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► **To cite this version:**

Benoît Geslin, Melissa Oddie, Morgane Folschweiller, Gaëlle Legras, Colleen L. Seymour, et al.. Spatiotemporal changes in flying insect abundance and their functional diversity as a function of distance to natural habitats in a mass flowering crop. *Agriculture, Ecosystems & Environment*, 2016, 229, pp.21-29. 10.1016/j.agee.2016.05.010 . hal-01327223

HAL Id: hal-01327223

<https://hal.sorbonne-universite.fr/hal-01327223v1>

Submitted on 6 Jun 2016

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1 ORIGINAL PAPER

2 **Spatiotemporal changes in flying insect abundance and their functional diversity as a**
3 **function of distance to natural habitats in a mass flowering crop**

4

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26

27 **Abstract**

28 To meet the dietary requirements of a burgeoning human population, the demand for animal-
29 dependent crops continues to grow. To meet the demand, intensive farming practices are used.
30 The gains in food production associated with agricultural intensification may be offset by its
31 detrimental effects on pollinator populations through natural habitat fragmentation and
32 pesticide use. Abundance and species richness of pollinators have been found to decrease with
33 increasing distance to natural habitat in agroecosystems, reducing crop yields. A key aspect of
34 crop pollination lies in the diversity of functional traits (functional diversity, FD) of flower-
35 visitor communities within crop fields. Higher FD allows improved pollination success
36 through complementarity between flower-visitors' morphology, phenology and behaviour.
37 Many studies reported negative effects of increasing distance to natural habitats on the
38 abundance and richness of flower-visitor communities, but the link between FD and natural
39 habitat isolation is less well understood. Also, a more complete understanding of the
40 functional traits of flower-visitor communities within crops should consider potential
41 variations through time. Differences in resources availability between seasons are important
42 in tropical areas and could modify ecological responses of flower-visitor communities to
43 isolation. In this study, we surveyed the Hymenoptera and Diptera communities within mango
44 orchards of South Africa using pan traps at 100m, 200m and at the maximal distance possible
45 from any natural habitat. We measured the response of insect abundance, wing span and body
46 size as well as functional diversity to habitat isolation during mango flowering (dry season),
47 and during the wet season (after mango fruit harvest). Flying insect abundance decreased with
48 increasing distance to natural habitat during mango flowering, but no effect was detected
49 during the wet season. FD of flying insects declined with increasing distance to natural habitat
50 in both sampling periods. Insects captured during mango flowering were smaller but had

51 higher wing length/body length ratios than those caught during the wet season. This study
52 highlights that mango orchards are more inhospitable for flying insects during mango
53 flowering. This effect might be due to low palatability of mango flowers, or pesticide use in
54 mango fields. In order to maintain a high FD of flower-visiting species, and reduce the
55 detrimental effects of habitat isolation to ultimately ensure better crop pollination, we propose
56 establishment of patches of resource-rich habitats combined with judicious use of pesticides
57 within orchards.

58

59 **Keywords**

60 Body size, Flower-visitors, Functional diversity, Isolation from natural habitat, Mangoes,
61 Morphological traits, Wing span

62

63 **1. Introduction**

64 To ensure nutritional security to a burgeoning human population, the demand for animal-
65 pollinated crops is continually increasing (Eilers et al. 2011; Ehrlich and Harte, 2015). To
66 meet this demand, agricultural production has intensified in recent decades through
67 conversion of large areas to monocultures, with concomitant loss of natural and semi-natural
68 areas, and increasing use of agrochemicals (Tscharntke et al. 2005; Kennedy et al. 2013).
69 However, given the reported negative effects of agricultural intensification on pollinator
70 populations (Kremen et al. 2002; Vanbergen et al. 2013), the benefits of intensification for
71 animal-pollinated crop yield might be negated by ensuing pollinator loss (Garibaldi et al.
72 2011a; Leonhart et al. 2013; Deguines et al. 2014). By pollinating crops, insects provide a
73 critical ecosystem service estimated to be worth more than €153 billion worldwide (Klein et
74 al. 2003; Gallai et al. 2008; Winfree 2008). The decline of pollinators owing to agricultural
75 intensification therefore raises concerns for food security (Aizen et al. 2008; Garibaldi et al.
76 2011a) and highlights the need for sustainable agriculture that ensures agricultural production
77 whilst conserving biodiversity (Garibaldi et al. 2015, 2016).

