

Temporal resource availability

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Abstract

Patterns of bee abundance and diversity across different spatial scales have received thorough research consideration. However, the impact of short and long term temporal resource availability on biodiversity has been less explored. This is highly relevant in tropical agricultural systems for pollinators, as many foraging periods of pollinators extend beyond flowering of any single crop species. In this study, we sought to understand how bee communities in tropical agroecosystems changed between seasons, and if short and long term floral resource availability influenced their diversity and abundance. We used a threshold analysis approach in order to

explore this relationship at two time scales. This study took place in a region dominated by coffee agroecosystems in Southern Mexico. This was an ideal system because the landscape offers a range of coffee management regimes that maintain heterogeneity in floral resource availability spatially and temporally.

We found that the bee community varies significantly between seasons. There were higher abundances of native social, solitary and managed honeybees during the dry season when coffee flowers. Additionally, we found that floral resources from groundcover, but not trees, were associated with bee abundance. Further, the temporal scale of the availability of these resources is important, whereby short-term floral resource availability appears particularly important in maintaining high bee abundance at sites with lower seasonal complementarity. We argue that in addition to spatial resource heterogeneity, temporal resource heterogeneity is critical in explaining bee community patterns, and should thus be considered to promote pollinator conservation.

Key Words: temporal resource availability, seasonal complementarity, bee community, coffee, agroecosystem

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1 **Introduction**

2 Land-use change, which includes habitat modification, fragmentation, and degradation, is
3 a major contributor to changes in resource availability and thus bee population declines
4 (Winfree et al., 2011a; Potts et al., 2016). According to the Food and Agricultural Organization
5 (FAO), agriculture is one of the strongest drivers of land use change, with over 40% of earth's
6 terrestrial surface dominated by agriculture (Foley, 2006). The highest rates of agricultural
7 intensification have been found in the tropics (FAO), which subsequently decreases the spatial
8 and temporal availability of foraging resources for bees in tropical regions (Peters et al., 2013;
9 Peters et al., 2016). Still, agricultural landscapes are not inherently unsuitable for biodiversity
10 (Perfecto et al., 1996), and can in fact positively impact biodiversity (IPBES), particularly in the
11 tropics (Gonthier et al., 2014). Whether agricultural landscapes foster biodiversity, particularly
12 bee populations, appears highly dependent on the level of management (Jha & Vandermeer,
13 2010; Winfree et al., 2011b; Mandelik et al., 2012), as it influences resource availability across
14 spatial (Ferreira et al., 2015; Kennedy et al., 2013; Kremen et al., 2007; Williams et al., 2010)
15 and temporal scales (Mandelik et al., 2012; Leong et al., 2016; Cerdeira Morellato et al., 2016;
16 Geslin et al., 2016).

17 Coffee agricultural systems have become model systems to explore how agricultural
18 intensification influences biodiversity and ecological interactions (Perfecto, Vandermeer, &
19 Philpott, 2014); coffee is managed across a large gradient of intensification, from farms that
20 structurally resemble forests, with coffee grown underneath a diversity of shade trees, to sun
21 coffee farms, without any non-crop vegetation. The ability of a coffee agroecosystem to support
22 bee populations depends on its ability to maintain necessary foraging and nesting resource
23 requirements (Michener, 1969). In coffee farms in Indonesia, (Klein et al., 2003) found that
24 farms with greater resource heterogeneity supported a greater diversity of pollinators. While
25 resource availability across multiple spatial scales has been shown to influence bee abundance
26 and diversity in tropical landscapes (Tylianakis et al., 2008; Basu et al., 2016), the impact of
27 temporal resource heterogeneity (differences in availability of resources throughout time) on
28 biodiversity has been less explored (Mandelik et al., 2012; Leong et al., 2016; Cerdeira
29 Morellato et al., 2016; Geslin et al., 2016). Bees use resources from an array of plant species to
30 satisfy different nutrition requirements throughout their foraging season, which typically extends
31 beyond the flowering event of a single plant species (Baker, 1963; Olesen, 2008). Thus, sites that

32 have floral resources available throughout the year satisfy bee foraging requirements, whether by
33 a single flowering species that is always in flower or through multiple plants that flower at
34 different times (seasonal complementarity) (Bluthgen & Klein, 2011; Mandelik et al, 2013).
35 Understanding seasonal resource patterns is particularly important in the tropics because tropical
36 bees forage all year long (Roubik, 1989). Further, because the tropics maintain less seasonal
37 extremes than temperate zones, seasonal variation imposed by climate change may have more
38 dramatic effects on flowering phenologies (Ceirdera-Morellato, 2016; Buckley and Huey, 2016).

39 In this study we sought to understand how seasonal complementarity of non-crop floral
40 resources influences bee diversity and abundance in a coffee agroecosystem with two well-
41 defined seasons. Coffee farms offer a valuable opportunity to explore these patterns because they
42 are managed under a variety of shade tree regimes (Moguel & Toledo, 1999). This leads to a
43 natural gradient of temporal floral resource availability, from farms that provide no floral
44 resources outside of the coffee flowering, to farms where non-crop floral resources are staggered.
45 We addressed the following questions: 1) How does the community composition of bees change
46 across seasons in a tropical coffee agroecosystem? 2) Is pollinator diversity and abundance better
47 explained by available floral resources or seasonal complementarity in floral resources (i.e., short
48 versus long temporal scales)?

49 For question one, we predicted that the community composition of bees would change
50 between the two different seasons, as bee communities have been found to vary in composition
51 due to temporal drivers (Aranda & Graciolli, 2015; Rollin, et al, 2015; Samnegård et al., 2015) .
52 There are fewer floral resources from trees in the rainy season, so we expected native social bees
53 to be favored in the dry season, when there are more floral resources to sustain their nests. We
54 predicted native solitary bees to be favored in the rainy season, as they are generally smaller
55 bodied, which have been found to be favored in the rainy season in previous studies (Samnegård
56 et al., 2015). We did not expect the managed honeybee (*Apis mellifera scutellata*) to change
57 during the different seasons, as they are given supplemental resources consistently throughout
58 the year and are thus buffered from resource fluctuatons (E. Jiminez-Soto, *pers. comm*).

59 Building on previous spatial studies to address question two, where local and landscape
60 level patterns interact to explain bee abundance (Tschardt et al, 2005), we predicted that short
61 and long temporal scales would also interact to explain bee abundance and richness, as the longer
62 temporal scale controls the shorter scale. We predicted that more continuous levels of site-level

63 floral resources during the sampling event from trees would explain high bee abundance and
64 richness (Jha & Vandermeer). Similarly, we predicted that habitats with more continuous levels
65 of local-floral resources from trees throughout different seasons (seasonal complementarity)
66 would also generate high bee abundance and richness (Kovacs-Hostyanszki et al., 2013). More
67 specifically, we predicted that sites with more even resources across longer temporal scales
68 would limit the importance of floral resource availability at shorter scales. Further, we predicted
69 that the temporal interaction of floral resource availability would vary depending on the sociality
70 group (ie. native solitary, native social, or managed social), due to differences in foraging
71 strategies (Rollin et al., 2015).

