

**Collateral effects of beekeeping: impacts on pollen-nectar resources and wild bee communities**

Anna Torné-Noguera<sup>a,\*</sup>, Anselm Rodrigo<sup>a,b</sup>, Sergio Osorio<sup>a</sup>, Jordi Bosch<sup>a</sup>

<sup>a</sup> CREAM, 08193 Cerdanyola del Vallès, Spain

<sup>b</sup> Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Spain

Accepted manuscript

This is the author's version of a work that was accepted for publication in Basic and applied ecology (Ed. Elsevier). Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in Torné-Noguera, A., et al. "Collateral effects of beekeeping: impacts on pollen-nectar resources and wild bee communities" in Basic and applied ecology, vol. 17, issue 3 (May 2016), p. 199-209. DOI 10.1016/j.baae.2015.11.004

\*Corresponding author. Tel.: +34 93 5814851; fax: +34 93 5814151.

E-mail address: a.torne@creaf.uab.cat.

1 **Abstract**

2 Due to the contribution of honey bees (*Apis mellifera*) to wild flower and crop pollination,  
3 beekeeping has traditionally been considered a sustainable practice. However, high honey bee  
4 densities may have an impact on local pollen and nectar availability, which in turn may  
5 negatively affect other pollinators. This is exacerbated by the ability of honey bees to recruit  
6 foragers to highly rewarding flower patches. We measured floral resource consumption in  
7 rosemary (*Rosmarinus officinalis*) and thyme (*Thymus vulgaris*) in 21 plots located at different  
8 distances from apiaries in the scrubland of Garraf Natural Park (Barcelona), and related these  
9 measures to visitation rates of honey bees, bumblebees (*Bombus terrestris*) and other  
10 pollinators. In the same plots, we measured flower density, and used pan traps to characterize  
11 the wild bee community. Flower resource consumption was largely explained by honey bee  
12 visitation and marginally by bumblebee visitation. After accounting for flower density, plots close  
13 to apiaries had lower wild bee biomass. This was due to a lower abundance of large bee  
14 species, those more likely to be affected by honey bee competition. We conclude that honey  
15 bees are the main contributors to pollen/nectar consumption of the two main flowering plants in  
16 the scrubland, and that at the densities currently occurring in the park (3.5 hives / km<sup>2</sup>) the wild  
17 bee community is being affected. Our study supports the hypothesis that high honey bee  
18 densities may have an impact on other pollinators via competition for flower resources.

19

20 **Zusammenfassung**

21 Wegen des Beitrages der Honigbiene (*Apis mellifera*) bei der Bestäubung von Wildblumen und  
22 Nutzpflanzen wurde die Bienenhaltung traditionell als eine nachhaltige Aktivität angesehen.  
23 Indessen können hohe Honigbiendichten Auswirkungen auf die lokale Verfügbarkeit von  
24 Nektar und Pollen haben, was wiederum andere Bestäuber negativ beeinflussen könnte. Dies  
25 wird verstärkt durch die Fähigkeit der Honigbiene, Sammlerinnen zu lohnenden Sammelstellen  
26 zu dirigieren. Im Buschland des Garraf-Naturparks bei Barcelona maßen wir den Verbrauch von  
27 Blütenressourcen an Rosmarin (*Rosmarinus officinalis*) und Thymian (*Thymus vulgaris*) an 21  
28 Standorten, die unterschiedlich weit von Bienenständen entfernt lagen, und setzten diese Werte  
29 in Bezug zu den Besuchsraten von Honigbienen, Hummeln (*Bombus terrestris*) und sonstigen  
30 Bestäubern. An den gleichen Standorten bestimmten wir die Blütendichte und setzten

31 Farbschalen ein, um die Wildbienengemeinschaft zu erfassen. Die Nutzung der Blüt enressou  
32 wurde weitgehend durch die Besuchsraten der Honigbiene erklärt und in geringfügigem Maße  
33 durch Hummelbesuch. Nach Berücksichtigung der Blütendichte wiesen Standorte in der Nähe  
34 von Bienenständen eine geringere Wildbienen-Biomasse auf. Dies war auf eine geringere  
35 Abundanz der großen Wildbienenarten zurückzuführen, also der Arten, die wahrscheinlich  
36 durch die Konkurrenz der Honigbiene beeinträchtigt werden. Wir schließen, dass Honigbienen  
37 den größten Beitrag zum Pollen- bzw. Nektarverbrauch bei den beiden wichtigsten  
38 Blütenpflanzen des Gebietes leisten und dass die Wildbienengemeinschaft bei den  
39 gegenwärtigen Honigbienendichten im Park (3.5 Völker/km<sup>2</sup>) beeinflusst wird. Unsere  
40 Untersuchung unterstützt die Hypothese, dass hohe Honigbienendichten durch Konkurrenz um  
41 Blütenressourcen einen Einfluss auf andere Bestäuber haben könnten.

42

43 **Keywords:** Bee conservation; Exploitative competition; Honey bees; Pollinator community;

44 Resource consumption.

45

46

Accepted manuscript

47 **Introduction**

48

49 The introduction of large populations of highly competitive species into a new area may affect  
50 resident populations, ultimately resulting in changes in the structure of native communities  
51 (Ehrenfeld, 2010; Levine et al., 2003). This may occur when exotic species, introduced either  
52 accidentally or intentionally, turn invasive and compete for limited resources with local species  
53 occupying a similar niche (Byers, 2000; Petren & Case, 1996). In addition to exotic species,  
54 domesticated species may also affect resident species. A clear example is the presence of  
55 cattle or sheep in natural or semi-natural areas, potentially competing with large herbivores for  
56 pasture (Stewart, Bowyer, Kie, Cimon, & Johnson, 2002; Young, Palmer, & Gadd, 2005).  
57 Domesticated animals benefit from human assistance, including protection against predators  
58 and veterinary care, and therefore may have a competitive advantage over wild species.

59

60 Among domesticated animals, the European honey bee (*Apis mellifera*) is undoubtedly one of  
61 the globally most spread. Native to Eurasia and Africa, honey bees are now kept in all  
62 continents except Antarctica, initially for honey production (Crane, 1990), but mostly for crop  
63 pollination (Free, 1993), being, by far, the main managed pollinator worldwide (Aizen & Harder,  
64 2009; Breeze et al., 2014; Garibaldi et al., 2013). Consequently, beekeeping has traditionally  
65 been considered a beneficial practice, and its sustainability has been taken for granted. This is  
66 reflected in the current lack of specific legislation in most countries worldwide, whereby  
67 beekeeping is considered to be beneficial and is usually allowed in nature reserves and other  
68 types of protected areas, including some National Parks. In many cases, beekeeping in these  
69 areas is not only allowed but even promoted as a traditional, sustainable activity (information  
70 obtained from natural park and wildlife managers from 8 European countries, see  
71 acknowledgements). It is therefore not surprising that *A. mellifera* is routinely reported as a  
72 dominant species in plant-pollinator networks worldwide, even in studies conducted in natural  
73 habitats (Forup et al. 2008, Bosch et al. 2009, Kaiser-Bunbury et al. 2009, Valido et al. 2014;  
74 see Davila & Wardle 2008 for a rare exception). However, as in other kinds of animal  
75 husbandry, large apiaries resulting in high densities of foragers may have an impact on local  
76 food resources (pollen and nectar in this case), which ultimately may negatively affect other

77 flower-visiting insects. Because they live in large colonies comprising tens of thousands of  
78 individuals and because they maintain elevated hive temperatures even during the winter  
79 (Seeley, 1985), honey bees have high energetic requirements, and their foraging ranges span  
80 several kilometres (Visscher & Seeley, 1982). In addition, honey bees have the ability (unique to  
81 them and some stingless bees) to communicate the location of flower resources to nest mates,  
82 thus concentrating large numbers of foragers in highly rewarding patches (von Frisch, 1967).  
83 Thus, honey bees are highly efficient pollen-nectar foragers and, when present in large  
84 densities, may potentially create a competition scenario with other pollinators.

