

1 **Male and female bees show large differences in floral preference**

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3 Michael Roswell mroswell.rutgers@gmail.com

4 Graduate program in ecology and evolution, Rutgers University

5 14 College Farm Road, New Brunswick, NJ 08904

6

7 Jonathan Dushoff

8 Department of biology, McMaster University

9 1280 Main St. West, Hamilton, Ontario ON L8S 4K1

10

11 Rachael Winfree

12 Department of ecology, evolution, and natural resources, Rutgers University

13 14 College Farm Road, New Brunswick, NJ 08904

14 **Abstract**

15

16 1. Intraspecific variation in foraging niche can drive food web dynamics and
17 ecosystem processes. Field studies and theoretical analysis of plant-pollinator
18 interaction networks typically focus on the partitioning of the floral community
19 between pollinator species, with little attention paid to intraspecific variation
20 among plants or foraging bees. In other systems, male and female animals
21 exhibit different, cascading, impacts on interaction partners. Although the
22 foraging ecology of male bees is little known, we expect foraging preferences to
23 differ between male and female bees, which could strongly impact plant-
24 pollinator interaction outcomes.

25 2. We designed an observational study to evaluate the strength and
26 prevalence of sexually dimorphic foraging preferences in bees.

27 3. We observed bees visiting flowers in semi-natural meadows in New
28 Jersey, USA. To detect differences in flower use against a shared background
29 resource availability, we maximized the number of interactions observed within
30 narrow spatio-temporal windows. To distinguish observed differences in bee use
31 of flower species, which can reflect abundance patterns and sampling effects,
32 from underlying differences in bee preferences, we analyzed our data with both a
33 permutation-based null model and random effects models.

34 4. We found that the diets of male and female bees of the same species
35 were often as dissimilar as the diets of bees of different species. Furthermore, we
36 demonstrate differences in preference between male and female bees, and
37 identify plant species that are particularly attractive to each sex. We show that
38 intraspecific differences in preference can be robustly identified within
39 interactions between hundreds of species, without precisely quantifying resource
40 availability, and despite high phenological turnover.

41 5. Given the large differences in flower use and preference between male
42 and female bees, ecological sex differences should be integrated into studies of
43 bee demography, plant pollination, and coevolutionary relationships between
44 flowers and insects.

45

46 **Key Words**

47 dimorphism, dissimilarity, Morisita-Horn, phenology, plant-pollinator interaction,
48 pollination, pollinator habitat, preference

49

50 **Introduction**

51 Intraspecific variation in traits and behavior, including foraging niche, has
52 important consequences for species interactions and conservation (Bolnick et al.,
53 2011; Durell, 2000). Sexual dimorphism is a large source of individual niche
54 variation, and an important factor in plant-animal interactions, such as seed
55 dispersal (Zwolak, 2018). Sexual dimorphism underlies adaptation, speciation,
56 and the way in which animals exploit their ecological niche (Butler, Sawyer, &
57 Losos, 2007; Temeles, Miller, & Rifkin, 2010). Morphological, behavioral, and life-
58 history dimorphisms can also drive the form and function of ecosystems, for
59 example when predator sex ratio drives the community composition of lower

60 trophic levels, shown experimentally (Start & De Lisle, 2018) and in nature,
61 where responses extended to water chemistry as well (Fryxell, Arnett, Apgar,
62 Kinnison, & Palkovacs, 2015).

63
64 Though ecological dimorphisms were first studied in vertebrates (Selander,
65 1966), they are common across taxa, including insects (Shine, 1989).
66 Surprisingly, in bees (Hymenoptera, Apoidea) for which both foraging (P.
67 Willmer, 2011) and sexual dimorphism (Alcock et al., 1978) have been well
68 studied, sexually dimorphic foraging has rarely been documented. Intraspecific
69 variation in floral preference is well known in social (Heinrich, 1979) and to a
70 lesser extent, solitary bee species (Bruninga-Socolar, Crone, & Winfree, 2016;
71 Tur, Vigalondo, Trøjelsgaard, Olesen, & Traveset, 2014), yet most community-
72 level studies focus on species-level interaction networks, and furthermore, on the
73 foraging preferences of only female bees.

74
75 Male bees differ from their better-studied female counterparts in their life history
76 and ecology. Female bees construct, maintain, provision, and defend nests,
77 whereas male bees primarily seek mates (P. G. Willmer & Stone, 2004). Both
78 sexes drink floral nectar for their own caloric needs, but only females collect
79 pollen to provision young, and thus forage at greater rates. While the pollen from
80 each flower species (the term we use throughout for the flowers from a species
81 of plant) tends to be morphologically and nutritionally distinct, interspecific
82 variation in the chemical composition of nectar is comparatively subtle (Cane &
83 Sipes, 2006). Thus, we expect the foraging ecology, including floral preferences,
84 of male and female bees to differ as well.

85
86 Male bees prove to be important pollinators when studied, both in specialized oil-
87 or scent-collecting pollination systems (Eltz et al., 2007; Etl, Franschitz, Aguiar,
88 Schönenberger, & Dötterl, 2017; Janzen, 1971) and also when males are
89 foraging for nectar and pollen (Cane, 2002; Cane, Sampson, & Miller, 2011;
90 Ogilvie & Thomson, 2015). Male bees may also be particularly relevant for bee
91 conservation. Males may be limiting in declining populations, either because
92 genetic diversity is necessary for the development of female offspring as a result
93 of complementary sex determination, or because mate or sperm limitation results
94 from poor male condition (Elias, Dorn, & Mazzi, 2010; Straub et al., 2016). As the
95 dispersing sex in most bee species, males may be crucial for gene flow and
96 metapopulation persistence even when they are not locally limiting (López-Uribe,
97 Morreale, Santiago, & Danforth, 2015; Ulrich, Perrin, & Chapuisat, 2009).

98
99 Foraging niche is only partly described by resource use. Indeed, resource
100 preferences may be more important than use alone in many contexts, including
101 conservation. Preference—the use of a resource in excess of its relative
102 availability—is challenging to measure, because both resource use and
103 availability must be known. Floral resource availability for pollinators is
104 particularly hard to quantify outside an experimental context because the
105 appropriate scale and units of floral resource availability are unclear. The

106 composition, amount, and supply rate of pollen and nectar per flower, the number
107 of flowers per inflorescence, of inflorescences per individual, and the number and
108 distribution of individual plants over the square kilometers of a bee's foraging
109 range are all important components of availability (Hicks et al., 2016).
110 Furthermore, floral availability can change rapidly over time. However,
111 differences in flower use between bees foraging at the same place and time
112 indicate differences in preference, which may occur between species, or between
113 individuals of the same species.

114
115 In this study, we assess differences between floral preferences of male and
116 female bees in the wild. We collected bees foraging on flowers in meadows in
117 New Jersey, USA. In order to observe preference differences, we collected as
118 many individuals as possible during replicated, short (3-day) windows, during
119 which we assumed floral availability and bee abundance were constant at each
120 site. We compare the species composition of flowers visited by males and
121 females of the most common bee species across the entire study as a naïve
122 measure of differences in preference between the sexes. Then, using random
123 effects models, we assess when differential flower species *use* by male and
124 female bees likely arises from sex-specific floral *preference*, as opposed to
125 shifting overlap between foragers and floral resources (i.e. changes in *availability*
126 without differences in preference). Specifically, we ask

- 127
128 1) How much do male and female bee diets overlap?
129 2) To what degree are particular flower species disproportionately visited by
130 bees of one sex?
131 3) To what extent are differences in floral use driven by preference, rather
132 than phenological differences between male and female bees?

133

134 **Materials and Methods**

135

136 **Study design and data collection**

137

138 Because absolute preference is nearly impossible to observe outside of an
139 experiment, we designed our study to reveal differences in preference between
140 groups of bees. In order to collect a large number of males and females from
141 many native bee species, we selected six meadows (sites) in New Jersey, USA
142 with a high abundance and diversity of flowers. These meadows were managed
143 for pollinator-attractive, summer-blooming forbs through seed addition, and a
144 combination of mowing, burning, and weed removal. Most flower species present
145 in the meadows are native to the eastern United States. We collected our data
146 during peak bloom and maximum day length (6 June to 20 August, 2016), and
147 during good weather (sunny enough for observers to see their own shadow, no
148 precipitation). We visited each site for three consecutive good weather days over
149 five evenly spaced sampling rounds in the 11-week period of our study. In all
150 analyses, we assume that bees and flowers detected at a site within one 3-day
151 sampling round co-occurred. In contrast, we assume that turnover of both plant

152 species in bloom and bee species activity can occur in the ~10 days between
153 sampling rounds.

154

155 During each 3-day sampling round, an observer walked parallel transects
156 through the meadow (which ranged in size from 0.8–2.2 ha; mean=1.4 ha),
157 observing every open flower within a moving 1-m semicircle, and net-collecting
158 any bee seen actively foraging, which we defined as contacting anthers or
159 collecting nectar from a flower (Fig. S1). We collected all bee species except
160 *Apis mellifera* L., the domesticated western honey bee, because *Apis* males do
161 not forage. Observations began as soon as pollinator activity picked up in the
162 morning (7–9 am) and continued into the late afternoon or evening until pollinator
163 activity slowed substantially. Observers sampled nearly continuously, in 30-
164 minute timed collection bouts with short breaks in between. If inclement weather
165 precluded a minimum of six 30-minute sampling bouts in a day, we added an
166 additional day to the sampling round as soon as weather permitted.

167

168 Flower species were identified in the field by the data collector. Bee species were
169 identified using a dissecting microscope and published keys; Jason Gibbs
170 (University of Manitoba), Joel Gardner (University of Manitoba), and Sam Droege
171 (USGS) assisted with identification for bees in the genera *Andrena*, *Anthophora*,
172 *Coelioxys*, *Halictus*, *Heriades*, *Hoplitis*, *Hylaeus*, *Lasioglossum*, *Megachile*,
173 *Melissodes*, *Nomada*, *Osmia*, *Pseudoanthidium*, *Ptilothrix*, *Sphecodes*, *Stelis*,
174 and *Triepeolus*, and at least one of them confirmed voucher specimens for every
175 species. We determined every specimen to species except for the following four
176 complexes: Most bees in the genus *Nomada* with bidentate mandibles (*ruficornis*
177 group) were treated as one species. All specimens from the *Hylaeus* species
178 complex that includes *Hylaeus affinis*, *H. modestus*, and at least one additional
179 species, informally dubbed “species A,” were treated as a single species,
180 denoted *Hylaeus affinis-modestus*, because females cannot be reliably
181 distinguished. There is a cryptic species in the genus *Halictus* unlikely to occur in
182 our area, *Halictus poeyi*, which is not morphologically distinct from *H. ligatus*; we
183 treat all specimens in this complex as *Halictus ligatus*. We could not confidently
184 separate all specimens of the two closely related *Lasioglossum* species
185 *Lasioglossum hitchensi* and *L. weemsi*. Thus, we treat all specimens from either
186 species as one, denoted *Lasioglossum hitchensi-weemsi*. All bee specimens are
187 curated in the Winfree lab collection at Rutgers University, and the data used in
188 this paper are available from the Dryad Digital Repository
189 <http://dx.doi.org/XXXXXXX> (Roswell et al.)

190

191 **Analytical methods**

192

193 We performed all statistical analyses and simulations using R 3.5.1 (R Core
194 Team, 2018).

195

196 **1) How much do male and female bee diets overlap?**

197

198 To compare the diets of male and female bees, we used the Morisita-Horn index
199 of resource overlap (Horn, 1966; Morisita, 1959). This dissimilarity index
200 compares the proportion of all female bees found on each flower species to the
201 proportion of all male bees found on each flower species. In other words, it
202 compares the contribution of each flower species to female diets (where this term
203 includes the food that females collect for themselves and also to feed to young)
204 to the contribution of the same flower species to male diets. The Morisita-Horn
205 index ranges from zero (completely similar) to one (maximally dissimilar), and
206 has several good properties for our purposes. First, it uses proportions, placing
207 visits from male and female bees on the same scale, even though most visits
208 come from females. Second, it is much more sensitive to large proportions than
209 to small ones, thereby down-weighting the contribution of flower species for
210 which we have little information. Third, the Morisita-Horn estimates are resilient
211 to undersampling and uneven sample size between groups (Barwell, Isaac, &
212 Kunin, 2015).

213
214 To determine whether the male-female differences we observed exceeded those
215 expected by chance, we compared the observed compositional dissimilarity
216 between flower visits from male and from female bees to dissimilarity measures
217 from a null model that randomly permuted the bee sex associated with each
218 flower-visit record. This permutation holds constant the total number of male and
219 of female visits, and the total number of visits to each flower species from both
220 sexes combined (Fig. S2). The range of dissimilarity values from this simulation
221 is the difference we would observe in our sample, if there were no true difference
222 in flower species use between males and females of the same bee species. We
223 evaluated the hypothesis that male and female diets overlap less than would be
224 expected by chance; thus we use a one-sided alpha of $p < 0.05$. We iterated this
225 null simulation 9999 times, which was sufficient to stabilize p-values near our
226 chosen alpha (North, Curtis & Sham 2002). When the observed dissimilarity was
227 greater than 9500 of the 9999 simulated dissimilarities, we concluded that we
228 had detected a difference in the pattern of floral visitation between conspecific
229 male and female bees, given the observed diet breadth and abundance of each
230 sex.

