

1 **Pollinator traits and competitive context shape dynamic foraging behavior in bee**
2 **communities.**

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9 **Abstract**

10 Interspecific interactions (e.g. competition) can dynamically shape individual and species-level
11 resource use within communities. Understanding how interspecific competition between
12 pollinators species shapes resource use is of particular interest because pollinator foraging
13 behavior (“floral fidelity”) is directly linked to plant reproductive function through the
14 movement of conspecific pollen. Through targeted species removals, this study aims to gain a
15 predictive understanding of how interspecific competition can influence pollinator foraging
16 behavior. We explore how traits—specifically pollinator tongue length, known to dictate
17 pollinator resource partitioning—influence behavioral plasticity and drive dynamic interspecific
18 interactions. Our results demonstrate that bee species vary in their floral fidelity and that tongue
19 length explains a large part of this variation. Bees with shorter tongues move between plant
20 species (floral infidelity) more often than bees with longer tongues. We did not find significant
21 variation in the response of bee species to a reduction in interspecific competition, but rather saw
22 a guild-wide reduction in floral fidelity in response to the removal of the dominant bee species
23 Finally, our results suggest that tongue length of the most abundant bee species, a site-level
24 attribute, explains much of the site-to-site variation in pollinator foraging behavior. In particular,
25 we found that as the tongue length of the most abundant bee in the site increases, the site level
26 foraging fidelity decreases. With global pollinator populations on the decline, novel interactions
27 between plants and pollinators are likely to occur. Exploring how the competitive landscape
28 shapes foraging plasticity will help us generalize to other plant pollinator systems and begin to
29 better predict the functional implications of competitive interactions.

30 **Introduction**

31 Differences in traits among species may reduce interspecific competition and maintain
32 diversity within a community (Grant 2006, Mayfield and Levine 2010). Generally, we still have
33 a poor understanding of which traits influence the outcome of competition and community
34 structure (McGill et al. 2006, Messier et al. 2010, HilleRisLambers et al. 2012). Traits such as
35 body size (Wells 1988) or bill size/shape (Wiens and Rotenberry 1981, Grant 2006) and plant
36 traits related to resource acquisition, such as root depth (Stubbs and Bastow 2004, Adler et al.
37 2010), can limit competition thus encouraging species coexistence. Our study explores the role
38 of traits in mediating competition within a community context, via pollinator foraging behavior.

39 Pollinator foraging behavior directly affects plant reproductive output and ecosystem
40 function through the transfer of pollen between plant individuals within a single foraging bout. If
41 pollinators move between different plant species they can transfer heterospecific pollen,
42 potentially reducing reproductive output (Ashman and Arceo-Gomez 2013, Briggs et al. 2016).
43 Given the functional significance of pollinator resource use, it is important to understand the
44 factors driving pollinator foraging behavior. The plants on which pollinators forage is a function
45 of a number of factors including innate and learned preference, morphological traits, as well as
46 direct and indirect competition with other pollinators in the community (Pimm et al. 1985,
47 Cnaani et al. 2006, Stang et al. 2009, Brosi and Briggs 2013).

48 Decades of research has demonstrated that interspecific competition can influence pollinator
49 foraging behavior. Largely in line with expectations derived from ecological theory, the range of
50 resources that a species utilizes contracts as the strength of interspecific competition increases
51 (Morse 1977, Hubbell and Johnson 1978, Inouye 1978, Pimm et al. 1985, Bolnick et al. 2010,
52 Brosi and Briggs 2013, Fründ et al. 2013). In one example, Pimm et al. (1985) found that in the

53 presence of one dominant competitor species, two other hummingbird species spent more time at
54 a less rewarding feeder. In contrast, *without* interspecific competition from the dominant
55 hummingbird, individuals of the other two species visited a feeder with high sucrose
56 concentrations. Brosi and Briggs (2013) found that after a release from interspecific competition,
57 bumble bees decreased their ‘floral fidelity’: pollinators moved more often between plant species
58 within a single foraging bout. These changes in foraging behavior were associated with a
59 significant decrease in reproductive output in a common alpine plant species. Fründ et al. (2013)
60 provide another example in which pollinators’ flower preferences can be flexible and depend on
61 community context (i.e., interspecific competition with other pollinator species present). In
62 simplified experimental plant-pollinator communities, as competition between pollinator species
63 increased, species often reduced their niche overlap by shifting to new plant species, which
64 resulted in increased reproduction across the plant community. Thus, we know bees respond to
65 competition and often do so strongly; but we don’t know if bee species vary in their response to
66 competition in complex assemblages of bee species or what traits are important in determining
67 how they will respond.