85

86 Competition may take place through interference or through resource exploitation (Tilman,  
87 1982). Interference competition occurs directly between individuals through aggressive  
88 encounters (e.g., honey bees chasing other pollinators out of a flower or flower patch). Such  
89 aggressive interactions have sometimes been observed (e.g. Pinkus-Rendon et al. 2005), but  
90 the fact that most studies do not report aggressive encounters indicates that they are not  
91 common (e.g. Roubik 1978, Hudewenz & Klein 2013). After several years of field work, we can  
92 assert that such interactions are very rare in our study area. Exploitative competition occurs  
93 indirectly between individuals through a limiting resource, such as food or nesting sites.  
94 Competition for nesting resources can be ruled out in this case because wild bees in temperate  
95 zones do not nest in the kind of large cavities used by honey bees, and because feral colonies  
96 are very rare in our study area, as in most of Europe (Jaffé et al., 2009). Competition for flower  
97 resources is much more likely to occur because honey bees are highly generalistic in pollen and  
98 nectar use, and their diet widely overlaps with that of other flower-visiting species.

99

100 Various studies have explored potential adverse effects of honey bees on local pollinator  
101 communities. However, demonstrating a competition scenario is extremely difficult owing to the  
102 large foraging ranges of honey bees (several km) (Goulson, 2003; Seeley, 1985), combined  
103 with their ability to communicate the location of rich flower patches, thus allowing colonies to  
104 adjust their foraging areas and flower choices as pollen-nectar standing crops vary through time  
105 and space (Visscher & Seeley, 1982). For this reason, most studies have so far focused on  
106 indirect evidences of competition between honey bees and wild bees, such as resource overlap

107 (Steffan-Dewenter & Tscharntke, 2000), changes in flower choice (Forup & Memmott, 2005;  
108 Valido et al., 2014), foraging activity (Thomson, 2004), and visitation rates (Hudewenz & Klein,  
109 2013; Roubik, 1978) of wild pollinators confronted with different honey bee scenarios. Other  
110 studies have measured changes in population abundance and richness of wild bees under  
111 different honey bee densities (Forup & Memmott, 2005; Roubik & Wolda, 2001; Roubik, 1978;  
112 Steffan-Dewenter & Tscharntke, 2000). Fewer studies have looked for more direct evidence of  
113 competition, such as changes in reproductive success (Elbgami, Kunin, Hughes, & Biesmeijer,  
114 2014; Goulson & Sparrow, 2009; Steffan-Dewenter & Tscharntke, 2000; Thomson, 2004), and  
115 the outcomes of these studies are not consistent. Some have found negative effects of honey  
116 bees (Goulson & Sparrow, 2009; Thomson, 2004) while others have not (Roubik & Wolda,  
117 2001; Steffan-Dewenter & Tscharntke, 2000).

118  
119 For exploitative competition to occur, floral resources should be limiting. However, to our  
120 knowledge, no study has hitherto measured the effects of honey bee abundance on pollen and  
121 nectar availability. This is important because we currently do not know the magnitude of the  
122 impact of honey bees on flower resources compared to resident pollinators. In this study we  
123 address the potential effects of beekeeping on wild bee communities in an environmentally  
124 protected natural area. Our objective is to study the impact of honey bee flower visitation on  
125 pollen and nectar consumption and the effect of beekeeping on the abundance, richness and  
126 composition of the local wild bee community. Because honey bees are very abundant and given  
127 their ability to recruit large numbers of foragers to the most rewarding flower patches, we have  
128 three hypotheses: (1) Honey bees will be the main contributors to flower resource consumption.  
129 We therefore expect pollen and nectar levels to be lower in areas close to apiaries; (2) Structure  
130 of the wild bee community will be modified by high honey bee densities. We expect wild bee  
131 richness and abundance to be lower close to apiaries; (3) Among wild bees, we expect large  
132 species (with higher feeding requirements; Müller et al., 2006), to be most affected.

133

## 134 **Materials and methods**

135

### 136 ***Study area***

137

138 This study was conducted in the Natural Park of el Garraf (Barcelona, Catalonia, NE Spain), a  
139 Mediterranean scrubland dominated by *Quercus coccifera*, *Pistacia lentiscus*, *Rosmarinus*  
140 *officinalis* and *Thymus vulgaris*. Over the last years, we identified 64 entomophilous plant  
141 species and 288 insect pollinator species in the park.

142

143 The Natural Park of el Garraf is classified as category V of the International Union for  
144 Conservation of Nature (IUCN) (Dudley, 2008), which includes the majority (62%) of the  
145 environmentally protected land in the Mediterranean region (López Ornat, Pons Reynés, &  
146 Noguera, 2007). Category V parks are defined as protected areas with an important biological,  
147 ecological, cultural and picturesque value based on the interaction between human populations  
148 and the environment via traditional management practices. In Catalonia, current policies  
149 regulating environmental impacts of human activities do not mention beekeeping (Law 20/2009,  
150 DOGC 5524). Rather, beekeeping is considered an innocuous activity and *A. mellifera* is  
151 declared a “species of special interest” (Decree 110/2003, DOGC 3870).

152

153 Our study area is entirely located in the park, encompassing a surface of 32 km<sup>2</sup>. We selected  
154 21 plots of 40 m x 40 m distributed more or less regularly across the study area. Distances  
155 between nearest plots ranged from 585 to 1354 m. Based on the information provided by the  
156 Department of Agriculture and subsequently verified *in situ*, we located 21 apiaries close to the  
157 study area for a total of 475 hives (see Appendix A). Minimum distance of our plots to the  
158 nearest apiary ranged from 262 m to 5122 m.

159

### 160 **Flower resource surveys**

161

162 To study flower resource consumption, we worked on rosemary (*Rosmarinus officinalis*) and  
163 thyme (*Thymus vulgaris*). These two species are, by far, the most abundant entomophilous  
164 species in the study area, producing 70-90% of the flowers in the scrubland (Bosch et al., 2009;  
165 Flo, 2014). In addition, the two species are very attractive to honey bees and are considered  
166 highly desirable for honey production (Bonet, Rita, & Sebastià, 1985; Cambra, 2008). In addition

167 to honey bees, rosemary and thyme attract a variety of other pollinators. We have recorded 46  
168 and 47 species visiting rosemary and thyme, respectively (Bosch et al. 2009). Of these, 13 and  
169 17 species are wild bees, including some early-flying *Andrena* (*A. angustior*, *A. nigroaenea*) and  
170 *Anthophora* (*A. acervorum*, *A. dispar*) that concentrate most of their foraging on these two plant  
171 species. All surveys were conducted in 2011 under fair weather.

172

### 173 *Pollen*

174

175 Rosemary pollen surveys were conducted in March, when the species was in full bloom. In each  
176 plot, we selected between 20 and 30 plants on which we marked 8 recently-opened flowers  
177 (with fresh, fully pollen-loaded stamens). Before the onset of pollinator activity (9:00), we  
178 collected 4 of the marked flowers per plant, and stored them together in a vial filled with ethanol  
179 70%. After 18:00, when foraging activity had ceased, the remaining 4 flowers per plant were  
180 collected and preserved following the same procedure.

181

182 Thyme pollen surveys were conducted in April, during peak bloom of this species. We selected  
183 between 20 and 30 thyme plants per plot and marked 4 recently-opened flowers in each of  
184 them, following the same criteria as for rosemary. Before 9:00 we collected the two stamens of  
185 one side (left or right) of each flower, and stored them together in a vial filled with ethanol 70%.  
186 After 18:00 we collected the two remaining stamens of each flower.