231
232 To compare the diet overlap we observed between sexes to a meaningful
233 benchmark, interspecific diet overlap, we repeated the same null model analysis,
234 this time comparing females of the focal species to females of other species. We
235 performed one analysis for each bee species for which we collected at least 20
236 visitation records for each sex (19 species). This sample size threshold is
237 arbitrary, but null model variance shrinks with sample size, such that apparent
238 patterns for species with smaller sample sizes are rarely interpretable (Fig. S3).
239 Because we analyze 19 bee species, females of each species are compared to
240 18 others. We then compared the male-female difference (observed minus mean
241 null dissimilarity in flower communities visited) to the analogous species-species
242 difference (observed minus null dissimilarity).

243

244 For this analysis, which evaluates holistic differences between male and female
245 bees of the same species, we combined observations across the full season and
246 all sites. This allows us to observe foraging niche differences that are driven by
247 flower and/ or bee phenology, in addition to any sex-specific floral preference.

248

249 **2) To what degree are particular flower species disproportionately visited by bees**
250 **of one sex?**

251

252 This analysis uses our entire data set of 153 bee species to determine whether
253 particular flower species are disproportionately visited by male or female bees,
254 and whether the answer varies by bee species. We can infer a preference
255 difference between male and female bees for a flower species when predicted
256 odds of visitors to that flower species being male are especially high or low. To
257 do this, we use a random effects model in which bee sex is the response, and
258 flower species, bee species, site, and their interactions are random effects. We
259 statistically control for variation in the overall sex ratio across bee species
260 through a random intercept of bee species, and variation in sex ratios across
261 sites, through random intercepts for site, and the site-bee species and site-flower
262 species interactions. Because it is unlikely that, within bee species, sex ratios at
263 birth vary greatly across space, any variability attributed to site terms would likely
264 result from differential overlap of bee foraging activity and flower bloom across
265 space.

266

267 We call this model the “summed model” because we sum interactions observed
268 across the entire season (all five sampling rounds) at each site. In the summed
269 model, the relationship between phenological overlap and the odds of flower-
270 visiting bees being male would be incorporated into the species effects. This
271 perspective is helpful for considering flower species’ contributions to the overall
272 diets of male versus female bees. We fit the model with the R package lme4
273 (Bates, Maechler, & Walker, 2016) with the following call:

274

275 ***Summed model***

```
276 lme4::glmer(bee_sex ~ (1|site)+(1|flower_species)+(1|bee_species)+  
277 (1|flower_species:bee_species)+(1|site:bee_species)+  
278 (1|site:flower_species), family="binomial", data=data)
```

279

280 We included bee species and site as random, rather than fixed, effects to directly
281 compare the variability in bee sex associated with each of these predictors to the
282 variability associated with flower species (preference). Comparing the overall
283 variability across these groups was more important to us than assessing
284 predictions on a per-site or per-bee-species basis. We fit flower species, the
285 primary covariate of interest, as a random effect to facilitate model fitting (fewer
286 degrees of freedom) as well as interpretation. In our summed model, we included
287 all two-way interactions, but omitted the three-way interaction, bee species by
288 flower species by site. Although the sort of context-dependent preference this
289 term could represent (e.g. males from bee species 1 prefer flower A at one site

290 (relative to females), but shun it at another) may exist in nature, it is unlikely we
291 would estimate it accurately in our model.

292

293 We confirmed model convergence by comparing several fitting methods using
294 the allFit function in lme4 (Bates et al., 2016), which all showed similar parameter
295 estimates (Table S1). We tested whether residuals from our model fit were
296 overdispersed using Bolker's function "overdisp" (Bolker, 2017), and visually
297 assessed our additivity assumptions with binned residual plots (Gelman & Hill,
298 2007) (Fig. S4).

299

300 **3) To what extent are differences in floral use driven by preference, rather than**
301 **phenological differences between male and female bees?**

302

303 Over the 11 weeks of our study, we observed turnover in bee species, in flower
304 bloom, and within-bee species changes in sex ratio. Therefore, phenological
305 overlap between male versus female bees and the bloom period of particular
306 flower species, rather than preference of those bees for those flowers, may
307 explain much of the variation in sex ratio we observed across visitors. In question
308 3, we are explicitly interested in distinguishing sex-specific diet *preferences* from
309 variable *use* resulting from seasonal resource availability and male vs. female
310 abundance. We do this in the "seasonal model" by incorporating sampling round
311 (our measure of phenology) as an additional random intercept effect, along with
312 random intercepts for the interactions between sampling round and the other
313 covariates. We chose to include sampling round as a random effect because this
314 enables direct comparison to all other terms in both models. We ignored the
315 three- and four-way interactions between bee species, flower species, and other
316 covariates. We fit this model with the following call in the R package lme4, with
317 new terms in bold:

318

319 **Seasonal model**

```
320 glmer(bee_sex ~ (1|site)+(1|flower_species)+(1|bee_species)+  
321 (1|flower_species:bee_species)+(1|site:bee_species)+  
322 (1|site:flower_species)+ (1|sampling_round)+(1|site:sampling_round)+  
323 (1|flower_species:sampling_round)+  
324 (1| bee_species:sampling_round)+  
325 (1|site:bee_species:sampling_round)+  
326 (1|site:flower_species:sampling_round), family="binomial", data=data)
```

327

328 Our index of preference for both the *summed model* and the *seasonal*
329 *model* is the change in odds that a bee is male when the flower species it visits is
330 given. To describe the importance of model terms, we calculated a bootstrapped
331 median odds ratio using code from Seth (Seth, 2017), which gives the expected
332 difference in odds that a flower-visiting bee is male between levels of a predictor
333 (Merlo et al., 2006). For example, a median odds ratio of five for the main effect
334 of sampling round would indicate that the odds of a flower-visiting bee being
335 male differ by about a factor of five between sampling rounds, while a median

336 odds ratio of one would indicate that the odds of a flower-visiting bee being male
337 do not change across rounds. If the median odds ratio is large for flower species
338 in both models, we could say that there are intrinsic (i.e. not simply phenological)
339 properties of flower species identity that male or female bees prefer. If flower
340 species is a strong predictor of bee sex in the summed model but not in the
341 seasonal one, we would still conclude that flower species often contribute more
342 strongly to the diet of one sex than the other, though these differences may not
343 arise due to differing preferences. If the sampling round terms have large median
344 odds ratios, then accounting for phenology is critical for identifying differences in
345 preference in addition to differences in use.

346

347 **Results**

348

349 In total we collected 18,698 bee specimens belonging to 152 bee species (table
350 S2) from a total of 109 flower species (table S3), which together comprised 1417
351 unique species-species interactions. Roughly 18% of specimens were male
352 (n=3372). Thus, the overall ratio of male to female bees we collected was 0.22,
353 although this ratio varied markedly between flower species (Fig. 1).

354

355 *How much do male and female bee diets overlap?*

356

357 We found that male and female bee diets overlap significantly less than would be
358 expected at random (Fig. 2), and that the differences in diet composition between
359 male and female bees of several species were of similar magnitude to the
360 differences in diet between species of bee (Fig. 3).

361

362 *To what degree are particular flower species disproportionately visited by bees of*
363 *one sex?*

364

365 The sex ratio of flower-visiting bees varied across species of flower (Fig. 2). After
366 controlling for bee species identity (the strongest predictor of sex in our models,
367 Fig. 4), and site, we still found that some flower species received a
368 disproportionate number of male bee visitors (Figs 4–5). The median odds ratio
369 for the main effect of flower species was 3.6 (bootstrapped CI 3.0–4.2) in our
370 summed model, indicating that, typically, the visitor sex ratio differs between two
371 flower species by more than a factor of 3. Furthermore, we observed sex-based
372 differences in flower use specific to particular bee species: the median odds ratio
373 for the flower species by bee species interaction in our summed model was
374 nearly as large (median=3.1, bootstrapped CI 3.0–3.3) as the main effect of
375 flower species. By contrast, sex ratios are not expected to differ between sites
376 (median odds ratio for main effect of site=1).

377

378 *To what extent are differences in floral use driven by preference, rather than*
379 *phenological differences between male and female bees?*

380

381 The flower species blooming in our system turned over throughout our 11-week

382 sampling period, with several highly visited species blooming for only one of the
383 three months during which we sampled. This turnover, along with potential sex-
384 specific bee flight seasons, means that differences in diet between male and
385 female bees could reflect seasonal availability and use, without also indicating
386 preference differences between the sexes. Indeed, phenology predicts bee sex
387 somewhat, with the odds of a flower-visiting bee being male expected to change
388 by a factor of 1.5 (bootstrapped CI 1.1–1.9) between sampling rounds (Fig. 4).
389 Phenological patterns of male vs. female flight seasons vary across bee species;
390 the median odds ratio for the bee species by sampling round interaction is 2.2
391 (bootstrapped CI 2.1–2.3) (Fig. 4). Even after accounting for these effects,
392 however, there remains a strong association between the species of flower a bee
393 visits and its sex (Figs 4–5). The relative effects of each flower species on the
394 sex of its visitors were changed very little by accounting for phenology; Pearson
395 and Spearman correlations between the random effect of flower species in the
396 seasonal model and the same random effect in the simpler summed model were
397 both 0.98. In addition to finding overall preference difference between male and
398 females, we found evidence for bee-species-specific difference in floral
399 preferences between the sexes (median odds ratios in both models for the bee
400 species by flower species interaction > 2.8).

401

402 **Discussion**

403

404 We found strong differences between the flower species preferences of male and
405 female bees. The difference in floral visits between male and female bees of the
406 same species was similar in magnitude to differences between females of
407 different species. The partitioning of the floral community among bee species is a
408 primary focus of pollination ecology and ecological network analysis (Bascompte
409 & Jordano, 2014), but male bees are typically disregarded or lumped together
410 with their female counterparts. Our study suggests this may represent an
411 important oversight. Further, our study provides strong confirmation of the few
412 studies that investigate the foraging behavior of male bees, which found that
413 males play a unique role in plant pollination (Cane, 2002; Cane et al., 2011;
414 Ogilvie & Thomson, 2015; Pascarella, 2010). Our result also implies that male
415 bees contribute substantially to the complexity of plant-pollinator networks in
416 nature, and that network analyses might benefit from separating males and
417 females into different nodes (Bolnick et al., 2011; Zwolak, 2018).

418

419 Phenology, a previously reported mechanism for distinct use of floral resources
420 by male and female bees (Ogilvie & Thomson, 2015; Robertson, 1925),
421 explained some variation in the sex ratio of flower-visiting bees, but was less
422 important than flower species identity over the period of our study. We expected
423 to find an effect of phenology because both the identity of the flower species
424 blooming within sites, and also the sex ratio of foragers within bee species, vary
425 across the season. Males emerge first in most solitary bees; for social species,
426 initial broods usually consist primarily of female workers, then males and
427 reproductive females emerge at the end of the colony cycle (P. G. Willmer &

428 Stone, 2004). Surprisingly, however, phenology only weakly predicted the sex of
429 flower-visiting bees. This is despite the fact that, as predicted by natural history,
430 the sampling round(s) in which males were relatively more prevalent depended
431 on bee species (the bee species by sampling round interaction was much bigger
432 than the sampling round main effect; Fig. 4). This indicates that our evidence for
433 floral preference differences between male and female bees was robust to
434 accounting for seasonal turnover in flower species bloom, bee species flight
435 seasons, and the sex ratios within bee species.

436
437 Whereas female bees collect both nectar and pollen, male bees forage primarily
438 for nectar to fuel flight. Thus, we predicted that male bees would avoid flowers
439 that produce no nectar. Indeed, in both our models, the predicted odds of a bee
440 visiting a nectar-less flower species being male were approximately half that of a
441 bee visiting a flower species that produces nectar (Fig. S5). A second biological
442 difference between male and female bees is that adult male bee activities orient
443 around mate seeking (Alcock et al., 1978). These behaviors, such as patrolling
444 routes (Barrows, 1976) or seeking flowers visited by conspecific females (Rossi,
445 Nonacs, & Pitts-Singer, 2010) could generate differences from females via
446 complementarity (males visiting flower species not visited by females), or
447 nestedness (one sex primarily visiting a subset of species visited by the other).
448 We found evidence for both (Fig. S6). Divergent floral preferences between
449 sexes may reflect nutritional needs or mating behavior, or simply biases resulting
450 from previous flower encounters, or visual or olfactory sensitivities that differ
451 between the sexes (Robert, Frasnelli, Collett, & de Ibarra, 2016; Somanathan,
452 Borges, Warrant, & Kelber, 2017; Streinzer, Kelber, Pfabigan, Kleineidam, &
453 Spaethe, 2013).