78 In agricultural landscapes, natural areas provide habitat for wild insects and constitute sources
79 of flower-visitors for crops (Kennedy et al. 2013; Morandin and Kremen, 2013). Many
80 flower-visitors, such as bees, are central place foragers and usually visit plants close to their
81 nests (Cresswell et al. 2000). As distant resources are more energetically costly to visit than
82 proximate resources, it is predicted that flowers isolated from natural areas will be less
83 frequently visited (Schmid-Hempel et al. 1985, 1986; Steffan-Dewenter and Tscharntke
84 1999). In croplands, species richness of flower-visitors, visitation rates, and pollination
85 services all tend to decline with distance to natural areas (e.g. Ricketts et al. 2008; Carvalheiro
86 et al. 2010; Garibaldi et al. 2011b). Whether or not flower-visitors disperse from natural
87 habitats into the adjacent crop depends on many factors such as floral resource abundance,

88 floral reward level or type of management (e.g., Kennedy et al. 2013). In this respect,
89 pollinator functional traits can be key. Most studies on the effect of distance to natural patches
90 of vegetation have not considered flower-visitor traits or their functional diversity (e.g.
91 Ricketts et al. 2008; Farwig et al. 2009; Carvalheiro et al. 2010, 2012; Garibaldi et al. 2011b;
92 but see Jauker et al. 2009; Williams et al. 2010; Benjamin et al. 2014). Yet traits such as
93 flower-visitor body size are likely to affect pollination success as these traits can influence
94 insect behaviour, foraging distances and pollen deposition (Hoehn et al. 2008). For example,
95 foraging distance is primarily dictated by pollinator body size, and small flower-visitors will
96 forage closer to their nests (Araújo et al. 2004; Greenleaf et al. 2007; Benjamin et al. 2014).
97 Moreover, several studies have shown that functional diversity (FD) of flower-visitor
98 communities enhances pollination by providing complementary pollination services, for
99 example through niche partitioning of resource use in time and space (Fontaine et al. 2006;
100 Hoehn et al. 2008; Albrecht et al. 2012; Fründ et al. 2013). Studying the effects of isolation
101 from natural areas on traits and FD of flower-visitors can thus shed light on the factors which
102 affect both crop pollination and the persistence of diverse flower-visitor communities in agro-
103 ecosystems, informing effective land management strategies (Williams et al. 2010; Benjamin
104 et al. 2014).

105 Temporal dynamics of agricultural landscapes are also important. Cultivated areas exhibit
106 particularly large temporal variations in floral resources which could affect flower-visitor
107 communities (Westphal et al. 2003). Mass flowering crops such as mangoes (*Mangifera*
108 *indica* L., Anacardiaceae) constitute a super-abundant floral resource during a short period of
109 time, representing a resource pulse for flower-visitors (Orford et al. 2015). The relationship
110 between increasing distance to natural habitat and flower-visitor communities has been mostly
111 explored during crop mass flowering (e.g. Holzschuh et al. 2011) but negative effects of
112 distance on flower-visitors are likely to be stronger when the crop is not flowering, because

113 only flowering weeds then provide resources in cultivated fields. Seasonal variation of wild
114 floral resources and flower-visitor communities also contribute to temporal variation of
115 agroecosystems. Spatiotemporal turnover in flower-visitor assemblages varies between and
116 within years in temperate and tropical ecosystems (Oertli et al. 2005; Rollin et al. 2015;
117 Samnegård et al. 2015), with temporal changes in abundance or even functional traits of
118 flower-visitors varying because of food and nesting requirements (Tylianakis et al. 2005;
119 Rollin et al. 2015). Flower-visitor assemblages might respond differently to agricultural
120 perturbations in different seasons (Samnegård et al. 2015). For example, in tropical
121 environments, resources are more scarce and patchily-distributed during the dry season
122 relative to the wet season. Greater mobility may therefore be advantageous to crop flower-
123 visitors during the dry season (see Samnegård et al. 2015).

124 To explore those questions, we studied the response of potential flower-visitors (hereafter
125 referred to as “flying insects”) to increasing distance from natural vegetation in mango
126 orchards in north-eastern South-Africa in two different seasons. Mango is one of the most
127 important tropical fruits produced in the world, and is economically important for income and
128 employment-creation in the region (FAO, 2010). Research conducted in our study area in the
129 past has found clear effects of distance on pollination (Carvalho et al. 2010, 2012), pest
130 control (Henri et al. 2015) and bird assemblages (Ehlers Smith et al. 2015).

131 We used pan-traps to survey flying insects during mango flowering in the dry season (winter),
132 and during the wet season (summer, when mango is not flowering), along transects of
133 increasing distance to natural habitat. We hypothesised that the number of flying insects
134 caught in traps would decrease with distance to natural vegetation. If isolation from natural
135 areas is the only cause of the decrease in flying insect abundance, the effect should be
136 consistent between seasons. We also measured wing span and body length of each flying
137 insect and investigated distance effects on flower-visitor functional-trait diversity. We

138 hypothesised a decline of the FD with increasing distance from natural areas in both seasons,
139 since species loss caused by isolation is likely to result in loss of trait diversity. Finally, given
140 links between size and flight abilities, we predicted that average insect body size would be
141 larger with increasing distance to natural area.

142 **2. Materials and Methods**

143 **2.1 Study site**

144 Our study site was situated in the Kruger to Canyons Biosphere Region, Limpopo Province,
145 South Africa. This region includes agricultural areas and also two large protected areas
146 (Kruger National Park and Blyde River Canyon reserve; 24° 24'S 30°50'E). The entire area
147 retains more than 50% of intact vegetation unaffected by anthropogenic perturbations
148 (Coetzer et al. 2013).

