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3 Complementarity and redundancy in the functional niche of cider
4 apple pollinators

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17 **Short title**

18 Functional niche of apple pollinators

19 **Abstract**

20 The magnitude and the stability of pollination services in entomophilous crops both
21 depend not only on honeybee management but also on the diversity of wild pollinators,
22 which enable additive contributions and replacement of species. This work evaluated
23 the functional niche of cider apple pollinators in Spain and found a highly
24 heterogeneous community of pollinators in taxonomic and functional terms. Through
25 different niche dimensions, our results suggest complementarity (i.e. niche
26 differentiation) in the contribution of the various groups to pollination, through
27 differences in abundance, foraging behaviour, diet and daytime and canopy distribution
28 patterns, as well as redundancy (i.e. niche similarity) in their responses to environmental
29 conditions. Thus, quantitative and qualitative complementarity would promote an
30 additive effect of different insects on pollination, while similarity in environmental
31 response would provide insurance against potential honeybee loss.

32

33 **Keywords: crop pollination / environmental response / foraging behaviour / *Malus***
34 ***domestica* / spatio-temporal patterns**

35

36 **1. Introduction**

37 The importance of insect pollinators for global food production is now unquestionable
38 (Klein et al. 2007; Garibaldi et al. 2013), and it will intensify under the scenario of
39 increasing food needs and anthropogenic pollinator loss (Potts et al. 2010; Goulson et
40 al. 2015). Farmers worldwide typically rely on the domesticated honeybee (*Apis*
41 *mellifera*) to ensure pollination services in many crops (Aizen and Harder 2009;
42 Garibaldi et al. 2013). However, depending exclusively on honeybee has been
43 demonstrated to be ineffective, and even hazardous, as honeybees may be unable to
44 cover the massive, short-term flowering of some crops (Brittain et al. 2013b; Grass et al.
45 2018), or could suffer severe declines due to colony collapse disorder or disease
46 (vanEngelsdorp et al. 2009). In this context, wild pollinators would seem essential in
47 overcoming honeybee constraints and to provide pollination insurance in the case of
48 honeybee loss (Garibaldi et al. 2013; Rader et al. 2016). In fact, the magnitude and
49 stability of pollination services in entomophilous crops is known to depend on the
50 diversity and the species turnover of insect pollinators (Garibaldi et al. 2013; Rader et
51 al. 2016; Winfree et al. 2018).

52 Ascertaining the role of pollinator diversity in crop pollination requires an
53 understanding of the additive effects of various pollinators, as well as their potential for
54 replacement following possible extinction. This can be achieved through studying the
55 functional niche of pollinators (Blüthgen and Klein 2011), which represents the
56 heterogeneity between insects contributing to pollination, by means of different
57 dimensions. In this sense, functional niche may be addressed through insect abundance
58 (Winfree et al. 2015), diet composition (Thomson and Goodell 2001), traits related to
59 the function (Garibaldi et al. 2015), and foraging behaviours affecting access to flowers
60 and pollen (Brittain et al. 2013a; Park et al. 2016). Also, functional niche may represent

61 the response of a species to the filtering effects of environmental conditions, such as
62 temperature, humidity or wind (e.g. Bartomeus et al. 2013; Brittain et al. 2013a). Thus,
63 depending on the extent of segregation or overlap of their niche dimensions, pollinators
64 may be considered as either complementary or redundant (Blüthgen and Klein 2011).
65 This classification is not trivial given that complementarity in contributions may lead to
66 additive effects across pollinators (Winfree 2013). In addition, complementarity in
67 environmental responses may increase pollination resilience to climate change (Rader et
68 al. 2013) while redundancy would ensure pollination stability across existing
69 environmental gradients in the case of extinctions (Winfree and Kremen 2009; Winfree
70 2013). Although complementarity and redundancy are apparently two mutually
71 exclusive scenarios, they can emerge simultaneously across different dimensions of the
72 functional niche of pollinators.

73 Apple is a major fruit crop throughout the world (FAO 2018) and is heavily
74 dependent on insect pollination (Klein et al. 2007). Pollinators determine apple
75 production quantitatively, with 92 to 100% of apple yield relying on pollinators (Garratt
76 et al. 2014; Miñarro and García 2016), as well as qualitatively, by increasing apple
77 weight or sugar content (Geslin et al. 2017; Sapir et al. 2017). Besides honeybee, wild
78 insects, including bumblebees, solitary bees and hoverflies, visit apple blossoms (e.g.
79 Földesi et al. 2016; Martins et al. 2015; Russo et al. 2017). Importantly, the abundance
80 and diversity of wild pollinators positively affects apple yield (Földesi et al. 2016;
81 Martins et al. 2015; Blitzer et al. 2016). These positive effects seem to be related to the
82 additive contributions of various pollinators that differ in abundance and quality
83 depending on their foraging patterns (Thomson and Goodell 2001; Martins et al. 2015;
84 Park et al. 2016). Although the functional variability of apple pollinators has been
85 highlighted (Martins et al. 2015; Park et al. 2016; Russo et al. 2017), to date no study

86 has focused on whole sets of apple pollinators by addressing simultaneously foraging
87 differences and responses to environmental conditions (but see Vicens and Bosch
88 2000a; 2000b; for a comparison *A. mellifera-Osmia cornuta*).