187

188 In the laboratory, vials with stamens were sonicated for 10 minutes in an ultrasonic bath to  
189 dislodge pollen grains from the anthers. Afterwards, each anther was inspected under the  
190 stereomicroscope and pollen grains still adhering to the anthers were manually detached with  
191 the aid of an insect pin. Later, we took 8 drops of 2.5  $\mu$ l of the resulting pollen suspension and  
192 counted the number of pollen grains under the stereomicroscope. Previous trials showed that  
193 the number of drops necessary to stabilize pollen counts was 6. We then measured the  
194 remaining ethanol volume in the vial, and estimated the total number of pollen grains in each  
195 sample. From these data, we estimated the number of pollen grains per flower in the morning



196 and in the evening, which we used to calculate pollen consumption. Overall, we sampled 4005  
197 rosemary flowers and 2366 thyme flowers.

198

### 199 *Nectar*

200

201 Nectar consumption is difficult to measure because nectar secretion is a more or less  
202 continuous process (Pacini, Nepi, & Vesprini, 2003), so that consumption may be compensated  
203 by subsequent secretion. In some cases, secretion may be even stimulated by consumption  
204 (Castellanos, Wilson, & Thomson, 2002; Ordano & Ornelas, 2004). In addition, nectar secretion  
205 can be strongly conditioned by weather conditions (Jakobsen & Kristjánsson, 1994; Petanidou &  
206 Smets, 1996). We therefore decided to measure nectar standing crops at the end of the day as  
207 a surrogate for nectar consumption.

208

209 Thyme flowers produce very small amounts of nectar (Arnan, Escolà, Rodrigo, & Bosch, 2014),  
210 which may become difficult to extract, especially in warm dry days. For this reason, nectar  
211 surveys were only conducted on rosemary. At the end of each sampling day, we used 1- $\mu$ l  
212 capillary tubes to measure the volume of nectar remaining in the flowers. This was done on  
213 most of the flowers used in the evening pollen surveys. We measured nectar standing crops in  
214 1628 rosemary flowers (mean number of flowers per plot = 86; range = 33 - 117).

215

### 216 ***Pollinator visitation rates***

217

218 To relate pollen and nectar consumption to pollinator activity, we conducted pollinator surveys  
219 between 9:00 and 18:00 in each plot on the same day in which pollen and nectar measures  
220 were taken. At each plot, we selected 10 rosemary and 10 thyme plants. These plants were not  
221 the same used in pollen/nectar surveys to avoid potential accidental contact with flowers  
222 marked for pollen-nectar measures. On each marked plant we conducted a number of pollinator  
223 counts (mean= 10, range= 5-15) throughout the day. In each count, the selected plant was  
224 observed for 2 minutes and all pollinators contacting flowers were recorded. Total observation  
225 time was 72 h 48 min for rosemary and 76 h 34 min for thyme. At the end of the day, we

226 counted the number of open flowers in each plant. *Apis mellifera* and the bumblebee *Bombus*  
227 *terrestris* were, by far, the two most frequent pollinators visiting the two plant species. Therefore,  
228 we grouped pollinators into three categories: *A. mellifera*, *B. terrestris*, and other pollinators  
229 (mostly other bees, along with some dipterans and a few lepidopterans and coleopterans).  
230 Visitation rates of each pollinator group were calculated as the number of contacts per minute  
231 and per 1000 flowers.

232

### 233 ***Bee community***

234

235 To assess bee community structure and composition, we placed 6 sampling stations in each  
236 plot. Each sampling station consisted of a metal bar holding 3 pan traps painted yellow, white  
237 and blue respectively, one metre above the ground (Westphal et al. 2008). We conducted 8  
238 biweekly surveys from mid-March to late June 2010, in which traps were set at 8:00-9:00,  
239 before the onset of pollinator activity (around 9:30) and collected after 18:00. All plots were  
240 sampled on the same 8 days (see Torné-Noguera et al. (2014) for details). We captured 6580  
241 bee specimens, which were dried and pinned for identification. In addition, we netted and  
242 weighed a few individuals of each species/sex to obtain measures of fresh body weight (n=1-52  
243 specimens per species). Species were subsequently classed as small (body weight <55 mg) or  
244 large (>70 mg) (see Torné-Noguera et al. (2014) for details).

245

### 246 ***Flower abundance***

247

248 To estimate flower abundance in each plot, we considered the main flowering species in the  
249 scrubland (*R. officinalis*, *T. vulgaris*, *Dorycnium pentaphyllum*, *Cistus albidus*, *Cistus salvifolius*  
250 and *Cistus monspeliensis*), which together accounted for >70% of the flowers in each plot. We  
251 measured two perpendicular widths and the height of each flower patch in two 40 x 1 m  
252 perpendicular transects centered in the middle of the plot. Then we estimated the number of  
253 flowers of each species based on previously established equations relating patch volume and  
254 number of open flowers at peak bloom ( $r^2=0.36-0.63$ ,  $p=0.001-0.015$ ) (see Torné-Noguera et  
255 al., 2014). Because the three *Cistus* species were much less abundant than the other species,

256 and their flowering periods largely overlap, we lumped together these three species into a single  
257 category (*Cistus* abundance).

258

## 259 **Statistical analysis**

260

### 261 *Visitation rates and pollen/nectar consumption*

262

263 Preliminary analyses showed no correlation between explanatory variables (visitation rates of  
264 the different pollinator groups). In pollen analysis, honey bee visitation rate and other pollinators  
265 visitation rate were log-transformed because there was a logarithmic relationship between these  
266 variables and pollen consumption. We initially fit a generalized linear model (GLM) assuming a  
267 binomial error distribution (adequate for proportion data such as pollen consumption), with *A.  
268 mellifera* visitation rate, *Bombus terrestris* visitation rate, and other pollinators visitation rate as  
269 predictive variables. However, the model showed overdispersion. Therefore, we finally opted for  
270 a quasibinomial GLM. We then compared the saturated model with the various non-saturated  
271 models and chose the best one using ANOVA (as AIC cannot be calculated for quasi model  
272 families). Finally, we checked for normality and homoscedasticity of the residuals. We used  
273 pseudo- $R^2$  as a measure of the goodness-of-fit.

274

275 In nectar analyses, we log-transformed the explanatory variable other pollinators visitation rate  
276 because it showed a logarithmic relationship with the response variable. We fit a generalized  
277 linear model (GLM) with a Gaussian error distribution, with nectar standing crop as the  
278 response variable and visitation rate of the various pollinator groups as predictive variables. We  
279 selected the best model using the second-order Akaike Information Criterion (AICc), adequate  
280 for small samples.

281

### 282 *Bee community*

283

284 We used MiraMon SIG software (Pons, 2014) to establish the linear distance of each plot to the  
285 nearest apiary, a measure commonly used in honey bee studies (Elbgami et al., 2014;  
286 Hudewenz & Klein, 2013; Steffan-Dewenter & Tscharrntke, 2000; Thomson, 2004).

287

288 To evaluate the potential relationship between distance to the nearest apiary and wild bee  
289 community structure, we run GLM models for wild bee abundance, wild bee richness and wild  
290 bee biomass. Because wild bee community structure may also be influenced by flower  
291 availability (Torné-Noguera et al., 2014), we included flower abundance of *T. vulgaris*, *R.*  
292 *officinalis*, *D. pentaphyllum* and *Cistus* as predictor variables. Correlations between predictor  
293 variables were low (ranging from -0.27 to 0.33) and non-significant. We did not include nesting  
294 substrate availability in the analysis because we know from previous studies that this is not a  
295 good predictor of bee community structure and composition in the study area (Torné-Noguera et  
296 al., 2014).

297

298 Bee biomass was analyzed with a GLM with a Gaussian distribution. For bee abundance and  
299 bee richness models, we chose a GLM with a Poisson error distribution, adequate for count  
300 data. However, both models showed overdispersion, and thus we opted for models with a  
301 negative binomial distribution. In all three analyses, we selected the best model with the AICc  
302 criterion. Best models were later checked for normality and homoscedasticity. Because large  
303 bees might respond differently from small bees due to their higher feeding requirements (Müller  
304 et al., 2006), we run additional analyses separately for small (<55 mg) and large (>70 mg) bees.  
305 The best model explaining wild bee richness showed heteroscedasticity. Thus, we used White's  
306 heteroscedasticity-corrected covariance matrices to make inference.