149 Other than tourism, agriculture is an important source of employment in the area. Although in
150 some areas, there are small subsistence farms, in our study area, the farms are composed of
151 sets of large blocks of monoculture stands of mango, citrus or avocado. Mango farms
152 consisted of multiple plots of 0.66 to 3 ha (mean \pm sd= 1.39 \pm 0.87) separated by windbreaks
153 of tall *Casuarina sp.* trees. All the study farms provided similar water and nutrient supply and
154 made intensive use of herbicides (e.g., glyphosphates) and insecticides (neonicotinoids or
155 organophosphates). The sets of blocks of mango plantation are bordered by patches of natural
156 vegetation that vary in size, but are usually at least 250 m wide. These patches of natural
157 vegetation have not been ploughed, and differ from natural vegetation in neighbouring Kruger
158 National Park in that livestock have replaced wild herbivores. The vegetation in the area is
159 Granite Lowveld (Mucina and Rutherford, 2006), a savannah in which the woody component
160 is dominated by *Acacia (Senegalia) nigrescens* and *Sclerocarya birrea*, with a herbaceous
161 layer that includes *Digitaria eriantha*, *Panicum maximum* and *Aristida congesta*.

162 The primary flower-visitors to mango in this area include Diptera (mostly Calliphoridae and
163 Empididae families), and Hymenoptera (*Apis mellifera*, *Ceratina* spp. bees and species of
164 *Camponotus*, *Monomorium* and *Tetramorium* ants; Carvalheiro et al. 2010, 2012). Mango is
165 self-compatible, but only to a small extent: a bagging experiment found that there was 21%
166 fruit set for inflorescences from which pollinators had been excluded (100% of fruit set in

167 open inflorescences see Carvalheiro et al. 2010). Mango flowers do produce nectar, but only a
168 small amount of pollen (Eardley et al. 2007).

169 The first surveys were performed during mango flowering (July-August 2013, dry season
170 hereafter), with maximum temperatures averaging around 26°C and minima of 9°C. The lack
171 of rain during this time means that few flowering species are in bloom for flower-visiting
172 insects. We selected five mango farms separated from each other by between three to thirteen
173 kilometres. Within each farm, we established two transects perpendicular to the edge between
174 mango and natural vegetation. Along each transect, we sampled insects at 5 sampling points,
175 at 50m from the edge with mango in the natural vegetation, at the field edge (0m) and at 100,
176 200m and the maximal distance possible from any natural habitat within mango orchards.
177 Distance to natural vegetation was measured as the distance from each set of traps within the
178 blocks of mango to the border of the nearest patch of natural vegetation. During April-May
179 2014, we re-sampled insects in two transects in each of the three most accessible farms. April-
180 May coincides with the end of the wet season, when maximum and minimum temperatures
181 average 29°C and 12°C, respectively, and floral resources are fairly abundant, having
182 flourished during the rains.

183 At each sampling point, three coloured pan traps (radius=7.25 cm, depth=5 cm) painted with
184 UV-reflecting paints (yellow, blue and white) were placed and filled with 400 ml of water and
185 a drop of detergent (surfactant). Although pan trap sampling is known to under-sample some
186 insect groups like large bees (*Bombus*, *Colletes*), this method is nevertheless considered the
187 most efficient method to sample flying flower-visitors (Roulston et al. 2007; Westphal et al.
188 2008, Nielsen et al. 2011). It allows sampling of a large number of points simultaneously and
189 uniformly, obtaining standardized estimates of flower visitor abundance and diversity.

190

191 **2.2 Data collection**

192 In dry and wet seasons, we performed three sampling sessions in each transect (one every two
193 weeks) where traps were set out in the field for 24 hours before being collected (N = 720 pan
194 traps). Traps were set on warm sunny days (minimum of 15°C, no wind and clear sky). Once
195 collected, insects were stored in 70% ethanol before being rinsed, identified at the order level
196 and measured. We focused on potential pollinators including Hymenoptera, Lepidoptera and
197 Diptera, which are groups that are considered as mango pollinators (Sung et al. 2006).
198 Morphometric measures of insects were also taken, *i.e.* wing length (distance between the
199 wing tips) and body length using digital callipers (Digit-Cal MK IV 599-571, Brown and
200 Sharpe, USA, 0.01 mm).
201 Finally, we assessed the number of mango flowers and wild flowers in a perimeter of 15
202 meters around each sampling point. Within mango orchards, the herbaceous cover was
203 dominated by non-native weeds (e.g. *Tridax procumbens* (L.) and *Bidens pilosa* (L.), both
204 Asteraceae). Since mangoes exhibit “big bang” flowering with a massive number of flowers
205 per tree, we estimated the number of mango flowers by counting the number of flowers on
206 three different panicles and multiplying the average by the number of panicles for each tree (a
207 mature tree has 600-1000 panicles; Manning, 1995; Sung et al. 2006).