454
455 While natural and semi-natural habitats are critical landscape elements for many
456 bee species (Senapathi, Goddard, Kunin, & Baldock, 2016), what constitute
457 suitable and/ or limiting resources within these habitats remains less clear (De
458 Palma et al., 2015). Flowers, which provide food for adult and larval bees, are
459 likely among them (Roulston & Goodell, 2011). Whether floral diversity *per se*
460 tends to benefit individual pollinator taxa remains unclear (Spiesman, Bennett,
461 Isaacs, & Gratton, 2017; Sutter, Jeanneret, Bartual, Bocci, & Albrecht, 2017).
462 However, complementary flower species use between the sexes implies a
463 mechanism by which a bee species could benefit from a diversity of flower
464 choices. In addition, it is currently unknown how the distinct foraging niches of
465 male bees mediate either the robustness of pollinator communities to species
466 loss and environmental perturbations (Brosi & Briggs, 2013; Ramos-Jiliberto,
467 Valdovinos, Moisset de Espanés, & Flores, 2012; Tur et al., 2014), or the
468 effectiveness of different habitat ameliorations (Rundlöf, Persson, Smith, &
469 Bommarco, 2014; Rusterholtz & Erhardt, 2000; Williams & Lonsdorf, 2018). This
470 study suggests that both questions warrant further investigation.

471
472 Patterns in bee-flower interaction data can arise from the sampling process itself
473 (Blüthgen, 2010; Fründ, McCann, & Williams, 2016). Our analyses control for

474 these patterns. To evaluate diet overlap, we used a dissimilarity index that
475 downweights rare diet items, and implemented a null model that accounts for
476 differences that could arise from sampling and abundance effects. To evaluate
477 preference, we used random effects models that incorporated all (nearly 19,000)
478 observations, and shrank extreme values for rarely observed species-species
479 interactions towards the global mean for each effect. Thus, our estimates for sex-
480 specific preferences should be robust to the inevitable under-sampling of rarer
481 taxa. Establishing differences in preference between categories of bees such as
482 males and females, even when resource availability is seasonal and difficult to
483 quantify, is possible using methods such as these, though absolute preference
484 remains elusive.

485
486 Pollination ecology and pollinator conservation still face the question of how
487 important sexually dimorphic foraging is. Does it enhance or reduce the stability
488 of bee populations? Should pollinator restorations explicitly include “male bee”
489 flowers and “female bee” flowers? Are floral traits under selection to favor female
490 versus male visitors? While our study does not answer these questions, by
491 showing that the diets and preferences of male bees commonly differ from those
492 of their female conspecifics, we suggest they are worthy of future study.

493

494 **Author contributions**

495

496 MR and RW conceived the ideas and designed field methodology; MR, JD, and
497 RW designed statistical methodology. MR collected the data; MR, RW, and JD
498 analyzed the data; MR and RW led manuscript drafting. All authors contributed
499 critically to the drafts and gave final approval for publication.

500

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502

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514 **References**

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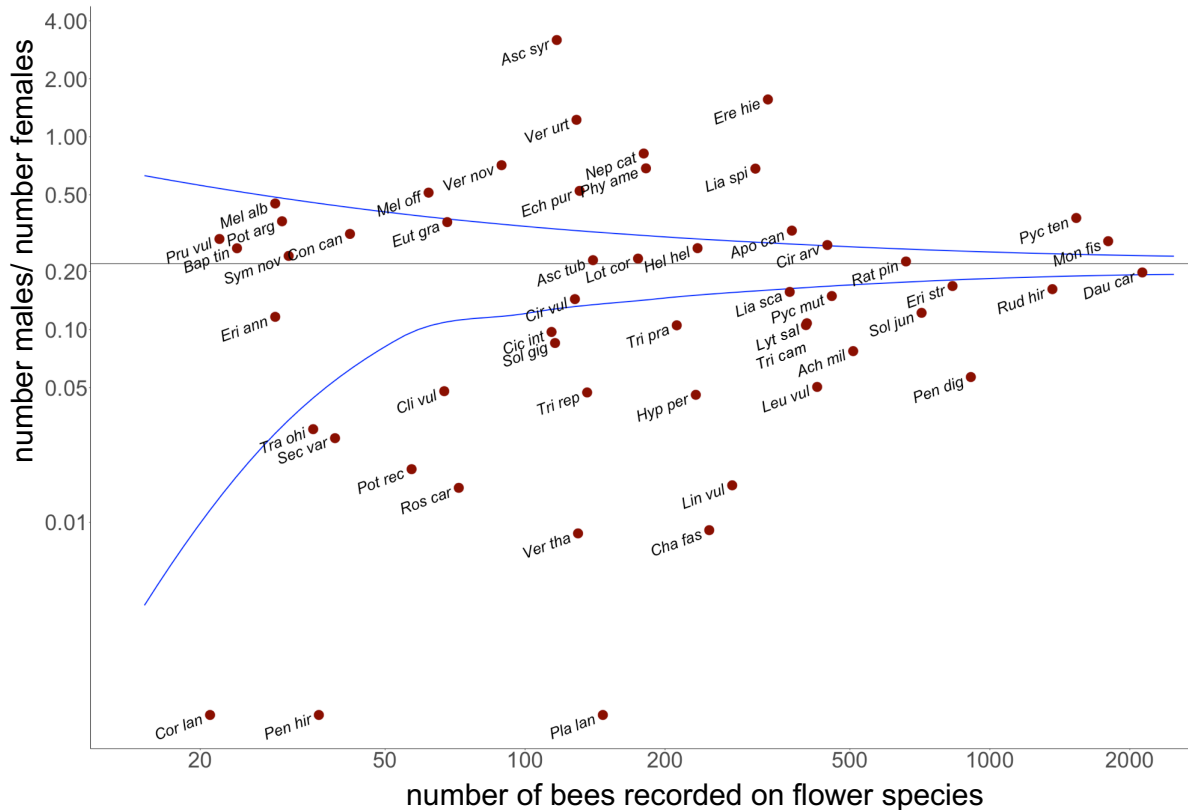
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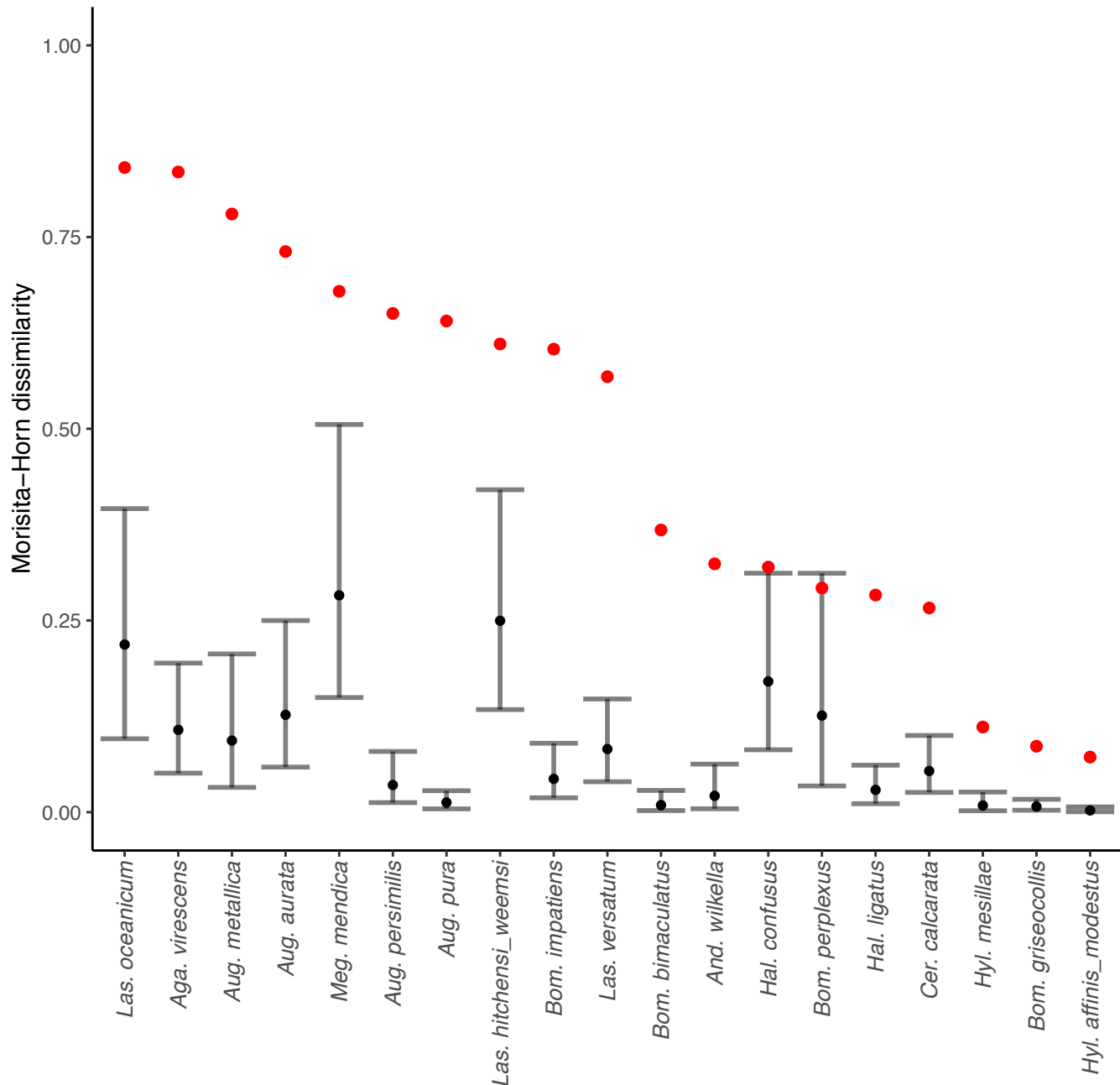
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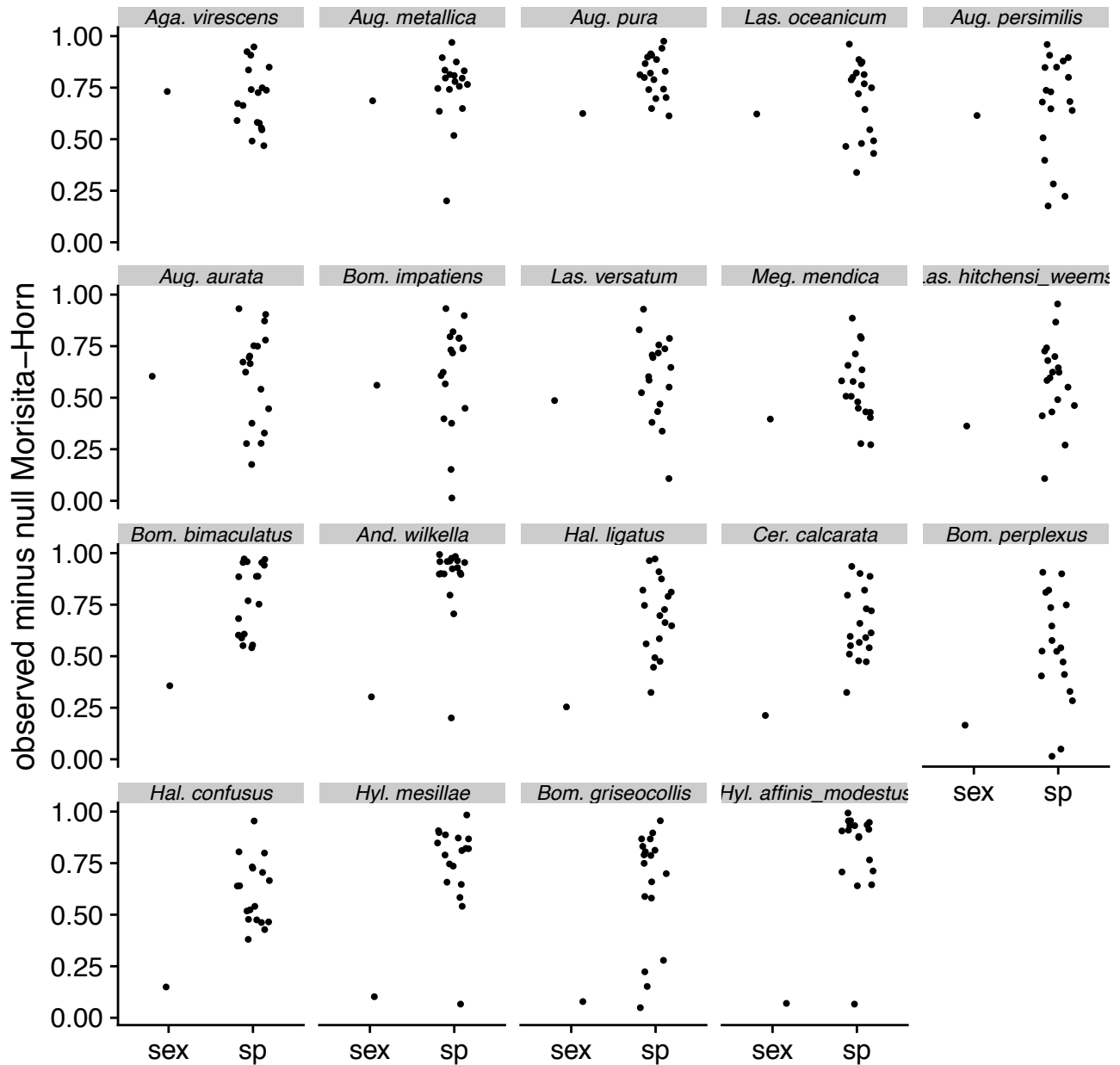
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701 **Figure 1.** The sex ratio (M:F) of flower-visiting bees varies across flower species.
 702 Each red point represents a flower species, the first three letters of the Latin
 703 genus and species names for the flower species label each point. The x-axis is
 704 the number of bees collected from that species, the y-axis is the ratio of male to
 705 female bees collected from the flower. Flower species that received >19 visits are
 706 plotted (n=54). Blue lines are smooth fits to the 97.5th and 2.5th percentiles of the
 707 binomial distribution given by the observed ratio of males to females in our
 708 overall dataset (M/F=0.22; i.e. $M/(M+F)=0.18$). This distribution represents our
 709 expectation for random variation in sex ratio across flower species, if the sex
 710 ratio of flower-visiting bees is independent of flower species identity (male and
 711 female bees exhibit the same floral preferences), and remains nearly constant
 712 across time and space.
 713