307

308 All analyses were computed with R (R Core Team, 2014).

309

## 310 **Results**

311

### 312 ***Pollen and nectar consumption***

313

314 *Apis mellifera* and *B. terrestris* accounted for the majority of visits to both rosemary (61.2 and  
315 30.1%, respectively) and thyme (39.5 and 34.8%). Visits of other pollinators amounted to 8.7  
316 and 25.7% of the visits to rosemary and thyme, respectively. Honey bee flower visits and  
317 bumblebee flower visits were not correlated (rosemary:  $\tau = 0.23$ ,  $p = 0.16$ ; thyme:  $\tau = 0.04$ ,  $p =$   
318 0.83). Honey bee visitation rate showed a negative relationship with distance to the nearest  
319 apiary ( $r^2 = 42.25$ ,  $p = 0.009$ ).

320

321 Mean  $\pm$  SE number of pollen grains in newly-opened rosemary flowers was  $5185 \pm 70$ , and  
322 these numbers decreased to  $1831 \pm 68$  by the end of the day. Pollen consumption in our plots  
323 ranged from 25.1% to 90.1% (mean  $\pm$  SE =  $65.6 \pm 4.0$ ). The best model for rosemary pollen  
324 consumption (pseudo- $R^2 = 0.54$ ) included *A. mellifera* visitation rate ( $p = 0.004$ ) and, marginally,  
325 *B. terrestris* visitation rate ( $p = 0.06$ ) (Fig. 1A and B).

326

327 Thyme flowers contained  $1220 \pm 30$  pollen grains in the morning and  $577 \pm 18$  at the end of the  
328 day. Thyme pollen consumption in the various plots ranged between 19.2% and 76.5% (mean  $\pm$   
329 SE =  $54.3 \pm 3.5$ ). The best model for thyme pollen consumption (pseudo- $R^2 = 0.42$ ) included *A.*  
330 *mellifera* visitation rate ( $p = 0.002$ ) and *B. terrestris* visitation rate ( $p = 0.04$ ) (Fig. 1C and D).

331

332 Rosemary nectar standing crops in the 21 plots ranged from 0 to  $6.31 \mu\text{L}/\text{flower}$  ( $0.26 \pm 0.39$ ).  
333 The best model explaining rosemary nectar levels (pseudo- $R^2 = 0.42$ ) included *A. mellifera*  
334 visitation rate ( $p = 0.04$ ) and, marginally, *B. terrestris* visitation rate ( $p = 0.05$ ) (Fig. 2).

335

### 336 **Bee community**

337

338 Pan trap surveys yielded 6580 bee specimens corresponding to 98 species. Sixty-three of the  
339 non-*Apis* species were small (fresh body weight  $< 55$  mg) and 34 were large ( $> 70$  mg). Honey  
340 bee abundance in the pan traps was negatively related to distance to the nearest apiary  
341 (logarithmic relationship,  $r^2 = 49.73$ ,  $p = 0.0004$ ).

342

343 No variables entered the model of wild bee richness (Table 1), and similar results were obtained  
344 when small and large bees were analyzed separately (Table 1). The best model for bee  
345 abundance (pseudo-R<sup>2</sup>= 0.48) included *Cistus* flower abundance (p= 0.002) and *T. vulgaris*  
346 flower abundance (p= 0.004). Similar results were obtained when only small bees were taken  
347 into account (pseudo-R<sup>2</sup>= 0.41; *Cistus* abundance (p= 0.008); *T. vulgaris* abundance (p= 0.03)).  
348 Instead, the best fit model for large bee abundance (pseudo-R<sup>2</sup>= 0.50) included distance to the  
349 nearest apiary (p= 0.02) and, marginally, *Cistus* abundance (p= 0.06) (Fig. 3A and B; Table 1).  
350 To be conservative, we re-ran the latter analysis without 3 possible leverage points (Cook's D =  
351 0.5 to 1), and obtained similar results with a lower goodness-of-fit (pseudo-R<sup>2</sup>= 0.28, distance to  
352 the nearest apiary p= 0.02, *Cistus* abundance p= 0.06). The best wild bee biomass model  
353 (pseudo-R<sup>2</sup>= 0.56) included *Cistus* flower abundance (p= 0.002) along with distance to the  
354 nearest apiary (p= 0.02). The best model for small bees (pseudo-R<sup>2</sup>= 0.27) included only *Cistus*  
355 abundance (p= 0.02) (Table 1). Conversely, the best model for large bees (pseudo-R<sup>2</sup>= 0.54)  
356 included distance to the nearest apiary (p= 0.007) and, marginally, *Cistus* abundance (p= 0.06)  
357 (Fig. 3C and D).

358

## 359 Discussion

360

361 Honeybees outnumbered the most frequent wild bee (the bumblebee *B. terrestris*) on rosemary  
362 and thyme flowers, the two main flowering plants in the study area. All workers of these two bee  
363 species collected nectar, and some of them also collected pollen. Our results demonstrate that  
364 honey bees were the main species contributing to pollen and nectar consumption. The  
365 contribution of *B. terrestris* was much lower, and other pollinators played a non-detectable role  
366 in flower resource consumption. In addition to being the most frequent visitors to rosemary and  
367 thyme, *A. mellifera* and *B. terrestris* visit more flowers per individual plant than other pollinators  
368 (Arnan et al., 2014). Mean pollen consumption per plot was slightly higher for rosemary (mean=  
369 65.6%, range= 25.1 - 90.1%) than for thyme (mean= 54.3%, range= 19.2 - 76.5%), but to a  
370 greater or lesser extent, most plots had considerable amounts of pollen and nectar available at  
371 the end of the day. This may suggest that flower resources are not a limiting factor for the bee  
372 community. However, the energetic gain obtained from flowers with pollen-nectar levels below a

373 certain threshold may be insufficient to compensate foraging costs, especially for large bees,  
374 with higher energetic demands (Heinrich, 1975). Bees have been shown to move away from  
375 less rewarding patches (Heinrich, 1979). Our pollen-nectar surveys were conducted during peak  
376 bloom of the two main flower species in the study area. By the end of April, flower resources are  
377 much scarcer in the Park, and overall visitation rates are much higher (Bosch et al., 2009; Filella  
378 et al., 2013; Flo, 2014). Consequently, we expect the potential effects of intensive honey bee  
379 foraging to be greater in late-spring. In the summer, when floral resources in the Park are very  
380 low, some beekeepers move their hives to mountain areas.

381

382 Our study also shows that the wild bee community is affected and modified in areas close to  
383 apiaries, with a lower overall wild bee biomass mediated by a lower abundance of large bees.  
384 Small bees require less energy to fly and sustain foraging and nesting activities (Heinrich,  
385 1975). In addition, small bees require smaller pollen/nectar amounts to produce an offspring  
386 (Müller et al., 2006). Thus, pollen and nectar standing crops in areas close to the apiaries may  
387 be sufficient for small bees but not for large bees. If so, large bees may be forced to nest  
388 somewhere else or widen their foraging ranges, which are well known to be positively related to  
389 body size (Gathmann & Tschardt, 2002; Greenleaf, Williams, Winfree, & Kremen, 2007;  
390 Guédot, Bosch, & Kemp, 2009). As for small bees, even if their abundance did not diminish  
391 close to apiaries, their fitness might still be affected by the lower pollen/nectar standing crops.  
392 At the intra-specific level, bee adult body size is directly related to the amount of pollen-nectar  
393 consumed by the larva (Bosch & Vicens, 2002; Ribeiro, 1994), and some studies have shown  
394 reductions in offspring body size in populations flying in areas with low levels of flower  
395 resources (Bosch, 2008; Peterson & Roitberg, 2006). Other studies have found that bumblebee  
396 colonies produce smaller workers in areas with managed honey bees, probably due to  
397 pollen/nectar scarcity (Elbgami et al., 2014; Goulson & Sparrow, 2009). Small offspring are  
398 more likely to die during development (Bosch, 2008) and during wintering (Bosch & Kemp,  
399 2004; Tepedino & Torchio, 1982). Smaller females are also less likely to found a nest (Bosch &  
400 Vicens, 2006; Tepedino & Torchio, 1982). Low levels of floral resources may also enhance  
401 parasitism in solitary bees (Goodell, 2003), as females are forced to make longer foraging trips  
402 to gather a pollen/nectar load, thus leaving the nest unguarded and exposed to cleptoparasites

403 (Seidelmann, 2006). In agreement with our results, some studies investigating the potential  
404 impact of honey bees on wild bee communities have found wild bee abundance to be lower  
405 near apiaries (Forup & Memmott, 2005; Thomson, 2006), but others have not (Roubik & Wolda,  
406 2001; Steffan-Dewenter & Tschardtke, 2000). On the other hand, and in agreement with other  
407 studies (Forup & Memmott, 2005; Roubik & Wolda, 2001; Steffan-Dewenter & Tschardtke,  
408 2000), bee richness was not influenced by proximity to apiaries in our study.