208

209 ***2.3 Functional Diversity***

210 Our dataset was comprised of individual insects, and not species, so we calculated functional
211 diversity of the individuals found in our samples. We used order, body length, wing span and
212 the ratio of body length to wing length as traits. Order was represented as a binary variable of
213 one or zero for each of three categories (Diptera, Hymenoptera or Lepidoptera), and therefore
214 order was represented by three “traits”. We therefore down-weighted order to one third the
215 value of the other traits to avoid biasing the analysis.

216 We calculated the FDis (Functional Dispersion, Laliberté and Legendre 2010) measure of
217 functional diversity, using the FD package in R (Laliberté et al. 2010). In this case, FDis is the
218 mean distance of individuals to the centroid calculated for all individuals in multidimensional
219 trait space. FDis is not affected by species richness (in our case, abundance), and is able to
220 handle missing values and qualitative as well as quantitative traits (Laliberté and Legendre
221 2010).

222

223 ***2.4 Data analysis***

224 We assessed how functional diversity and the value of each of the traits used to calculate
225 functional diversity (i.e. body length, wing length, and ratio of wing length over body length)
226 changed with season and habitat. Although functional diversity is a measure of the variation
227 in these traits, changes in the average values of traits yields insights into how the traits
228 themselves are affected by habitat and season. These two analyses therefore produce
229 complementary information.

230 We assessed the effects of sampling season (dry or wet season), habitat (natural vegetation or
231 mango fields) and distance to natural habitat, as well as the interactions between season and
232 distance or habitat effects, on flower abundance, abundance and traits of flying insects and on
233 flying insect functional diversity. To do so, for each response variable, we performed a model
234 averaging approach which allows comparison of all possible submodels from a global model
235 containing all the predictors of interest, in order to identify the best set of models describing
236 the observed variation (Grueber et al. 2011). With this approach, it is possible to account for
237 model uncertainty and to assess the relative importance of various predictor variables.

238 To analyse patterns in flower abundance, traits of flying insects and functional diversity FDis,
239 we used linear mixed-effect models on log-transformed response variables (except for FDis)
240 using distance to natural vegetation, sampling season, type of habitat, interactions between

241 distance and sampling season, and interactions between type of habitat and sampling season
242 as fixed variables. Farm, transect nested within farm and date of sampling were included as
243 random effects to avoid pseudo-replication (Crawley, 2007). Additionally, in models with
244 insect traits as a response variable, we included insect order as a random effect to account for
245 differences in trait values between orders.

246 To assess variations in abundance of flying insects, we carried out generalized linear mixed-
247 effect models (GLMER) with a Poisson distribution and a log-link using the same fixed and
248 random variables with the addition of flower abundance as a fixed variable. We included
249 flower abundance as an explanatory variable because pan-traps are known to be less attractive
250 to flower-visitors in resource-rich sites relative to resource-poor sites (Wilson et al. 2008).

251 The GLMERs were corrected for overdispersion by including observation-level random
252 factors (Harrison 2014).

253 For each response variable, we selected the set of models according to the Akaike information
254 criterion (AIC). More precisely, we kept the models that were within the range of four highest
255 AIC units and we used these "top models" to estimate the mean effects and confidence
256 intervals of each predictor variable using model averaging (natural average method, Grueber
257 et al. 2011). We also measured the relative importance of each predictor variable which is
258 expressed as the relative sum of the Akaike weights across all top models in which the
259 variable appears (relative importance is equal to 1 for variables present in all top models).

260 Additionally, we calculated the marginal R^2 values (fixed effects) and conditional R^2 values
261 (R^2 both fixed and random effects) to assess the amount of variance explained by the best
262 model (i.e. with highest AIC; Johnson 2014). All analyses were performed using the R
263 statistical interface (v 3.1.0, R Development Core Team, 2014); mixed models were
264 conducted using the package lme4 (Bates et al. 2014) and model comparison and averaging
265 were performed with the functions dredge, get.models and model.avg (package MuMIn;

266 Barton 2016). Model predictor variables were also centered and standardized with the
267 function `standardize` (package `arm`; Gelman and Su, 2015) to facilitate comparison between
268 the relative strengths of parameter estimates (Grueber et al. 2011). R^2 values were calculated
269 with the function `r.squared` GLMM (package `MuMIn`; Barton 2016).

270

271 **3. Results**

272 ***3.1. Abundance of flowers***

273 Distance to natural vegetation, as well as habitat type, sampling season and their interactions
274 (habitat×season and distance×season), were included in all top models describing the response
275 of flower abundance (Table 1). As expected, the abundance of flowers was greater in mango
276 fields in the dry than in the wet season, whereas we observed more flowers in the nearby
277 natural vegetation during the wet season (see parameter estimate and confidence interval of
278 the interaction between sampling season and habitat type in Table 1, Figure 1A). Flower
279 abundance was far higher in the mango fields than in the natural vegetation during the dry
280 season (Figure 1A), given that we did not observe any flowers in the neighbouring natural
281 vegetation in any of the sampling sessions in the five farms over the dry season. The
282 abundance of flowers also increased with increasing distance from natural vegetation (Figure
283 1A). The interaction between distance and season had only 35% relative importance to other
284 predictor variables and the confidence interval for this parameter estimate included 0. Thus
285 there was little evidence that the effect of distance from natural vegetation on flower
286 abundance differed between seasons.