72

73 **Methods**

74 *Study Area*

75 This study was conducted from June 2014 to April 2015 in the Soconusco region of
76 Chiapas (15°10'15"N; 92°20'33.192 W), a coffee growing region in Mexico. We selected sites
77 across three farms that ranged in management intensification (Moguel & Toledo, 1999; Philpott
78 et al., 2008). The rainy season takes place from May to November and the dry season takes
79 place from December to April. Twenty-five 20m × 20m sites were established based on the
80 estimated¹ temporal composition of floral availability provided by plant species within each site,
81 with 13 sites in a commercial polyculture farm and 12 sites distributed between two shaded
82 monoculture farms. All sites were at least 100 m apart. Sites were evenly distributed between the
83 commercial polyculture farm and between the two functionally similar shade monoculture farms.
84 However, we ultimately used only 22 sites due to significant tree removal at three sites half way
85 through the execution of this project.

86 Sites were selected according to a gradient of temporal floral resource availability from
87 shade trees, which have previously been found to be the most important resource strata for the
88 bee community at these farms (Jha & Vandermeer, 2010). Sites were selected if they conformed
89 to one of the following categories: 1) tree species with continuous floral resources available
90 throughout the year, or a combination of dry and rainy season flowering trees; 2) tree species

¹ Seasonal floral resource availability from trees was determined from previous personal observations at this field site, as well as from reported phenologies of specific species (missouribotanicalgarden.org).

91 with floral resources available only in the dry season; 3) floral resources available only in the
92 rainy season; and 4) trees without floral resources for animals (Table S1). The combination of
93 the four site types during one sampling event represented a gradient of short-term resource
94 availability. The four repeated sampling events across each site type produced a gradient of long-
95 term resource availability. All sites had coffee, which flowers in February during dry season
96 (Philpott et al., 2006) and flowering groundcover. Floral resources and bee abundance/richness
97 were measured twice at each site during the rainy season, June 2014 and July 2014 (n=35) and
98 twice during the dry season, January 2015 and February 2015 (n=44). For the July sampling
99 event, only sites in one farm were collected (n=13; Table S5) due to sampling limitations. We
100 performed vegetation and pollinator surveys simultaneously during each sampling event.

101 *Vegetation Survey*

102 Floral resources from trees, herbaceous groundcover (hereafter GC) and coffee were all
103 measured. The availability of floral resources from trees was estimated according to canopy
104 cover, proportion of trees in flowers, flowering tree abundance and flowering tree richness. The
105 availability of floral resources from GC was estimated according to richness of GC in flower
106 (based on morpho-species) and percentage of GC in flower. Canopy cover was measured at five
107 points throughout the site using a handheld spherical densitometer. The proportion of trees in
108 flower was calculated by counting the number of trees in flower over the total number of trees in
109 the site. GC was measured by randomly placing four 0.5×0.5 m quadrats within each site and
110 measuring the percent GC in each quadrat and the percentage of flowering herbs within each
111 quadrat. Percent GC in flower was calculated by taking the proportion of flowering herbs to the
112 total GC. When coffee was in flower (February), percentage of coffee in flower was determined
113 by selecting three coffee bushes and counting flowers and buds.

114 *Pollinator Survey*

115 To quantify pollinator abundance and diversity at each site during one sampling event,
116 pollinators were collected using pan traps and sweep nets. All bees collected during one
117 sampling event were combined into a single site-sampling event value. Thirty 148mL (Gordon's
118 Food Supply) plastic bowls (1/3 blue; 1/3 white; 1/3 yellow) were placed across each site in the
119 shape of an x through the center of each site (LeBuhn et al., 2003; Jha & Vandermeer, 2010).
120 Pan traps were set out before 9am and collected right before it began to rain in the rainy season
121 (around 1pm), and 2pm in the dry season. All insects caught in the pan traps were preserved in

122 alcohol in the field. Specimens were later separated and identified to species, or morpho-species,
123 in the lab with field guides (Michener et al, 1994), reference collections from El Colegio
124 Frontera Sur, and comparisons from previous studies (Jha & Vandermeer, 2010; Novelo et al.,
125 2007). We observed bee foraging at each site between the hours of 9am and 11am, optimum
126 foraging hours for bees in this region (Jha & Vandermeer, 2010). We performed observations for
127 10 minutes at each site on the same day pan traps were laid out. Bees found foraging on GC or
128 low trees were either identified on site, or collected for later identification. During coffee
129 flowering, coffee bushes were also observed for a period of 10 minutes.

130 *Statistical Methods*

131 We performed all the analyses considering representative month-pairs for each season:
132 June and July (rainy season), January and February (dry season). We analyzed the differences in
133 community composition between the month-pairs using a non-metric multidimensional scaling
134 analysis (NMDS). We then conducted an analysis of similarity (ANOSIM) using a Bray-Curtis
135 similarity index as the similarity measure in PAST (Hammer et al., 2001). The ANOSIM
136 compares the mean distance within a group to the mean distance between groups; this
137 statistically determines separation in species composition between the two different seasons
138 (Jimenez-Soto & Philpott, 2015).

139 To see what was explaining the differences in community composition between the
140 sampling events, we used generalized linear mixed models (GLMM) with Poisson error
141 distributions (Bolker, 2008) using the ‘glmer’ package lme4. We ran models with month
142 (sampling event) as a fixed effect, and site, as a factor of season, and farm as random effects to
143 account for any differences from site and farm level variation. We ran all models for the
144 following response variables: bee abundance, native social bee abundance, native solitary bee
145 abundance, and managed bee abundance. We then performed post-hoc analyses using the glht
146 function in the “mulcomp” package in R. This function performs pairwise comparisons of
147 categorical fixed effects. Finally, we used the “car” package to perform Wald Type III tests to
148 determine overall model significance.

149 To compare how short and long term temporal resource availability influence bee
150 abundance and richness, as well as to see if they interact, we created two metrics to quantify
151 floral resource availability at the two temporal scales, that we could statistically compare across
152 sites as well as between sampling events. The first metric combined individual floral resource

153 variables across the four sampling events to quantify long-term resource availability. This metric
154 was then divided into metric 1a, which represents long-term resource availability from trees
155 (abundance, richness, and % trees in flower), and metric 1b, which represents long-term resource
156 availability from GC (richness and % flowering GC). The second metric considered short-term
157 floral resources from trees at each sampling event [metric 2a] and short-term floral resources
158 from GC at each sampling event [metric 2b] (Table S2).