68 Bumble bee (*Bombus*) communities provide an excellent system in which to empirically
69 explore how trait differences drive foraging plasticity in response to interspecific competition.
70 *Bombus* assemblages are often species-rich, and sympatric species typically have substantial
71 overlap in their life history requirements (Goulson et al. 2008). Furthermore, traits that affect
72 resource acquisition and foraging efficiency can influence how species partition resources within
73 a community (Abrams and Chen 2002, Grant 2006). Tongue length is a trait that directly
74 determines which resources a bumble bee can access and how resource selection varies among
75 species (Heinrich 1976, Inouye 1978, McGill et al. 2006, Stang et al. 2009). In general, long-

76 tongued bumble bee foragers visit flowers with deep corollas and short-tongued bumble bees
77 forage on shallow flowers (Heinrich 1976, Stang et al. 2006, McGill et al. 2006). Still, bumble
78 bees are known to be labile in their foraging patterns if more rewarding floral resources become
79 available or the competitive landscape shifts (Inouye 1978, Gegear and Thomson 2004, Brosi
80 and Briggs 2013). Tongue length appears to be important for structuring foraging preferences but
81 we are lacking experimental work that evaluates how traits such as tongue length influence
82 pollinators' response to competition.

83 We systematically manipulated interspecific competition in bumble bee communities through
84 targeted single species removals and examined patterns of species-specific plasticity in resource
85 use in the remaining pollinators. Specifically we examined to what extent tongue length explains
86 species-specific difference in the pollinators' foraging behavior in response to release from
87 competition. We worked in spatially replicated plots in natural communities varying in plant and
88 bee community composition. Utilizing removals in these natural communities allowed us to
89 examine if the identity of the most abundant bee species (i.e. competitive context) influences bee
90 foraging behavior. We focused on the foraging response of the remaining bees in the community
91 with respect to floral fidelity, or, within plant species movements within a single foraging bout.
92 Floral fidelity is critical for many plants species' reproductive success because transfer of
93 conspecific pollen must occur in order for fertilization to take place.

94 We asked specifically (1) How do bee species vary in their overall patterns of floral fidelity?
95 (2) To what extent does tongue length explain variation in species-specific foraging behavior?
96 (3) How does the competitive context in which bees forage influence their floral fidelity, and is
97 there a systematic relationship between the traits (i.e. tongue length) of the dominant bee species
98 and the foraging patterns of the remainder of the bees at a given site?

99

100 **Methods.**

101 *Study Sites:* We worked in 28 subalpine meadow sites in the landscape surrounding the Rocky
102 Mountain Biological Laboratory (38° 57.5'N, 106°59.3'W, 2,900 m above sea level), in the
103 Gunnison National Forest, western Colorado, United States. Each site consisted of a 20 × 20-m
104 plot, all with the same dominant plant species (*Delphinium barbeyi*). A minimum distance of 1
105 km separated any two sites. We collected data over three summer growing seasons (June-
106 August), in 2010, 2011 and 2013.

107 *Manipulations.* We assessed each plot in a control state, waited one day, and then assessed each
108 plot in a manipulated state. We kept the interval between control and manipulated states short
109 because of the rapid turnover in flowering phenology in our high-altitude system, allowing us to
110 keep the plant community constant in our control–manipulation comparisons (Langenheim 1962,
111 Brosi and Briggs 2013). Manipulations reduce interspecific competition through the temporary,
112 non-destructive removal of the most abundant bumblebee species in each plot. We determined
113 the most abundant bee via inventory of *Bombus* species richness and abundance on the control
114 day using nondestructive aerial netting, with two field team members netting for a 20-min
115 period, not including handling time (the time from when a bee was in the net until it was in a
116 closed vial). To avoid double-counting, we kept each bee in an individual glass vial, identified to
117 species, and kept in a cool, dark cooler until the inventory time period was over, at which point
118 bees were released.

119 On the manipulation day we removed the most abundant bee species (as determined two
120 days previously in the control state). The removals were accomplished through targeted hand-
121 netting, and we minimized disturbance of other bees and vegetation by carefully placing the

122 insect net over entire inflorescence and allowing bee individuals to fly up into the net (Inouye
123 1978). Captured bees were transferred to vials and placed in a cooler during the manipulation
124 and released unharmed afterward. We used as much time as necessary to remove essentially all
125 individuals of the target species from the sample plot and immediately adjacent area (typically in
126 1-2 hours we would achieve ~98% removal). We left a period of at least 30 minutes between
127 manipulative bee removals and subsequent sampling to minimize the impact of the disturbance
128 on the foraging activities of other bees. We recorded both the abundance of removed (captured)
129 individuals, as well as the number of un-captured “escapees” of the most abundant species that
130 were observed during bee sampling. We assessed resource use (plant species visited within a
131 single foraging bout) in each site in both a control and a manipulated state. Each site was only
132 used once in a manipulated and controlled state per year (i.e., no sites were re-sampled within a
133 single season).