409

410 In addition to honey bee density, bee abundance and biomass may also be influenced by flower  
411 abundance and distribution. Our models show that *Cistus* flowers have an important role in  
412 structuring the Garraf bee community. The three *Cistus* species occurring in the park bloom in  
413 April, at a time when wild bee abundance and diversity are high, and flower resources show a  
414 strong decline after the blooming period of *R. officinalis* and *T. vulgaris* (Bosch et al., 2009;  
415 Filella et al., 2013; Flo, 2014). Other plants blooming at this time are either very scarce  
416 (*Gladiolus illyricus*, *Orobanche latisquama*), or produce smaller amounts of pollen and nectar  
417 (*D. pentaphyllum*) (Flo, 2014). Previous studies in the same area have shown that *C. albidus*  
418 and *C. salvifolius* constitute a hub in the Garraf pollination network, attracting higher numbers of  
419 pollinator species and receiving higher flower visitation rates than any other plant species  
420 (Bosch et al., 2009).

421

422 Our study provides evidence to support the hypothesis that high densities of managed honey  
423 bees have a negative impact on wild bee communities. Our results point to pollen-nectar  
424 depletion as a mechanism explaining this negative impact. To our knowledge, this is the first  
425 time flower resource consumption has been measured in studies exploring the potential effects  
426 of managed honey bees on wild pollinators. To confirm or refute this hypothesis, future studies  
427 should include long-term monitoring of wild bee populations and direct measures of fitness.

428 From a land management perspective, decisions on the number of hives allowed in an  
429 environmentally protected area should be based on the carrying capacity of the flower  
430 community at the landscape level. However, to provide a range of appropriate hive densities is  
431 extremely difficult for several reasons. First, even in a natural habitat such as the Garraf Natural  
432 Park, flower spatial distribution is far from homogeneous (Torné-Noguera et al., 2014). Second,



433 availability of flower resources in our study area changes dramatically throughout the season  
434 and from year to year (Flo, 2014). Third, foraging ranges of honey bees span several kilometers  
435 and are highly variable in time (Visscher & Seeley, 1982). Fourth, resource depletion may also  
436 depend on the abundance of wild pollinator populations. Given all these uncertainties, our study  
437 suggests that, in this particular habitat, wild bee communities are likely to be affected at  
438 densities over 3.5 hives per km<sup>2</sup> (475 hives / 134 km<sup>2</sup>).

439

#### 440 **Epilogue**

441

442 The Garraf Natural Park is partially located in the municipality of Olivella. In May 2012, the city  
443 council discussed a petition to install 357 new honey bee hives in the Park. The council  
444 examined a report commissioned by the board of directors of the Park cautioning about the  
445 potential effects of intensive beekeeping on other pollinators. The council finally approved the  
446 installation of the additional 357 hives based on current legislation considering beekeeping an  
447 "innocuous activity".

448

#### 449 **Acknowledgements**

450

451 We are thankful to H. Barril-Graells, I. Raya, O. Riera, S. Reverté, P. Cucurull, M. A.  
452 Requesens, I. Doncel, J. Prat, A. Lázaro, A. Revoltós, J. P. Vilellas, N. Mas, M. Viladés, A.  
453 Llavina, A. López, D. González, and L. Muñoz for their help with field and laboratory work, and  
454 to M. Fernández for his statistical advice. D. Duggan (DAHG, Ireland), H. Haller  
455 (Schweizerische Nationalpark, Switzerland), M. Heinonen (Metsähallitus, Finland), A. Korakis  
456 (Pindos National Park, Greece), J. Lanek (Jordbruksverket, Sweden), L. Pelle (Parco  
457 Nazionale dell'Aspromonte, Italy), J. Torrentó (Diputació de Barcelona, Spain) and H. P. Vicente  
458 (ICNF, Portugal) kindly provided information on beekeeping legislation in their respective  
459 countries. This study was supported by the Spanish Ministry of Science and Innovation  
460 (MICINN, projects CGL2005-00491, CGL2009-12646 and CSD2008-0040); and an FPI  
461 fellowship (BES-2010-042520) to A.T-N.; and by Diputació de Barcelona. S.O. was supported  
462 by a FI fellowship (2012 FI SO080484) from Generalitat de Catalunya.

463

464 **Appendix A. Supplementary data**

465

466 Supplementary data associated with this article can be found, in the online version, at XXXXX.

467

468 **References**

469

470 Aizen, M. A., & Harder, L. D. (2009). The global stock of domesticated honey bees is growing

471 slower than agricultural demand for pollination. *Current Biology*, 19(11), 915–918.

472 doi:10.1016/j.cub.2009.03.071

473 Arnan, X., Escolà, A., Rodrigo, A., & Bosch, J. (2014). Female reproductive success in

474 gynodioecious *Thymus vulgaris*: Pollen versus nutrient limitation and pollinator foraging

475 behaviour. *Botanical Journal of the Linnean Society*, 175, 395–408. doi:10.1111/boj.12173

476 Bonet, A., Rita, J., & Sebastià, M. T. (1985). *La flora mel·lífera de la circumscripció de*

477 *Barcelona*. Diputació de Barcelona.

478 Bosch, J. (2008). Production of undersized offspring in a solitary bee. *Animal Behaviour*, 75(3),

479 809–816. doi:10.1016/j.anbehav.2007.06.018

480 Bosch, J., & Kemp, W. P. (2004). Effect of pre-wintering and wintering temperature regimes on

481 weight loss, survival, and emergence time in the mason bee *Osmia cornuta*

482 (Hymenoptera: Megachilidae). *Apidologie*, 35, 469–479. doi:10.1051/apido:2004035

483 Bosch, J., Martín González, A. M., Rodrigo, A., & Navarro, D. (2009). Plant-pollinator networks:

484 adding the pollinator's perspective. *Ecology Letters*, 12(5), 409–19. doi:10.1111/j.1461-

