1 **Mass flowering crops in a patchy agricultural landscape can reduce bee**

2 **abundance in adjacent shrublands**

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Abstract

Pollinator spill-over among habitats can arise in order to fulfill the pollination function and whenever differences in floral offering change over time or space. Flowering crops offer pulsed and abundant floral resources (i.e., mass flowering crops) that might promote pollinator spill-over between cultivated and adjacent natural areas. We explored pollinator patterns in the mass flowering legume crop *Hedysarum coronarium* and its influence on the bee pollinator communities of adjacent shrublands in a heterogeneous and patchy agricultural landscape. We studied the temporal (i.e., during vs. after mass flowering in adjacent shrublands) and spatial (i.e., inside crops, adjacent and distant shrublands during mass flowering) functional pollinator spill-over. The honeybee was highly attracted to *Hedysarum* crops, yet its abundance and that of other bee species visiting native plants in adjacent shrublands did not differ during and after *Hedysarum* mass flowering. However, at the landscape scale, the honeybee and the other bee species were less abundant in shrublands adjacent to *Hedysarum* crops compared to distant ones; their visitation rates showing a similar trend. These results show that some mass flowering crops can influence pollinator patterns in the surrounding landscape by competing for generalist pollinators with native plants. The characteristics of the crop species and the landscape can modulate and determine the role of mass flowering crops as competitors or supporters of wild pollinators for adjacent natural areas.

1. Introduction

There is growing concern about local and regional declines in pollinator species and the pollination services they provide (Bartomeus et al., 2013; Potts et al., 2010). Moreover, plant-pollinator interactions may be even more sensitive than the species themselves (Tylianakis et al., 2008), and factors driving the decline of pollinators might interact in non-additive ways (González-Varo et al., 2013). More than 75% of the cultivated species depend on, or benefit from, animal mediated pollination (Klein et al., 2007), and the area devoted to pollinator-dependent crops is disproportionately growing (Aizen et al., 2008). In this context, during the last two decades, scientists have explored the role of remaining natural areas within agricultural landscapes as reservoirs of pollinators to provide pollination service to pollinator-dependent crops. Maintaining and restoring these areas in agricultural landscapes is one of the most commonly implemented agri-environment schemes. The underlying rationale is that remaining natural areas offer pollinators feeding resources and/or nesting sites not provided by the crop or not stable over time due to the inherent disturbance frequency (Westphal et al., 2003).

Pollinators move from one area to another in order to meet their feeding and/or nesting requirements. When such a movement results in the achievement of their functions (e.g. pollination), it is called functional spill-over (hereafter, spill-

over) (Blitzer et al., 2012). Spill-over can occur whenever the offer of required

floral resources differs between habitats; therefore, it can occur in both

directions. However, only recently has the spill-over of pollinators from

entomophilous mass flowering crops (MFCs, hereafter) to natural habitats

received the attention of scientists and managers (Blitzer et al., 2012;

Holzschuh et al., 2011). MFCs, despite offering only pulsed floral rewards, could

compensate for food resource limitation during periodic intervals, and help in

maintaining and enhancing pollinator communities in agricultural landscapes

(Westphal et al., 2003), as long as nesting sites and other feeding areas are

also available within the foraging ranges of pollinators. Thus, those natural

areas that offer alternative resources and that are close to MFCs could benefit

from a pollinator spill-over from MFCs. That is, the MFC could exert a magnet

effect (Johnson et al., 2003; Molina-Montenegro et al., 2008) over close natural

areas. This magnet effect would more likely occur in heterogeneous agricultural

landscapes (Blitzer et al., 2012).

In addition to spill-over between habitats with different resource offer at a given

period of time (i.e., spatial spill-over), differences in resource offer between

habitats can also arise at different moments in time (i.e. temporal spill-over). For

instance, the high floral rewards of a MFC compared to its surrounding habitats

can be reverted after the MFC flowering peak (Hanley et al., 2011).

Here we study the effect of the highly rewarding *Hedysarum coronarium* L. MFC

on the pollinator community in adjacent shrublands in a patchy and

heterogeneous Mediterranean agricultural landscape. We specifically focus on

the bee pollinator community because this MFC is mainly bee-pollinated (the

honeybee, *Apis mellifera* L., accounting for more than the 80% of its visits;

4

95   Montero-Castaño et al., 2014). We address the following questions: (a) Does

96   the MFC affect the bee community visiting plant species in adjacent shrublands

97   through a temporal bee spill-over during and after mass flowering? (b) Is there a

98   spatial bee spill-over from the MFC to adjacent shrublands during mass

99   flowering? (c) Is the role of the honeybee (the main pollinator of the MFC)

100 different from that of the other bee species, for both the temporal and spatial

101 spill-over?