134 *Foraging observations:* We directly followed the foraging sequences of *Bombus* individuals in
135 both the control and manipulated states. We recorded the identity of each plant species visited in
136 a foraging sequence. We discontinued an observation when the bee was lost from sight, when it
137 ventured more than 5 m outside of the plot, when it had been observed for 10 full minutes, or
138 when we had tallied 100 individual plants visited. We discarded observations of fewer than five
139 plants visited. The number of individuals observed per/state/site varied due to bee abundance
140 (mean = 33 individuals per site; range = 8–54).

141 *Tongue Length measurements:* The data on proboscis lengths of workers was taken from
142 published measurements of bumblebees collected on the Front Range of the Colorado Rocky
143 Mountains and overlap with the sites and species that we used for this study (Inouye 1980).
144 Measurements indicate the sum of the individual lengths of the prementum and glossa. The

145 mean tongue length of each bumble bee species was assigned to each individual bee and used in
146 the trait analysis ([see Table 1 for tongue lengths] Inouye 1978, 1980, Pyke 1982).

147

148 *Data analysis:*

149 *Quantifying Floral fidelity:* Floral fidelity was measured as the binomial counts of individual bee
150 foraging movements that were conspecific (between individuals of the same plant species) vs.
151 heterospecific (between individuals of different plant species) (Brosi and Briggs 2013). We used
152 GLMMs with binomial errors using the logit link in the lme4 package for R (Hothorn et al.
153 2013) to model the floral fidelity response variable. Data from individual bees foraging within a
154 site cannot be considered independent because bees within a site are likely to be closely related
155 genetically, and environmental conditions are similar; therefore, site was included as a random
156 intercept term (Bolker et al. 2009). Relative to a binomial distribution, our data were
157 overdispersed, which we corrected by including an individual-level (i.e. bee individual) random
158 intercept term (Elston et al. 2001). We used the R statistical programming language (R Core
159 Development Team 2012) for all models.

160 *Species Specific differences:* We first ran a null model (M0) that included only the two structural
161 random effects: one to control for pseudoreplication for site and another to correct for over-
162 dispersion in the binomial response variable (see above).

163 M0: fidelity ~ (1|site) + (1|unique bee ID)

164 These structural terms were retained in all models. We then added state (control or manipulation)
165 as a fixed effect to M0, giving M1 below, to assess whether the removal of the most abundant
166 bee had a guild-wide impact on foraging fidelity.

167 M1: fidelity ~ state + (1|site) + (1|unique bee ID)

168 We compared M1 and M0 through a likelihood ratio test (LRT) and retained state as a fixed
169 effect in all subsequent models (see Results, Table 2). Next, we estimated the magnitude of
170 between-bee species variation in foraging dynamics by adding bee species as a random intercept
171 (model M2) or as a random intercept and a random slope (model M2b) with respect to state to
172 model M1:

173 M2: fidelity ~ state + (1|site) + (1|unique bee ID) + (1|bee species).

174 M2b: fidelity ~ state + (1|site) + (1|unique bee ID) + (1+state|bee species).

175 These models allowed us to estimate how much bee species differ in both their base-line fidelity
176 (i.e. random intercept) and in their response to the manipulation (i.e. random slope) by estimating
177 a variance term for each. To test if the random effects associated with bee species improved the
178 model fit, we compared models M1 and M2, as well as M2b and M2, using LRT and by
179 computing differences in the values of Akaike's Information Criterion (ΔAIC) between the
180 models.

181 *Traits:* To examine if bee species-level traits explain the species-specific differences in foraging
182 behavior, we added tongue length as a continuous fixed factor to M2 yielding M3 below.

183 M3: fidelity ~ state + tongue length + (1|site) + (1|unique bee ID) + (1|bee species)

184 We then asked whether tongue length explains differences in base-line floral fidelity among bee
185 species. We did so by first comparing M3 to M2 via LRT and by calculating ΔAIC between
186 these models to determine the overall impact on the model of adding tongue length as a fixed
187 effect. If tongue length explained base-line differences in foraging behavior that was otherwise
188 modeled as a random effect, the variance estimate for bee species intercepts should be reduced in
189 M3 relative to M2. We calculate this relative reduction in variance as

190
$$C_{\alpha}(bee) = 1 - \frac{\sigma_{\alpha}^2(M3)}{\sigma_{\alpha}^2(M2)}$$

191 following Jamil (2013), where subscript α indicates random intercept terms. The numerator
192 indicates the “residual” variation among bee species after taking account of tongue length (M3),
193 while the denominator is the ‘total’ variance among bee species from the model without tongue
194 length (M2). $C_\alpha > 0$ suggests inter-specific differences in base-line fidelity may be explained by
195 differences in their tongue lengths.

196 We evaluated variability in the estimates for $\sigma_\alpha^2(M3)$ and $\sigma_\alpha^2(M2)$ —and thus, the
197 difference between them—through parametric bootstrapping, i.e. by simulating data from the
198 maximum likelihood fits of M3 and M2 and then re-fitting the model. This approach generates a
199 set of coefficient fits for $\sigma_\alpha^2(M3)$ and $\sigma_\alpha^2(M2)$. We then compared the bootstrap distributions for
200 the variance terms using the non-parametric two-sample Kolmogorov–Smirnov (KS) test, which
201 examines the null hypothesis that the boot strap replicates for the variance terms are not different
202 at the $p \leq 0.05$ level.

