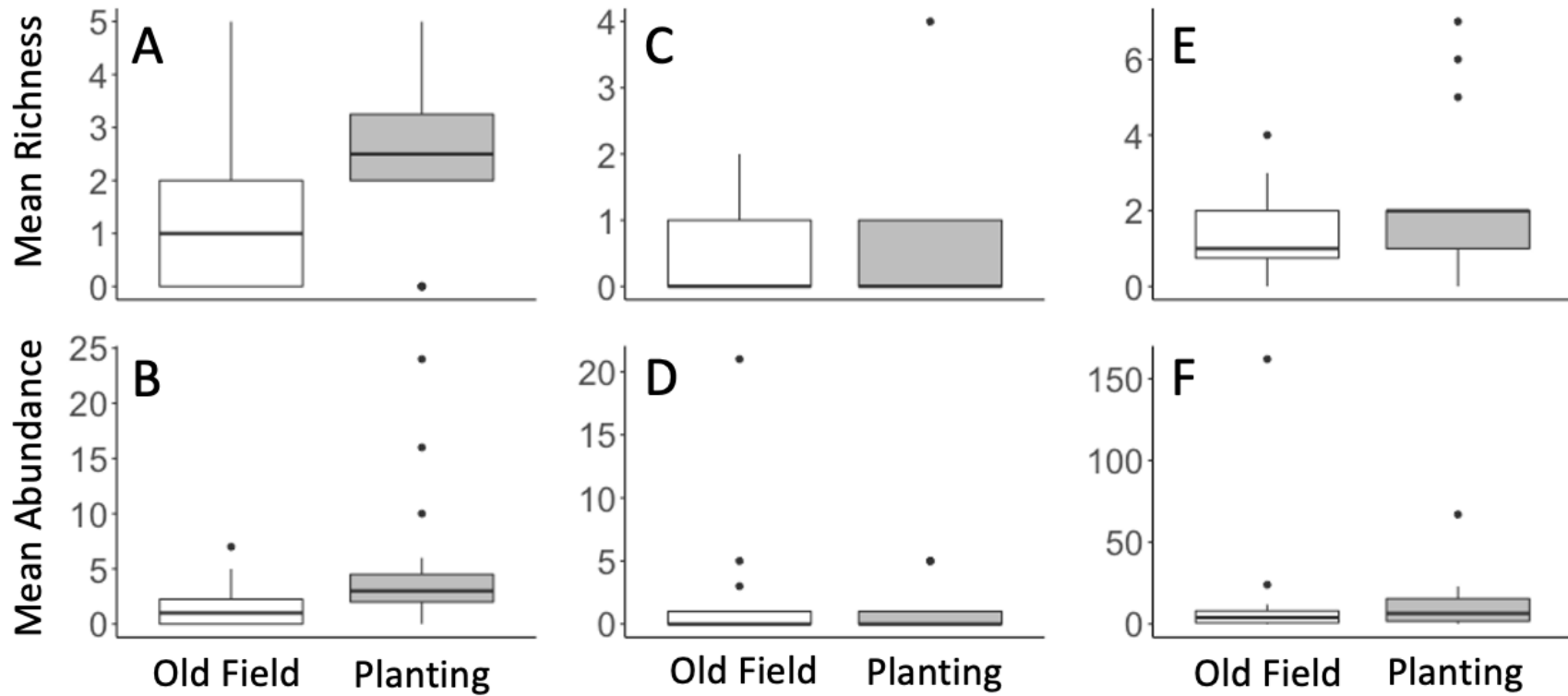


Figure 2. Rare species richness and abundance in old fields (white) and pollinator habitat (grey). Rarity metrics for A-B) Relative abundance, C-D) site occurrence frequency, and E-F) geographic range size.