287

288 ***3.2 Abundance of flying insects***

289 Distance to natural vegetation, sampling season, and the interaction between these two
290 variables, were included in all top models describing the response of abundance of flying

291 insects (Table 1). The abundance of flying insects was far higher during the wet season than
292 the dry season, which was expected since we captured 798 insects in the five farms during the
293 dry season but captured 1719 insects in only three of these farms during the wet season.
294 Abundance of flying insects declined with increasing distance from natural vegetation, but
295 only during the dry season (Table 1, Figure 1B). The difference in abundance of flying insects
296 between the two sampling periods was also more pronounced in mango fields (see parameter
297 estimate and confidence interval of the interaction between sampling season and habitat type
298 in Table 1), but there was weaker evidence for this effect (55% relative importance). Lastly,
299 there was very little evidence of an effect of flower abundance on the abundance of flying
300 insects (39% relative importance to distance and season, and the confidence interval for this
301 parameter estimate included 0).

302

303 ***3.3 Functional diversity***

304 Distance to natural vegetation and sampling season were included in all top models describing
305 the response of functional diversity (Table 1). Functional diversity of flying insects was
306 higher in the wet season than during the dry season and FD declined with increasing distance
307 from natural vegetation in both seasons (Figure 1C). Functional diversity was also higher in
308 nearby natural vegetation than in mango fields (79% relative importance to distance and
309 season, Table 1). The interaction between distance and season had only 23% relative
310 importance and the confidence interval for this parameter estimate included 0. Thus, there was
311 little evidence that the negative effect of distance from natural vegetation on functional
312 diversity differed between seasons.

313

314 ***3.4 Insect traits***

315 Only sampling season was included in all top models describing the responses of body length,
316 wing span and ratio of wing span to body length of flying insects (Table 2). Both body length
317 and wing span of flying insects were on average smaller during the dry than during the wet
318 season, whereas the ratio of wing span to body length was larger during the dry season
319 (Figure 2). Body length and wing span of flying insects also differed between habitat types,
320 insects being on average larger in natural vegetation than in mango fields (Figure 2, Table 2).
321 Although body length and wing span of flying insects tended to decrease with increasing
322 distance to natural vegetation during the dry season (Figure 2), this effect was not significant
323 (the confidence interval for the corresponding estimate included 0). There was very little
324 evidence of any effect of habitat type and distance to natural vegetation on the ratio of wing
325 span to body length of flying insects (Table 2). In addition, the marginal R^2 of the models
326 were very low (about 0.02, see Table 2), indicating that on average variance in insect traits
327 explained by effects of distance, habitat type and sampling season was only 2% whereas
328 random factors (which represented insect order, as well as sample position and date)
329 explained between 40 and 50% of the variation.

330

331

332 **4. Discussion**

333 This study highlights that mango orchards are more inhospitable for flying insects during the
334 dry (mango flowering) than during the wet season, despite the abundance of mango flowers
335 available in the orchards. We found declines in insect abundance with increasing distance to
336 natural areas during the dry season whereas no pattern was found during the wet season. The
337 functional diversity (FD) of flying insects declined with increasing distance to natural habitat
338 in both sampling periods, however, and insects were on average smaller in mango orchards
339 than in natural vegetation. Taken together, our results suggest impacts on crop yield, given
340 that as a rule, rate of flower visitation (Vázquez et al. 2005, Garibaldi et al. 2013) and
341 functional diversity (Fontaine et al. 2006, Hoehn et al. 2008, Albrecht et al. 2012, Fründ et al.
342 2013) increase crop fruit set. Creating patches of habitat rich in native floral resources that
343 flower before and during mango flowering within orchards could mitigate the detrimental
344 effects of isolation from natural habitats and increase mango production (Carvalho et al.
345 2012).

346

347 **4.1 Seasonal variation in flying insect abundance**

348 Agricultural landscapes show strong temporal variation in the floral resource offer. Mass
349 flowering crops, during their flowering season, are expected to exert a strong magnet effect on
350 pollinators from adjacent areas (Blitzer et al. 2012). We did not find this effect, however, and
351 this was somewhat surprising, given that there are few other floral resources in the landscape
352 at this time. It is possible that this pulse of floral resources is too short-lived to enable
353 invertebrate populations to respond to this sudden availability in floral resources. This finding
354 highlights the importance of considering seasonal variation in the value of agricultural patches
355 for pollinators.