203
204 *Site level attributes:* Finally, we explored if the community in which bees are locally embedded
205 influenced their foraging patterns. Specifically, we asked whether site-level variance in base-line
206 foraging patterns of the observed bees is a function of the identity of the most abundant bee
207 species at that site. We consider this a site-level attribute and a stand-in for competitive context
208 for the observed bees. To do so, we added a term to M3 for the tongue length of the bee species
209 that was the most locally abundant at the site, and thus the bee that we non-destructively
210 removed from the site in our manipulations (‘manip. tongue length’), as a continuous fixed
211 factor, giving M4 below:

212 M4: fidelity \sim state + tongue length + manip. tongue length + (1|site) + (1|unique bee ID)
213 + (1|bee species)

214 To assess overall effects on model fit of adding this additional term, we compared M4 to M3
215 using LRT and by calculating ΔAIC . We compared variance estimates for the site intercept from
216 M4 to that from M3 by calculating $C_\alpha(\text{site})$, with site variance from M4 in the numerator and
217 that from M3 in the denominator. This comparison examines to what extent the trait of the most
218 abundant species at a site captures site-to-site variance in baseline fidelity that would otherwise
219 be contained within the random intercept term for site. Again, a result of $C_\alpha > 0$ indicates that
220 the traits of locally abundant bee species explain site-to-site variance (Jamil 2013). The
221 distributions for $\sigma_\alpha^2(M3)$ and $\sigma_\alpha^2(M2)$ for site were compared using a KS test.

222

223 **Results.**

224 *Overall effect of manipulation:* The addition of manipulated state as a fixed effect in M1
225 confirmed that the removal of the most abundant bee resulted in a guild-wide reduction in
226 foraging fidelity when examined across the three year study period (Coeff = 0.93, SE = 0.22, $p =$
227 3.87×10^{-5} ; Table 2; Fig. 1), consistent with previous work that analyzed only the first two years
228 of this dataset (Brosi and Briggs 2013). Furthermore, we found that M1 was a significantly better
229 model when compared to the M0 ($\Delta\text{AIC} = -15.29$, LRT: $p = 3.2 \times 10^{-5}$), we therefore retained
230 state as well as the structural random effects (site and bee individual) in all subsequent models.

231

232 *Species-specific differences:* Adding bee species as a random intercept (M2) and as a random
233 slope term (M2b) to M1 significantly improved model fit over M1 (M2 vs. M1: $\Delta\text{AIC} = -28$,
234 LRT: $p = 4.8 \times 10^{-7}$; M2b vs. M1: $\Delta\text{AIC} = -26$, LRT: $p = 4.8 \times 10^{-7}$). Model M2b revealed only
235 slight interspecific variation in the *response* to the manipulation that was not already captured by
236 the main effect of state (variation in the random slope term for bee species = 0.10, see Table 2).

237 While M2b was a better model than M1, it did not improve model fit compared to M2 ($\Delta\text{AIC} =$
238 1.72, LRT: $p > 0.5$). In contrast, model M2 reveals substantial interspecific variation in the
239 *baseline* floral fidelity of bees (variation in the random intercept term for bee species = 0.24;
240 Table 2). Subsequent model comparisons were made with model M2. The fixed effect of state
241 remained highly significant (Coeff = 0.72, SE = 0.26, $p = 0.005$, see Table 2) in this model.

242

243 *Traits:*

244 *Baseline differences in species specific fidelity:* The addition of the trait level fixed effect in M3
245 largely explained the *baseline* variation in inter-specific floral fidelity (when compared to M2).
246 The baseline fidelity of bees with shorter tongues is lower than that of bees with longer tongues
247 (i.e. short tongue bees move between plant species more often) (Fig. 2, S2). The variance
248 estimate for the random intercept term for bee species dropped from 0.444 in M2 to 0.164 in M3
249 , giving $C_\alpha(\text{bee}) = 0.63$. Furthermore, M3 is a significantly better model than M2 ($\Delta\text{AIC} = 2$,
250 LRT: $p = 0.043$, Table 2), indicating the importance of tongue length as an explanatory factor for
251 floral fidelity. The bootstrapped distribution of estimates for the bee species random effect from
252 M3 substantially overlapped 0, while that for M2 was well above zero (Fig. S1). Further
253 supporting our interpretation of this term, a KS-test of the difference between these bootstrapped
254 distributions was highly significant ($p < 10^{-10}$).