485 0248.2009.01296.x

486 Bosch, J., & Vicens, N. (2002). Body size as an estimator of production costs in a solitary bee.

487 *Ecological Entomology*, 27, 129–137. doi:10.1046/j.1365-2311.2002.00406.x

- 488 Bosch, J., & Vicens, N. (2006, December 16). *Relationship between body size, provisioning*  
489 *rate, longevity and reproductive success in females of the solitary bee Osmia cornuta.*  
490 *Behavioral Ecology and Sociobiology*. doi:10.1007/s00265-005-0134-4
- 491 Breeze, T. D., Vaissière, B. E., Bommarco, R., Petanidou, T., Seraphides, N., Kozák, L., ...  
492 Potts, S. G. (2014). Agricultural policies exacerbate honeybee pollination service supply-  
493 demand mismatches across Europe. *PLoS ONE*, 9(1). doi:10.1371/journal.pone.0082996
- 494 Byers, J. E. (2000). Competition between two estuarine snails: implications for invasions of  
495 exotic species. *Ecology*, 81(5), 1225–1239. doi:10.1890/0012-  
496 9658(2000)081[1225:CBTESI]2.0.CO;2
- 497 Cambra, J. (2008). Flora mel·lífera de Catalunya. In *Apicultura i producció de mel a Catalunya.*  
498 *Dossier tècnic.* (p. 20). Generalitat de Catalunya. Departament d'Agricultura, Alimentació i  
499 Acció Rural.
- 500 Castellanos, M. C., Wilson, P., & Thomson, J. D. (2002). Dynamic nectar replenishment in  
501 flowers of *Penstemon* (Scrophulariaceae). *American Journal of Botany*, 89(1), 111–118.  
502 doi:10.3732/ajb.89.1.111
- 503 Crane, E. (1990). *Bees and beekeeping: science, practice and world resources.* Oxford, UK:  
504 Heinemann Newnes.
- 505 Davila, Y. C., & Wardle, G. M. (2008). Variation in native pollinators in the absence of  
506 honeybees: implications for reproductive success of an Australian generalist-pollinated  
507 herb *Trachymene incisa* (Apiaceae). *Botanical Journal of the Linnean Society*, 156, 479–  
508 490. doi:10.1111/j.1095-8339.2007.00774.x
- 509 Dudley, N. (2008). *Guidelines for applying protected area management categories.* (N. Dudley,  
510 Ed.). Gland, Switzerland: IUCN.
- 511 Ehrenfeld, J. G. (2010). Ecosystem consequences of biological invasions. *Annual Review of*  
512 *Ecology, Evolution, and Systematics*, 41(1), 59–80. doi:10.1146/annurev-ecolsys-102209-  
513 144650

- 514 Elbgami, T., Kunin, W. E., Hughes, W. O. H., & Biesmeijer, J. C. (2014). The effect of proximity  
515 to a honeybee apiary on bumblebee colony fitness, development, and performance.  
516 *Apidologie*, 45(4), 504–513. doi:10.1007/s13592-013-0265-y
- 517 Filella, I., Primante, C., Llusà, J., Martín González, A. M., Seco, R., Farré-Armengol, G., ...  
518 Peñuelas, J. (2013). Floral advertisement scent in a changing plant-pollinators market.  
519 *Scientific Reports*, 3, 3434. doi:10.1038/srep03434
- 520 Flo, V. (2014). *Eight-year variability in flowering patterns in a Mediterranean scrubland*  
521 *community: consequences on pollen-nectar composition*. MSc Thesis. Autonomous  
522 University of Barcelona.
- 523 Forup, M. L., Henson, K. S. E., Craze, P. G., & Memmott, J. (2008). The restoration of  
524 ecological interactions: plant-pollinator networks on ancient and restored heathlands.  
525 *Journal of Applied Ecology*, 45(3), 742–752. doi:10.1111/j.1365-2664.2007.01390.x
- 526 Forup, M. L., & Memmott, J. (2005). The relationship between the abundances of bumblebees  
527 and honeybees in a native habitat. *Ecological Entomology*, 30(1), 47–57.  
528 doi:10.1111/j.0307-6946.2005.00660.x
- 529 Free, J. B. (1993). *Insect pollination of crops*. Academic Press, London.
- 530 Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S.  
531 A., ... Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey  
532 bee abundance. *Science*, 339(6127), 1608–11. doi:10.1126/science.1230200
- 533 Gathmann, A., & Tschardtke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal*  
534 *Ecology*, 71(5), 757–764. doi:10.1046/j.1365-2656.2002.00641.x
- 535 Goodell, K. (2003). Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae)  
536 foraging, reproduction, and brood parasitism. *Oecologia*, 134(4), 518–27.  
537 doi:10.1007/s00442-002-1159-2

538 Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of*  
539 *Ecology, Evolution, and Systematics*, 34(1), 1–26.  
540 doi:10.1146/annurev.ecolsys.34.011802.132355

541 Goulson, D., & Sparrow, K. R. (2009). Evidence for competition between honeybees and  
542 bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation*, 13(2),  
543 177–181. doi:10.1007/s10841-008-9140-y

544 Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and  
545 their relationship to body size. *Oecologia*, 153(3), 589–96. doi:10.1007/s00442-007-0752-  
546 9

547 Guédot, C., Bosch, J., & Kemp, W. P. (2009). Relationship between body size and homing  
548 ability in the genus *Osmia* (Hymenoptera; Megachilidae). *Ecological Entomology*, 34(1),  
549 158–161. doi:10.1111/j.1365-2311.2008.01054.x

550 Heinrich, B. (1975). Energetics of pollination. *Annual Review of Ecology and Systematics*, 6,  
551 139–170. doi:10.1146/annurev.es.06.110175.001035

552 Heinrich, B. (1979). Resource heterogeneity and patterns of movement in foraging bumblebees.  
553 *Oecologia*, 40, 235–245. doi:10.1007/BF00345321

554 Hudewenz, A., & Klein, A.-M. (2013). Competition between honey bees and wild bees and the  
555 role of nesting resources in a nature reserve. *Journal of Insect Conservation*, 17(6), 1275–  
556 1283. doi:10.1007/s10841-013-9609-1

557 Jaffé, R., Dietemann, V., Allsopp, M. H., Costa, C., Crewe, R. M., Dall'Olio, R., ... Moritz, R. F.  
558 A. (2009). Estimating the density of honeybee colonies across their natural range to fill the  
559 gap in pollinator decline censuses. *Conservation Biology*, 24(2), 583–93.  
560 doi:10.1111/j.1523-1739.2009.01331.x

561 Jakobsen, H. B., & Kristjánsson, K. K. (1994). Influence of temperature and floret age on nectar  
562 secretion in *Trifolium repens* L. *Annals of Botany*, 74, 327–334.  
563 doi:10.1006/anbo.1994.1125

- 564 Kaiser-Bunbury, C. N., Memmott, J., & Müller, C. B. (2009). Community structure of pollination  
565 webs of Mauritian heathland habitats. *Perspectives in Plant Ecology, Evolution and*  
566 *Systematics*, 11(4), 241–254. doi:10.1016/j.ppees.2009.04.001
- 567 Levine, J. M., Vilà, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., & Lavelle, S. (2003).  
568 Mechanisms underlying the impacts of exotic plant invasions. *Proceedings. Biological*  
569 *Sciences / The Royal Society*, 270(1517), 775–81. doi:10.1098/rspb.2003.2327
- 570 López Ornat, A., Pons Reynés, A., & Noguera, M. (2007). *Use of IUCN protected areas*  
571 *management categories in the Mediterranean region*. (A. López Ornat, A. Pons Reynés, &  
572 M. Noguera, Eds.). Consejería de Medio Ambiente of Junta de Andalucía, Sevilla, Spain  
573 and IUCN, Gland, Switzerland and Malaga, Spain.
- 574 Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., & Dorn, S. (2006). Quantitative pollen  
575 requirements of solitary bees: Implications for bee conservation and the evolution of bee–  
576 flower relationships. *Biological Conservation*, 130(4), 604–615.  
577 doi:10.1016/j.biocon.2006.01.023
- 578 Ordano, M., & Ornelas, J. F. (2004). Generous-like flowers: nectar production in two epiphytic  
579 bromeliads and a meta-analysis of removal effects. *Oecologia*, 140(3), 495–505.  
580 doi:10.1007/s00442-004-1597-0
- 581 Pacini, E., Nepi, M., & Vesprini, J. L. (2003). Nectar biodiversity: A short review. *Plant*  
582 *Systematics and Evolution*, 238, 7–21. doi:10.1007/s00606-002-0277-y
- 583 Petanidou, T., & Smets, E. (1996). Does temperature stress induce nectar secretion in  
584 Mediterranean plants? *New Phytologist*, 133(3), 513–518. doi:10.1111/j.1469-  
585 8137.1996.tb01919.x
- 586 Peterson, J. H., & Roitberg, B. D. (2006). Impacts of flight distance on sex ratio and resource  
587 allocation to offspring in the leafcutter bee, *Megachile rotundata*. *Behavioral Ecology and*  
588 *Sociobiology*, 59(5), 589–596. doi:10.1007/s00265-005-0085-9