89 We therefore evaluate here the functional niche of apple pollinators, interpreting
90 niche differences in terms of complementarity or redundancy. We studied the cider
91 apple crops of the Asturias region in northern Spain, considering it to be a suitable
92 model for evaluating pollinator functionality because: 1) a species-rich pollinator
93 community is expected due to biogeographical and management factors (Miñarro et al.
94 2011); 2) the management of honeybee hives is not standardized in the locality, which
95 allows for high variability in the density of managed pollinators; and 3) regional
96 weather conditions vary widely during apple bloom, including rain and low
97 temperatures, providing large environmental gradients for pollinators. We hypothesised
98 that honeybee and wild pollinators would show complementarity in both their
99 contribution to pollination (Martins et al. 2015) and their response to climatic gradients
100 (Bartomeus et al. 2013). Specifically, we sought to apply a multi-dimensional niche
101 approach based on: 1) the structure and composition of the pollinator community; 2) the
102 foraging behaviour and pollen-vs-nectar preferences of the different insect groups; 3)
103 daytime temporal patterns; and 4) responses to daytime temperature and humidity.

104

105 **2. Materials and Methods**

106 **2.1. Study site**

107 Cider is a valuable traditional product with Protected Denomination of Origin status in
108 Asturias (northern Spain). Indeed, almost the entire regional apple yield (up to 50,000
109 tons per year) is devoted to cider production. Apple orchards are planted with selected
110 local cultivars that are tolerant to common apple diseases. As, in addition, the cultural

111 tolerance of growers to pests is high in general because aesthetic damage is of no
112 importance for cider apples, the use of fungicides and insecticides is not common.
113 These orchards are embedded in a highly variegated landscape and are typically
114 surrounded by natural woody vegetation (Miñarro and Prida 2013; García et al. 2018).
115 The low degree of agricultural intensification in these orchards and the surrounding
116 landscape thus allows for high animal diversity within orchards, including natural
117 enemies (Miñarro et al. 2011; García et al. 2018).

118

119 **2.2. Structure and composition of the pollinator community**

120 We aimed to identify the insect groups and species that comprised the pollinator
121 community in the cider orchards, as well as to assess their abundances. To do so we
122 surveyed apple pollinators in 2015-2016 in 26 cider apple orchards in Asturias (see
123 García et al. 2018, for a comprehensive description of sites). All orchards comprised
124 several cultivars, but sampling was carried out on a single local cultivar, ‘Regona’,
125 given that flower visits by pollinators may depend on cultivar (Garratt et al. 2016). Only
126 two orchards managed pollination by introducing honeybee hives.

127 Both in 2015 and in 2016, each orchard was surveyed three times, each time by a
128 different observer and at a different time in the day (from 1100 h to 1300 h, from 1300 h
129 to 1500 h or between 1500 h and 1700 h) in order to cover the maximum range of
130 pollinator activity. Surveys were made under standard climatic conditions: dry
131 vegetation, clear to lightly overcast skies, temperatures $>13^{\circ}\text{C}$, wind speed $<2.5\text{ m}\cdot\text{s}^{-1}$,
132 and when the ‘Regona’ cultivar was in full bloom. In each orchard, prior to full bloom
133 we marked five target trees (at least 15 m from the edge to avoid a potential edge effect;
134 Campbell et al. 2017), and then in each survey we observed a 1-m diameter area of the
135 canopy of each target tree for a period of 5 min, recording the number of insect visits

136 and the number of flowers in the selected area. In total, therefore, each orchard
137 accounted for 75 minutes of observation (3 visits * 5 trees * 5 min) per year. To avoid
138 disrupting floral visits, no insects were collected during the surveys and, therefore, we
139 were only able to reliably identify the most easily recognised species (e.g. *Apis*
140 *mellifera*, *Bombus* species, *Andrena pilipes*, *Episyrphus balteatus*, *Oxythreya funesta*,
141 etc.). Most visitors were, thus, assigned to one of the following groups: bumblebees,
142 wild bees (categorised according to body size as either large, medium or small, when,
143 respectively, bigger, similar or smaller than honeybees), hoverflies (predatory hoverflies
144 with aphidophagous larvae, *Eristalis* hoverflies), flies (Diptera other than hoverflies),
145 beetles, butterflies and “other”. In order to better assess species richness, we also made
146 separate assessments of apple pollinators by walking slowly along tree rows and
147 catching all floral visitors, during a 10 min period at during each survey event (i.e. a
148 sum of 30 min per orchard per year). Captured specimens were identified in the
149 laboratory.

150

151 **2.3. Foraging behaviour**

152 To estimate the differences in foraging behaviour between pollinator groups, we
153 quantified visitation rate (the number of flowers a pollinator visits in a minute), how the
154 insect approaches the flower (from the top or from the side), and tree canopy
155 distribution (part of tree canopy, upper or lower, visited by insects). We also assessed
156 inter-tree and inter-row movements (how often a pollinator left a tree to visit another,
157 and whether the new tree was in a different row). Apple cultivars are auto-incompatible
158 and thus, the frequent movement of pollinators between trees and tree rows is important
159 to secure pollen transfer between cultivars (Ramírez and Davenport 2013).

160 During the observations of floral visits across the 26 orchards studied (see 2.1),
161 we recorded the way in which the visitor approached flowers, distinguishing two
162 behaviours that can affect the pollination outcome (Thomson and Goodell 2001,
163 Martins et al. 2015; Russo et al. 2017): 1) ‘top-working’, when insects approached the
164 top of the flower, increasing the probability of contacting both anthers and stigma and
165 subsequently pollen removal; and 2) ‘side-working’, when insects landed on the petals
166 and approached the flower from the side, inserting their tongue in the base of stamens to
167 collect nectar without coming into contact with anthers or stigma. Insects gathering
168 pollen always contact the sexual organs of the flower (at least the anthers), and such
169 visits can be considered legitimate in terms of pollination, as they contribute to pollen
170 transfer. On the contrary, nectar-gathering insects can approach either from the side
171 (illegitimate visit: nectar is collected without contribution to pollination) or from the top
172 (legitimate visit). We calculated the frequency of top-working for each pollinator group.