356 The decline in insect abundance with increasing distance to natural vegetation that we
357 observed during the dry season is a pattern that has been observed in numerous studies in
358 agricultural systems (e.g. Ricketts et al. 2008; Garibaldi et al. 2011b). This pattern appears
359 stronger in tropical than temperate regions (Ricketts et al. 2008) and has been particularly
360 well documented by Carvalheiro et al. (2010) in our study system. This latter study notably
361 showed that even in a biodiversity rich area, with a high proportion of intact natural habitat,
362 the abundance of flying insects was impacted by isolation from natural habitats, which in turn
363 impacted crop fruit set. Because several flying insects such as bees are central place foragers
364 (*i.e.* individuals that return to their nests after foraging (for nectar and/or pollen; Williams and
365 Kremen, 2007), this decline in insect abundance with increasing distance to natural area is
366 commonly attributed to the distance from nesting sites and foraging resources available in
367 natural habitats (e.g. Ricketts et al. 2008; Farwig et al. 2009; Williams et al. 2010; Garibaldi
368 et al. 2011b; Samnegård et al. 2015).

369 But intriguingly, in complete contrast to the dry season when mango is flowering, we did not
370 observe any effect of distance to natural area on insect abundance during the wet season.
371 These contrasting results might be explained by the seasonal dynamics of wild floral
372 resources and pollinator communities. Flying insects were more abundant and had higher
373 functional diversity during the wet than dry season, which is expected since the wet season
374 coincides with spring/summer, when more floral resources are available and temperatures are
375 higher. The link between plant richness and abundance and flower-visitor richness and
376 abundance has been well documented in the scientific literature for croplands (e.g., Holzschuh
377 et al., 2007; Kennedy et al., 2013). The higher diversity of native flowering plant during the
378 wet season, and the increasing availability of weed flowers with increasing distance from
379 natural vegetation within mango orchards might explain the absence of a relationship between
380 isolation from natural habitat and insect abundance. It is also worth noting that mango flowers

381 yield only small amounts of pollen, although they do offer some nectar (Eardley et al. 2007),
382 and so are not very attractive to many insects (Free and Willams 1976). Thus, the lack of
383 attractiveness of mango mass flowering might explain the strong negative effect of isolation
384 from natural habitat we observed during the dry season. This idea is supported by an earlier
385 study in which small planted patches of native flowering plants within mango orchards were
386 associated with an increased abundance of flower-visitors to mango flowers, which mitigated
387 to some extent the effects of isolation (Carvalho et al. 2012).

388 In addition to the limitations in floral resources, alternative explanations exist that might
389 explain seasonal variation in distance effects on flying insects in the crop. Pesticides are used
390 in mango fields, even during mango flowering. Many studies have reported on the negative
391 effect of pesticides on flower-visitors (Henry et al. 2012; Goulson et al. 2015; Stanley et al.
392 2015), and Carvalho et al. (2012) also previously highlighted the detrimental effect of
393 pesticide use on flying insect along gradients of increasing distance to natural area in our
394 study system. Varying pesticide applications might thus also explain the different effects of
395 distance to natural area on insect abundance between the two sampling seasons.

396 Pan-traps are widely considered to provide accurate surveys of bee assemblages (Roulston et
397 al. 2007, Westphal et al. 2008, Geslin et al. 2016), but are also prone to some bias. Pan-traps
398 under-sample large insects and their attractiveness can vary with the amount of flowers
399 locally present (Wilson et al. 2008, Popic et al. 2013). The relative attractiveness of pan-traps
400 decreases as floral resources increase because pan traps compete with flowers for flying insect
401 attention. However, it is unlikely that our results are an artefact of pan-trapping. We included
402 floral abundance as an explanatory variable in our statistical models, and this variable did not
403 have a significant effect on insect abundance. Secondly, in both seasons, more flowers were
404 observed in mango orchards compared to natural habitats and the decline in insect abundance

405 with increasing distance to natural habitat was observed uniquely during the dry season, with
406 the same capture method.

407

408 **4.2 Functional diversity**

409 Although flying insect abundance decreased with increasing distance from natural habitat
410 during the dry season only, declines in functional diversity with increasing isolation were
411 consistent in the two sampling seasons. A recent study highlighted that farmed landscapes
412 were detrimental to the maintenance of functional-trait diversity of flying insects (Forrest et
413 al. 2015), and our findings support this view.

414 FD is increasingly recognized as being more important than species diversity to ecosystem
415 functioning (Gagic et al. 2015) and has been suggested to be the major component of diversity
416 (Tilman et al. 1997; Hulot et al. 2000; Hoehn et al. 2008). The main reason for the importance
417 of FD lies in the complementarity of pollination services through niche partitioning of
418 resource use in time and space (Fontaine et al. 2006; Hoehn et al. 2008; Albrecht et al. 2012;
419 Fründ et al. 2013). The value of greater FD to pollination services has been demonstrated both
420 experimentally (Fontaine et al. 2006) and empirically (Hoehn et al. 2008), and a recent
421 example in apple orchards highlighted that fruit and seed set was mainly mediated by bee FD
422 (Martins et al. 2015, but see Garibaldi et al. 2015).