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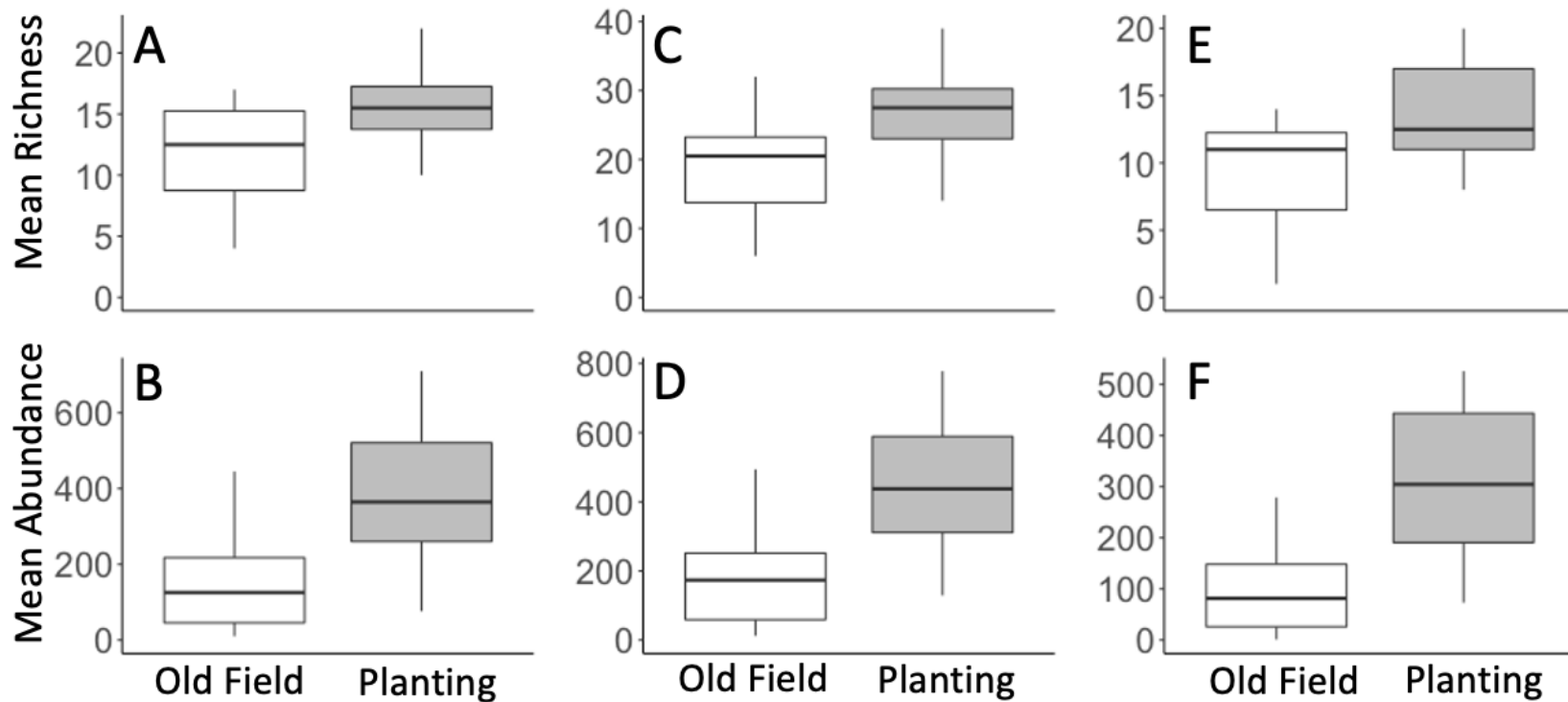
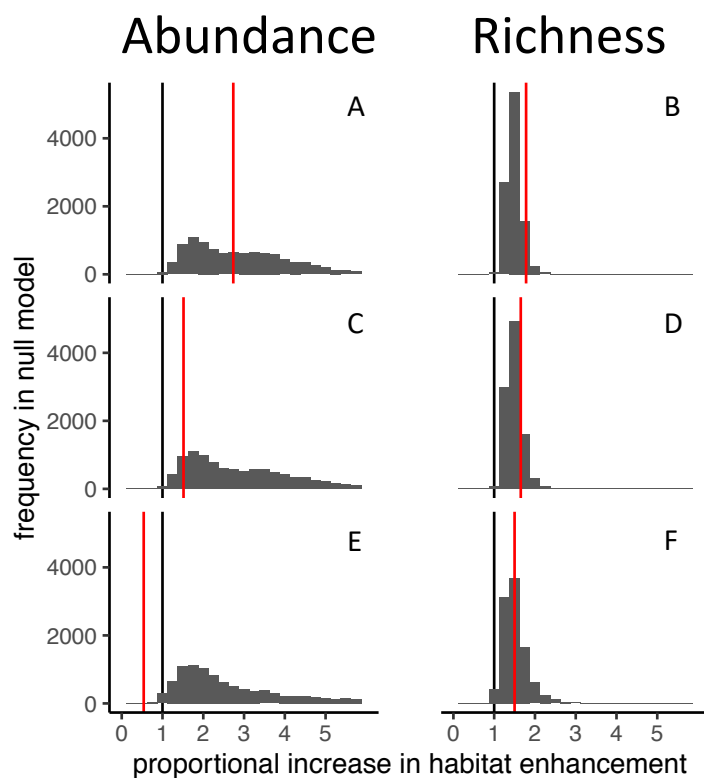


Figure 3. Common species richness and abundance in old fields (white) and pollinator habitat (grey). Rarity metrics for A-B) Relative abundance, C-D) site occurrence frequency, and E-F) geographic range size.