159 These metrics were determined using a threshold analysis approach, which have
160 previously been employed in other studies to integrate effects of multiple variables into a single
161 metric (Byrnes et al., 2014; Lefcheck et al., 2015). This approach assigns a value only to
162 variables that exceed a threshold percentage for resource level. The threshold represents a
163 percentage of the maximum value of the variable across sites sampled. We used this approach
164 because to account for variation in amount of resources available, rather than average resource
165 availability or variability in resources (CV) across time.

166 In order to combine multiple variables into one metric, each individual variable (ie. Tree
167 variables or GC variables) that is put into the metric is considered as a response variable.
168 Theoretically considering one variable across four sampling events, if the response variable
169 exceeds the selected threshold percentage, then that variable receives a value of 1 for that
170 sampling event and if it is below then it receives a value of 0, with a maximum value of 4 (the
171 variable exceeding the threshold percentage during four sampling events) and minimum value of
172 0 (the variable never exceeding the threshold percentage). To select the best threshold
173 percentage, all possible threshold percentages from 5-95% were run to generate values for the
174 relevant variable and compared with bee richness. The threshold percentage was selected based
175 on which percentage's value was best correlated with bee richness (Fig. S1; Fig. S2).

176 Each variable that was included in metric 1a or 1b was given a threshold value. Then
177 these individual values were summed for the temporal floral resources from trees [metric 1a]
178 metric or for temporal floral resources from GC [metric 1b]. Metric 1a had a final range from 0-
179 11, and Metric 1b had a final range from 0-6. The 0-11 range for metric 1a is produced from two
180 variables (tree abundance and tree richness) measured during four sampling events, and one
181 variable (percentage of trees in flower) measured during only three sampling events, due to
182 limited sampling in July. GC species richness and percentage of GC in flower were used to

183 calculate metric 1b and these variables were only quantified during three sampling events, June,
184 January and February.

185 To quantify short-term resources from trees, [metric 2a], the three variables that
186 characterize floral resources from trees were quantified together to select the best threshold
187 percentage (Fig. S1). Values were assigned to each site for every time period based on how many
188 of the three variables exceeded the threshold. All possible threshold percentages, from 5-95%,
189 were run to generate values for the metric, which were then compared to bee richness in order to
190 select the most predictive percentage (Fig. S2). The percentage used to calculate the metric was
191 selected based on which percentage's value was best correlated with bee richness, or had the
192 highest slope (Fig. S2). Metric 2a has a range from 0-3. This was then repeated for metric 2b
193 (short-term resources from GC), which included the two variables that quantified floral resources
194 from GC (Fig. S1). Metric 2b has a range from 0-2.

195 We tested all of the final metric values for collinearities by calculating correlation
196 coefficients using linear regressions (Table S3). To understand the effect of short and long-term
197 floral resource availability on the following response variables: bee abundance, bee richness,
198 native social bee abundance, native solitary bee abundance, and managed social bee abundance,
199 we used generalized linear mixed effect models (GLMM) using the 'glmer' package lme4. All
200 models were run with a Poisson error distribution and logit link function (Bolker et al., 2008).
201 We constructed five candidate models with the following fixed effects: 1) interaction between
202 short and long term resource availability from trees (ITR), interaction between short and long
203 term resource availability from GC (IGCR) + coffee +season; 2) ITR+coffee+season; 3)
204 IGCR+coffee+season; 4) ITR+IGCR+coffee; 5) ITR+IGCR+season. For each model, site, as a
205 factor of season, and farm were included as random effects to account for any differences from
206 site and farm level variation. We then used the package 'AICcmodavg' to conduct maximum
207 likelihood comparisons to select the best model according to Akaike's information criterion
208 (AIC). To determine term significance for the best-fit models, we compared nested models,
209 starting with the best-fit model as the global model, and performed likelihood ratio tests with the
210 package 'lmerTest.' To see if predictor variables correlated with response variables, we ran
211 Spearman rank correlations, to account for non-parametric data. Finally, we ran % canopy cover
212 as a predictor variable, as canopy cover has previously been found to impact bee community
213 composition.

214 Because some of our sites were only 100 m apart, the degree of spatial autocorrelation in
215 the residuals of the best-fit models was tested using Moran's I test for spatial autocorrelation
216 with the 'ape' package (Table S4). We did not find spatial autocorrelation at any of our sites
217 (Table S4) and thus considered our sites to be spatially independent. All statistical analyses were
218 performed with the software R-Studio v. 0.98.1103 for Macintosh and PAST v. 3.04.

219

220 **Results**

221 We identified 796 bees of 31 species in 3 families. Most bees collected were in the family
222 Apidae (62.9% of individuals collected) and Halictidae (37% of individuals collected). The most
223 abundant species was *Apis mellifera scutellata*, the Africanized honeybee, which are kept in
224 managed hives on the farm. The second most abundant species was *Ceratina ignara*, a solitary
225 Apidae species. Across sites and months, bee abundance ranged from 0 to 35 within a sampling
226 period, with an average of 8.9 bees per site. Bee richness ranged from 0 to 12, with an average of
227 3.8 species per site. A total of 312 bees were caught during the rainy season and 484 bees were
228 caught during the dry season. Flowering vegetation varied between sites and seasons. Flowering
229 tree richness ranged from 0 to 4 species in flower at a given sampling event at one site.
230 Flowering tree abundance ranged from 0 to 10 trees. The percentage of trees in flower ranged
231 from 0 to 63%. The percentage of GC in flower ranged from 0 to 35% and the richness of GC in
232 flower ranged from 0 to 7 species (Table S2).

233 *Changes in the bee community based on season*

234 Bee community composition differed between the two seasons, and differed between
235 each sampling event ($R=0.2406$). The NMDS comparing the four months showed an apparent
236 difference (Stress=0.4606; Fig. 4) visually. We confirmed this difference statistically with an
237 analysis of similarity (ANOSIM) and found significant differences in the bee community
238 between June and July, both in the rainy season ($p=0.0018$), between January and February, both
239 in the dry season ($p=0.0066$), and between the dry and rainy season (Table S6).