715 **Figure 2:** Flower visit patterns of male and female bees of the same species
 716 differed significantly. Red points are observed Morisita-Horn dissimilarities
 717 between flower communities visited by all male and all female bees of a
 718 particular species across all sites and sampling rounds. Black points are the
 719 mean dissimilarity (gray bars, 95% CI) from a permutation-based null model that
 720 randomly shuffles the sex associated with each visit record, maintaining the total
 721 number of males, females, and overall combined visits to each floral species.
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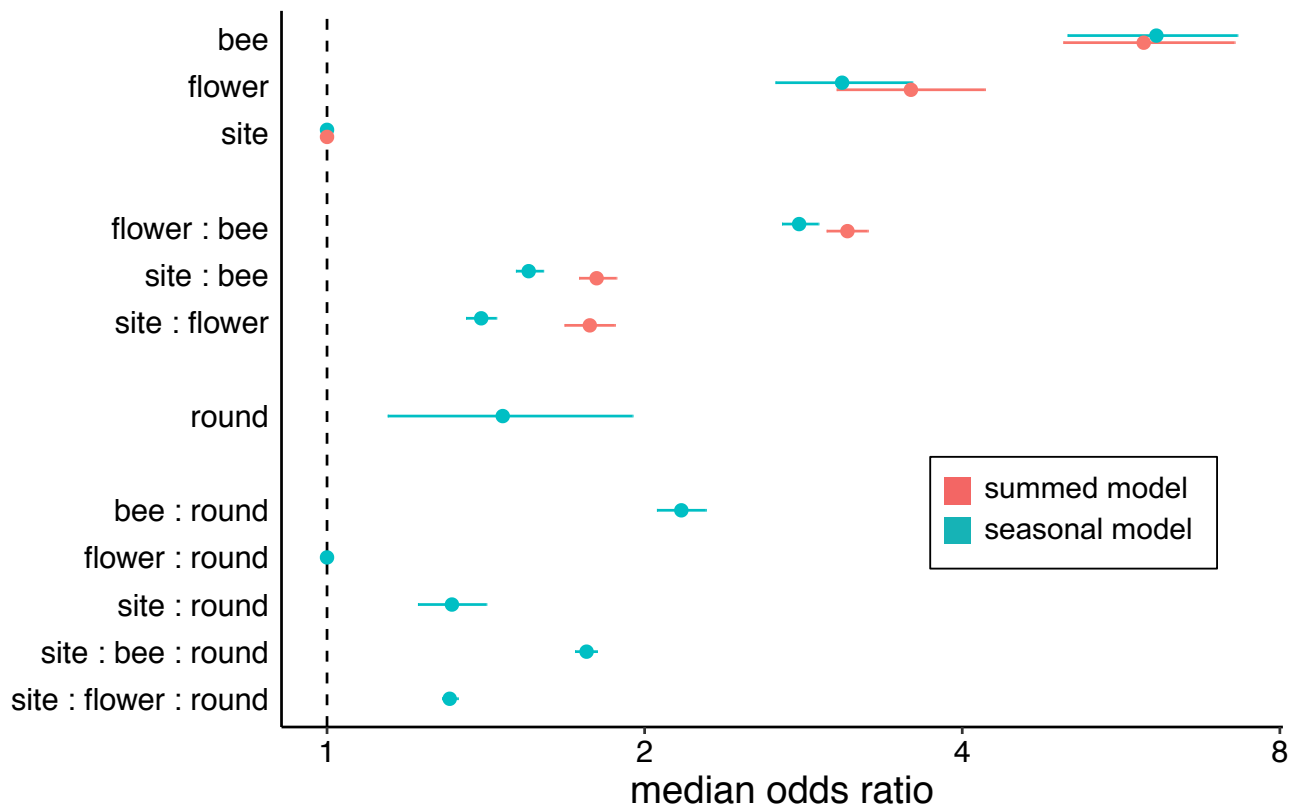
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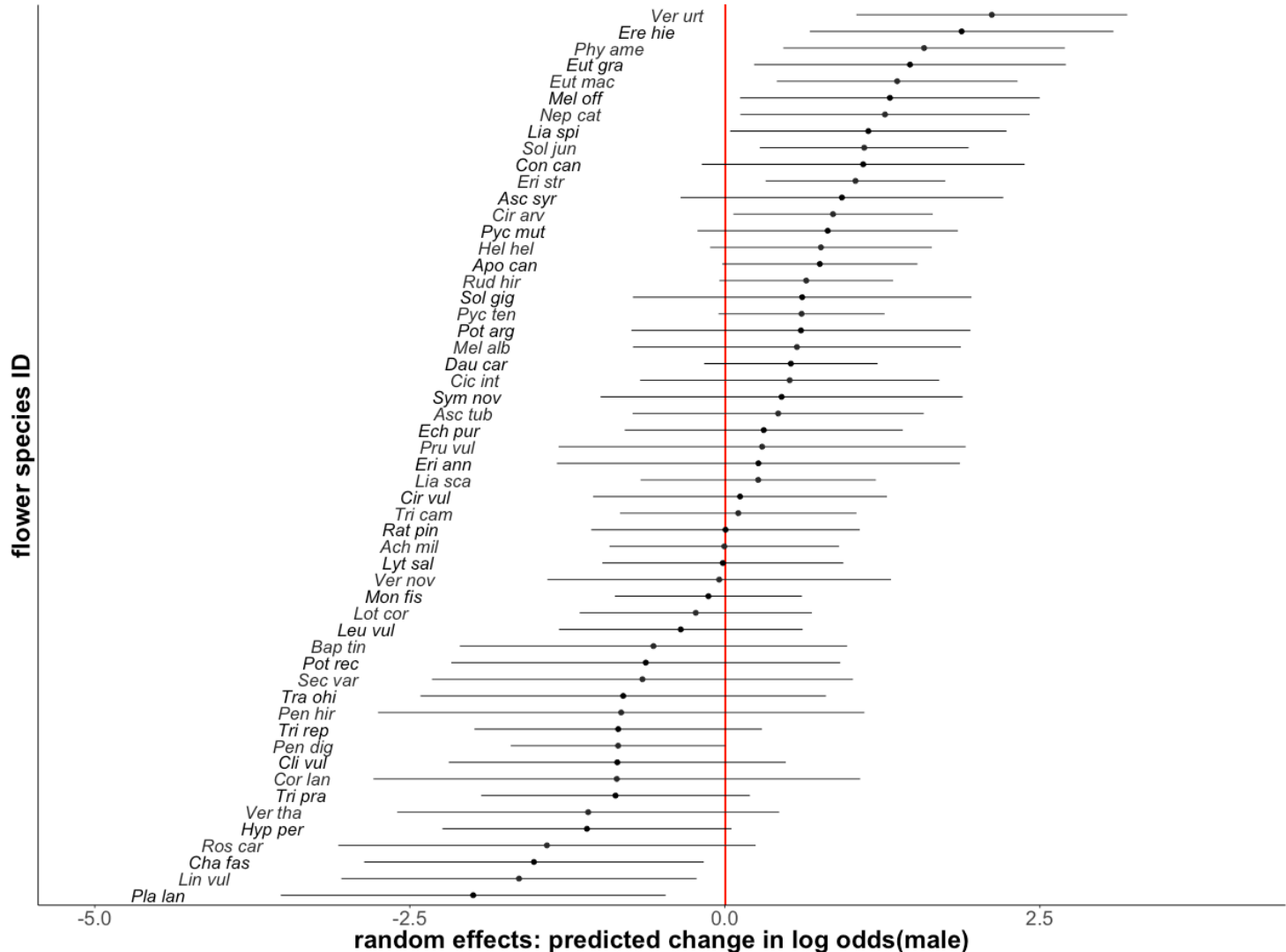
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Figure 3. The diets of male and female bees of the same species can be as dissimilar as the diets of females of two different bee species. Dissimilarities in this figure are the observed statistic minus, for each pairwise comparison, the mean dissimilarity in the null model. Each panel focuses on a bee species (panel name) and shows: above the label “sex”, observed diet dissimilarity between male and female bees of the focal species, minus the average null dissimilarity resulting from randomly permuting the sex identity of each visit record; above the label “sp”, observed diet dissimilarity between female bees of the focal species and each other bee species, minus the average null dissimilarity resulting from randomly permuting the species identity of each visit record.

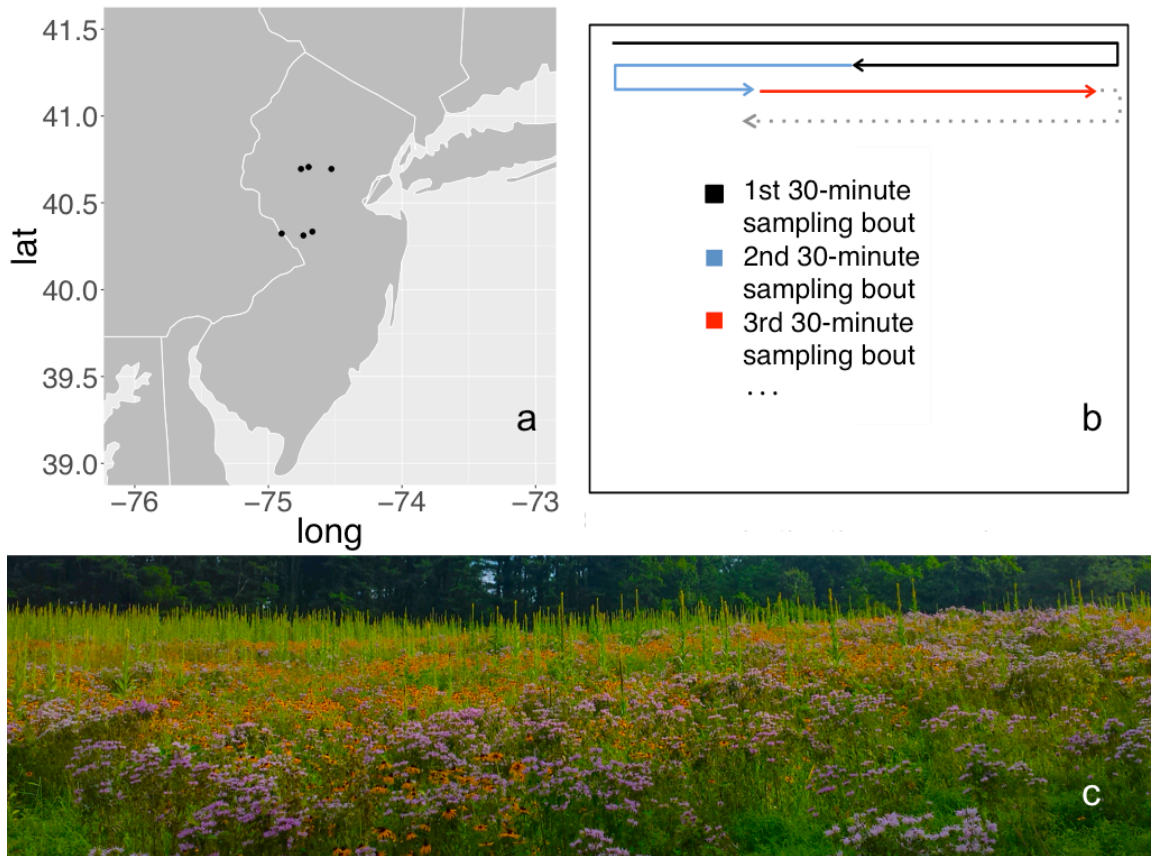
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736 **Figure 4.** Flower species, along with bee species, predicts the sex of visiting
 737 bees, which suggests floral preferences differ between male and female bees.
 738 Flower species is an important predictor of bee sex even after accounting for
 739 phenology (seasonal model). For each term (“bee”= bee species, “flower”=flower
 740 species, “round”=sampling round) in each model, the median odds ratio (+/- 95%
 741 bootstrapped credible interval) indicates the expected difference in odds that a
 742 flower-visiting bee is male between two levels. For example, a median odds ratio
 743 of 3.7 for the flower species term means the odds of a visitor being male are
 744 expected to differ by a factor of 3.7 between two randomly selected species of
 745 flower.