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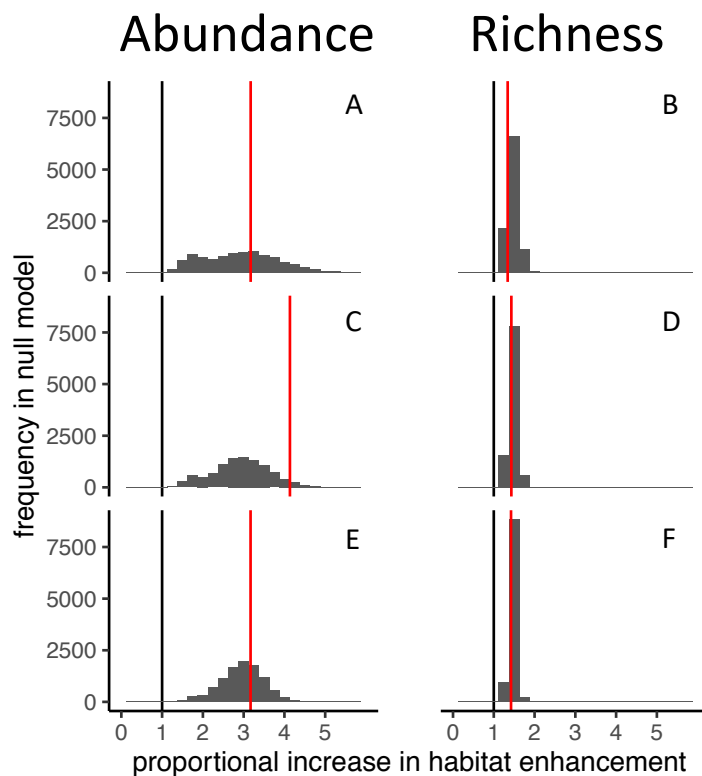
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Figure 4. Comparison of outputs for model simulations and empirical models for rare species. x-axis values represent proportional increase in abundance or richness in habitat enhancements relative to old field controls. Histograms represent the frequency of each proportional change in richness or abundance in the null model, which designates randomly selected species as “rare.” Black lines represent no difference in response variable between treatment and control ( $x=1$ ). Red lines represent model output for the real data, for which species were defined as rare based on regional relative abundance (A,B), regional site occurrence frequency (C,D), or geographic range size (E, F).

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Figure 5. Comparison of outputs for model simulations and empirical models for common species. x-axis values represent proportional increase in abundance or richness in habitat enhancements relative to old field controls. Histograms represent the frequency of each proportional change in richness or abundance in the null model, which designates randomly selected species as “common.” Black lines represent no difference in response variable between treatment and control ( $x=1$ ). Red lines represent model output for the real data, for which species were defined as common based on regional relative abundance (A,B), regional site occurrence frequency (C,D), or geographic range size (E, F).



631 **Table S1. Supplementary Information on the datasets used to classify rarity**

632 **Dataset Name:** dryad\_amnh

633 Use in manuscript: site occurrence frequency

634 Number bee individual specimens used in this study: 7633

635 Number bee species used in this study: 331

636 Number of sites: 751

637 Published in: (Bartomeus *et al.* 2011, 2013a, b)

638

639 **Dataset Name:** bef\_scale\_spec

640 Use in manuscript: site occurrence frequency, local relative abundance

641 Number bee individual specimens used in this study: 7359

642 Number bee species used in this study: 90

643 Number of sites: 25

644 Unpublished

645

646 **Dataset Name:** cape\_may

647 Use in manuscript: site occurrence frequency, local relative abundance

648 Number bee individual specimens used in this study: 8217

649 Number bee species used in this study: 85

650 Number of sites: 1

651 Published in: (MacLeod *et al.* 2016, 2020; Genung *et al.* 2017)

652

653 **Dataset Name:** forest\_spec

654 Use in manuscript: site occurrence frequency, local relative abundance

655 Number bee individual specimens used in this study: 543

656 Number bee species used in this study: 59

657 Number of sites: 33

658 Published in: (Smith *et al.* In Press.; Volenec & Smith 2021)

659

660 **Dataset Name:** male\_bee\_project

661 Use in manuscript: site occurrence frequency, local relative abundance

662 Number bee individual specimens used in this study: 15110

663 Number bee species used in this study: 145

664 Number of sites: 8

665 Published in: (Roswell *et al.* 2019a, b)

666

667 **Dataset Name:** njpa\_ha

668 Use in manuscript: site occurrence frequency, local relative abundance

669 Number bee individual specimens used in this study: 4822

670 Number bee species used in this study: 72

671 Number of sites: 54

672 Unpublished

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674 **Dataset Name:** nsf0607\_spec

675 Use in manuscript: site occurrence frequency, local relative abundance

676 Number bee individual specimens used in this study: 683

677 Number bee species used in this study: 70

678 Number of sites: 18

679 Published in: (Winfree *et al.* 2014)

680

681 **Dataset Name:** pinelands\_2003

682 Use in manuscript: site occurrence frequency, local relative abundance

683 Number bee individual specimens used in this study: 1967

684 Number bee species used in this study: 124

685 Number of sites: 44

686 Published in: (Winfree *et al.* 2007)

687

688 **Dataset Name:** bh\_spec

689 Use in manuscript: site occurrence frequency, local relative abundance

690 Number bee individual specimens used in this study: 5641

691 Number bee species used in this study: 162

692 Number of sites: 27

693 Published in: (Harrison *et al.* 2017, 2018b, a)

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695 **Dataset Name:** swg

696 Use in manuscript: site occurrence frequency, local relative abundance

697 Number bee individual specimens used in this study: 7943

698 Number bee species used in this study: 192

699 Number of sites: 51

700 Unpublished

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