173 Visitation rate and pollinator movements between trees and rows were sampled
174 in 2016 only, in a single orchard with an abundant and rich pollinator community. To do
175 this, any flower visitor detected during a slow walk along tree rows was visually tracked
176 until lost, recording tracking time, number of flowers visited, and whether each visited
177 flower was on the same or another tree and in the same or another tree row. Thus, we
178 calculated the visitation rate (number of flowers visited per minute), the frequency of
179 inter-tree movements (number of movements between trees per minute) and the
180 frequency of inter-row movements (number of movements between rows per minute)
181 for honeybees (N=45), bumblebees (74), wild bees (75) and hoverflies (44). Flies and
182 beetles were very passive and their movements were not recorded.

183 The distribution between the different parts of the tree canopy of pollinator visits
184 was studied in five orchards in 2017. We stood in front of a given focal tree (N=72; tree

185 height from ~3 to 5 m) for 1 min, recording for each flower visit whether the insect
186 visited the upper or the lower half of the canopy. In this way we were able to estimate
187 the frequency of visits to upper and lower canopy for honeybees, bumblebees, wild
188 bees, hoverflies, flies and beetles.

189 Differences between pollinator groups in terms of visitation rate and inter-tree
190 and inter-row movement rates were measured by means of Kruskal-Wallis tests (with
191 post-hoc between-pairs Mann-Whitney tests). We used Chi-square tests to analyse
192 whether a given pollinator group differed from a random distribution in the frequency of
193 top- versus side-working frequency, and in their frequency of visits to upper versus
194 lower canopy. We also used Chi-square tests to compare the frequencies of top-working
195 and of visits to upper canopy between pairs of pollinator groups.

196

197 **2.4. Trophic behaviour: pollen vs. nectar gathering**

198 Apple flower visitors may, as mentioned above, consume either one single resource
199 (pollen or nectar) or two (both pollen and nectar). During the surveys of all 26 orchards
200 (see 2.2), we also recorded the frequency of whether visitors were gathering pollen or
201 nectar, or both when visitors gathered pollen and nectar from the same flower or from
202 the consecutive flowers they visited. In such cases we summed one to the frequency of
203 each behaviour (pollen and nectar gathering). Departures from random in the frequency
204 of pollen versus nectar gathering for pollinator groups, as well as differences between
205 pairs of pollinator groups, were examined with Chi-square tests.

206

207 **2.5. Daytime temporal patterns**

208 In an experimental 1-ha orchard planted with a collection of more than 350 apple
209 cultivars, we studied the distribution of flower visits at different times of the day by

210 assigning visits to one of ten different hours (from 0900 h to 1800 h; hours hereafter).
211 Observations were made in censuses on 22 days (9 days in 2014 and 13 in 2016). In
212 each of the 220 censuses, one observer stood for 1 minute in front of 20 different trees,
213 counting and visually identifying all floral visitors belonging to six pollinator groups
214 (honeybees, bumblebees, wild bees, hoverflies, beetles and flies). For each pollinator
215 group and hour, we pooled all observations across days. We then made comparisons
216 between pairs of pollinator groups of the distribution of observations for the different
217 hours using Kolmogorov-Smirnov tests.

218

219 **2.6. Response to temperature and relative humidity**

220 We studied pollinator response to temperature and relative humidity within the same
221 sampling set up as in 2.5. The richness of cultivars in the experimental orchard enabled
222 sampling to take place over the long overall blooming period resulting from the
223 sequential bloom of different cultivars, which ensured that a variety of weather
224 conditions prevailed on the observation days. The temperature and humidity data used
225 in the analyses were from a weather station located 150 m away from the study site.

226 We used a spatially-explicit approach to evaluate the distribution of pollinator
227 abundances in an environmental, bi-dimensional space of temperature and relative
228 humidity. We estimated the degree of clumpiness (i.e. significant non-random
229 aggregation of abundance) within this environmental space for each pollinator group,
230 and quantified overlap/segregation between pollinator groups (i.e.
231 concordance/discordance in the distribution across environmental space). We used
232 Spatial Analysis by Distance Indices (SADIE, using Sadie Shell 2.0; Perry et al. 2002),
233 to calculate, for each pollinator group, an aggregation index (I_a) that measured
234 clumpiness in the distribution of abundance (with values $I_a = 1$ representing random, I_a

235 >1 clumped, and $I_a < 1$ regular distribution patterns). The degree of significance of I_a
236 (i.e. departure from a random distribution) was checked with a randomization procedure
237 (Perry et al. 2002). SADIE also provided a sampling point-level clustering index (v),
238 which quantified the degree to which the count at a given sampling point was
239 contributing to the overall clumpiness. The clustering indexes of different pollinator
240 groups may be correlated among themselves, in order to estimate overlap/segregation
241 between pairs of groups, through an association index Xp (Perry and Dixon 2002) that
242 ranges from + 1 (complete spatial association) to -1 (complete dissociation, 0 indicating
243 spatial independence), and whose statistical significance was quantified by the Dutilleul
244 method (it corrects the amount of degrees of freedom in the presence of spatial
245 autocorrelation).

246 In order to establish the environmental space for the analysis, we first considered
247 the complete gradients of temperature and relative humidity recorded during the
248 sampling. Temperature gradient (range: 11.8°C-22.4°C) was divided into eleven one-
249 degree intervals (11.5°C-12.4°C, ..., 21.5°C-22.4°C; hereafter 12°, ..., 22°) while we
250 considered the relative humidity gradient (34.8%-91.8%) to comprise nine five-percent
251 intervals (45.0%-49.9%, ..., 85.0%-90%; hereafter 45%, ..., 85%). Extreme values were
252 incorporated into the lowest or highest intervals as appropriate. A total of 99 (11x9)
253 combinations of temperature and relative humidity were possible, and data were
254 available for 58 of them (due to the negative correlation between temperature and
255 relative humidity; $r = -0.566$, $P < 0.0001$, $N = 220$). After this we considered a narrower
256 scale with the central range of environmental conditions by using seven (15°-21°)
257 temperature and five (50%-70%) relative humidity intervals (data available for 29 of 35
258 possible combinations). Aggregation indexes were estimated for all groups of insects at

259 the two study scales, as well as association indexes with respect to all possible pairings
260 of pollinator groups.