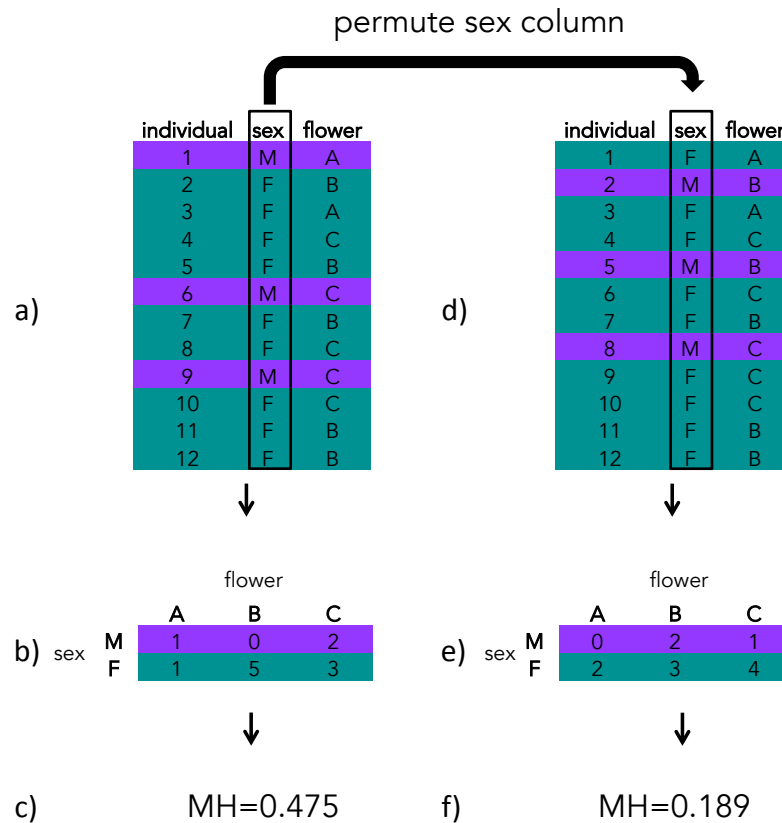


747 **Figure 5.** Male bee preferences for and against flower species vary across
 748 flower species. Each point is the conditional mode of the random effects
 749 prediction (the random-effects analog to an estimate), for a flower species that
 750 received at least 20 visits, on the logit scale. Zero represents the odds of a visitor
 751 being male on a random flower, and -2 or 2 indicates a ~7 fold decrease or
 752 increase in those odds, given flower species identity. Error bars are the square
 753 root of the conditional variances on the conditional mode * 1.96, and can be
 754 interpreted as the expected range in which the random effect for a particular
 755 flower truly lies, analogous to 1.96 times the standard error of the mean for a
 756 fixed effect.
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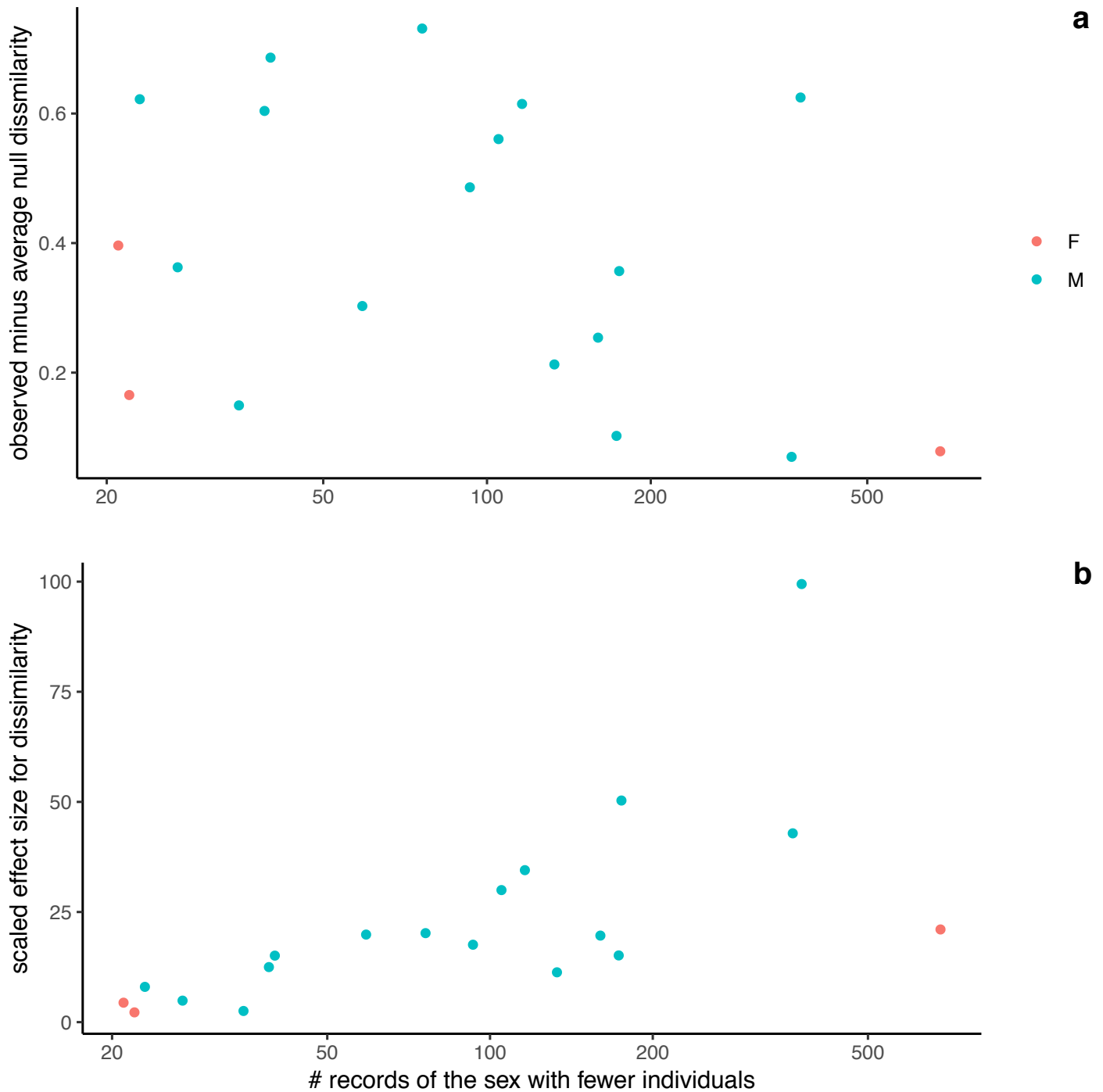
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759 **Figure S1:** Sampling scheme. (a) The six study sites in central New Jersey,
760 USA. (b) Schematic sampling diagram (not to scale). One observer walked
761 parallel 2m transects covering the entire sampling area. Each 30-minute
762 sampling bout resumed where the previous one left off; observers typically
763 covered the entire meadow once over a 3-day sampling round. (c) The
764 southwestern-most site in peak bloom.

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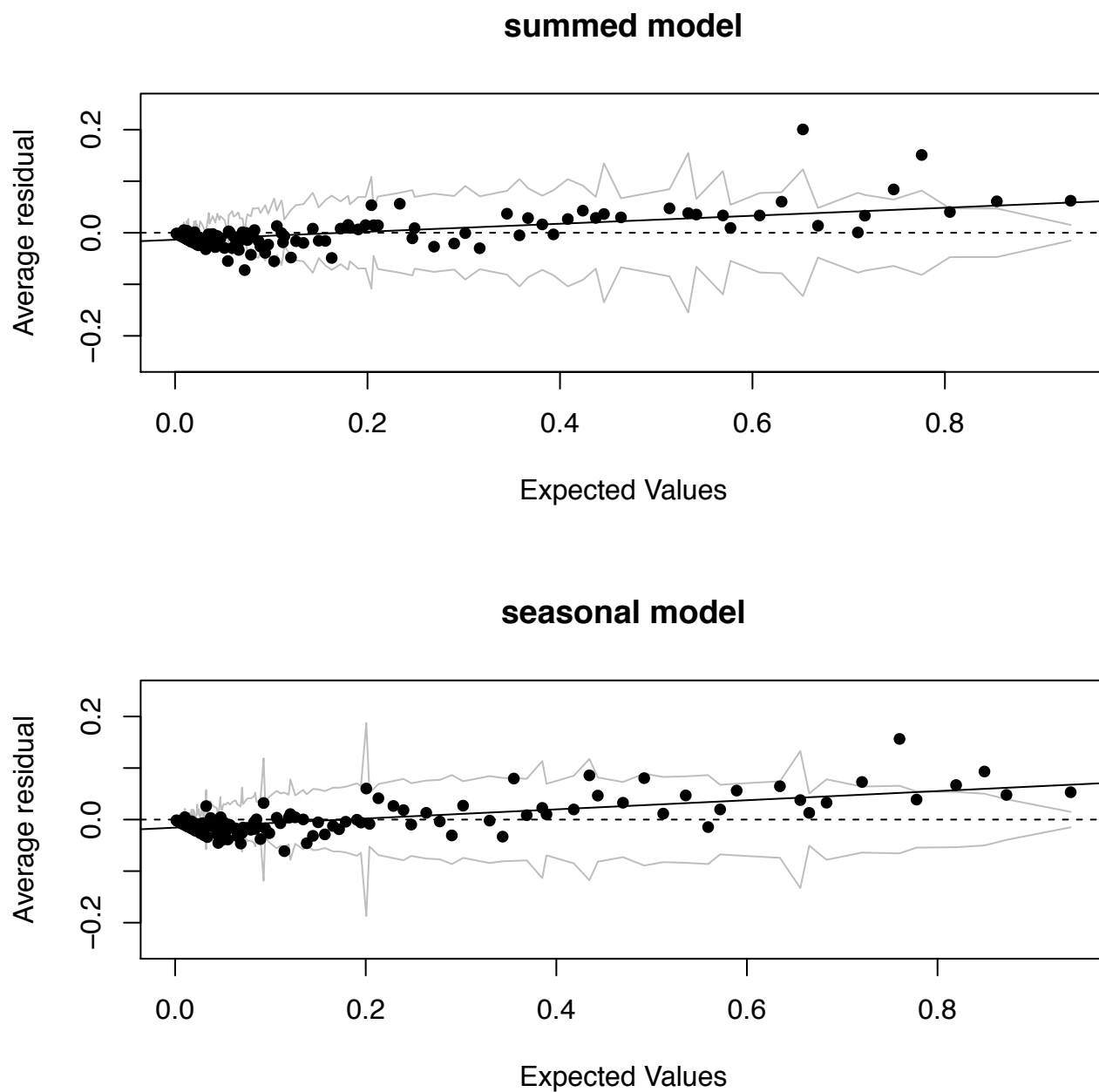


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Figure S2. Schematic cartoon of our simulation for the dissimilarity values associated with our null hypothesis that diets of male and female bees do not differ. (a) Each collection record for each bee species associates the sex of an individual bee to the flower species from which it was collected. (b) To compute the dissimilarity between males and females, we compare all visits to each flower species from males (purple vector) to all visits to each flower species from females (green vector). (c) The Morisita-Horn index summarizes the differences between the two vectors as a value between 0 (identical) and 1 (maximally dissimilar). (d) For our null model, we shuffle the sex column from our observation table. (e) This produces two null vectors. The row and column sums for the matrices in (b) and (c) are identical, but the elements can differ. (f) For our null model, we compute the dissimilarity between the null vectors. We repeated steps d-f 9999 times to generate confidence intervals for the null hypothesis that the sex of a visiting bee is unrelated to the flower species it is collected from. When comparing the flower species visited by different species of bee, we conducted an analysis identical except that rather than comparing two sexes of the same species, we compared two species of the same sex (i.e. exchanging “sex” and “species” throughout figure S1).