- 589 Petren, K., & Case, T. J. (1996). An experimental demonstration of exploitation competition in  
590 an ongoing invasion. *Ecology*, 77(1), 118–132. doi:10.2307/2265661
- 591 Pinkus-Rendon, M. A., Parra-Tabla, V., & Meléndez-Ramírez, V. (2005). Floral resource use  
592 and interactions between *Apis mellifera* and native bees in cucurbit crops in Yucatán,  
593 México. *The Canadian Entomologist*, 137(04), 441–449. doi:10.4039/n04-043
- 594 Pons, X. (2014). MiraMon. Geographic Information System and Remote Sensing Software.  
595 *Geographical Information System and Remote Sensing Software*. Barcelona: CREA.
- 596 R Core Team. (2014). R: A language and environment for statistical computing. Vienna, Austria:  
597 R Foundation for Statistical Computing.
- 598 Ribeiro, M. F. (1994). Growth in bumble bee larvae: relation between development time, mass,  
599 and amount of pollen ingested. *Canadian Journal of Zoology*, 72(11), 1978–1985.  
600 doi:10.1139/z94-270
- 601 Roubik, D. W. (1978). Competitive interactions between neotropical pollinators and africanized  
602 honey bees. *Science*, 201, 1030–1032. doi:10.1126/science.201.4360.1030
- 603 Roubik, D. W., & Wolda, H. (2001). Do competing honey bees matter? Dynamics and  
604 abundance of native bees before and after honey bee invasion. *Population Ecology*, 43(1),  
605 53–62. doi:10.1007/PL00012016
- 606 Seeley, T. D. (1985). *Honeybee ecology: a study of adaptation in social life*. Princeton, New  
607 Jersey: Princeton University Press.
- 608 Seidelmann, K. (2006). Open-cell parasitism shapes maternal investment patterns in the Red  
609 Mason bee *Osmia rufa*. *Behavioral Ecology*, 17(July), 839–848.  
610 doi:10.1093/beheco/arl017
- 611 Steffan-Dewenter, I., & Tschamntke, T. (2000). Resource overlap and possible competition  
612 between honey bees and wild bees in central Europe. *Oecologia*, 122(2), 288–296.  
613 doi:10.1007/s004420050034

- 614 Stewart, K. M., Bowyer, R. T., Kie, J. G., Cimon, N. J., & Johnson, B. K. (2002). Temporospatial  
615 distributions of elk, mule deer, and cattle: resource partitioning and competitive  
616 displacement. *Journal of Mammalogy*, 83(1), 229–244. doi:10.1644/1545-  
617 1542(2002)083<0229:TDOEMD>2.0.CO;2
- 618 Tepedino, V. J., & Torchio, P. F. (1982). Phenotypic variability in nesting success among *Osmia*  
619 *lignaria propinqua* females in a glasshouse environment: (Hymenoptera: Megachilidae).  
620 *Ecological Entomology*, 7(4), 453–462. doi:10.1111/j.1365-2311.1982.tb00688.x
- 621 Thomson, D. M. (2004). Competitive interactions between the invasive European honey bee  
622 and native bumble bees. *Ecology*, 85(2), 458–470. doi:10.1890/02-0626
- 623 Thomson, D. M. (2006). Detecting the effects of introduced species: a case study of competition  
624 between *Apis* and *Bombus*. *Oikos*, 114(3), 407–418. doi:10.1111/j.2006.0030-  
625 1299.14604.x
- 626 Tilman, D. (1982). *Resource competition and community structure*. Princeton, New Jersey:  
627 Princeton University Press.
- 628 Torné-Noguera, A., Rodrigo, A., Arnan, X., Osorio, S., Barril-Graells, H., Correia da Rocha-  
629 Filho, L., & Bosch, J. (2014). Determinants of spatial distribution in a bee community:  
630 nesting resources, flower resources, and body size. *PLOS ONE*, 9(5), e97255.  
631 doi:10.1371/journal.pone.0097255
- 632 Valido, A., Rodriguez-Rodriguez, M. C., & Jordano, P. (2014). Impacto de la introducción de la  
633 abeja doméstica (*Apis mellifera*, Apidae) en el Parque Nacional del Teide (Tenerife, Islas  
634 Canarias). *Ecosistemas*, 23(3), 58–66.
- 635 Visscher, P. K., & Seeley, T. D. (1982). Foraging strategy of honeybee colonies in a temperate  
636 deciduous forest. *Ecology*, 63(6), 1790–1801. doi:10.2307/1940121
- 637 Von Frisch, K. (1967). *The dance language and orientation of bees*. Harvard University Press.  
638 Cambridge, MA.



639 Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Petanidou, T., Potts, S. G., ... Vaissi, E.  
640 (2008). Measuring bee diversity in different European habitats and biogeographical  
641 regions. *Ecological Monographs*, 78(4), 653–671. doi:10.1890/07-1292.1

642 Young, T. P., Palmer, T. M., & Gadd, M. E. (2005). Competition and compensation among  
643 cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological*  
644 *Conservation*, 122(2), 351–359. doi:10.1016/j.biocon.2004.08.007

645

Accepted manuscript

**Table 1.** Results of GLMs analyzing wild bee richness, abundance and biomass in 21 plots as a function of distance to the nearest apiary, and abundance of *Cistus* spp., *Thymus vulgaris*, *Rosmarinus officinalis* and *Dorycnium pentaphyllum* flowers. P-values are only given for variables entering the models. Pseudo-R<sup>2</sup> is provided as a measure of goodness-of-fit.

Response variable		Explanatory variables					Pseudo-R <sup>2</sup>
		Distance to apiary	<i>Cistus</i>	<i>T. vulgaris</i>	<i>R. officinalis</i>	<i>D. pentaphyllum</i>	
Wild bee richness	Large species <sup>1</sup>	ns	ns	ns	ns	ns	--
	Small species <sup>2</sup>	ns	ns	ns	ns	ns	--
	All species	ns	ns	ns	ns	ns	--
Wild bee abundance	Large species <sup>1</sup>	p=0.019	p= 0.061	ns	ns	ns	0.50
	Small species <sup>2</sup>	ns	p= 0.008	p= 0.030	ns	ns	0.41
	All species	ns	p= 0.002	p= 0.042	ns	ns	0.48
Wild bee biomass	Large species <sup>1</sup>	p= 0.007	p= 0.059	ns	ns	ns	0.54
	Small species <sup>2</sup>	ns	p= 0.016	ns	ns	ns	0.27
	All species	p= 0.017	p= 0.016	ns	ns	ns	0.56

<sup>1</sup> Body weight >70 mg: <sup>2</sup> Body weight <55 mg.

646 **Fig.1.** Partial regression plots showing the contribution of honey bee and bumblebee visitation  
647 rates to rosemary and thyme pollen consumption in 21 plots, once the effect of other  
648 explanatory variables entering the GLMs has been removed (bumblebee visitation rate in (A)  
649 and (C); honey bee visitation rate in (B) and (D))

650

651 **Fig. 2.** Partial regression plots showing the contribution of honey bee and bumblebee visitation  
652 rates to rosemary nectar standing crops in 21 plots, once the effect of other explanatory  
653 variables entering the GLMs has been removed (bumblebee visitation rate in (A); honey bee  
654 visitation rate in (B))