261

262 **3. Results**

263 **3.1. Pollinator community**

264 We recorded 3,405 insect visits to apple flowers (Figure 1) in 2015 and 2016 across 26
265 orchards. Hymenoptera (71.3%) were the dominant order, followed by Diptera
266 (26.7%), Coleoptera (1.3%) and Lepidoptera (0.4%). Overall, the honeybee (*Apis*
267 *mellifera*) was the most abundant taxon, followed by hoverfly, where *Eristalis* spp.
268 dominated over predatory species. Among the wild bees, those categorised as small
269 (mostly Halictidae) dominated over those categorised as medium or large (mostly
270 Andrenidae), while *Bombus terrestris* was the most abundant bumblebee.

271 Of the 82 species of floral visitors identified (Table S1), Hymenoptera was the
272 richest order (44 species), followed by Diptera (29 species). Wild bees, the richest
273 group, were dominated by Halictidae and Andrenidae. The group of hoverflies, with 21
274 species, was the richest of the dipterans.

275 *Apis mellifera* was ubiquitous (Table S1) and also the most abundant (>50% of
276 all pollinator visits in 21 of the 26 orchards; Figure S1). Another seven species (*Bombus*
277 *terrestris*, *Eristalis tenax*, *Episyrphus balteatus*, *Eristalis similis*, *Sphaerophoria scripta*,
278 *Bombus pratorum* and *Andrena nigroaenea*) occurred in 10 or more sites, in both years.

279

280 **3.2. Foraging behaviour**

281 Pollinator groups differed in the number of apple flowers visited per minute (Kruskal-
282 Wallis $\chi^2=144.7$; $df=3$; $P<0.001$; Mann-Whitney $U<429.0$; $P<0.001$ for all paired
283 comparisons, but for wild bees-hoverflies, $U=1430.0$; $P=0.226$; Figure 2A).

284 Bumblebees showed the highest visitation rate (16.7 ± 6.9 flowers.min⁻¹; mean \pm SD),
285 almost double that of honeybees (8.7 ± 2.4 flowers.min⁻¹). Wild bees and hoverflies
286 were the visitors which spent most time per flower during their visits (they visited only
287 4.8 ± 2.9 and 4.7 ± 4.4 flowers.min⁻¹, respectively).

288 Honeybees, bumblebees, hoverflies and wild bees mostly approached the
289 flowers from the top (χ^2 tests; $P < 0.001$ in all cases; Figure 2B), although with different
290 frequencies (bumblebees = hoverflies > wild bees > honeybees; χ^2 tests; $P < 0.001$ in all
291 paired combinations, but in bumblebee-hoverfly, $P = 0.385$). Flies were detected resting
292 in the petals or collecting nectar from the flower from the side in most cases ($P < 0.001$).
293 No differences in the frequency of top- and side-visits were detected for beetles
294 ($P = 0.095$).

295 Pollinators differed in the frequency of changing tree (KW $\chi^2 = 10.25$; $df = 3$;
296 $P < 0.017$; excluding flies and beetles due to lack of observations), with honeybees
297 changing between trees more frequently than wild bees ($U = 1300.5$; $P < 0.017$; Table S2).
298 In contrast, pollinators did not differ in the frequency of movement between tree rows
299 (KW $\chi^2 = 5.09$; $df = 3$; $P < 0.160$; Table S2).

300 Bumblebees, wild bees and hoverflies showed a preference in terms of tree
301 canopy part (Figure 2C), with bumblebees being more frequent in the upper canopy (χ^2
302 test; $P = 0.008$), with wild bees ($P = 0.037$) and hoverflies ($P = 0.009$) mostly appearing in
303 the lower canopy. The bumblebee preference for the upper canopy was significantly
304 stronger than in all other groups except beetles (χ^2 test $P = 0.095$ for bumblebees-beetles).

305

306 **3.3. Trophic behaviour: pollen vs. nectar gathering**

307 There was a preference for collecting nectar in honeybees (χ^2 test, $P < 0.001$), hoverflies
308 ($P < 0.001$) and flies ($P < 0.001$) (Figure 2D). However, no statistically significant

309 preferences for pollen or nectar were found for either bumblebees (χ^2 test, $P=0.394$) or
310 wild bees ($P=0.122$), although these groups did show a higher frequency of pollen
311 gathering than the other pollinators (χ^2 tests; $P<0.001$ for all pair combinations). Similar
312 differences emerged when comparing honeybees with hoverflies and flies (χ^2 tests;
313 $P<0.001$ for all pair combinations).

314

315 **3.4. Daytime temporal patterns**

316 Sampling in the experimental orchard provided 10,725 visits to flowers. The pollinator
317 community was dominated by honeybees (67.9%), bumblebees (15.8%), hoverflies
318 (10.0%), wild bees (4.2%), beetles (1.9%) and flies (0.3%). Pollinator groups differed in
319 how their daytime visits to flowers were distributed (Figure 3; Table S3). Namely,
320 honeybees, hoverflies and flies were more active than other groups in the first hours
321 (0900 h -1100 h), wild bees and beetles concentrated most of their activity in the central
322 hours (1200 h to 1500 h) and bumblebees were the most vespertine group, with 40% of
323 their visits occurring between 1600 h and 1800 h.