102 We expect the MFC to attract a large number of bees and to exert a magnet

103 effect on adjacent shrublands. That is, increasing the abundance of bees in

104 adjacent shrublands compared to shrublands away from MFCs (i.e. spatial spill-

105 over). Additionally, after mass flowering, bees may spill-over from the MFC to

106 adjacent shrublands (i.e. temporal spill-over). We expect both temporal and

107 spatial spill-over to be largely mediated by the honeybee, as it is the main

108 pollinator of the MFC.

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110 **2. Materials and methods**

111

112 *2.1. Crop species*

113

114 The MFC species studied was *H. coronarium* L. (Fabaceae; hereafter

115 *Hedysarum*). *Hedysarum* is a short-lived N-fixing perennial (Bullitta et al., 2000;

116 Sulas et al., 2000) that can reach a height of 1.5 m (Bustamante et al., 1998;

117 Montes Pérez, 1993/94). Its inflorescences are racemes with up to 30 pink

118 flowers rich in pollen and nectar that bloom during April and May. Its flowers are

119 self-compatible, although they need to be tripped, and have high out-crossing

120   rates (Louati-Namouchi et al., 2000; Yagoubi and Chriki, 2000). Bees are the

121   primary pollinators of *Hedysarum* with the honeybee being the most abundant

122   (Louati-Namouchi et al., 2000; Montero-Castaño et al., 2014; Satta et al., 2000).

123

124   *2.2.   Study sites*

125

126   We conducted our study in Menorca (Balearic Islands, Spain), where

127   *Hedysarum* was introduced between the end of the 18th and the beginning of

128   the 19th centuries (Ortells and Campos, 1983). Since 1860 it has been used in a

129   traditional cyclical agro-farming system (Bustamante et al., 2007) which

130   consists of growing crops of *Hedysarum* for two consecutive years, followed by

131   cereal cropping in the third year, and leaving the land fallow during the fourth

132   year (Bustamante et al., 2007). To some extent, this traditional system is still

133   present in the extensive and heterogeneous agricultural landscape of the island,

134   but the area devoted to it has been reduced by 97% in the last three decades

135   due to land use intensification (Bustamante et al., 2000; Díaz-Ambrona

136   Medrano et al., 2014). Currently, the public administration is attempting to

137   restrain this trend by subsidizing *Hedysarum* crops.

138   *Hedysarum* is the only spring MFC on the island. Most *Hedysarum* crops are

139   harvested during the flowering peak, when the balance between plant yield and

140   its nutritional value is greatest (Bustamante et al., 2005), in order to provide

141   feed for cattle during the summer.

142   In 2009, to explore whether there was a temporal bee spill-over between

143   *Hedysarum* crops and adjacent shrublands, we selected four Mediterranean

144   shrublands adjacent to *Hedysarum* crops (≤ 10 m apart), which were studied

145   during and after mass flowering (i.e., after crops were harvested during the

146   flowering peak). The distance among study shrublands ranged from 500 m to

147   12.01 km. Although honeybees and bumblebees can fly distances greater than

148   500 m (Greenleaf et al., 2007; Osborne et al., 2008), pollinators do not usually

149   travel very far when rewards are available in the vicinity (Greenleaf et al., 2007;

150   Johnson et al., 2003; Wolf and Moritz, 2008). Moreover, due to the

151   heterogeneity of the Minorcan agricultural landscape, we considered 500 m to

152   be a sufficient minimum distance to assure shrubland independence.

153   In 2010, in order to investigate whether there was a spatial bee spill-over at the

154   landscape scale, we selected four *Hedysarum* crops (inside, hereafter) and six

155   Mediterranean shrublands, four adjacent to the selected *Hedysarum* crops (i.e.,

156   ≤ 10 m apart; adjacent, hereafter) and two without *Hedysarum* crops in the

157   surrounding 500 m radius landscape (distant, hereafter). The distance among

158   study shrublands ranged from 690 m to 15.27 km.

159   For the two study years, the area of MFCs ranged from 2240 to 21066 m^2 with a

160   mean flower density of 557.40 ± 142.85 flowers/m^2. Study shrublands had an

161   area that ranged from 133 to 29743 m^2 (Table 1). They were early successional

162   shrublands of *Quercus ilex* L. and *Olea europaea* L. subsp. *sylvestris* Brot.

163   (Carreras et al., 2007) with a rich herbaceous understory. The flowering

164   community slightly differed among study shrublands but was mainly composed

165   by Leguminosae and Compositae species. The species that overlapped their

166   flowering peak with *Hedysarum* and that contributed the most to the total

167   abundance of floral units (hereafter flowers, according to Dicks et al., 2002)

168   were all legumes, either *Calicotome infesta* (C. Presl) Guss., *Lotus*

169   *angustissimus* L.*, Lotus ornithopodioides* L. and/or *Trifolium campestre* Schreb.

170   There were no honeybee hives within any of the 500 m radius surrounding

171   landscapes (landowners' *personal communication*).