423 The loss of FD with increasing isolation can reduce the efficiency of pollination (Forrest et al.
424 2015; Wood et al. 2015) reducing yield for trees at the centre of mango orchards. Carvalheiro
425 et al. (2010, 2012), demonstrated that agricultural production and proximity to natural habitat
426 are positively correlated in the mango orchards we studied. Yet, easily implementable
427 management practices might ameliorate, to some extent, the negative effects of isolation.
428 Creating patches of flowering rich habitat has been shown to increase crop yield in mango
429 orchards (Carvalheiro et al. 2012). FD of flying insects has been shown to improve with only

430 modest enhancements of floral diversity (Orford et al. 2016). Given that isolation from natural
431 habitat together with loss of flower-visitor abundance and diversity are now well established
432 as critical drivers of limitation in crop yield (Garibaldi et al. 2016), we encourage the
433 establishment of those simple management practices to enhance food production.

434

435 **4.3 Traits of flying insects**

436 In contrast to functional diversity, there was weak evidence of distance effects on average
437 insect trait values, and the traits were only weakly affected by habitat type. Although a large
438 part of the variance in insect traits was related to size differences between orders, sampling
439 season had also a significant effect on flying insect average body length and wing span.
440 During the dry season in tropical environments, resources are scarcer and more patchily-
441 distributed compared to the wet season (Samnegård et al. 2015). Because the foraging range
442 of flying insects is positively correlated with their body size (Araújo et al. 2004; Greenleaf et
443 al. 2007), we initially hypothesized that we would trap larger flying insect during the dry
444 season. However, our results show that insects were smaller during the dry season. This
445 finding is more consistent with the findings of Wray et al. (2014), who found large-bodied
446 species to be favoured by increasing availability of floral resources (although this was in a
447 landscape context of urbanisation). Indeed, large-bodied species may have larger resource
448 needs and smaller population sizes (Kremen and McGonigle, 2015), which could
449 disadvantage them during the dry season. We nevertheless did detect a greater ratio of wing to
450 body length during the dry season, which might indicate greater mobility of insects relative to
451 their size than during the wet season. Insect size differences between seasons might also arise
452 from differences in climatic conditions such as temperature. Some studies reported that higher
453 wing to thorax size ratios could be selectively advantageous at lower temperatures (e.g.,
454 Azevedo et al. 1998), which is in agreement with what we found during the dry/winter season.

455 Species turnover between seasons likely explains the difference in insect sizes between
456 seasons. The distribution of insect body size/tongue size has been found to closely match the
457 distribution of flower corolla tube depth (Agosta and Janzen 2005, Stang et al. 2006; 2009)
458 and to determine the abundance of interactions in pollinator webs (Stang et al. 2006, Geslin et
459 al. 2013). The distribution of the size of insects might be due to the predominance of flowers
460 with short corollas during the dry season because mango flowers, as well as the dominant
461 non-native weeds *T. procumbens* and *B. pilosa* have short corollas. This is supported by the
462 fact that the few large individuals of flying insect we found during the dry season were
463 trapped in natural habitat where plants such as *Grewia* spp., have flowers that present a more
464 tubular and deep corolla structure. Finally, we observed larger insects, in both seasons, in the
465 natural vegetation compared to mango orchards. Some studies have found large-bodied flying
466 insects to be more prone to extinction in response to land use intensity and habitat loss
467 (Larsen et al. 2005, Bartomeus et al. 2013; Rader et al 2014), whereas others have found non-
468 significant effects (Williams et al. 2010), and several authors found small insects to be more
469 negatively affected by isolation and habitat loss than larger ones (Bommarco et al. 2010;
470 Öckinger et al. 2010; Jauker et al. 2013). Here, large-bodied species seemed more sensitive to
471 agricultural perturbations than small bodied ones and were thus less abundant in mango
472 orchards. Moreover, flowers within mango orchards may be less attractive to large bodied
473 insects because of the nectar and pollen offerings of mango flowers relative to wild flower
474 species.

475

476 **5. Conclusion**

477 Our study provides new evidence of the detrimental effects of isolation from natural habitats,
478 even in a biodiversity rich area, on abundance and functional diversity of flying insects in
479 different seasons. Although these deleterious effects were season-dependent for insect

480 abundance (i.e. negative effects of distance from natural vegetation only during crop
481 flowering), functional diversity declined consistently with increasing distance from natural
482 habitat in both dry and wet seasons. This study thus sheds a light on the importance of
483 providing patches of resource-rich habitat within orchards over the year to mitigate the
484 detrimental effects of isolation and maintain functionally-diverse insect communities. Such
485 management practices are easily achievable in mango orchards and should be encouraged.
486 Finally, this study also underlines the temporal variability within a year of patch use by flying
487 insect communities within an agricultural landscape. Agricultural landscapes and mechanisms
488 that structure flying insect communities should thus be studied at various spatial and temporal
489 scales. We encourage new studies regarding links between morphological traits of insects and
490 agricultural intensification, contributing to a synthesis that can untangle the relative
491 importance of temporal and spatial contexts, crop and management practices.
492

493 **Acknowledgments**

494 We are grateful to Floriane Flacher, Lavhelesani Simba, Lyndre Nel, Anne-Sophie Bonnet-
495 Lebrun, Pierre Quévieux, Thomas Aubier and Kejun Zou for their help with data collection.
496 BG thanks Lucas A. Garibaldi and Boris Leroy for useful discussions. This work was
497 supported by the European Commission Marie Curie *International Research Staff Exchange*
498 *Scheme* (IRSES) ('NETWORK' project, Grant agreement: PIRSES-GA-2012-318929). .