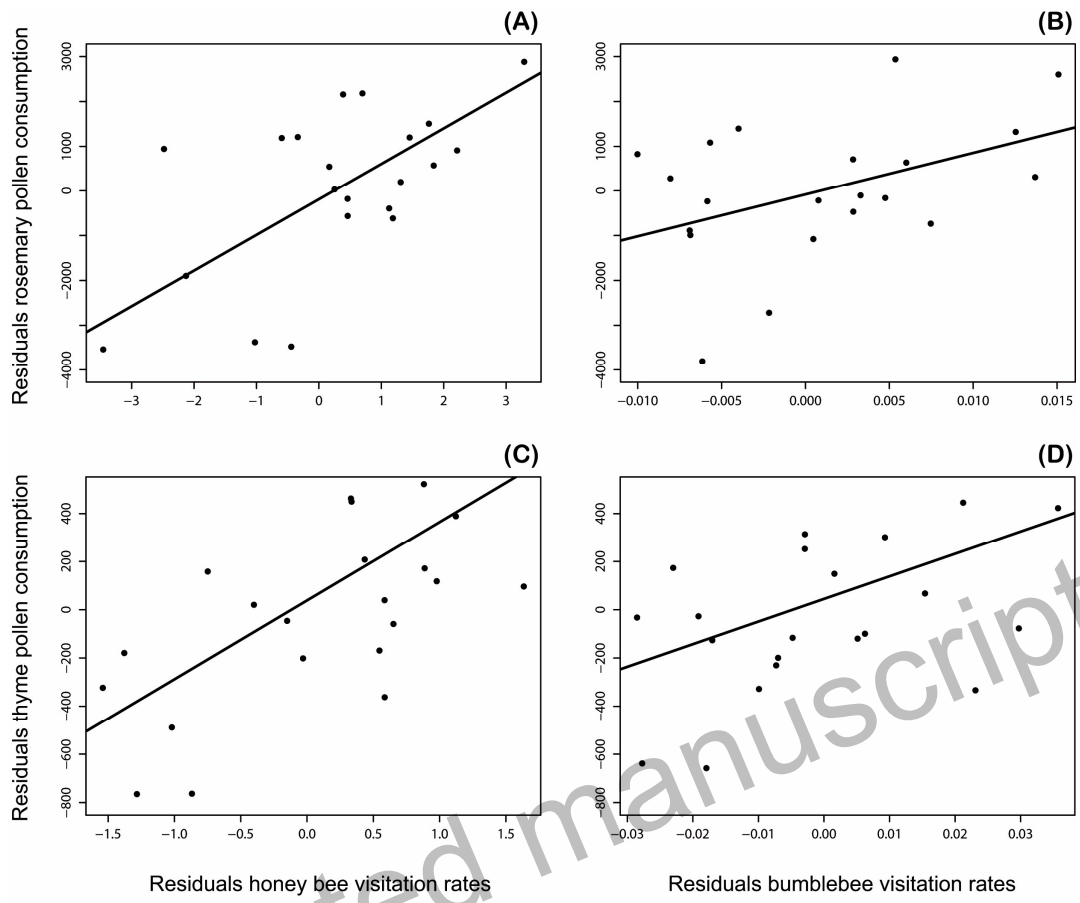
655

656 **Fig. 3.** Partial regression plots showing the relationship between distance to the nearest apiary  
657 and large bee (body weight >70 mg) abundance and biomass in 21 plots, once the effect of  
658 other explanatory variables entering the GLMs has been removed (*Cistus* flower abundance in  
659 (A) and (C); distance to the nearest apiary in (B) and (D))

660

Accepted manuscript

661 **Fig.1.**  
662

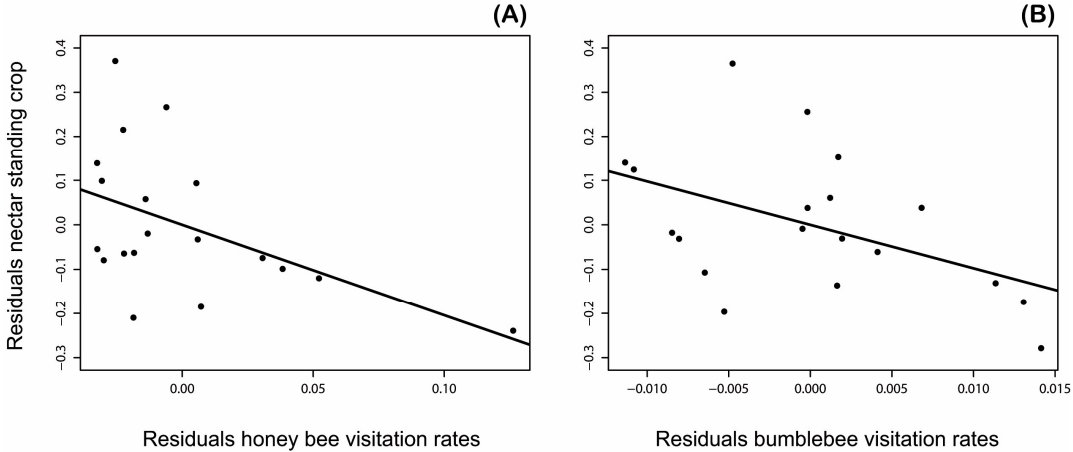


663

Accepted manuscript

664  
665

**Fig.2.**

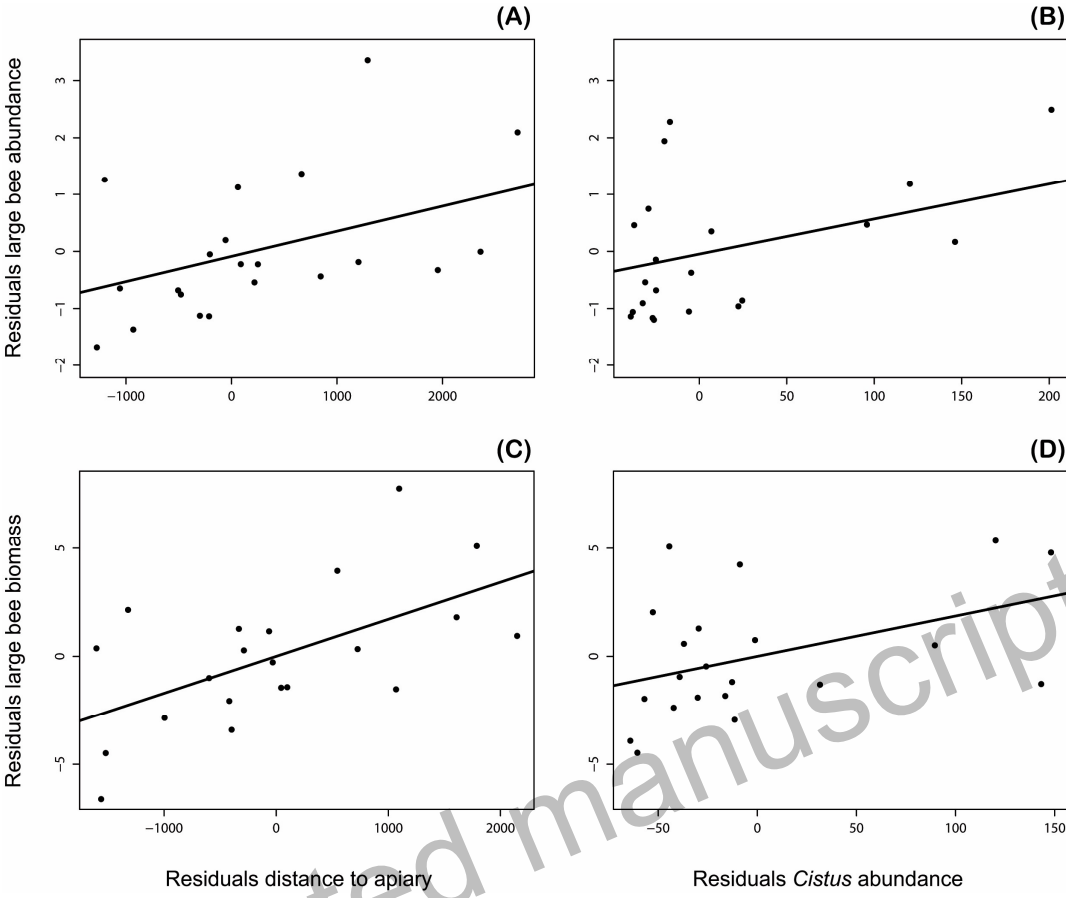


666

Accepted manuscript

667  
668

Fig.3.



669