172   Adjacent and distant shrublands in our 2010 study had similar flowering plant

173   species richness (0.46 ± 0.04 and 0.43 ± 0.03 species/m^2, respectively; t = -

174   0.067, p-value = 0.950), similar total flower density (100.12 ± 24.49 and 163.24

175   ± 30.95 flowers/m^2, respectively; t = 0.616, p-value = 0.571) and showed a

176   proportional similarity index of 0.37 (see below for vegetation surveys and index

177   calculation details).

178

179   *2.3.   Pollination censuses*

180

181   We conducted pollination censuses during the flowering peak of *Hedysarum*

182   (from 30th April to 25th May and from 28th April to 24th May in 2009 and 2010,

183   respectively) on sunny, warm (≥ 17 ºC) and non-windy days, from 10 am to 6

184   pm. In both years weather conditions fell within the average ranges for these

185   months in the study area (Agencia Estatal de Meteorología).

186   Unidentified bee pollinator species in the field were caught and sorted into

187   distinct morphospecies for later identification by specialists. Voucher specimens

188   are deposited at Doñana Biological Station (EBD-CSIC).

189

190   *2.3.1. Temporal bee spill-over*

191   In 2009, in each adjacent shrubland we surveyed two or three target plant

192   species out of seven: *Asphodelus aestivus* Brot., *Cistus albidus* L., *Daucus*

193   *carota* L., *Galactites tomentosa* Moench, *Hypochoeris achyrophorus* L., *Oxalis*

194   *pes-caprae* L. and *Urospermum dalechampii* (L.) Scop. ex F. W. Schmidt

195   (Supplementary material, Appendix A). They all shared pollinators with

196   *Hedysarum* and were in their flowering peak during the study period. Moreover,

197   we selected target plant species with low-restrictive flower morphologies

198   because we expected them to attain higher visitation rates than those with more

199   restrictive flower morphologies (Córdoba and Cocucci, 2011).

200   For each target species we conducted focal censuses that lasted 15 min during

201   which we noted the number and identity of bee pollinators and counted the

202   number of open flowers of the observed target plants. A visitor was considered

203   a pollinator when it entered a flower and touched its reproductive structures.

204   Censuses were taken daily for 13 days and on average were conducted 3.50 ±

205   1.35 days before and after crop harvesting. The order of observation of each

206   site, plant species and individual was randomly established. We conducted a

207   total of 134 focal censuses (33.5 h), including 66 during and 68 after

208   *Hedysarum* mass flowering. Each plant species was observed an average of

209   1.84 ± 0.09 h and 1.89 ± 0.08 h during and after mass flowering, respectively.

210   For statistical analyses, data for each target plant species was pooled.

211

212   *2.3.2. Spatial bee spill-over*

213   In 2010, during the mass flowering, we conducted bee censuses in the adjacent

214   and distant shrublands by walking along 20 m long and 1 m width parallel

215   transects, for a duration of 10 min. During those 10 min, we noted the identity,

216   number and visits of bees and the identity of the plants visited.

217   In each shrubland we marked between three and 17 parallel transects,

218   depending on the area of the shrubland. In total, we marked 36 and 16 parallel

219   transects in adjacent and distant shrublands, respectively. Each transect was

220   walked an average 5.35 ± 0.35 times (0.89 ± 0.06 h), ranging from two to 11

221   times. Overall, we conducted a total of 278 transect walks (46.33 h): 164 (27.33

222   h) in adjacent and 114 (19.00 h) in distant shrublands, respectively.

223   The sampling order of shrublands and of transects within shrublands was

224   randomly established. We sampled shrublands until we found no new plant-bee

225   pollination interaction after six or more transect walks according to rarefaction

226   curves (Supplementary material, Appendix B), which we considered a good

227   compromise between sampling effort and data accuracy. For statistical

228   analyses, data for each study shrubland or crop was pooled.

229   To account for the abundance and richness of flowers in the shrublands,

230   quadrats (0.4 x 0.4 m) were laid at every meter along each transect in the

231   shrublands. All plant species were identified and all open flowers were counted.

232   In total we observed 46 plant species belonging to 34 genera and 17 families:

233   38 species in adjacent shrublands and 24 in distant ones.

234   Simultaneously, we conducted censuses in the four *Hedysarum* crops (i.e.,

235   inside) following the same methodology as in the shrublands. We marked a total

236   of 21 transects (three to seven transects per crop). Each transect was walked

237   an average of 5.24 ± 0.39 times (0.87 ± 0.07 h) accounting for a total of 18.33 h

238   of crop sampling. Quadrats were also laid every meter along each transect

239   inside the crops to account for the abundance of *Hedysarum* flowers.

240

241   *2.4.   Data analyses*

242

243   We explored the similarity of bee communities, in terms of their identity and

244   relative abundance across time (during vs. after mass flowering, in 2009), and

245 across space (inside, adjacent and distant, in 2010) with the proportional

246 similarity index (PS; Hurlbert, 1978). PS was calculated as:

247 $PS = \sum_{i=1}^{n} \min(p_{ia}, p_{ib})$ where for *n* species p_{ia} is the relative abundance of

248 species *i* at time *a* (i.e., during or after *Hedysarum* mass flowering) or at

249 distance a (i.e., inside, adjacent or distant to *Hedysarum* crops) and p_{ib} is the

250 relative abundance of species *i* at time or distance *b. PS* values range from 0

251 (no overlap between species composition) to 1 (complete overlap).