255

256 *Site level attributes:* We found that adding the tongue length of the removed bee as a fixed effect,
257 (a site-level attribute), largely accounted for site-to-site variation in bees' floral fidelity (over and
258 above species-level differences) ($\Delta\text{AIC} = -8.7$; LRT: $p = 0.001$). That is, site level variation in
259 bumble bee floral fidelity is largely explained by the tongue length of the most abundant bee

260 species (i.e., the species removed experimentally): variance estimates for the site intercept
261 dropped from 0.918 in M3 to 0.178 in M4, giving $C_{\alpha}(\text{site}) = 0.80$, suggesting that there is little
262 variance left to explain after accounting for site level variation (Table 2). The three fixed effects,
263 state, tongue length and the tongue length of the removed bee species, are also statistically
264 significant in M4 (Coeff = 0.937, SE = 0.242, $p = 0.0001$, Coeff = 0.734, SE = 0.276, $p = 7.46 \times$
265 10^{-8} , Coeff = 0.301, SE = 0.081, $p = 0.0001$, respectively; Table 2, Fig. 2). Furthermore, the
266 bootstrapped distribution of estimates for the site level random effect from M4 substantially
267 overlapped 0, while that for M3 was well above zero (Fig. S1). Further supporting our
268 interpretation of this term, a KS-test of the difference between these bootstrapped distributions
269 was highly significant ($p < 10^{-10}$).

270

271 **Discussion.**

272 Our results demonstrate that bees vary in their floral fidelity and that tongue length explains a
273 large part of this variation. Bees with shorter tongues move between plant species (floral
274 infidelity) more often than bees with longer tongues. We did not find significant variation in the
275 response of bee species to a reduction in interspecific competition, but rather saw a guild-wide
276 reduction in floral fidelity in response to the removal of the dominant bee species (following
277 Brosi and Briggs 2013). Finally, our results suggest that tongue length of the most abundant bee
278 species, a site-level attribute, explains much of the site-to-site variation in pollinator foraging
279 behavior. In particular, we found that as the tongue length of the most abundant bee (i.e. the
280 species that was experimentally removed) increases, the site level foraging fidelity decreases
281 (Fig. 2).

282 We found that bumble bee species vary in the degree to which they move between different
283 plant species within a single foraging bout, and tongue length explains much this variation. Some
284 suggest that long tongued bees should exhibit broader resource usage patterns because their traits
285 permit them access to a wider range of flower types (Santamaría and Rodríguez-Gironés 2007) .
286 In contrast, short-tongued bees should act as specialists, with a more restricted range of resource
287 use options, rarely able to access the nectar at the base of the flowers with long corollas (Harder
288 1985, Graham and Jones 1996). Our results suggest the opposite pattern, that shorter tongue bees
289 are more labile with their foraging patterns and on average move between plant species within a
290 single foraging bout more often than longer tongue bees. We suggest the following
291 interpretation: because long tongues enable bees to access flowers with better rewards (e.g. long-
292 corolla flowers) and maintain a monopoly on those rewards, they may have less incentive than
293 short-tongued species to move between plant species while foraging. While longer tongue
294 bumble bees are capable of foraging on flowers with short corollas (Heinrich 1976, Plowright
295 and Plowright 1997) it would provide less energetic gain, making behavioral plasticity less
296 profitable (Inouye 1980). In contrast, the shorter-tongued bees in our system tend to have smaller
297 bodies and are more likely to depend on resources within a more restricted foraging range
298 (Westphal et al. 2006). These limitations could favor a labile foraging habit, with shorter tongue
299 bees constantly assessing the resource availability and competitive context in their community.
300 As such, shorter-tongued bees more readily switch between plant species.

301 We found an overall reduction in floral fidelity across sites after the removal of the most
302 abundant bee species. Our results build on the findings of Brosi and Briggs (2013), reaffirming a
303 guild-wide reduction in floral fidelity in response to a reduction in interspecific competition. This

304 study adds an additional two years, 8 sites and 165 bee individuals to our previous study,
305 confirming that the guild-wide results found in Brosi and Briggs (2013) are robust.

306 Variation in bumble bee floral fidelity is largely explained by the tongue length of the most
307 abundant (i.e. removed) bee species in each site. This means that pollinator foraging behavior is
308 context dependent and is determined (at least in part) by the most abundant bee species. In
309 general, short tongue bees exhibit lower floral fidelity than long tongued bees but when they are
310 in a site that has a long tongue bee removal, their reduction in floral fidelity is magnified.