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797 **Table 1:** Model selection for flower abundance, insect abundance and functional diversity. *N*
798 corresponds to the number of models selected in the top 4AIC_c, R²_m and R²_c correspond
799 respectively to the marginal and conditional R² values of the best model. Est. corresponds to
800 the parameter estimate (for centralized and standardized predictor variables), CI to its 95%
801 confidence interval and Imp. to the parameter relative importance. * Mango field was the
802 reference habitat and § the dry season was the sampling season of reference.

| Parameter | Flower abundance (<i>N</i> = 2 models) R ² _m = 0.40 ; R ² _c = 0.68 | | | Insect abundance (<i>N</i> = 6 models) R ² _m = 0.54 ; R ² _c = 0.67 | | | Functional diversity (<i>N</i> = 6 models) R ² _m = 0.32 ; R ² _c = 0.41 | | |
|----------------------|---|---------------------|------|---|---------------------|------|---|----------------------|------|
| | Est. | CI | Imp. | Est. | CI | Imp. | Est. | CI | Imp. |
| Intercept | 2.867 | (2.056, 3.679) | | 1.402 | (1.120, 1.683) | | 0.069 | (0.059, 0.082) | |
| Habitat * | -2.563 | (-3.033, -2.093) | 1.00 | 0.255 | (-0.082, 0.592) | 0.68 | 0.017 | (0.0002, , 0.033) | 0.79 |
| Season § | -1.427 | (-1.756, -1.098) | 1.00 | 1.393 | (1.033, 1.751) | 1.00 | 0.048 | (0.033, 0.063) | 1.00 |
| Distance | 0.538 | (0.187, 0.889) | 1.00 | -0.632 | (-0.940, -0.325) | 1.00 | -0.026 | (-0.042, -0.011) | 1.00 |
| Habitat X Season | 2.363 | (1.632, 3.093) | 1.00 | -0.517 | (-0.962, -0.072) | 0.55 | 0.015 | (-0.007, 0.038) | 0.45 |
| Distance X Season | 0.326 | (-0.346, 0.999) | 0.35 | 0.687 | (0.227, 1.148) | 1.00 | -0.006 | (-0.036, 0.023) | 0.23 |
| Flower abundance | | | | -0.119 | (-0.328, 0.089) | 0.39 | | | |

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804

805 **Table 2:** Model selection for body length, wing span and ratio of wing span over body length.

806 Same legend as Table 1. * Mango field was the reference habitat and § the dry season was the

807 sampling season of reference.

| Parameter | Body length (N = 7 models) | | | Wing span (N = 7 models) | | | Ratio of wing span over body length (N = 5 models) | | |
|----------------------|--|--------------------|------|--|--------------------|------|---|---------------------|------|
| | R ² _m = 0.037 ; R ² _c = 0.45 | | | R ² _m = 0.015 ; R ² _c = 0.54 | | | R ² _m = 0.02 ; R ² _c = 0.40 | | |
| | Est. | CI | Imp. | Est. | CI | Imp. | Est. | CI | Imp. |
| Intercept | 0.556 | (0.271, 0.840) | | 0.805 | (0.433, 1.177) | | 0.248 | (0.155, 0.342) | |
| Habitat* | 0.049 | (0.0007, 0.097) | 0.89 | 0.052 | (0.006, 0.099) | 0.93 | -0.0004 | (-0.013, 0.013) | 0.24 |
| Season§ | 0.168 | (0.112, 0.225) | 1.00 | 0.126 | (0.067, 0.186) | 1.00 | -0.042 | (-0.061, -0.022) | 1.00 |
| Distance | -0.047 | (-0.109, 0.014) | 0.68 | -0.018 | (-0.095, 0.028) | 0.52 | 0.002 | (-0.011, 0.015) | 0.28 |
| Habitat X Season | -0.023 | (-0.10, 0.053) | 0.32 | -0.008 | (-0.097, 0.048) | 0.32 | 0.003 | (-0.019, 0.025) | 0.07 |
| Distance X Season | 0.060 | (0.004, 0.117) | 0.53 | 0.016 | (-0.011, 0.109) | 0.32 | -0.009 | (-0.028, 0.009) | 0.10 |

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810 **Figures**

811 **Figure 1:** Effect of distance to the natural habitat (m), habitat type and sampling period on: A.
812 abundance of flowers (log+1), B. abundance of insects, and C. functional diversity of insects.
813 Lines represent model predicted values. In all panels, mango flowering period (dry season) is
814 represented in dark grey and mango non-flowering period (wet season) is represented in light
815 grey.

816

817 **Figure 2:** Relationship between body length (mm) and wing span (mm) of flying insects (A),
818 and effect of distance to the natural habitat (m) and habitat type on insect body length (B).
819 Mango flowering period (dry season) is represented in dark grey and mango non-flowering
820 period (wet season) is represented in light grey.

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