252 To explore the temporal and spatial spill-over, we built generalized mixed

253 models with bee species richness and abundance per target plant species (in

254 2009) or per study shrubland or crop (in 2010) as response variables. In 2010,

255 bee visitation rate and plant-bee pollination interaction richness were also

256 explored as response variables.

257

258 *2.4.1. Temporal bee spill-over*

259 In 2009, for the response variable bee richness, time (during vs. after mass

260 flowering) was included as a fixed factor in the model. For the response variable

261 bee abundance, pollinator group (honeybee vs. other bees) and its interaction

262 with time were also included as fixed factors. In both models target plant

263 species nested in study shrubland was included as a random factor. The

264 logarithm of the flowers under observation and the logarithm of the hours of

265 observation of each target plant species were included as offsets. Poisson was

266 used as the error distribution family. Post hoc comparisons were conducted by

267 building contrast matrices.

268 We also explored whether the effect of time and pollinator group in these

269 response variables differed for each target plant species and site by conducting

270 Wilcoxon tests (Supplementary material, Appendix C).

271

272   *2.4.2. Spatial bee spill-over*

273 In 2010, for the response variable bee species richness, distance (inside,

274 adjacent and distant) was included as a fixed factor in the model and study site

275 as a random factor. For the response variables bee abundance and visitation

276 rate, pollinator group (honeybee vs. other bees) and its interaction with distance

277 were also included as fixed factors and study site as a random factor. In the

278 three models, the logarithm of the number of 10 min transect walks conducted

279 in each shrubland or crop was included as offset. Poisson was used as the error

280 distribution family. Post hoc comparisons were conducted by building contrast

281 matrices.

282 We are aware that the number of replicates is unbalanced among treatments

283 with distant shrublands underrepresented. To account for this limitation, we

284 repeated the analyses by randomly excluding two MFC and two adjacent

285 shrublands while keeping the geographical spatial distribution of the study sites.

286 The results obtained did not qualitatively differ from those including all study

287 sites (Supplementary material, Appendix D).

288 Additionally, we explored whether the richness of plant-bee pollination

289 interactions differed between adjacent and distant shrublands by conducting

290 Wilcoxon tests.

291

292   All analyses were conducted in R (R Development Core Team, 2014). We used

293   the library *nlme* for building the generalized mixed models and the library

294   *multcomp* for building the post hoc comparisons. Mean ± SE values are given

295   throughout the text unless otherwise specified.

296

297

298   **3. Results**

299

300   Pooling the 2009 and 2010 data, we observed a total of 25 bee species

301   belonging to 16 genera, all of them considered native in the study area. Nine

302   species visited *Hedysarum* crops while 23 species visited plants in shrublands

303   (19 in adjacent and 14 in distant ones). All bee species that visited *Hedysarum*

304   were shared with shrubland plants except two, *Bombus terrestris* L. and *Eucera*

305   *numida* Lepeletier, which were exclusive to *Hedysarum* MFC (Table 2).

306

307   *3.1.   Temporal bee spill-over*

308

309   In adjacent shrublands there were not significant differences in bee species

310   richness in target plant species during and after *Hedysarum* mass flowering

311   (during = 0.028 ± 0.008 and after = 0.035 ± 0.014 species/flower/h, Table 3).

312   Despite that, the composition and relative abundance of the species partially

313   differed during and after mass flowering, as indicated by the proportional

314   similarity index PS = 0.65.

315 Honeybee abundance did not differ between during and after mass flowering,

316 and neither did the combined abundance of all other bee species (Fig. 1, Table

317 3).

318 When analyzing each target plant species in each site separately, the trend was

319 not consistent. For example, after mass flowering, honeybee abundance

320 marginally decreased in one target plant species (*A. aestivus*) while in other two

321 target plant species (*C. albidus* and *G. tomentosa* in the *Binicalaf* site) the

322 abundance of other bees increased (Fig. C.2). *Hedysarum* mass flowering also

323 affected bee species richness in three target plant species. In *C. albidus* and *G.*

324 *tomentosa* at the *Mila1* site, bee species richness increased after mass

325 flowering while in *G. tomentosa* at the *Binicalaf* site it decreased.