311 Bumble bees are large bodied insects that require many floral resources to keep their colony
312 growing throughout the (often short) growing season. As such, we might expect strong
313 competition between these species, and tongue length, arguably one of the traits most relevant
314 for resource acquisition, could dictate how resources are partitioned within a community,
315 ultimately driving the assembly of bumble bees within communities (Heinrich 1976, Harmon-
316 Threath and Ackerly 2013). Pyke (1982) proposed that bumble-bee species with similar tongue
317 lengths could not exist in his altitudinal alpine transects presumably because the bees compete
318 for floral resources. But later studies did not support this pattern (Ranta 1982, Goulson et al.
319 2008), and, as in our study, found that bumble bee species with similar tongue lengths co-occurred
320 within a community. This has left researchers to wonder if the coexistence of many bee species
321 with substantial overlap in their life history requirements is possible because bumble bee species
322 compete for something other than flower resources (i.e. nesting sites) allowing so many similar
323 species to co-occur (Goulson et al. 2008). Our study suggests that in our system, bumble bees do
324 in fact compete for floral resources and that longer tongue bees seem to elicit competition that is
325 experienced across the range of trait values seen in our sites (see Table 1). The willingness of
326 short tongue bees to exhibit behavioral plasticity may allow for such a large number of

327 seemingly similar bee species to coexist in a community (Valdovinos et al. 2016). Future work
328 should examine the extent to which this plasticity is adaptive and assess the fitness costs (or
329 benefits) that may result from the willingness to switch floral resources in response to a
330 reduction in interspecific competition.

331 Most pollinators are generalist foragers that can switch between plant species within a single
332 foraging bout (Waser et al. 1996, Brosi and Briggs 2013). When pollinators move between plant
333 species, they can transfer heterospecific pollen to plant stigmas which in turn can reduce plant
334 reproduction (Morales and Traveset 2008, Mitchell et al. 2009, Ashman and Arceo-Gomez 2013,
335 Briggs et al. 2016). We found an effect in which competition from a long tongued bee changes
336 the foraging behavior of the rest of the bees in a way that could be detrimental to plant
337 reproduction. From a plant's perspective, not only do short tongue bees exhibit behavior that
338 likely results in the transfer of heterospecific pollen, but when short tongue bees are in
339 communities in which a longer tongue bee is most abundant, they exhibit even greater floral
340 infidelity, making the likelihood of heterospecific pollen deposition even greater (see Fig. 2).

341 Pollinator species are on the decline globally (Potts et al. 2010). Bumble bees in particular
342 are experiencing population range contractions due to climate change (Kerr et al. 2015) as well
343 reductions in abundance due to disease (Cameron et al. 2011), agricultural intensification and
344 pesticide use (Goulson et al. 2015). In a changing world where we are likely to experience an
345 emergence of new interactions, exploring how the competitive landscape shapes foraging
346 plasticity will help us generalize to other plant pollinator systems and begin to better predict the
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486 **Figure 1: Species specific response to pollinator removals. A.** Mean effect of experimental
487 state ('C' = control, 'M' = manipulation) on the probability that foraging moves are between
488 heterospecific plant species, plotted for each bee species. Bee species panels are arranged left to
489 right in increasing order of their tongue length. 95% CI around the mean heterospecific move
490 probability calculated on the basis of pooled counts for each state for each bee species.

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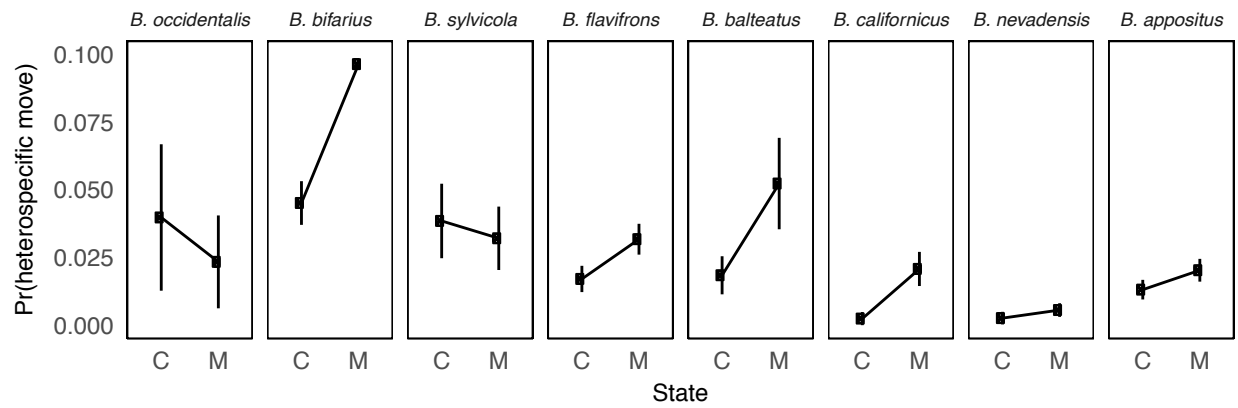
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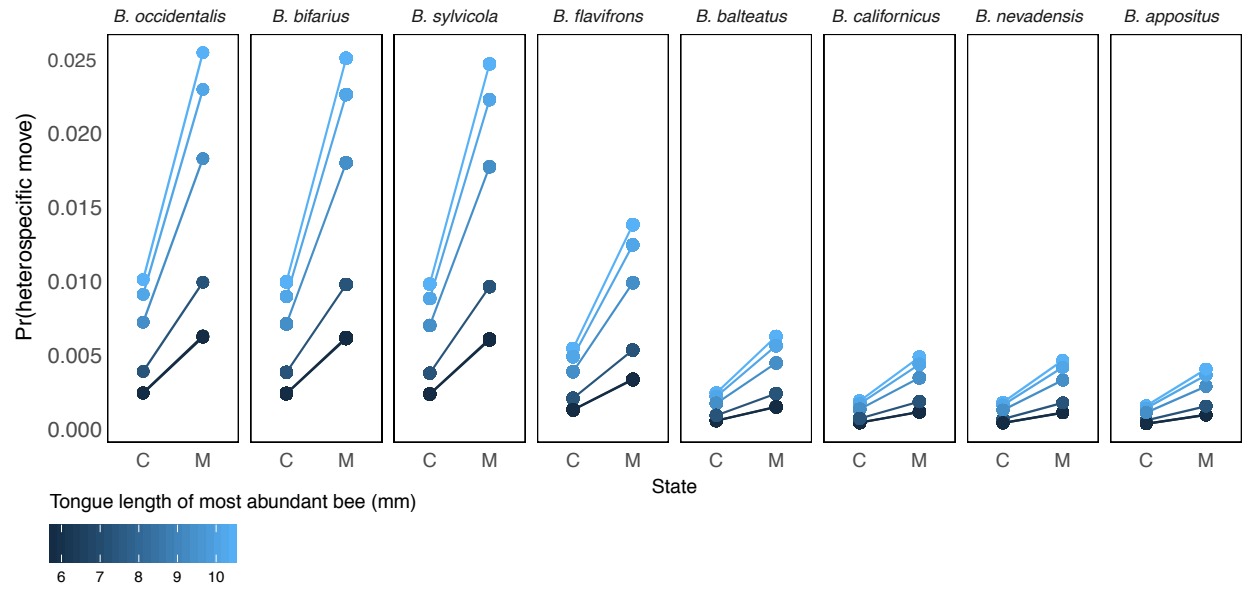