240 *Temporal changes in bee abundance and richness*

241 Bee abundance across all sites was significantly higher in February, when the coffee was
242 flowering, than any other sampling event ($X^2=43.4$; $Df=3$; $p<0.001$, Fig. 2). Coffee flowering
243 was positively correlated with bee abundance and bee richness, while canopy cover negatively
244 correlated with bee richness (Table 1). Short and long term temporal availability of floral

245 resources from GC interacted to influence bee abundance ($X^2=43.4$, $p<0.001$; Table S7) at
246 individual sites. At sites with low seasonal complementarity in floral resources from GC, high
247 short-term floral resources from GC was positively associated with bee abundance. However, at
248 sites with floral GC resources more consistently available between the two seasons, short-term
249 floral resources did not significantly correlate with bee abundance (Fig. 3). Thus, high short-term
250 floral resource availability from GC was important in explaining bee abundance at sites that did
251 not maintain consistent floral resources throughout the year. Floral resources from trees were not
252 included in the best model for bee abundance, but long-term tree floral resources were for bee
253 richness (Table 2). However, long-term floral resources from trees did not significantly correlate
254 with bee richness. High seasonal complementarity in floral resources from GC was positively
255 correlated with bee richness, but short-term floral resources from GC did not (Table 1).

256 *Temporal changes between sociality groups*

257 *Native Bee Abundance*

258 Abundance of native social bees remained constant between the four sampling events,
259 except for in January of the dry season, where it was significantly lower ($X^2=43.4$, $Df=3$,
260 $p<0.001$; Fig. 2). Native social bee abundance was positively correlated with coffee flowering
261 and negatively correlated with canopy cover (Table 1). Short and long-term temporal resource
262 availability from GC interacted to influence native social bee abundance ($X^2=12.9$; $p<0.001$;
263 Table S7). At sites with less seasonal complementary in floral resources from GC, high short-
264 term resource availability from GC positively impacted native bee abundance. At sites with more
265 consistent floral resources from GC between the two seasons, high, short-term resource
266 availability did not significantly impact native social bee abundance (Fig. 3). This suggests that
267 short-term floral resource pulses are important in explaining native bee abundance patterns at
268 sites that do not have consistent floral resources seasonally, similar to what was found for total
269 bee abundance.

270 *Solitary Bee Abundance*

271 Native solitary bee abundance remained constant throughout the four sampling events,
272 except during February, where it significantly increased ($X^2=79.8$, $Df=3$, $p<0.001$; Fig. 2).
273 Native solitary bee abundance was found to significantly correlate with coffee flowering (Table
274 1), which occurs in February. Long-term floral resources from trees were kept in the best model
275 predicting solitary bee abundance (Table 2), and were found to positively correlate with solitary

276 bee abundance (Table 1). Canopy cover was also negatively correlated with solitary bee
277 abundance (Table 1).

278 *Managed Honeybee Abundance*

279 The abundance of managed honeybees was significantly higher during the period in
280 which coffee was flowering ($X^2=84.2$, $Df=3$, $p<0.001$; Fig. 1). Short-term resources from trees
281 and coffee flowering were positively correlated with honeybee abundance (Table 1).

282 **Discussion**

283 Seasonal resource complementarity is important to support the bee community in which
284 complementarity in floral resources through time functions to satisfy foraging requirements of
285 bees throughout their foraging season. In coffee agroecosystems, coffee is grown under shade
286 trees and in the presence of flowering GC. These agroecosystems have the potential to support
287 bee resource requirements seasonally, depending on the intensity of their management. We found
288 more bees to be active during the dry season, which can be explained by the greater abundance
289 of flowering plants. Still, bees were found foraging in the rainy season, as well as in the dry
290 season outside of major flowering events. The bee community differed between the two seasons,
291 as well as between sampling events. The presence of bee foraging during the two seasons, as
292 well as differences in the bee community, exemplifies the importance of understanding seasonal
293 resource complementarity. We found that short-term and long-term temporal resource
294 availability from GC, but not from trees, interact to explain bee abundance. In fact, we only
295 found floral resources from trees to be important in explaining managed honeybee abundance,
296 but not native bee abundance or richness. This was surprising, as these resources have previously
297 been found to be critical for native bees (Cairns et al, 2005; Jha & Vandermeer, 2010).

298 Previous studies have considered the impact of seasonal complementarity on bee
299 abundance and richness from theoretical perspectives (Bluthgen & Klein, 2011), complementary
300 habitat use between seasons (Mandelik et al., 2012), effects of steady state floral resource
301 availability from a single non-crop plant (Peters et al., 2013) and seasonal shifts in bee
302 abundance and richness (Leong et al., 2016). These studies have been foundational in
303 understanding how seasonal flowering phenologies impact bee abundance and diversity, which
304 has been arguably understudied. However, no studies to date have explored how seasonal
305 flowering phenologies interact within the same site across different time scales.

306 *Changes in the bee community based on season*

307 We found that bee community composition differs between the two seasons, and the four
308 sampling events. Each sampling event had different combinations of floral resources available.
309 The floral resources available are determined by flowering phenologies of trees and coffee.
310 However, the availability of GC on the farm is more reflective of management decisions, than
311 intrinsic phenology. Under normal management, GC is completely removed several times per
312 year, which disrupts available floral resources for bees from this source. However, GC grows
313 back and flowers within a few weeks (K. Fisher, *personal observation*). We speculate that the
314 flowering species, and strata (trees, GC, etc), during a sampling event impact how and where
315 bees forage for resources. Previous empirical studies have reported how bee foraging behavior
316 shifts with seasonal variation in resource availability across tropical landscapes (Aleixo et al.,
317 2016; Aranda & Graciolli, 2015; Kaluza et al., 2016). Native bees foraging on high quality
318 resources have been found to be displaced in the presence of managed honeybees (Roubik &
319 Wolda, 2001). If there are other resources available concurrently with the displacement, they will
320 persist by foraging on the other resources, possibly of lower quality, which may explain why
321 managed honeybees responded to short-term resource availability from trees but not other bees.
322 Similarly, if one group is displaced by another on coffee, they can still be found foraging on
323 flowering trees or herbaceous GC. Since each sampling event has a different combination of
324 floral resource strata (ie. GC, trees, coffee), with varying abundances and richness, we see strong
325 differences in community composition of bees during the different seasons.

326 *Temporal changes in bee abundance and richness*

327 Bee abundance did not respond to floral resources from trees, which was unexpected as
328 previous studies have shown the importance of trees in predicting bee abundance and richness
329 (Jha & Vandermeer, 2010; Klein et al., 2003) in the tropics. The variation we found in floral
330 resources from trees across our sites was much smaller than the previous study in this system
331 (Jha & Vandermeer, 2010), which may have reduced its impact. Further, between the years of
332 these studies, one of the farms we sampled significantly reduced the number of shade trees (I.
333 Perfecto, *pers. communication*). Additionally, native bees may respond to a larger spatial scale
334 than we used for this study (Jha & Vandermeer, 2010). Floral resources from GC however, were
335 very important in explaining total bee abundance throughout the year. These resources interacted
336 between the two time scales, where short-term resource availability was more impactful at sites
337 with less consistent seasonal complementarity. Our results suggests that sites with higher

338 seasonal complementarity can sustain bee foraging requirements, even at times where short-term
339 resources are low. Previous studies have found that bees shift from agricultural habitats, when
340 there are fewer floral resources available from crops, to more consistent resources in semi-
341 natural habitats surrounding farms (Mandelik et al., 2012). Because we explored our question in
342 a coffee system that had sites with floral resources from multiple species and strata, we were able
343 to find patterns of complementarity within a single habitat rather than across habitats.