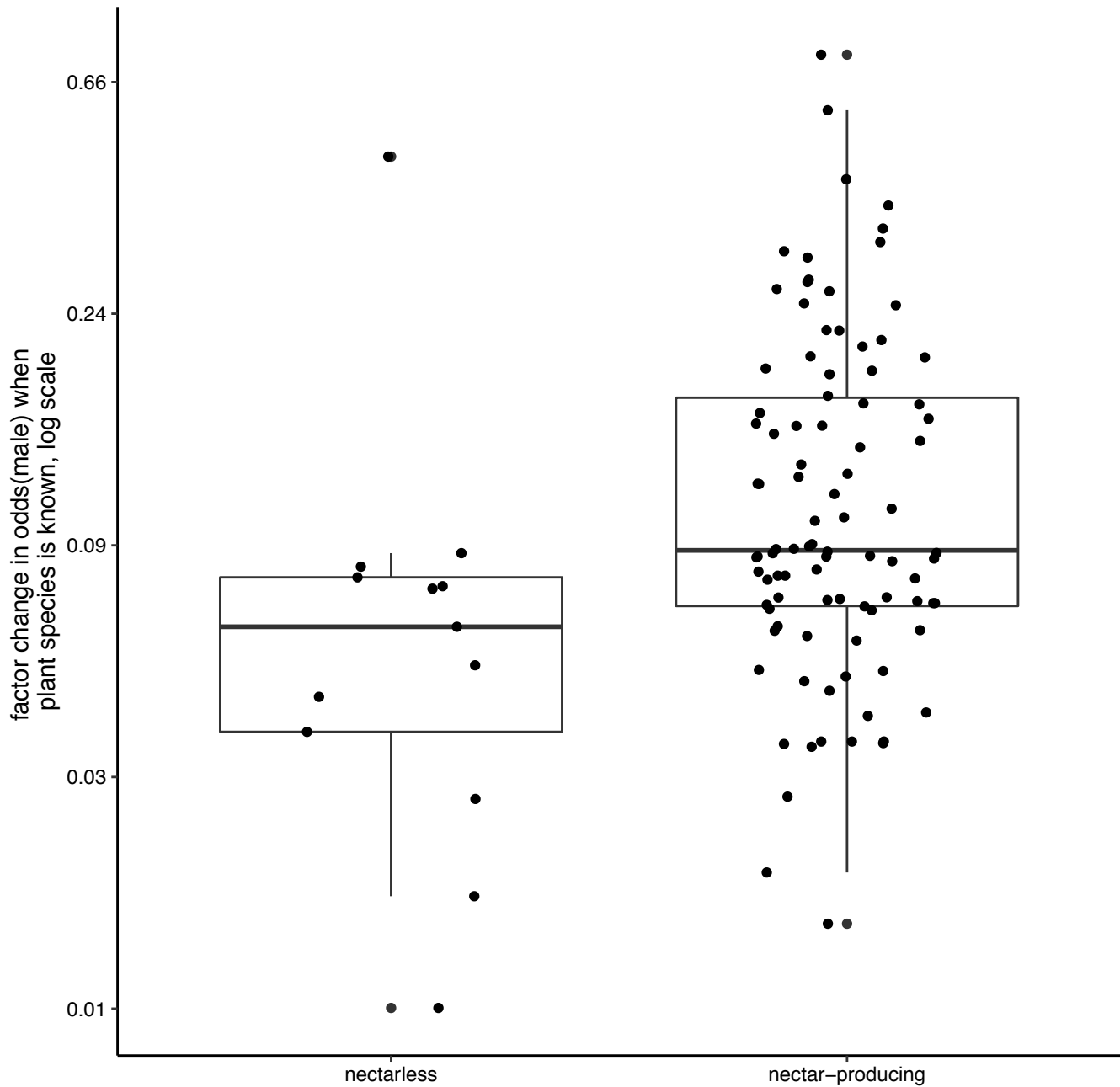


787 **Figure S3.** Effect size for diet dissimilarity is independent of sample size, while
788 standardized effect is strongly driven by the number of individuals of the sex with
789 the fewest records. a) Observed Morisita-Horn dissimilarity in flower communities
790 visited by male and female bees of a single species, minus average null
791 dissimilarity vs. the number of records for the less frequently observed sex. b)
792 Observed minus null dissimilarity in composition of flowers visited by male and
793 female bees of a single species, scaled by the variation in the null model, versus
794 the number of records for the less frequently observed sex.

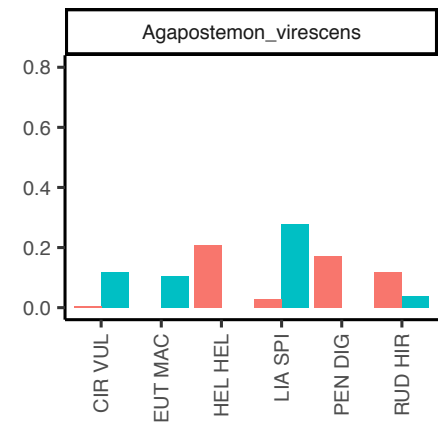
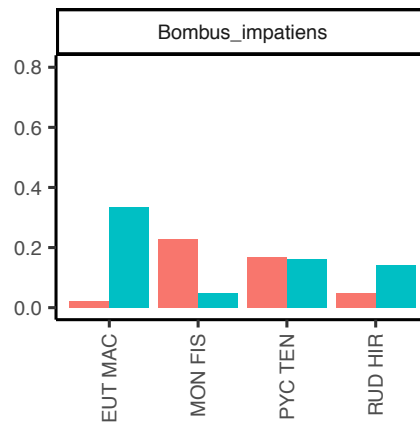
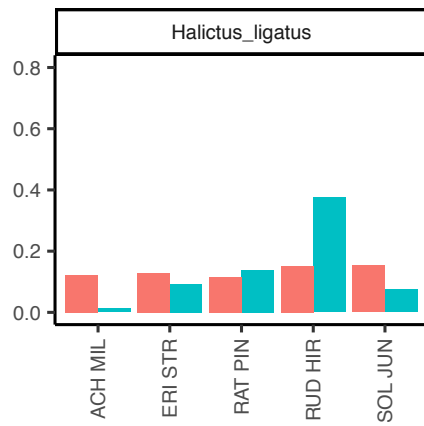
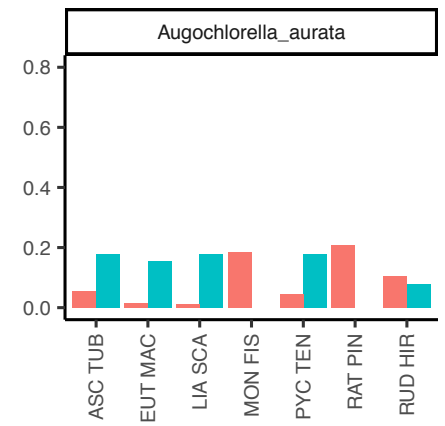
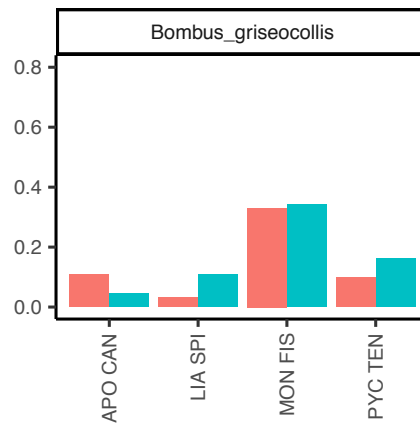
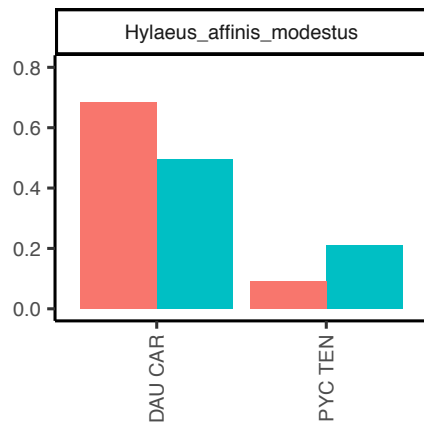
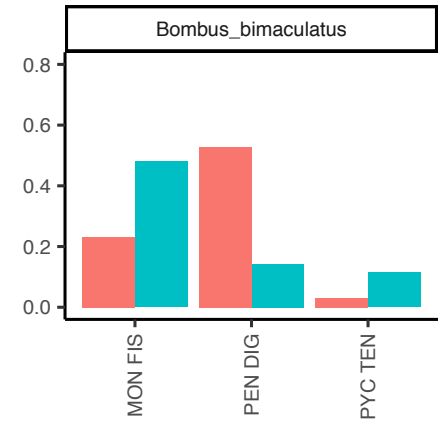
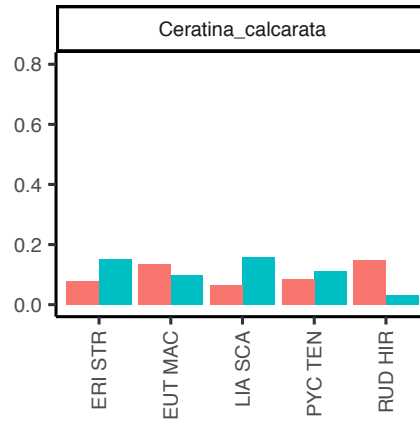
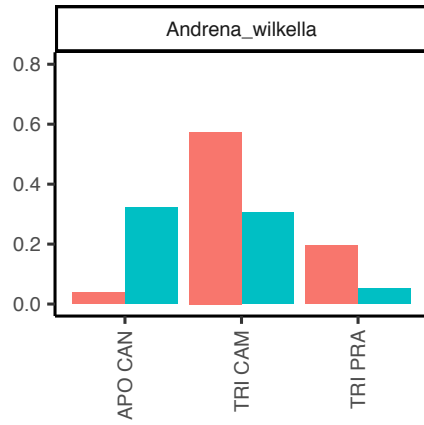


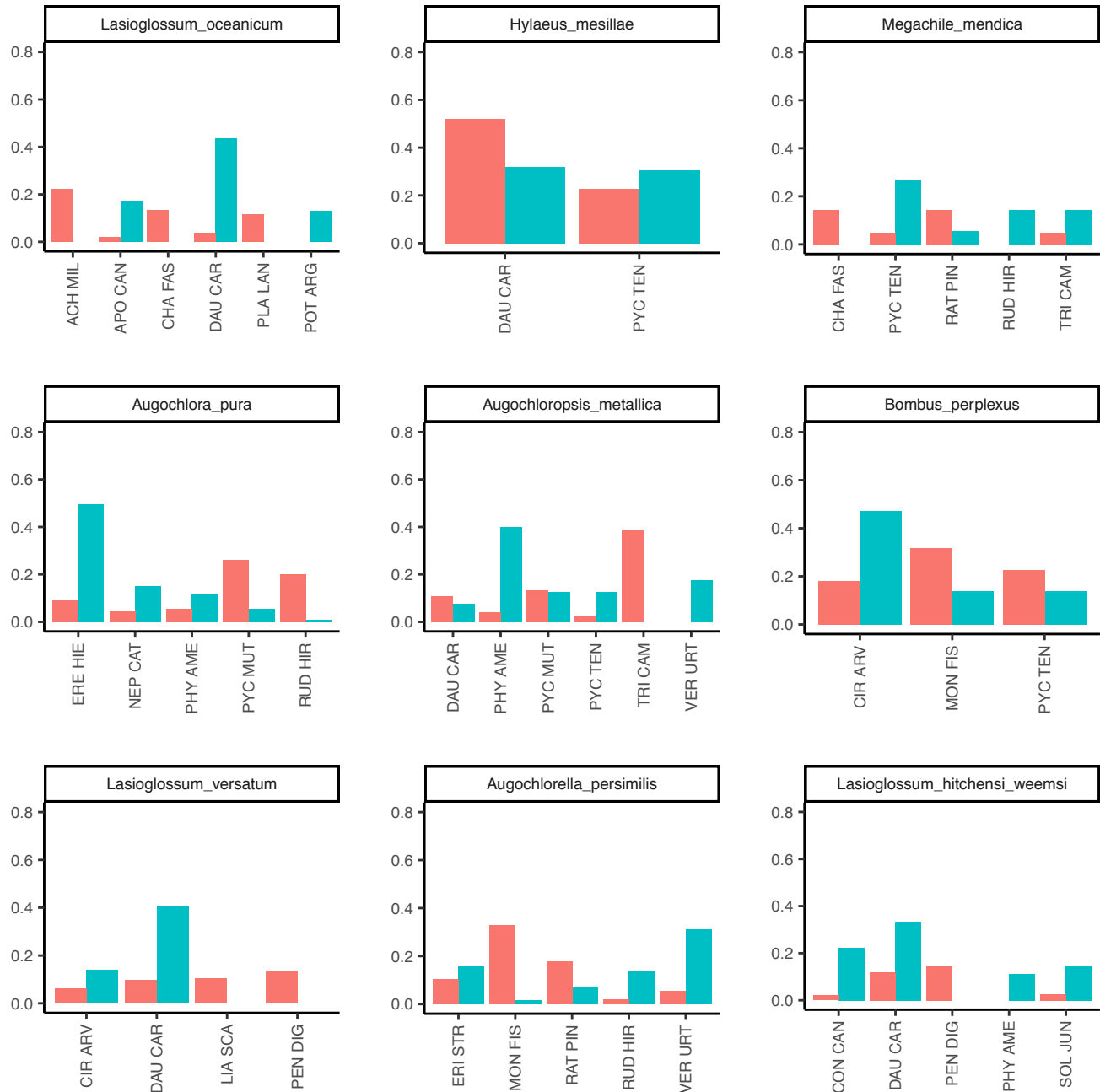
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Figure S4. Binned residual plots for each model show minor violation of the additivity assumption. Residuals and predicted values on the probability scale.