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Figure 2: Predicted impacts of the fixed effects from model M4 on the probability of heterospecific foraging moves. Contribution of random effects to the variance in heterospecific moves are not displayed in order to reveal the how the three fixed effects (see Table 2) shape foraging fieldity. Shown are the predicted mean foraging behavior of each bee species in each state ('C' = control, 'M' = manipulation) across a gradient of sites where the manipulated bee varies in tongue length ('tongue length of most abundant bee'). Bee species panels are arranged left to right as shortest to longest tongue length.



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597 **Tables.**

<i>Bombus</i> Species	mean mm	sd	N sites in which sp. was removed
<i>B. occidentalis</i>	5.71	0.25	0
<i>B. bifarius</i>	5.75	0.37	6
<i>B. sylvicola</i>	5.79	0.58	1
<i>B. flavifrons</i>	7.31	0.8	9
<i>B. balteatus</i>	9.36	0.62	4
<i>B. californicus</i>	10.01	0.75	0
<i>B. nevadensis</i>	10.13	0.68	2
<i>B. appositus</i>	10.48	0.95	5

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599 **Table 1:** Tongue lengths of sympatric *Bombus* spp. Mean and standard deviation of 50
600 individuals per species from Inouye (1976).

model	Fixed effects			Random effects			Model Comparison			
	state	TL	MTL	Species α/β	Site	Individual	AIC	R ² C	R ² M	LRT
MO	--	--	--	--	0.880	5.240	2079	0.093	0.000	--
M1	0.93***	--	--	--	0.930	5.000	2064	0.122	0.022	0:1, $p = 3.2 \times 10^{-5}$
M2	0.72**	--	--	0.444	1.159	3.900	2036	0.199	0.021	1:2, $p = 4.5 \times 10^{-8}$
M2b	0.726**	--	--	0.10/0.24	1.115	3.959	2038	0.199	0.022	2:2b, $p = 0.319$
M3	0.899***	-0.274**	--	0.160	0.920	4.170	2034	0.176	0.055	2:3, $p = 0.035$
M4	0.937***	-0.389***	0.301***	0.000	0.178	6.404	2025	0.127	0.112	3:4, $p = 0.003$

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603 **Table 2:** Results of generalized linear mixed-effects models with binomial errors *P < 0.05; **P
604 < 0.01; ***P < 0.001; TL = tongue length MTL = manipulated tongue length (i.e. tongue length
605 of the species removed from each site); R²C = describes the proportion of variance explained by
606 both the fixed and random factors; R²M describes the proportion of variance explained by the
607 fixed factors alone; LRT = likelihood ratio test.