324

325 **3.5. Response to temperature and relative humidity**

326 Aggregation indexes indicated significant clumpiness in the abundances of pollinators
327 across the sampled environmental space (Table 1). Numbers of observations for all
328 groups gradually increased from low temperature -high humidity to high temperature-
329 low humidity conditions (Figure 4). An almost monotonic pattern was specially marked
330 for honeybees. There was significant concordance (i.e. overlap) in the large-scale
331 environmental distribution of all paired combinations of pollinator groups (Table 2).
332 Nevertheless, aggregation and concordance trends changed when the environmental
333 space was narrowed. Although most groups still showed clumpy distributions at this

334 smaller scale, fly and beetle abundances appeared randomly distributed (Table 1; Figure
335 4). More importantly, spatial concordance was not generalised, with bumblebee, fly and
336 beetle abundance patches occurring independent of those of honeybees, as was also the
337 case for wild bees and hoverflies (Table 2).

338

339 **4. Discussion**

340 In this study we characterized the whole community of insects visiting cider apple
341 flowers across a regional extent in northern Spain using non-manipulative sampling to
342 evaluate insect behaviour and environmental responses which are important to
343 pollination. We found a highly heterogeneous community of apple pollinators in both
344 taxonomic and functional terms. Through various dimensions of the functional niche of
345 pollination, our results suggest complementarity (i.e. niche segregation) in the different
346 pollinator groups' contribution to pollination (through differences in abundance,
347 foraging behaviour, diet and daytime distribution patterns), as well as scale-dependent
348 redundancy (i.e. niche overlap) in their response to environmental conditions.

349

350 **4.1 The cider apple pollinator community**

351 Our study was based on direct observation and capture of flower visitors, hence
352 providing conservative but unbiased information (compared with trap-sampling, Gibbs
353 et al. 2017), and widened the scope beyond the usual focus of bees (see also Rader et al.
354 2016). We detected an abundant and rich community of flower visitors of over 80
355 species, of which 48% were non-bee pollinators. This is not a surprising result, as apple
356 is an attractive flower resource due to the massive bloom (Grab et al. 2017) and easy
357 accessibility to nectar and pollen (Ramírez and Davenport 2013). As such, pollinator

358 pools very rich in wild species have also been found in apple crops in other regions (e.g.
359 Földesi et al. 2016; Martins et al. 2015; Campbell et al. 2017).

360 In terms of visitation rate, the community studied was dominated by *Apis*
361 *mellifera*, even though managed hives were present in only two of the orchards (see also
362 Joshi et al. 2016). The common presence of non-professional, honey-devoted hives in
363 farms around apple orchards, as well as the occurrence of some feral populations, would
364 explain honeybee dominance in Asturian apple. Nevertheless, this dominance was not
365 widespread: in several orchards honeybee represented less than 20% of floral visitors,
366 and in more than a third of orchards, almost 40% of visits were by wild pollinators
367 (Figure S1). In sum, despite being a –quantitatively– honeybee-dominated crop, cider
368 apple in Asturias benefits from a rich coterie of wild pollinators which are able to
369 ensure high visitation rates when honeybee is rare. As a result, orchards with a low
370 proportion of honeybees show visitation rates similar to those numerically dominated by
371 honeybees (Figure S1).

372

373 **4.2. Foraging and trophic behaviour**

374 We recorded notable differences among pollinator groups in terms of foraging and
375 trophic behaviour. First, pollinators differed in their speed of visiting flowers, with
376 bumblebees being faster than honeybees and, especially, wild bees or hoverflies (see
377 also Martins et al. 2015; Park et al. 2016, but see Vicens and Bosch 2000a). Second,
378 pollinators differed in the way they approached flowers, with bumblebees, wild bees
379 and hoverflies being mostly top-workers, whereas honeybees and flies showed
380 increased rates of side-working. Similar differences have been noted in other regions
381 (Vicens and Bosch 2000a, Martins et al. 2015; Park et al. 2016). Third, pollen vs. nectar
382 foraging also varied among groups, with bumblebees and wild bees, again, showing

383 higher frequencies of pollen gathering behaviour than honeybees, which is probably
384 associated with their higher dependence on pollen for reproduction and larval
385 development (Vaudo et al. 2015). Dipterans were, however, almost exclusively nectar
386 foragers. This, is to be expected because, despite female hoverflies can occasionally
387 feed on pollen to mature their ovaries and reach sexual maturity (Haslett 1989), they,
388 unlike bees, do not use pollen for feeding larvae (e.g. Owen and Gilbert 1989).
389 Nonetheless, hoverflies probably received and delivered high pollen loads as they
390 usually accessed nectar from the flower top, thus their hairy body would come into
391 contact with the flowers reproductive parts (e.g. *Eristalis* spp.). In honeybees, side-
392 working and nectar-gathering behaviour have been related with lower pollen removal
393 and deposition (Thomson and Goodell, 2001).

394 In this study we found honeybees moving between trees with a higher frequency
395 than other groups. The lower tolerance of honeybees to interspecific aggressive
396 encounters in trees could underpin this pattern (Brittain et al. 2013b; Sapir et al. 2017).
397 Nevertheless, we did not observe differences between pollinator groups in the frequency
398 of movements between tree rows (but see Campbell et al. 2017). We did however
399 register some spatial segregation of pollinators within tree canopies, with bumblebees
400 being more frequently observed in the upper part, wild bees and hoverflies at the
401 bottom, while honeybees were observed throughout the canopy. Irrespective of the
402 mechanism which provokes segregation (e.g. interspecific competition; Brittain et al.
403 2013a), it may have a positive impact on apple crop yield as different parts of the
404 blossom canopy would be setting fruit thanks to different insects (Brittain et al. 2013a).