799 **Figure S5.** Seasonal model predictions are consistent with the hypothesis that
800 male bees avoid flower species that do not produce nectar, relative to females.
801 Each point is the random effect prediction (change in odds that a bee visiting that
802 flower is male) for a flower species.
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Figure S6. Dissimilarity in flower communities visited by male and female bees arise due to complementarity in addition to nestedness patterns. For each bee species, the proportion of male (blue) and female (red) visits to each flower species that received >10% of at least one sex's visits are pictured. Due to omitted flower species, bars may sum to <1.

813 **Table S1.** Model convergence confirmed based on similar parameter estimates across fitting routines. For each model,
 814 the estimate for each term is given for each of 6 fitting algorithms in the R package lme4. Subsequent analyses used
 815 parameter estimates in yellow, in both cases tied for the highest estimated likelihood with other very similar fits.

term	model	bobyqa	Nelder_Mead	nlminbw	optimx.L-BFGS-B	nloptwrap.NLOPT_LN_NELDERMEAD	nloptwrap.NLOPT_LN_BOBYQA
intercept	summed	-2.43	-2.43	-2.43	-2.43	-2.43	-2.43
bee species	summed	2.04	2.04	2.04	2.04	2.04	2.04
flower species	summed	1.40	1.40	1.40	1.40	1.40	1.40
site	summed	0.00	0.00	0.00	0.00	0.00	0.00
bee species:flower species	summed	1.21	1.21	1.21	1.21	1.21	1.21
site:bee species	summed	0.62	0.62	0.62	0.62	0.62	0.62
site:flower species	summed	0.61	0.61	0.61	0.61	0.61	0.61
intercept	seasonal	-2.38	-2.45	-2.38	-2.38	-2.45	-2.45
bee species	seasonal	2.09	2.14	2.09	2.09	2.13	2.13
flower species	seasonal	1.25	1.27	1.25	1.25	1.27	1.27
site	seasonal	0.00	0.00	0.00	0.00	0.00	0.00
bee species:flower species	seasonal	1.09	1.10	1.09	1.09	1.10	1.10
site:bee species	seasonal	0.46	0.47	0.46	0.46	0.47	0.47
site:flower species	seasonal	0.35	0.35	0.35	0.35	0.35	0.35
sampling round	seasonal	0.38	0.36	0.38	0.38	0.36	0.36
sampling round:bee species	seasonal	0.83	0.84	0.83	0.83	0.84	0.84
sampling round:flower species	seasonal	0.00	0.00	0.00	0.00	0.00	0.00
sampling round:site	seasonal	0.29	0.29	0.29	0.29	0.29	0.29
sampling round:site:bee species	seasonal	0.60	0.60	0.60	0.60	0.60	0.60
sampling round:site:flower species	seasonal	0.28	0.29	0.28	0.28	0.28	0.28

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Table S2. Bee species with number of female and male specimens collected.
This table will be removed from the final submission when data are deposited on Dryad.

family	genus	species	females	males
Andrenidae	<i>Andrena</i>	<i>brevipalpis</i>	1	0
Andrenidae	<i>Andrena</i>	<i>carlini</i>	3	0
Andrenidae	<i>Andrena</i>	<i>commoda</i>	3	0
Andrenidae	<i>Andrena</i>	<i>cressonii</i>	16	0
Andrenidae	<i>Andrena</i>	<i>fragilis</i>	2	0
Andrenidae	<i>Andrena</i>	<i>hippotes</i>	4	0
Andrenidae	<i>Andrena</i>	<i>imitatrix</i>	6	0
Andrenidae	<i>Andrena</i>	<i>krigiana</i>	14	0
Andrenidae	<i>Andrena</i>	<i>nasonii</i>	13	0
Andrenidae	<i>Andrena</i>	<i>nuda</i>	2	0
Andrenidae	<i>Andrena</i>	<i>pruni</i>	6	0
Andrenidae	<i>Andrena</i>	<i>robertsonii</i>	8	0
Andrenidae	<i>Andrena</i>	<i>rudbeckiae</i>	8	11
Andrenidae	<i>Andrena</i>	<i>rugosa</i>	1	0
Andrenidae	<i>Andrena</i>	<i>spiraeana</i>	1	0
Andrenidae	<i>Andrena</i>	<i>vicina</i>	6	0
Andrenidae	<i>Andrena</i>	<i>wilkella</i>	277	59
Andrenidae	<i>Andrena</i>	<i>wilmattae</i>	2	0
Andrenidae	<i>Calliopsis</i>	<i>andreniformis</i>	4	1
Apidae	<i>Anthophora</i>	<i>abrupta</i>	4	0
Apidae	<i>Anthophora</i>	<i>terminalis</i>	3	2
Apidae	<i>Bombus</i>	<i>auricomus</i>	1	0
Apidae	<i>Bombus</i>	<i>bimaculatus</i>	577	175
Apidae	<i>Bombus</i>	<i>citrinus</i>	0	5
Apidae	<i>Bombus</i>	<i>fervidus</i>	18	0
Apidae	<i>Bombus</i>	<i>griseocollis</i>	681	815
Apidae	<i>Bombus</i>	<i>impatiens</i>	2358	105
Apidae	<i>Bombus</i>	<i>perplexus</i>	22	36
Apidae	<i>Bombus</i>	<i>vagans</i>	14	2
Apidae	<i>Ceratina</i>	<i>calcarata</i>	1417	133
Apidae	<i>Ceratina</i>	<i>dupla</i>	151	19
Apidae	<i>Ceratina</i>	<i>mikmaqi</i>	130	5
Apidae	<i>Ceratina</i>	<i>strenua</i>	285	13

Apidae	<i>Melissodes</i>	<i>agilis</i>	0	7
Apidae	<i>Melissodes</i>	<i>bimaculatus</i>	9	1
Apidae	<i>Melissodes</i>	<i>denticulatus</i>	7	73
Apidae	<i>Melissodes</i>	<i>desponsus</i>	1	7
Apidae	<i>Melissodes</i>	<i>subillatus</i>	31	6
Apidae	<i>Melissodes</i>	<i>trinodis</i>	1	7
Apidae	<i>Nomada</i>	<i>articulata</i>	4	0
Apidae	<i>Nomada</i>	<i>bidentate_gr</i>	7	0
Apidae	<i>Nomada</i>	<i>erigeronis</i>	1	0
Apidae	<i>Nomada</i>	<i>lehighensis</i>	1	0
Apidae	<i>Nomada</i>	<i>maculata</i>	2	0
Apidae	<i>Nomada</i>	<i>pygmaea</i>	15	0
Apidae	<i>Ptilothrix</i>	<i>bombiformis</i>	0	1
Apidae	<i>Triepeolus</i>	<i>cressonii</i>	0	1
Apidae	<i>Triepeolus</i>	<i>eliseae</i>	1	0
Apidae	<i>Triepeolus</i>	<i>remigatus</i>	1	0
Apidae	<i>Xylocopa</i>	<i>virginica</i>	137	13
Colletidae	<i>Hylaeus</i>	<i>affinis_modestus</i>	1376	363
Colletidae	<i>Hylaeus</i>	<i>fedorica</i>	1	0
Colletidae	<i>Hylaeus</i>	<i>leptocephalus</i>	1	3
Colletidae	<i>Hylaeus</i>	<i>mesillae</i>	575	173
Halictidae	<i>Agapostemon</i>	<i>sericeus</i>	5	5
Halictidae	<i>Agapostemon</i>	<i>virescens</i>	203	76
Halictidae	<i>Augochlora</i>	<i>pura</i>	1036	377
Halictidae	<i>Augochlorella</i>	<i>aurata</i>	397	39
Halictidae	<i>Augochlorella</i>	<i>persimilis</i>	434	116
Halictidae	<i>Augochloropsis</i>	<i>metallica</i>	121	40
Halictidae	<i>Dufourea</i>	<i>novaeangliae</i>	0	1
Halictidae	<i>Halictus</i>	<i>confusus</i>	174	35
Halictidae	<i>Halictus</i>	<i>ligatus</i>	2432	160
Halictidae	<i>Halictus</i>	<i>parallelus</i>	6	18
Halictidae	<i>Halictus</i>	<i>rubicundus</i>	31	19
Halictidae	<i>Lasioglossum</i>	<i>abanci</i>	6	0
Halictidae	<i>Lasioglossum</i>	<i>admirandum</i>	15	0
Halictidae	<i>Lasioglossum</i>	<i>anomalum</i>	17	0
Halictidae	<i>Lasioglossum</i>	<i>atwoodi</i>	7	1
Halictidae	<i>Lasioglossum</i>	<i>birkmanni</i>	1	0
Halictidae	<i>Lasioglossum</i>	<i>bruneri</i>	6	4
Halictidae	<i>Lasioglossum</i>	<i>callidum</i>	54	0

Halictidae	<i>Lasioglossum</i>	<i>cattellae</i>	14	4
Halictidae	<i>Lasioglossum</i>	<i>coeruleum</i>	2	0
Halictidae	<i>Lasioglossum</i>	<i>coreopsis</i>	1	0
Halictidae	<i>Lasioglossum</i>	<i>coriaceum</i>	14	0
Halictidae	<i>Lasioglossum</i>	<i>cressonii</i>	16	5
Halictidae	<i>Lasioglossum</i>	<i>ellisiae</i>	0	3
Halictidae	<i>Lasioglossum</i>	<i>ephialtum</i>	1	0
Halictidae	<i>Lasioglossum</i>	<i>foxii</i>	2	2
Halictidae	<i>Lasioglossum</i>	<i>fuscipenne</i>	9	0
Halictidae	<i>Lasioglossum</i>	<i>gotham</i>	74	2
Halictidae	<i>Lasioglossum</i>	<i>hitchensi_weemsi</i>	152	27
Halictidae	<i>Lasioglossum</i>	<i>illinoense</i>	70	7
Halictidae	<i>Lasioglossum</i>	<i>imitatum</i>	462	15
Halictidae	<i>Lasioglossum</i>	<i>leucocomum</i>	2	0
Halictidae	<i>Lasioglossum</i>	<i>leucozonium</i>	2	0
Halictidae	<i>Lasioglossum</i>	<i>nigroviride</i>	2	0
Halictidae	<i>Lasioglossum</i>	<i>oblongum</i>	4	2
Halictidae	<i>Lasioglossum</i>	<i>obscurum</i>	7	1
Halictidae	<i>Lasioglossum</i>	<i>oceanicum</i>	104	23
Halictidae	<i>Lasioglossum</i>	<i>oenotherae</i>	1	0
Halictidae	<i>Lasioglossum</i>	<i>paradmiraandum</i>	50	0
Halictidae	<i>Lasioglossum</i>	<i>pectorale</i>	3	0
Halictidae	<i>Lasioglossum</i>	<i>pilosum</i>	2	0
Halictidae	<i>Lasioglossum</i>	<i>platyparium</i>	2	3
Halictidae	<i>Lasioglossum</i>	<i>rozeni</i>	15	11
Halictidae	<i>Lasioglossum</i>	<i>smilacinae</i>	4	0
Halictidae	<i>Lasioglossum</i>	<i>subviridatum</i>	5	1
Halictidae	<i>Lasioglossum</i>	<i>tegulare</i>	31	2
Halictidae	<i>Lasioglossum</i>	<i>trigeminum</i>	44	0
Halictidae	<i>Lasioglossum</i>	<i>truncatum</i>	2	0
Halictidae	<i>Lasioglossum</i>	<i>versatum</i>	681	93
Halictidae	<i>Lasioglossum</i>	<i>viridatum</i>	11	2
Halictidae	<i>Lasioglossum</i>	<i>zephyrum</i>	12	1
Halictidae	<i>Sphecodes</i>	<i>atlantis</i>	0	1
Halictidae	<i>Sphecodes</i>	<i>dichrous</i>	3	5
Halictidae	<i>Sphecodes</i>	<i>heraclei</i>	10	5
Megachilidae	<i>Anthidiellum</i>	<i>notatum</i>	4	1
Megachilidae	<i>Anthidium</i>	<i>manicatum</i>	7	8
Megachilidae	<i>Anthidium</i>	<i>oblongatum</i>	18	19