326

327 *3.2.   Spatial bee spill-over*

328

329 Bee species richness did not differ with distance to *Hedysarum* crops (0.128 ±

330 0.033, 0.201 ± 0.075 and 0.150 ± 0.017 species/transect, for inside, adjacent

331 and distant sites, respectively; Table 4). However, composition and relative

332 abundance of the species partially differed across distances as indicated by the

333 proportional similarity indexes. The similarity in bee communities was the

334 highest between adjacent and distant shrublands (PS = 0.58), in which the

335 honeybee and the wild bee *Eucera oraniensis* Lepeletier were the most

336 abundant species (Fig. 2). Meanwhile, the bee community in *Hedysarum* crops

337 was largely dominated by the honeybee but lacked *E. oraniensis.* The similarity

338 of *Hedysarum* crop with adjacent (PS = 0.30) and distant (PS = 0.36)

339 shrublands was low (Fig. 2). When the bee pollinator communities of

340   *Hedysarum* crops and adjacent shrublands were pooled together, the similarity

341   with distant shrublands was PS = 0.62.

342   Distance to *Hedysarum* crops affected bee abundance, and the effect differed

343   between pollinator groups (Fig. 3a and Table 4). The abundance of honeybees

344   and other bees was almost two times higher in distant than in adjacent

345   shrublands. Inside *Hedysarum* crops, the two pollinator groups showed different

346   trends. The abundance of the honeybee was one order of magnitude higher

347   than in shrublands, while the abundance of other bee species was lower than in

348   distant shrublands and did not differ from that in adjacent shrublands (Fig. 3a

349   and Table 4). When excluding *E. oraniensis* from the analysis, differences in the

350   abundance of other bees were not significant among distances (Table 4).

351   Visitation rates showed the same trends as abundance of bees (Fig. 3b and

352   Table 4). There were no significant differences in plant-bee pollination

353   interaction richness between adjacent and distant shrublands (0.304 ± 0.053

354   and 0.303 ± 0.086 interactions/transect, respectively; N = 6, W = 4, p-value = 1).

355   The most frequently observed interactions in both types of shrublands were

356   between *G. tomentosa* and honeybees (20.37%) and *E. oraniensis* (30.73%).

357

358

359   **4. Discussion**

360

361   *4.1.   No temporal bee spill-over from* Hedysarum *MFCs to adjacent*

362   *shrublands*

363

364 Contrary to what we expected, we did not observe a temporal spill-over of

365 honeybees from the MFC to adjacent shrublands after *Hedysarum* mass

366 flowering. During mass flowering, the floral offer of MFCs seems to cover all the

367 requirements of the honeybee so that the crops monopolize their visits.

368 However, after mass flowering, due to their large foraging ranges (Greenleaf et

369 al., 2007; Osborne et al., 2008), capacity to locate highly rewarding resources at

370 greater distances (Cresswell and Osborne, 2004) and developed

371 communication skills (Steffan-Dewenter and Kuhn, 2003), honeybees

372 might move to other still unharvested MFCs or to other highly rewarding plant

373 communities within their foraging ranges, such as old-fields (Gathmann et al.,

374 1994). For instance, in our study system, communities with abundant *G.*

375 *tomentosa* might be highly attractive to the honeybee. Therefore, the temporal

376 spill-over effect mediated by honeybees in patchy and heterogeneous

377 agricultural landscapes might be spatially diluted.

378 A temporal spill-over of other bees from MFC to adjacent areas was also not

379 observed. We did not expect the other bee species to be strongly attracted to

380 *Hedysarum* crops as prior studies have shown that most *Hedysarum* visits in

381 cultivated and naturalized populations are made by the honeybee (Montero-

382 Castaño et al., 2014; Satta et al., 2000).The pollinator survey conducted in 2010

383 inside *Hedysarum* crops also supported this observation, as the other bee

384 species represented only 3.87% of the total visitors. Thus, even if a temporal

385 spill-over of a particular bee species could occur, it would be difficult to detect it

386 due to their low abundance. In our study system, this was the case for

387 *Megachile pilidens* Alfken and *Osmia caerulescens* L. Despite that the

388 phenologies of these species overlapped with the flowering peak of *Hedysarum*

389 (they were observed visiting *Hedysarum* crops); in adjacent shrublands they

390 were only observed after mass flowering.

391 Therefore, the lack of a significant general pollinator temporal spill-over is due

392 to both non-significant trends for most of target plant species, and to significant

393 but opposed trends that nullify each other for few target plant species.

394 In addition, other bee species able to access the restrictive flowers of

395 *Hedysarum* are medium to large-sized ones (Córdoba and Cocucci, 2011) with

396 medium-large foraging ranges (Greenleaf et al., 2007), so that their potential

397 temporal spill-over could also be spatially diluted. Nonetheless, we would

398 expect this spatial dilution to occur at shorter distances than in the case of the

399 honeybee because maximum foraging distances for wild bees, which are mostly

400 solitary central place foragers, fall below the ones described for honeybees

401 (Gathmann and Tscharntke, 2002; Steffan-Dewenter and Kuhn, 2003)*.*

402

403   *4.2.   No spatial spill-over from* Hedysarum *MFCs to adjacent shrublands*

404   *but the reverse*

405

406 We did not observe a spatial spill-over from the MFC to adjacent shrublands

407 neither of honeybees nor of other bee species. However, the explanation for

408 this result differs between the two pollinator groups.