405

406 **4.3. Daytime temporal patterns and response to temperature and relative humidity**

407 Flowers received pollinators during all the 10 hours over which observations were
408 conducted, although there were differences in how the different groups distributed their
409 visits throughout the day: wild bees, hoverflies and flies were early visitors, whereas
410 bumblebees showed a higher frequency of afternoon visits. This temporal segregation
411 could have positive consequences for apple pollination, leading to better coverage of the
412 daily interval of stigmatic receptivity and opening of anthers (Herrera 1990). Among the
413 potential mechanisms underlying the differences found may be differences in life
414 histories (e.g. some flies overwinter on petals taking advantage of radiation reflection
415 early in the morning; Vicens and Bosch 2000b), thermoregulation ability (small-sized
416 wild bees may depend more on day central temperatures; Bishop and Armbruster 1999),
417 but also interspecific competition (Brittain et al. 2013a).

418 Our spatial approach showed a significant overlap among pollinator groups in
419 their response to temperature and relative humidity. All pollinator groups increased in
420 abundance as conditions became warmer and dryer, and were able to cope with the
421 recorded range of weather conditions (temperature: 11.8-22.4°C, relative humidity:
422 34.8-91.8%). The absence of differences may result, nevertheless, from the limitation of
423 the observational space to detect the relevance of extreme or rare values, given the
424 strength of the large-scale, monotonic gradient based on the negative correlation
425 between temperature and humidity. In fact, when the response to environmental
426 conditions was analysed at a finer scale (i.e. reducing the magnitude of the
427 environmental gradient), some differences between pollinators groups arose under hot
428 and dry conditions, with bumblebees prevailing over honeybees, and flies and beetles
429 showing distributions less affected by the environmental gradients. Although we cannot
430 exclude competitive avoidance as an alternative explanation, such a fine-scale

431 segregation in the environmental space may also be due to different thermoregulation
432 constraints between species (Rader et al. 2013).

433

434 **4.4. Complementarity and redundancy in the cider apple pollination niche**

435 Our approach seeks to interpret the contribution of different flower visitors to cider
436 apple pollination by integrating different dimensions of functional niche. Importantly,
437 we found significant differences between pollinator groups in all niche components
438 assumed to impact on the magnitude of pollination: abundance, visitation rate, trophic
439 and foraging behaviour and spatio-temporal distribution. Thus, we consider that,
440 although numerically dominated by *Apis mellifera*, cider apple in Asturias is far from
441 being a honeybee-dependent crop. This is because wild pollinators show diverse
442 behaviours that may qualitatively compensate for their usually lower abundances (see
443 also Garratt et al. 2016). For example, the high visitation rate of the less common
444 bumblebees would mean a high proportion of flowers pollinated by this group.
445 Similarly, a higher frequency of legitimate visits (i.e. an enhanced effectiveness of
446 pollination) is expected from the predominantly top-working behaviour of bumblebees,
447 wild bees and hoverflies, as well as from the higher frequency of pollen collection
448 behaviour by bumblebees and wild bees. Therefore, by means of quantitative and
449 qualitative complementarity, we may expect an additive effect of the different insect
450 groups on pollination (Martins et al. 2015; Garratt et al. 2016).

451 Unlike the behavioural dimensions, and in contrast to our initial hypothesis, no
452 clear evidence of niche segregation in the pollinator response to environmental
453 conditions were found in our study. Some differences in the environmental distribution
454 were observed at the fine scale, for example between honeybees and bumblebees, flies
455 and beetles. These subtle differences could also mean additive contributions to

456 pollination, especially for non-bee pollinators (Rader et al. 2016). Nevertheless, the
457 wide overlap among pollinator taxa suggested a redundant response along the larger
458 environmental gradients studied here. This also means that, despite the frequent much
459 higher abundance of honeybees, when wild pollinators are considered all together, they
460 covered all the conditions in which honeybees occurred. Thus, in a scenario of
461 honeybee locally extinct (e.g. by colony collapse disorder), the local community of wild
462 insects could fulfil pollination requirements over the complete environmental gradients
463 covered by the managed species. This sort of redundancy may be thought to be positive
464 for the stability of apple yield, when providing ecological insurance under events of
465 honeybee collapse and high meteorological variation during apple bloom (Vicens and
466 Bosch 2000b). In fact, both types of events are particularly relevant in the context of
467 climate change (Bartomeus et al. 2013; Rader et al. 2013).

468 As a final remark, we would highlight that, as has been shown for other crops
469 (Garibaldi et al. 2013; Rader et al. 2016), both wild insects and honeybees are probably
470 necessary to optimize the global service of pollination in cider apple. We encourage,
471 therefore, actions to promote wild pollinator diversity through habitat management
472 (floral cover in orchards and surrounding woody hedgerows; Miñarro and Prida 2013;
473 Dicks et al. 2016; Campbell et al. 2017), in parallel with honeybee management regimes
474 that are non-harmful for wild species (Geldmann and González-Varo 2018).

475

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485

486 **Authors Contribution**

487 MM and DG conceived and designed the research, collected field data, analysed the
488 data and wrote the manuscript, which both authors have approved.

489

490 **Conflict of interest**

491 The authors declare that they have no potential conflict of interest.

492

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628

629 **Figure captions**

630 **Fig 1.** Community of insects visiting apple flowers in 26 cider orchards in Asturias
631 (NW Spain) in 2015 and 2016.

632

633 **Fig 2.** Foraging and trophic behaviour of cider-apple pollinators. A) Visitation rate
634 (number of flowers visited per minute), B) frequency of top-working, C) frequency of
635 visits recorded in the upper half of the canopy and D) frequency of individuals gathering
636 pollen. Numbers at the top of each column indicate sample size. Different letters
637 indicate differences between pollinator groups. Asterisks over the columns on B), C)
638 and D) reflect deviations from 1:1 for each pollinator (***: $P \leq 0.001$, **: $P \leq 0.01$, *: P
639 ≤ 0.05). For A), boxplots indicate 25-75% quartiles (box boundaries), median (thick
640 horizontal bar), largest and smallest observed values (whiskers), outliers (small circles)
641 and extreme values (asterisks).