Megachilidae	<i>Coelioxys</i>	<i>alternatus</i>	1	2
Megachilidae	<i>Coelioxys</i>	<i>banksi</i>	1	0
Megachilidae	<i>Coelioxys</i>	<i>germanus</i>	0	1
Megachilidae	<i>Coelioxys</i>	<i>hunteri</i>	0	1
Megachilidae	<i>Coelioxys</i>	<i>modestus</i>	0	1
Megachilidae	<i>Coelioxys</i>	<i>obtusiventris</i>	1	0
Megachilidae	<i>Coelioxys</i>	<i>octodentatus</i>	1	1
Megachilidae	<i>Coelioxys</i>	<i>porterae</i>	0	1
Megachilidae	<i>Coelioxys</i>	<i>sayi</i>	2	6
Megachilidae	<i>Heriades</i>	<i>carinatus</i>	31	2
Megachilidae	<i>Heriades</i>	<i>leavitti</i>	1	6
Megachilidae	<i>Heriades</i>	<i>variolosus</i>	10	0
Megachilidae	<i>Hoplitis</i>	<i>pilosifrons</i>	46	1
Megachilidae	<i>Hoplitis</i>	<i>producta</i>	8	0
Megachilidae	<i>Hoplitis</i>	<i>spoliata</i>	2	1
Megachilidae	<i>Lithurgus</i>	<i>chrysurus</i>	0	6
Megachilidae	<i>Megachile</i>	<i>brevis</i>	25	3
Megachilidae	<i>Megachile</i>	<i>campanulae</i>	6	18
Megachilidae	<i>Megachile</i>	<i>exilis</i>	11	29
Megachilidae	<i>Megachile</i>	<i>frugalis</i>	26	6
Megachilidae	<i>Megachile</i>	<i>gemula</i>	4	2
Megachilidae	<i>Megachile</i>	<i>georgica</i>	1	0
Megachilidae	<i>Megachile</i>	<i>inimica</i>	4	0
Megachilidae	<i>Megachile</i>	<i>integra</i>	1	0
Megachilidae	<i>Megachile</i>	<i>melanophaea</i>	0	1
Megachilidae	<i>Megachile</i>	<i>mendica</i>	21	56
Megachilidae	<i>Megachile</i>	<i>montivaga</i>	15	9
Megachilidae	<i>Megachile</i>	<i>petulans</i>	0	2
Megachilidae	<i>Megachile</i>	<i>pugnata</i>	2	3
Megachilidae	<i>Megachile</i>	<i>rotundata</i>	11	8
Megachilidae	<i>Megachile</i>	<i>sculpturalis</i>	17	32
Megachilidae	<i>Megachile</i>	<i>xylocopoides</i>	2	1
Megachilidae	<i>Osmia</i>	<i>albiventris</i>	3	0
Megachilidae	<i>Osmia</i>	<i>atriventris</i>	9	0
Megachilidae	<i>Osmia</i>	<i>bucephala</i>	21	0
Megachilidae	<i>Osmia</i>	<i>distincta</i>	7	0
Megachilidae	<i>Osmia</i>	<i>georgica</i>	5	0
Megachilidae	<i>Osmia</i>	<i>pumila</i>	30	0
Megachilidae	<i>Pseudoanthidium</i>	<i>nanum</i>	0	1

Megachilidae	<i>Stelis</i>	<i>lateralis</i>	1	0
Megachilidae	<i>Stelis</i>	<i>louisae</i>	1	2

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Table S3. Number of male and female visitors to each plant species, and bias towards attracting male bee visitors. This bias is the random effect prediction from the seasonal model, which indicates the change in log(odds) that a visiting bee is male when the species of flower it visits is given; greater values indicate male bias.

family	genus	species	female visits	male visits	random effect
Alliaceae	<i>Allium</i>	<i>vineale</i>	3	0	-0.224
Apiaceae	<i>Daucus</i>	<i>carota</i>	1778	350	0.526
Apiaceae	<i>Eryngium</i>	<i>yuccifolium</i>	2	0	-0.225
Apiaceae	<i>Sanicula</i>	<i>canadensis</i>	1	0	-0.049
Apocynaceae	<i>Apocynum</i>	<i>cannabinum</i>	283	92	0.754
Asclepidaceae	<i>Asclepias</i>	<i>incarnata</i>	7	0	-0.736
Asclepidaceae	<i>Asclepias</i>	<i>syriaca</i>	28	89	0.929
Asclepidaceae	<i>Asclepias</i>	<i>tuberosa</i>	114	26	0.423
Asteraceae	<i>Achillea</i>	<i>millefolium</i>	472	36	-0.004
Asteraceae	<i>Bidens</i>	<i>trichosperma</i>	1	0	-0.015
Asteraceae	<i>Carduus</i>	<i>nutans</i>	1	0	-0.366
Asteraceae	<i>Centuarea</i>	<i>stoebe</i>	321	50	0.265
Asteraceae	<i>Cichorium</i>	<i>intybus</i>	104	10	0.516
Asteraceae	<i>Cirsium</i>	<i>arvense</i>	351	96	0.858
Asteraceae	<i>Cirsium</i>	<i>discolor</i>	5	2	0.349
Asteraceae	<i>Cirsium</i>	<i>vulgare</i>	112	16	0.121
Asteraceae	<i>Conyza</i>	<i>canadensis</i>	32	10	1.097
Asteraceae	<i>Coreopsis</i>	<i>lanceolata</i>	21	0	-0.857
Asteraceae	<i>Coreopsis</i>	<i>tinctoria</i>	1	0	-0.069
Asteraceae	<i>Crepis</i>	<i>capillaris</i>	6	0	-0.236
Asteraceae	<i>Doellingeria</i>	<i>umbellata</i>	1	0	-0.052
Asteraceae	<i>Echinacea</i>	<i>purpurea</i>	86	45	0.309
Asteraceae	<i>Erechtites</i>	<i>hieraciifolius</i>	130	203	1.878
Asteraceae	<i>Erigeron</i>	<i>annuus</i>	26	3	0.266
Asteraceae	<i>Erigeron</i>	<i>strigosus</i>	712	119	1.037
Asteraceae	<i>Euthamia</i>	<i>graminifolia</i>	50	18	1.467
Asteraceae	<i>Eutrochium</i>	<i>maculatum</i>	461	166	1.368
Asteraceae	<i>Gaillardia</i>	<i>aristata</i>	4	0	-0.274
Asteraceae	<i>Helianthus</i>	<i>angustifolius</i>	11	0	-0.411

Asteraceae	<i>Helianthus</i>	<i>strumosus</i>	1	1	0.517
Asteraceae	<i>Heliopsis</i>	<i>helianthoides</i>	186	49	0.763
Asteraceae	<i>Hieracium</i>	<i>pilosella</i>	2	0	-0.148
Asteraceae	<i>Krigia</i>	<i>biflora</i>	19	0	-0.542
Asteraceae	<i>Lactuca</i>	<i>serriola</i>	4	0	-0.257
Asteraceae	<i>Leucanthemum</i>	<i>vulgare</i>	405	20	-0.349
Asteraceae	<i>Liatris</i>	<i>spicata</i>	186	127	1.137
Asteraceae	<i>Ratibida</i>	<i>pinnata</i>	539	121	0.005
Asteraceae	<i>Rudbeckia</i>	<i>hirta</i>	1174	189	0.645
Asteraceae	<i>Solidago</i>	<i>altissima</i>	8	0	-0.586
Asteraceae	<i>Solidago</i>	<i>canadensis</i>	8	2	0.816
Asteraceae	<i>Solidago</i>	<i>gigantea</i>	107	9	0.613
Asteraceae	<i>Solidago</i>	<i>juncea</i>	636	77	1.106
Asteraceae	<i>Solidago</i>	<i>rugosa</i>	1	0	-0.015
Asteraceae	<i>Symphotrichum</i>	<i>novae-angliae</i>	25	6	0.451
Asteraceae	<i>Vernonia</i>	<i>noveboracensis</i>	52	37	-0.045
Brassicaceae	<i>Barbarea</i>	<i>vulgaris</i>	3	0	-0.114
Campanulaceae	<i>Lobelia</i>	<i>inflata</i>	12	3	1.147
Campanulaceae	<i>Lobelia</i>	<i>siphilitica</i>	2	0	-0.034
Caryophyllaceae	<i>Dianthus</i>	<i>armeria</i>	3	0	-0.280
Commelinaceae	<i>Tradescantia</i>	<i>ohiensis</i>	34	1	-0.805
Convolvulaceae	<i>Calystegia</i>	<i>silvatica</i>	5	0	-0.538
Cornaceae	<i>Swida</i>	<i>amomum</i>	4	0	-0.250
Cornaceae	<i>Swida</i>	<i>racemosa</i>	12	1	0.546
Fabaceae	<i>Baptisia</i>	<i>tinctoria</i>	19	5	-0.566
Fabaceae	<i>Chamaecrista</i>	<i>fasciculata</i>	246	2	-1.514
Fabaceae	<i>Desmodium</i>	<i>paniculatum</i>	6	1	-0.138
Fabaceae	<i>Lotus</i>	<i>corniculatus</i>	142	33	-0.231
Fabaceae	<i>Melilotus</i>	<i>albus</i>	20	9	0.571
Fabaceae	<i>Melilotus</i>	<i>officinalis</i>	41	21	1.309
Fabaceae	<i>Securigera</i>	<i>varia</i>	38	1	-0.654
Fabaceae	<i>Senna</i>	<i>hebecarpa</i>	5	5	1.678
Fabaceae	<i>Trifolium</i>	<i>aureum</i>	1	0	-0.033
Fabaceae	<i>Trifolium</i>	<i>campestre</i>	365	39	0.106
Fabaceae	<i>Trifolium</i>	<i>hybridum</i>	11	7	0.739
Fabaceae	<i>Trifolium</i>	<i>pratense</i>	192	20	-0.869
Fabaceae	<i>Trifolium</i>	<i>repens</i>	130	6	-0.847
Fabaceae	<i>Vicia</i>	<i>tetrasperma</i>	1	0	-0.048
Gentianaceae	<i>Sabatia</i>	<i>angularis</i>	1	0	-0.034

Hypericaceae	<i>Hypericum</i>	<i>perforatum</i>	223	10	-1.095
Hypericaceae	<i>Hypericum</i>	<i>punctatum</i>	1	0	-0.176
Iridaceae	<i>Sisyrinchium</i>	<i>angustifolium</i>	9	0	-0.351
Lamiaceae	<i>Clinopodium</i>	<i>vulgare</i>	64	3	-0.854
Lamiaceae	<i>Monarda</i>	<i>fistulosa</i>	1397	400	-0.131
Lamiaceae	<i>Monarda</i>	<i>punctata</i>	0	1	1.242
Lamiaceae	<i>Nepeta</i>	<i>cataria</i>	99	81	1.270
Lamiaceae	<i>Prunella</i>	<i>vulgaris</i>	17	5	0.296
Lamiaceae	<i>Pycnanthemum</i>	<i>muticum</i>	398	59	0.811
Lamiaceae	<i>Pycnanthemum</i>	<i>tenuifolium</i>	1113	421	0.609
Lamiaceae	<i>Pycnanthemum</i>	<i>verticillatum</i>	5	8	0.886
Lamiaceae	<i>Teucrium</i>	<i>canadense</i>	3	0	-0.104
Loniceraceae	<i>Lonicera</i>	<i>japonica</i>	1	0	-0.131
Lythraceae	<i>Lythrum</i>	<i>salicaria</i>	364	38	-0.016
Onagraceae	<i>Oenothera</i>	<i>biennis</i>	2	0	-0.143
Onagraceae	<i>Oenothera</i>	<i>fruticosa</i>	2	1	0.221
Oxalidaceae	<i>Oxalis</i>	<i>stricta</i>	8	0	-0.249
Phytolaccaceae	<i>Phytolacca</i>	<i>americana</i>	108	74	1.580
Plantaginaceae	<i>Plantago</i>	<i>lanceolata</i>	147	0	-1.997
Poaceae	<i>Glyceria</i>	<i>grandis</i>	1	0	-0.187
Poaceae	<i>Sorghastrum</i>	<i>nutans</i>	1	0	-0.092
Polygonaceae	<i>Fallopia</i>	<i>convolvulus</i>	3	4	1.044
Polygonaceae	<i>Persicaria</i>	<i>pensylvanica</i>	4	0	-0.391
Polygonaceae	<i>Persicaria</i>	<i>setacea</i>	3	1	0.158
Ranunculaceae	<i>Ranunculus</i>	<i>hispidus</i>	1	0	-0.057
Rosaceae	<i>Drymocallis</i>	<i>arguta</i>	22	8	0.604
Rosaceae	<i>Potentilla</i>	<i>recta</i>	56	1	-0.628
Rosaceae	<i>Rosa</i>	<i>carolina</i>	71	1	-1.412
Rosaceae	<i>Rosa</i>	<i>multiflora</i>	5	0	-0.264
Rosaceae	<i>Rubus</i>	<i>flagellaris</i>	1	0	-0.027
Rosaceae	<i>Rubus</i>	<i>pensilvanicus</i>	7	0	-0.241
Rubiaceae	<i>Galium</i>	<i>mollugo</i>	4	0	-0.369
Scrophulariaceae	<i>Linaria</i>	<i>vulgaris</i>	275	4	-1.633
Scrophulariaceae	<i>Penstemon</i>	<i>digitalis</i>	862	48	-0.847
Scrophulariaceae	<i>Penstemon</i>	<i>hirsutus</i>	36	0	-0.822
Scrophulariaceae	<i>Verbascum</i>	<i>blattaria</i>	15	0	-0.721
Scrophulariaceae	<i>Verbascum</i>	<i>thapsus</i>	129	1	-1.085
Solanaceae	<i>Solanum</i>	<i>carolinense</i>	14	0	-0.518
Verbenaceae	<i>Verbena</i>	<i>hastata</i>	8	3	0.927

Verbenaceae	<i>Verbena</i>	<i>simplex</i>	11	3	0.482
Verbenaceae	<i>Verbena</i>	<i>urticifolia</i>	58	71	2.118

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