344 Bee richness responded to more consistent seasonal complementarity of floral resources
345 from GC, but not short-term availability. This may be because different bee species' dependence
346 on GC varies throughout the year depending on species and strata-specific floral resource
347 availability.

348 *Changes between among sociality groups between the sampling events*

349 Floral resource availability influenced bee groups differently as we expected, except for
350 their response to coffee flowering, which was always positively impacted. This is reasonable, as
351 coffee is a mass flowering, high quality resource that is abundant throughout the landscape when
352 it flowers. Bees employ different recruitment strategies in response to mass flowering crops
353 depending on sociality: managed honeybees forage with a concentration effect, whereas native
354 solitary and social bees exhibit a dilution effect in their foraging response to increases in floral
355 resources. Additionally, different groups have been shown to respond to resources at different
356 spatial scales; native social and solitary bees respond to resources at smaller spatial scales than
357 managed honeybees (Jha & Vandermeer, 2009). This may explain why they responded to
358 temporal availability in resources in different ways in our system.

359 The abundance of native social bees did not significantly change between sampling
360 events, except for significantly decreasing in January, which had the lowest number and richness
361 of trees in flower (Table S1). Previous studies have found this group to respond the strongest to
362 increases in floral resource availability from trees (Jha & Vandermeer, 2010), which may explain
363 why their abundances decreased during this sampling event. But neither short-term or long-term
364 temporal floral resources from trees were found to correlate with native bee abundance. Like
365 total bee abundance, native social bee abundance responded to an interaction between short-term
366 and long-term temporal resource availability from GC.

367 Both foraging and nesting resources from trees have been found to be important for
368 native social bees (Jha & Vandermeer, 2010). Abundance may have been lower in January

369 because they avoided floral resources occupied by other species (Johnson & Hubbel, 1974;
370 Nagamitsu & Inoue, 1997) by shifting resource use (Roubik, 1978; Roubik et al, 1986; Cairns et
371 al, 2005). Native social bees have been found to respond negatively to greater distance to forest (
372 Klein et al, 2003; Ricketts, 2004; Brosi & Briggs, 2013). In a previous study at the farms we
373 sampled in, distance to forest did not impact bee abundance. This was explained by the diversity
374 of within farm resources being sufficient in sustaining resource requirements (Jha &
375 Vandermeer, 2010). But since the significant shade tree removal in 2012, the forest fragments
376 adjacent to the farms may now be relatively more valuable than they were during the previous
377 study. The native social bees may have shifted to forest fragments during this time, which would
378 explain their relatively low numbers on the farm.

379 Native solitary bees did not change in their abundance during the four sampling events,
380 except increasing in February. Native solitary bees strongly correlated with presence of coffee
381 and seasonal complementarity in floral resources from GC. This is similar to other studies which
382 have found solitary bees to respond to flowering GC (Klein et al., 2003b; Mandelik et al., 2012)
383 and species richness of flowering herbs (Jha & Vandermeer, 2010). High percentages of canopy
384 cover has also been found to be important for these bees because it provides access to nesting
385 sites (Jha & Vandermeer, 2010), however, canopy cover actually negatively correlated with bee
386 abundance. This may be because high percentages of canopy cover decrease availability of
387 herbaceous GC (Jha & Vandermeer, 2010). While most solitary bees forage on coffee flowers
388 (Klein et al., 2003b), they will switch to GC resources when social bees are foraging (Willmer &
389 Stone, 1989; Klein et al. 2002). This may explain why they have high abundances during the
390 coffee flowering event, despite increases in other bee groups.

391 Managed honeybees were found in the highest proportions during the dry season when
392 coffee was flowering (February). This is contrary to what we expected, as we predicted that their
393 proportion would remain the same as they were given supplemental resources at the apiaries
394 during our sampling events. Social bees have been found to positively correlate with blossom
395 cover of coffee (Klein et al., 2003). The Africanized honeybee exhibits a concentration effect in
396 response to mass flowering, where they increase visitation with increases in floral resource
397 abundance (Jha & Vandermeer, 2009; Veddeler et al., 2006). Managed honeybees only
398 correlated with coffee flowering (February) and short-term resources from trees. Coffee flowers
399 are high quality and abundant resources for bees when they are available. As the managed

400 honeybees have been found to be the best competitor in obtaining high quality floral resources
401 (Roubik, 1978; Roubik et al., 1986; Cairns et al., 2005) it is reasonable that they would
402 significantly respond to coffee flowering. Still, floral resources from trees may also offer higher
403 quality resources outside the coffee flowering event. As Africanized honeybees have been found
404 to be better competitors, they may be displacing the other social groups from foraging on trees.

405

406 *Conclusion*

407 Floral resource availability, which is determined by management decisions in agricultural
408 landscapes, is a key driver of species abundance and richness (Tylianakis et al, 2008). It has been
409 shown that changes in land use can lead to resource mediated pollinator declines (Holzschuh et
410 al, 2008; Kennedy et al., 2013). Previous studies have found that resource heterogeneity at the
411 local and landscape spatial scale interact to explain diversity, where diversity is positively
412 impacted by improvements in local resource availability in more simplified landscapes
413 (Tscharrntke et al, 2005). We used this idea as a model to explore how bees respond to different
414 temporal scales. Similar to bee patterns across spatial scales, we found that short-term temporal
415 resource availability was more important for bee abundance at sites that had less consistent long-
416 term resource availability, a novel finding to our knowledge. In addition to spatial resource
417 heterogeneity, temporal resource heterogeneity is also critical in explaining patterns of bee
418 abundance and richness.

419 The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
420 recently evaluated knowledge of pollinators and pollination (2016) and concluded that
421 agricultural systems have the potential to support pollinators. In conjunction with this report,
422 (Dicks et al, 2016) suggested the following policy objectives: policies should be implemented
423 that support agroecological (ecological intensification) farming practices, which support
424 ecological functions like pollination and pest control. As part of these complementary objectives,
425 we suggest that seasonal, or temporal, availability of resources should be considered to
426 understand patterns of bee abundance and diversity and to implement successful conservation
427 strategies. Specifically, farms can support pollinators by maintaining complementarity in floral
428 resources available from both crop and non-crop plants as part of diversification of their farms.
429 Future studies should further investigate the physiological and ecological mechanisms driving
430 these patterns. Particularly, they should consider how specific bee groups shift resource use

431 depending on the what plant species is in flower and relative availability, physiological
432 requirements at different life history stages (nesting, nutritive, immune, etc.) and competition
433 with other insects.