642

643 **Fig 3.** Distributions of frequencies of visits to apple flowers of each pollinator group
644 throughout the day (from 0900 to 1800 h). Numbers at the top of each column indicate
645 number of pollinators observed in each group.

646

647 **Fig 4.** Response surfaces of all the insects visiting apple flowers in relation to
648 temperature and relative humidity. Dots in the first plot indicate the combinations of
649 temperature and humidity registered during sampling (censuses). Coloured contours are
650 interpolated from the number of visits in censuses. The colour scales represent the
651 number of visits; note scale differences between insect groups. The inner rectangle
652 indicates the small-scale observational space that considers a narrower, central range of
653 environmental conditions (15°-21° C temperature and 50%-70% relative humidity).
654 This small-scale subset accumulated more than 65% of sampled abundances for all
655 insect groups.

656

657 **Table 1.** Index of aggregation (I_a) measuring the degree of global clumpiness (i.e.
658 aggregation of counts in space) and its significance (P), indicating the degree in which
659 the aggregated distribution departs from a random distribution. Data for large and small
660 scales are shown.

Group	Large scale		Small scale	
	I_a	P	I_a	P
Honeybees	3.83	0.001	1.58	0.048
Bumblebees	3.77	0.001	1.61	0.042
Wild bees	3.70	0.001	1.96	0.006
Hoverflies	3.27	0.001	1.78	0.018
Flies	2.44	0.001	1.30	0.134
Beetles	2.45	0.013	1.35	0.112

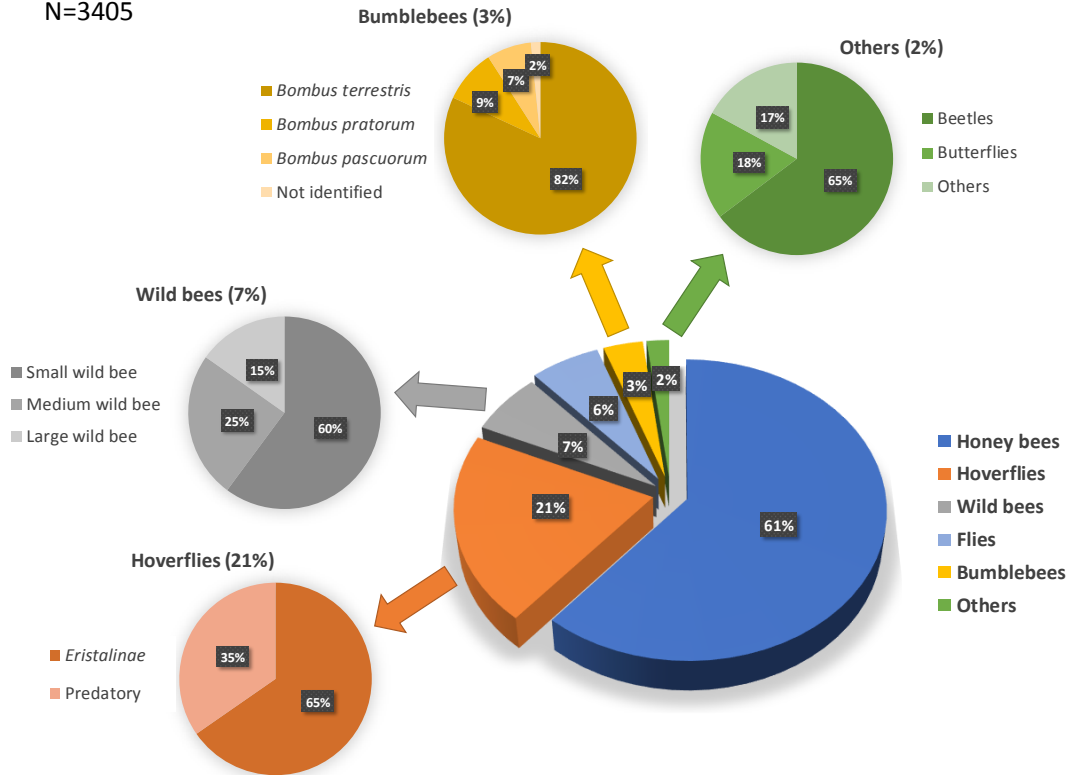
661
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663 **Table 2.** Index of association (X_p) representing the concordance between clusters of two
664 different count variables. It can be used as a measure of niche overlap (positively
665 significant) or segregation (null or negatively significant). Values corresponding to the
666 large scale are in the upper half-matrix, and those to the small scale in the lower half-
667 matrix (***: $P \leq 0.001$, **: $P \leq 0.01$, *: $P \leq 0.05$, n.s.: $P > 0.05$).
668

	Honeybees	Bumblebees	Wild bees	Hoverflies	Flies	Beetles
Honeybees	-	0.692 ***	0.795 ***	0.795 ***	0.653 ***	0.587 ***
Bumblebees	0.087 n. s.	-	0.745 ***	0.605 ***	0.634 ***	0.646 ***
Wild bees	0.624 ***	0.397 *	-	0.792 ***	0.663 ***	0.651 ***
Hoverflies	0.409 *	0.391 *	0.148 n. s.	-	0.789 ***	0.751 ***
Flies	0.199 n. s.	0.584 **	0.461 *	0.574 *	-	0.729 ***
Beetles	0.052 n. s.	0.667 ***	0.545 **	0.466 **	0.523 **	-