409 The honeybee preferentially selected *Hedysarum* crops and did not spill-over to

410 adjacent shrublands. Pollinators, seek to optimize their floral rewards intake

411 (Armbruster and Herzig, 1984) and might benefit greatly from MFCs, where the

412 relative abundance and quality of available floral resources are usually high

413 (Dietzsch et al., 2011). This behavior is amplified if they have an intensive

414   foraging behavior with short flying distances between consecutive flower visits,

415   as is the case of the honeybee (Gross, 2001). In fact, the predominance of the

416   honeybee in MFCs is not exclusive to *Hedysarum* crops as in many parts of the

417   world crop pollination relies on this single species (Winfree et al., 2007).

418   In the case of the other bee species, they did not highly select *Hedysarum*

419   MFCs and, consequently, they did not significantly spill-over to adjacent

420   shrublands. We suggest three non-exclusive explanations for the pool of other

421   bee species not highly selecting the MFC. First, flower constancy at the

422   individual level might be more highly associated with social pollinators like the

423   honeybee (Leonhardt and Blüthgen, 2012) than with solitary bees. Therefore,

424   monospecific areas like MFCs do not fulfill the individual requirements of

425   solitary bees. Second, other bee species could be excluded from MFCs due to

426   competition with the honeybee for the use of floral resources (Paini, 2004;

427   Roubik, 1983) or by physical disturbance (Gross and Mackay 1998). Floral

428   resources would not be expected to be limiting in MFCs. However, interspecific

429   competition depends on the relative abundance of interacting species (Steffan-

430   Dewenter and Tscharntke, 2000), and we cannot disregard the possibility of

431   competition to arise due to the high abundance of honeybees inside crops.

432   Third, other factors co-varying with the presence of MFCs (for instance, some

433   agricultural practices like the use of pesticides), could lead to the avoidance of

434   MFCs by bee species.

435   Nevertheless, despite that the pool of other bee species did not highly select

436   *Hedysarum* MFCs, it did not avoid them either, as indicated by the similar

437   abundance inside crops and in adjacent shrublands for the pool of other bee

438   species. That is, some particular species might spill-over from MFCs to adjacent

439   shrublands. Most wild bees are central placed foragers (Cresswell et al., 2000)

440   and due to their more restrictive foraging ranges compared to honeybees, their

441   spill-over occurs at smaller spatial scales. However, due to the low abundance

442   of other bee species, we could not conduct analyses for particular species

443   separately to elucidate such specific responses.

444   Finally, some bee species did not profit from the resources offered by

445   *Hedysarum*. Moreover, they seemed to prefer landscapes without *Hedysarum*

446   MFCs. That was the case for *E. oraniensis,* whose relative abundance was

447   twofold in distant shrublands than in adjacent ones, and in fact, it was the main

448   responsible for the higher bee abundance in distant shrublands compared with

449   adjacent ones. In general, medium to large-sized bees (Greenleaf et al., 2007)

450   are able to perceive their landscapes at larger spatial scales (Steffan-Dewenter

451   et al., 2002). Therefore, regardless of the reason for their not exploiting a

452   particular crop species, these bees can chose landscapes without such MFCs

453   and with high concentrations of their preferred required resources (e.g. nesting

454   sites, food) (Tscharntke et al., 2012).

455   Our approach allowed us to detect a spatial bee spill-over, not from *Hedysarum*

456   MFC to adjacent natural habitats, but rather the reverse. As *Hedysarum* crops

457   are part of a cyclical agro-farming system (Bustamante et al., 2007) and are

458   grown a maximum of two consecutive years in the same field, their negative

459   effect in the abundance of bee pollinators in adjacent areas could be buffered in

460   the long term. Therefore, we would not expect the observed spill-over to alter

461   the demography of neither pollinator populations nor of the entomophilous wild

462   plants in adjacent shrublands. However, at larger spatial scales than the one

463   considered here, *Hedysarum* MFCs could have an indirect positive effect on the

464 abundance of wild bees in natural areas. If honeybee hives are spread across

465 the Minorcan landscape and *Hedysarum* MFCs attract honeybees not only from

466 adjacent but also from distant shrublands, MFCs could be reducing the

467 abundance of honeybees in natural areas at a large spatial scale. As this

468 species can outcompete wild pollinators (Gross and Mackay, 1998; Paini, 2004;

469 Roubik, 1983), these latter could profit from the decrease of honeybee

470 abundance and increase their visitation rates, as we have observed at smaller

471 spatial scales (Montero-Castaño and Vilà, *unpublished result*). At such large

472 spatial scale, the rotation of crops might not dilute the effect on pollinators and

473 entomophilous wild plants. It would have been very interesting, though not

474 feasible, to test this hypothesis by manipulating the presence and absence of

475 honeybee hives at larger spatial scales like Valido et al., (2014) did.