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457 **Literature Cited**

458 Aleixo, K. P. A., Enezes, C. M., Lúcia, V., Onseca, I. M. F., Inês, C., & Ilva, S. (2016). Seasonal
459 availability of floral resources and ambient temperature shape stingless bee foraging
460 behavior (*Scaptotrigona aff . depilis*). *Apidologie*. [http://doi.org/10.1007/s13592-016-](http://doi.org/10.1007/s13592-016-0456-4)
461 0456-4

- 462 Aranda, R., & Gracioli, G. (2015). Spatial–temporal distribution of the Hymenoptera in the
463 Brazilian Savanna and the effects of habitat heterogeneity on these patterns. *Journal of*
464 *Insect Conservation*, 19(6), 1173–1187. <http://doi.org/10.1007/s10841-015-9832-z>
- 465 Basu, P., Parui, A. K., Chatterjee, S., Dutta, A., Chakraborty, P., Roberts, S., & Smith, B. (2016).
466 Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural
467 landscapes. *Ecology and Evolution*, 6(19), 6983–6992. <http://doi.org/10.1002/ece3.2360>
- 468 Bluthgen, N., & Klein, A. M. (2011). Functional complementarity and specialisation: The role of
469 biodiversity in plant-pollinator interactions. *Basic and Applied Ecology*, 12(4), 282–291.
470 <http://doi.org/10.1016/j.baae.2010.11.001>
- 471 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., &
472 White, J. S. (2008). Generalized linear mixed models : a practical guide for ecology and
473 evolution. *Trends in Ecology and Evolution*, 24(3), 127–135.
474 <http://doi.org/10.1016/j.tree.2008.10.008>
- 475 Brosi, B. J., & Briggs, H. M. (2013). Single pollinator species losses reduce floral fidelity and
476 plant reproductive function. *Proceedings of the National Academy of Sciences of the United*
477 *States of America*, 110(32), 13044–8. <http://doi.org/10.1073/pnas.1307438110>
- 478 Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., ... Emmett
479 Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem
480 multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, 5(2), 111–
481 124. <http://doi.org/10.1111/2041-210X.12143>
- 482 Cairns, C. E., Villanueva-Gutiérrez, R., Koptur, S., & Bray, D. B. (2005). Bee populations, forest
483 disturbance, and Africanization in Mexico. *Biotropica*, 37(4), 686–692.
484 <http://doi.org/10.1111/j.1744-7429.2005.00087.x>
- 485 FAO (2015): Food and Agriculture Organization of the United Nations Global Forest Resources
486 Assessment 2015
- 487 Ferreira, P. A., Boscolo, D., Carvalheiro, L. G., Biesmeijer, J. C., Rocha, P. L. B., & Viana, B. F.
488 (2015). Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic
489 Rainforest. *Landscape Ecology*, 30(10), 2067–2078. [http://doi.org/10.1007/s10980-015-](http://doi.org/10.1007/s10980-015-0231-3)
490 0231-3
- 491 Gonthier, D. J., Ennis, K. K., Farinas, S., Hsieh, H., Iverson, A. L., Batáry, P., ... Perfecto, I.
492 (2014). Biodiversity conservation in agriculture requires a multi-scale approach

493 Biodiversity conservation in agriculture requires a multi-scale approach. *Proceedings of the*
494 *Royal Society B*, 281.

495 IPBES (2016): Summary for policymakers of the assessment report of the Intergovernmental
496 Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination
497 and food production. S.G. Potts et al. Secretariat of the Intergovernmental Science-Policy
498 Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

499 Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software
500 package for education and data analysis. Retrieved from [http://palaeo-](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)
501 [electronica.org/2001_1/past/issue1_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)

502 Jha, S., & Vandermeer, J. H. (2009). Contrasting foraging patterns for Africanized honeybees,
503 native bees and native wasps in a tropical agroforestry landscape. *Journal of Tropical*
504 *Ecology*, 25, 13. <http://doi.org/10.1017/S026646740800566X>

505 Jha, S., & Vandermeer, J. H. (2010). Impacts of coffee agroforestry management on tropical bee
506 communities. *Biological Conservation*, 143(6), 1423–1431.
507 <http://doi.org/10.1016/j.biocon.2010.03.017>

508 Jimenez-Soto, E., & Philpott, S. M. (2015). Size matters: Nest colonization patterns for twig-
509 nesting ants. *Ecology and Evolution*, 5(16), 3288–3298. <http://doi.org/10.1002/ece3.1555>

510 Kaluza, B. F., Wallace, H., Heard, T. A., Klein, A., & Leonhardt, S. D. (2016). Urban gardens
511 promote bee foraging over natural habitats and plantations. *Ecology and Evolution*, 1–13.
512 <http://doi.org/10.1002/ece3.1941>

513 Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., ...
514 Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild
515 bee pollinators in agroecosystems. *Ecology Letters*, 16(5), 584–599.
516 <http://doi.org/10.1111/ele.12082>

517 Klein, A.-M., Steffan-Dewenter, I., & Tschardtke, T. (2003). Bee Pollination and Fruit Set of
518 *Coffea Arabica* and *C. Canephora* (Rubiaceae). *American Journal of Botany*, 90(1), 153–
519 157.

520 Klein, A., Steffan-Dewenter, I., & Tschardtke, T. (2003). Pollination of *Coffea canephora* in
521 relation to local and regional agroforestry management. *Journal of Applied Ecology*, 40,
522 837–845.

523 Kovacs-Hostyanszki, A., Haenke, S., Batary, P., Jauker, B., Baldi, A., Tschardtke, T., &

524 Holzschuh, A. (2013). Contrasting effects of mass-flowering crops on bee pollination of
525 hedge plants at different spatial and temporal scales. *Ecological Applications*, 23(8), 1938–
526 1946. <http://doi.org/10.1890/12-2012.1>

527 Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., ...
528 Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile
529 organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*,
530 10(4), 299–314. <http://doi.org/10.1111/j.1461-0248.2007.01018.x>

531 LeBuhn, G., Griswold, T., Minckley, R., Droege, S., Roulston, T., Cane, J., ... Messenger, O.
532 (2003). *A standardized method for monitoring Bee Populations – The Bee Inventory (BI)*
533 *Plot*.