608 **Supplemental Information.**

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612 **Figure S1: Parametric bootstrap estimates for variance terms.** To evaluate the significance
613 of the reductions in estimated random effects variances, we conducted parametric bootstrapping
614 of models M2, M3, and M4 (1000 replicates each) and compared the distribution of estimates for
615 σ^2 (M2) and σ^2 (M3) for the bee species random intercept ('bee.species'), as well as σ^2 (M3) and
616 σ^2 (M4) for the site-level random intercept ('site'). Plotted are the distribution of estimates for
617 each variance term in the models, with the individual level random effect ('unique.bee.ID')
618 added for comparison.

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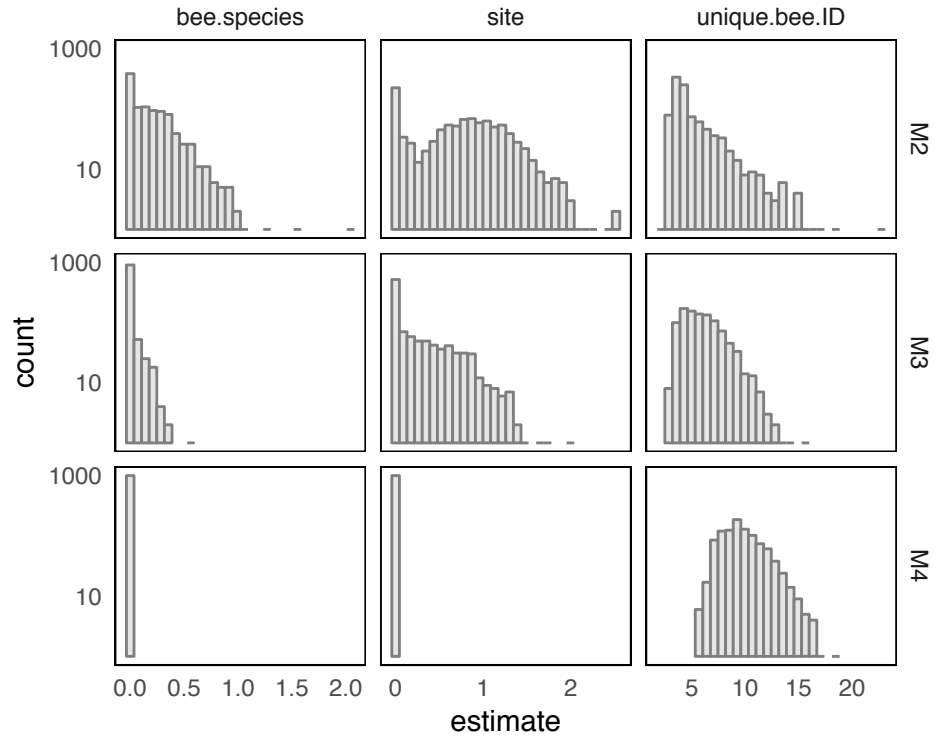
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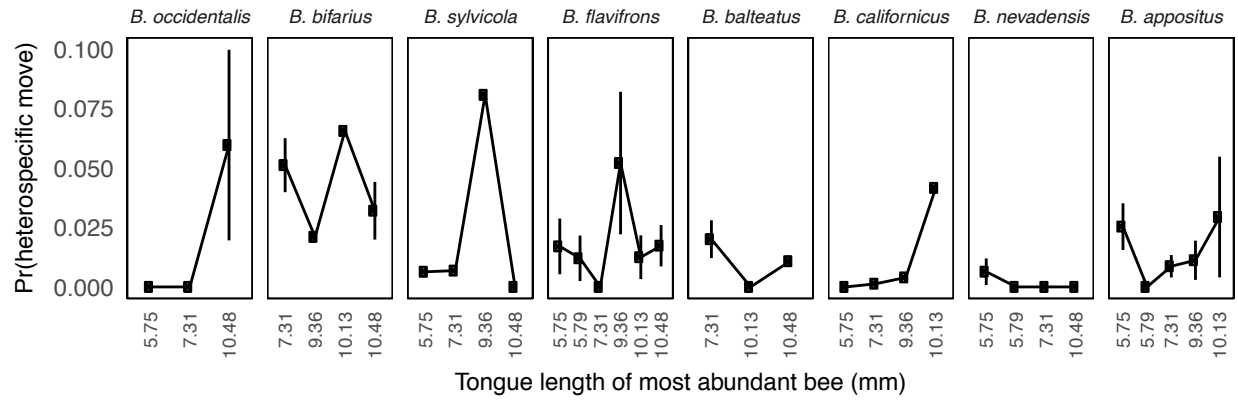
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666 **Figure S2: Trait based response to pollinator removals.** Heterospecific move probability for
667 each bee species as a function of trait-based competitive context (i.e. tongue length of the most
668 abundant bee species at that site). Plotted are data from the Control condition only to reveal
669 standing variation in foraging behavior in relation to site-level variation in the abundant bee
670 species. Plotted are means and 95% CIs calculated on the basis of pooled counts for each bee
671 species for a given context, as in Figure 1.
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