476 In addition, and though the study years were representative of the average

477 weather conditions for the study area (Agencia Estatal de Meteorología),

478 pollinator communities show a high interannual variability (Williams et al., 2001).

479 Thus, a long term study would be necessary to elucidate whether the observed

480 pattern is maintained in the long-term or if *Hedysarum* crops support and

481 enhance the abundance of generalist pollinators and provide a benefit through

482 greater pollinator service overall (Holzschuh et al., 2011; Mitchell et al., 2009).

483 Finally, the extrapolation of our results to other MFCs should be done cautiously

484 and taking into account the particular characteristics of our study crop species,

485 specially its restrictive flower morphology and its high attractiveness to

486 honeybees. For instance, *Hedysarum* MFC can only directly compete for or

487 share with natural areas those pollinators able to access its floral rewards

488 (Córdoba and Cocucci, 2011). Meanwhile, other MFCs with non-restrictive

489 flower morphologies, such as sunflower (*Helianthus annuus* L.) and oilseed

490 rape (*Brassica napus* L.), might compete for or share with natural areas a

491 broader array of pollinators including bees, butterflies, flies and beetles

492 (Bommarco et al., 2012) potentially showing larger spill-over effects on one

493 direction or another.

494

495 *4.3. Conclusions*

496

497 In the studied agricultural landscape in Menorca the presence of *Hedysarum*

498 MFCs decreased pollinator abundance in adjacent shrublands by monopolizing

499 the visits of the honeybee, and by attracting some wild bees away from the

500 surrounding natural areas. Thus, the proposed role of MFCs as supporters and

501 sources of wild pollinators for surrounding natural areas should be cautiously

502 analyzed for each particular system. Factors such as the flower morphology

503 (i.e., restrictive or easy access to floral resources) of the crop species, the

504 presence of honeybees and their preference for the crop species and the

505 landscape configuration, might modulate and determine the role of MFCs as

506 supporters and sources of wild pollinators for surrounding natural areas.

507

508

509 **Acknowledgements**

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528 **Supplementary data**

529

530 **Appendix A.** Focal study plants

531 **Appendix B.** Rarefaction curves for 2010 field campaign

532 **Appendix C.** Temporal spill-over per species and site in 2009

533 **Appendix D.** Statistical analyses balancing the number of sites per treatment

534

535

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Figure captions

Figure 1. Temporal spill-over. Mean + SE abundance of the honeybee and other bee species in plants in shrublands adjacent to *Hedysarum* MFCs during (black) and after (bold) mass flowering.

Figure 2. Pollinator communities similarity. Percentage of bee species inside, adjacent and distant to *Hedysarum* MFCs. The honeybee is represented in black, the wild bee *Eucera oraniensis* in grey and the rest of species in white. Total number of individuals observed in each habitat type is given above each pie chart. Below brackets values for the proportional similarity index (PS) are given.

Figure 3. Spatial spill-over. Mean + SE (a) abundance and (b) visitation rate of the honeybee and other bee species inside (grey), adjacent (black) and distant (bold) to *Hedysarum* MFCs. Different letters above bars represent significant differences within pollinator groups.

714 **Table 1.** Location, area and flower density of each study shrubland or *Hedysarum* MFC. The land uses of the 500 m radius

715 surrounding landscape of each study shrubland are also given. Landscape characterization was based on the land-use cover map

716 (Carreras et al., 2007).

Site	Treatment	Year	Latitude	Longitude	Area (m²)	Flower density (flowers/m²)	% Land-uses 500 m landscape			
							MFC	Other crops	Natural areas	Non-natural areas*
Binicalaf	adjacent MFC	2009	39°52'14.81"N 39°52'16.99"N	4°10'2.49"E 4°10'1.25"E	2940.30 3844.45	54.65 208.75	0.49	34.82	55.17	9.14
Binixabó	adjacent MFC	2009	39°56'12.04"N 39°56'12.82"N	4° 6'57.23"E 4° 6'56.60"E	873.54 3379.52	11.43 216.88	0.43	47.03	47.95	4.48
Mila1	adjacent MFC	2009	39°55'29.35"N 39°55'28.61"N	4°15'12.05"E 4°15'15.34"E	151.53 15542.47	283.78 1038.37	4.47	58.60	34.46	2.45
Mila2	adjacent MFC	2009	39°55'40.88"N 39°55'39.50"N	4°15'21.39"E 4°15'16.90"E	15837.37 20522.74	145.05 1295.31	4.59	55.36	35.89	2.14
Albufera	distant	2010	39°56'27.50"N	4°15'21.11"E	29742.80	215.63	0.00	4.37	82.03	9.81
Binigurdó	adjacent MFC	2010	39°59'56.09"N 39°59'54.93"N	4° 6'2.40"E 4° 6'0.63"E	2707.70 2240.15	24.28 494.51	0.29	60.54	36.48	2.35
Favaraix	distant	2010	39°58'26.19"N	4°13'39.69"E	13745.07	110.86	0.00	61.86	34.14	2.25
Molí	adjacent MFC	2010	39°59'50.42"N 39°59'48.71"N	4° 5'34.13"E 4° 5'35.22"E	455.82 11487.12	38.45 308.52	1.46	79.30	13.65	5.52
Mongofre	adjacent MFC	2010	39°59'3.85"N 39°59'3.14"N	4°13'18.29"E 4°13'17.40"E	3090.83 21065.59	42.43 589.37	2.68	63.94	32.98	0.00
Palafanguer	adjacent MFC	2010	39°55'35.74"N 39°55'34.61"N	4°14'15.21"E 4°14'15.38"E	132.95 6110.35	323.35 307.50	0.78	44.23	54.09	0.88