534 Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., ... Duffy,
535 J. E. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and
536 habitats. *Nature Communications*, 6, 6936. <http://doi.org/10.1038/ncomms7936>

537 Mandelik, Y., Winfree, R., Neeson, T., & Kremen, C. (2012). Complementary habitat use by
538 wild bees in agro-natural landscapes. *Ecological Applications*, 22(5), 1535–1546.
539 <http://doi.org/10.1890/11-1299.1>

540 Michener, C. D., McGinley, R. J., & Danforth, B. N. (1994). *The Bee Genera of North and*
541 *Central America (Hymenoptera: Apoidea)*.

542 Moguel, P., & Toledo, V. M. (1999). Biodiversity Conservation in Traditional Coffee Systems of
543 Mexico. *Conservation Biology*, 13(1), 11–21.

544 Perfecto, I., Rice, R. A., Greenberg, R., & Voort, M. E. Van Der. (1996). Shade Coffee : A
545 Disappea Refuge for Biodiversity. *BioScience*, 46(8), 598–608.

546 Perfecto, I., Vandermeer, J., & Philpott, S. M. (2014). Complex Ecological Interactions in the
547 Coffee Agroecosystem. *Annual Review of Ecology, Evolution, and Systematics*, 45, 37–58.
548 <http://doi.org/10.1146/annurev-ecolsys-120213-091923>

549 Philpott, S. M., Arendt, W. J., Armbrrecht, I., Bichier, P., Diestch, T. V., Gordon, C., ... Zolotoff,
550 J. M. (2008). Biodiversity loss in Latin American coffee landscapes: Review of the
551 evidence on ants, birds, and trees. *Conservation Biology*, 22(5), 1093–1105.
552 <http://doi.org/10.1111/j.1523-1739.2008.01029.x>

553 Philpott, S. M., Uno, S., & Maldonado, J. (2006). The importance of ants and high-shade
554 management to coffee pollination and fruit weight in Chiapas, Mexico. *Biodiversity and*

555 *Conservation*, 15(1), 487–501. <http://doi.org/10.1007/s10531-005-0602-1>

556 Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D.,
557 ... Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being.
558 *Nature*, 540(7632), 220–229. <http://doi.org/10.1038/nature20588>

559 Ricketts, T. H. (2004). Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee
560 Crops. *Conservation Biology*, 18(5), 1262–1271.

561 Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L., & Henry, M. (2015). Habitat, spatial and
562 temporal drivers of diversity patterns in a wild bee assemblage. *Biodiversity and*
563 *Conservation*, 24(5), 1195–1214. <http://doi.org/10.1007/s10531-014-0852-x>

564 Roubik, D. W. (1978). Competitive Interactions between neotropical pollinators and africanized
565 honey bees. *Science*, 201(4360), 1010–1032.

566 Roubik, D. W., Moreno, J. E., Vergara, C., & Wittman, D. (1986). Sporadic Food Competition
567 with African Honey Bee: Projected Impact on Neotropical Social Bees. *Journal of Tropical*
568 *Ecology*, 2(2), 97–111.

569 Roubik, D. W., & Wolda, H. (2001). Do competing honey bees matter? Dynamics and
570 abundance of native bees before and after honey bee invasion. *Population Ecology*, 43(1),
571 53–62. <http://doi.org/10.1007/PL00012016>

572 Samnegård, U., Hambäck, P. A., Eardley, C., Nemomissa, S., & Hylander, K. (2015). Turnover
573 in bee species composition and functional trait distributions between seasons in a tropical
574 agricultural landscape. “*Agriculture, Ecosystems and Environment*,” 211, 185–194.
575 <http://doi.org/10.1016/j.agee.2015.06.010>

576 Tylianakis, J. M., Rand, T. A., Kahmen, A., Klein, A. M., Buchmann, N., Perner, J., &
577 Tscharrntke, T. (2008). Resource heterogeneity moderates the biodiversity-function
578 relationship in real world ecosystems. *PLoS Biology*, 6(5), 0947–0956.
579 <http://doi.org/10.1371/journal.pbio.0060122>

580 Veddeler, D., Klein, A. M., & Tscharrntke, T. (2006). Contrasting responses of bee communities
581 to coffee flowering at different spatial scales. *Oikos*, 112(3), 594–601.
582 <http://doi.org/10.1111/j.0030-1299.2006.14111.x>

583 Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G.
584 (2010). Ecological and life-history traits predict bee species responses to environmental
585 disturbances. *Biological Conservation*, 143(10), 2280–2291.

586 <http://doi.org/10.1016/j.biocon.2010.03.024>
 587 Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011a). Native pollinators in anthropogenic
 588 habitats. *Annual Review of Ecology, Evolution, and Systematics*, 42, 1–22.
 589 <http://doi.org/10.1146/annurev-ecolsys-102710-145042>
 590 Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011b). Native Pollinators in Anthropogenic
 591 Habitats. *Annual Review of Ecology, Evolution, and Systematics*, 42(1), 1–22.
 592 <http://doi.org/10.1146/annurev-ecolsys-102710-145042>

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 595 Supporting Information

596 Additional supporting information may be found in the online version of this article at
 597 <http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/supinfo>

598
 599 Data Availability

600 Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4s51m>

601
 602 **Tables**

603 Table 1: Results of spearman rank correlations; significant predictor variables are italicized.

	Df		S	Rho	p-value
Bee Abundance					
	<i>1</i>	<i>Coffee flowering</i>	<i>42292.71</i>	<i>0.48</i>	<i><0.001</i>
	1	Canopy Cover	98788,46	-2.02	0.07
Bee Richness	1	Trees Total	72769.87	0.1142	0.3159
	<i>1</i>	<i>GC Total</i>	<i>51830.34</i>	<i>0.369</i>	<i><0.001</i>
	<i>1</i>	<i>Coffee flowering</i>	<i>48243.82</i>	<i>0.4128</i>	<i><0.001</i>
	<i>1</i>	<i>Canopy Cover</i>	<i>104805.2</i>	<i>-0.275</i>	<i>0.013</i>
Native Social Bee	<i>1</i>	<i>Coffee</i>	<i>86541.15</i>	<i>0.23</i>	<i>0.02</i>

Abundance		<i>flowering</i>			
	<i>1</i>	<i>Canopy Cover</i>	<i>103412.6</i>	<i>-0.258</i>	<i>0.02</i>
Native Solitary Bee Abundance	<i>1</i>	<i>Trees Total</i>	<i>66040</i>	<i>0.196</i>	<i>0.08</i>
	<i>1</i>	<i>GC Total</i>	<i>46736</i>	<i>0.43115</i>	<i><0.001</i>
	<i>1</i>	<i>Coffee</i>	<i>58816.85</i>	<i>0.284</i>	<i>0.01</i>
	<i>1</i>	<i>Canopy Cover</i>	<i>103410.4</i>	<i>-0.258</i>	<i>0.02</i>
Managed Bee Abundance	<i>1</i>	<i>Present Trees</i>	<i>53627</i>	<i>0.32</i>	<i><0.001</i>
	<i>1</i>	<i>Canopy Cover</i>	<i>70395</i>	<i>0.1098</i>	<i>0.3386</i>
	<i>1</i>	<i>GC Present</i>	<i>71046</i>	<i>0.101</i>	<i>0.3762</i>
	<i>1</i>	<i>Coffee</i>	<i>28496</i>	<i>0.63</i>	<i><0.001</i>

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Table 2: Statistical results of generalized linear mixed effect models (GLMMs) analyzing the effect of short term and long term temporal resource availability from trees and their interaction, short term and long term temporal resource availability from GC and their interaction, presence of coffee flowering and season on bee abundance, richness and abundance of bee sociality groups.

Response Variable	Best Model	SGC	LGC	IGCR	ST	LT	ITR	CF	Season
Bee Abundance	SGC*LGC+CF +Season	<0.01	<0.001	<0.01	NA	NA	NA	<0.001	<0.001

Bee Richness	LT+LGC+CF	NA	<0.001	NA	NA	0.47	NA	<0.001	<0.001
Native Social Bee Abundance	SGC*LGC+CF	<0.001	<0.01	<0.001	NA	NA	NA	<0.001	<0.001
Native Solitary Bee Abundance	LT+LGC +CF	NA	<0.001	NA	NA	0.08	NA	<0.001	<0.001
Managed Bee Abundance	SGC+ST+CF	0.29	NA	NA	0.72	NA	NA	0.059	<0.001

616 Significance Levels: p<0.1; *p<0.05; **p<0.01; ***p<0.001

617 NA indicates that variable was not included in the best model

618 Numbers show p-values for predictor variables as determined by likelihood ratio tests.

619 (SGC: Short term GC availability; LGC: Long term GC availability; IGCR: Groundcover resource interaction; ST:

620 Short term tree resource availability; LT: Long term tree resource availability; ITR: tree resource interaction; CF:

621 coffee flowering).

622 Figure Legends

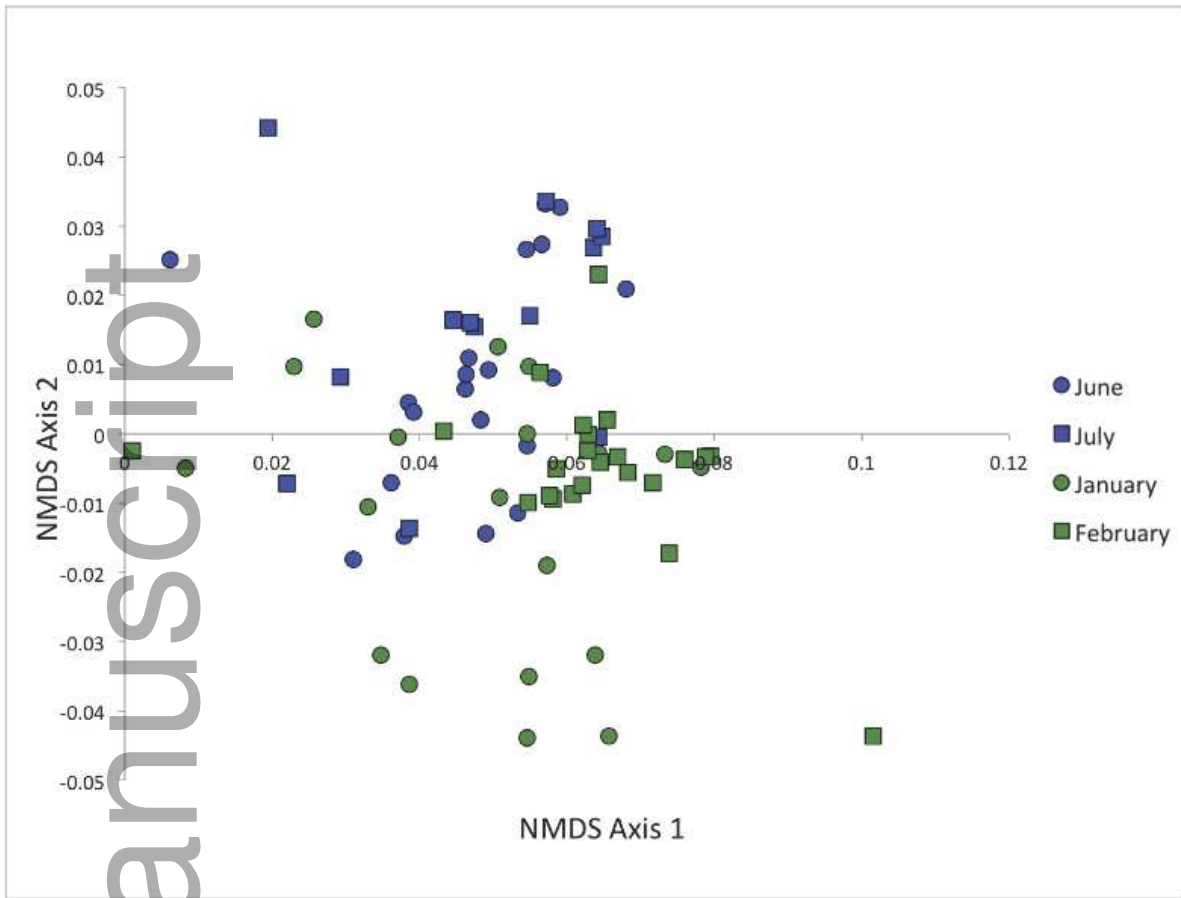
623 Figure 1: Results of Non Metric Multi-dimensional scaling analysis performed of community
624 composition of bees between each sampling event. There is an apparent difference in the bee
625 community between each sampling event (Stress=0.4606). Blue squares and diamonds represent
626 the months sampled during the rainy season; green squares and diamonds represent the months
627 sampled during the dry season.

628
629 Figure 2: Bar graphs showing average a) bee abundance, b) native social bee abundance, c)
630 native solitary bee abundance and d) managed bee abundance across all sites for each sampling
631 event. A) There are significantly more bees in February than the three other sampling months (;
632 B) There are significantly fewer native social bees in January than the other sampling events; C)
633 There are significantly more native solitary bees in February than the three other sampling
634 months; D) There are significantly more managed bees in February than the other three sampling
635 months.

636

637 Figure 3: The effect of the interaction between floral resources from GC on total bee abundance
638 (top) and native social bee abundance (bottom). The x-axis represents short-term resource
639 availability from GC. When there is lower complementarity in long-term resource availability
640 from GC, short-term resource availability from GC is more important in explaining bee
641 abundance.

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Figure 2