717 * Human settlements and infrastructures

Table 2. Bee pollinator species observed during 2009 and 2010 with indication of whether they were observed inside *Hedysarum* MFCs and/or in adjacent or distant shrublands.

Species	Family	MFC	Shrublands	
			Adjacent	Distant
Andrena flavipes	Andrenidae		X	
Andrena nigroolivacea	Andrenidae		X	X
Andrena ovatula	Andrenidae	X	X	
Andrena parviceps	Andrenidae		X	
Andrena tenuistriata	Andrenidae		X	
Anthophora plumipes	Apidae		X	
Apis mellifera	Apidae	X	X	X
Bombus terrestris	Apidae	X		
Ceratina cucurbitina	Anthophoridae		X	X
Ceratina dallatorreana	Anthophoridae		X	
Chalicodoma sicula	Megachilidae	X		X
Eucera numida	Apidae	X		
Eucera oraniensis	Apidae	X	X	X
Halictus gemmeus	Halictidae		X	X
Halictus scabiosae	Halictidae		X	X
Hoplitis praestans	Megachilidae			X
Hoplosmia ligurica	Megachilidae			X
Hylaeus clypearis	Megachilidae		X	
Hymenoptera *sp.1*	-			X
Lasioglossum sp.1	Halictidae		X	X
Lasioglossum sp.2	Halictidae			X
Megachile pilidens	Megachilidae	X	X	
Osmia caerulescens	Megachilidae	X	X	X
Osmia niveata	Megachilidae		X	
Rhodanthidium septemdentatum	Megachilidae	X	X	X
Scoliidae *sp.1*	Scoliidae		X	

Table 3. Effect of *Hedysarum* mass flowering time (i.e. during vs. after) on bee pollinator species richness and abundance in shrublands adjacent to *Hedysarum* MFCs. The effect on abundance is explored for the honeybee and other bee species separately.

Response variable	N	Group	Contrast	Estimate	SE	Z	p-value
Richness	18	-	After vs. During	0.366	0.402	0.911	0.362
Abundance	36	Honeybee	After vs. During	-0.225	0.459	-0.491	0.858
		Other bees	After vs. During	0.105	0.205	0.509	0.848

Table 4. Effect of distance to *Hedysarum* MFCs (i.e. inside, adjacent and distant) on bee pollinator species richness, abundance, visitation rate and on plant-bee pollination interactions richness. The effect on abundance is explored for the honeybee and other bee species separately and for other bees when excluding from the analysis the wild bee *Eucera oraniensis*. Significance levels: * p < 0.05, ** p < 0.01, *** p < 0.001.

Response variable	N	Pollinator group	Contrast	Estimate	SE	Z	p-value	
Richness	10	-	Distant vs. Adjacent	0.152	0.326	0.467	0.887	
			Inside vs. Adjacent	-0.080	0.353	-0.227	0.972	
			Inside vs. Distant	-0.233	0.368	-0.631	0.803	
Abundance	20	Honeybee	Distant vs. Adjacent	1.000	0.336	2.976	0.015	*
			Inside vs. Adjacent	3.887	0.167	23.301	<0.001	***
			Inside vs. Distant	2.887	0.294	9.808	<0.001	***
		Other bees	Distant vs. Adjacent	0.635	0.299	2.122	0.148	
			Inside vs. Adjacent	-0.339	0.170	-1.995	0.194	
			Inside vs. Distant	-3.861	0.196	-19.708	<0.001	***
	10	Other bees excluding *E. oraniensis*	Distant vs. Adjacent	-0.254	0.386	-0.659	0.778	
			Inside vs. Adjacent	0.107	0.184	0.580	0.824	
			Inside vs. Distant	0.361	0.390	0.925	0.612	
Visitation rate	20	Honeybee	Distant vs. Adjacent	0.913	0.267	3.425	0.003	**
			Inside vs. Adjacent	3.315	0.088	37.656	<0.001	***
			Inside vs. Distant	2.401	0.253	9.487	<0.001	***
		Other bees	Distant vs. Adjacent	1.050	0.259	4.056	<0.001	***
			Inside vs. Adjacent	-0.052	0.109	-0.479	0.982	
			Inside vs. Distant	-3.503	0.115	-30.375	<0.001	***