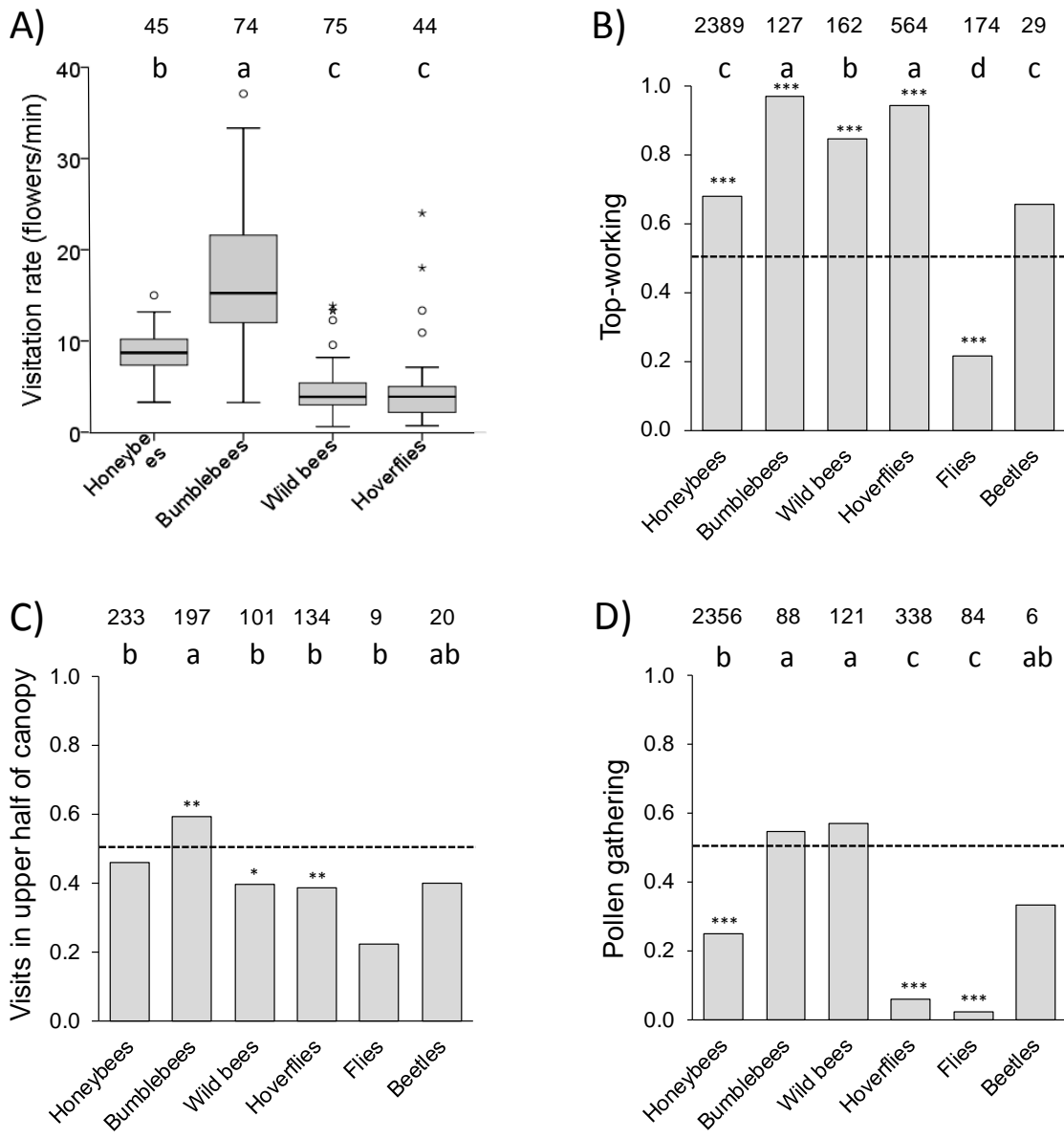
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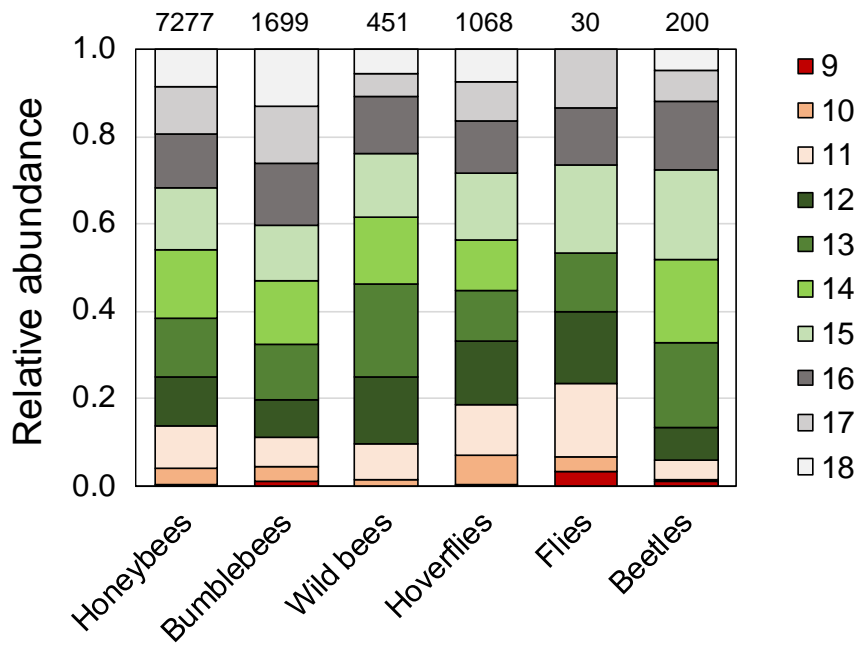
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Fig 1

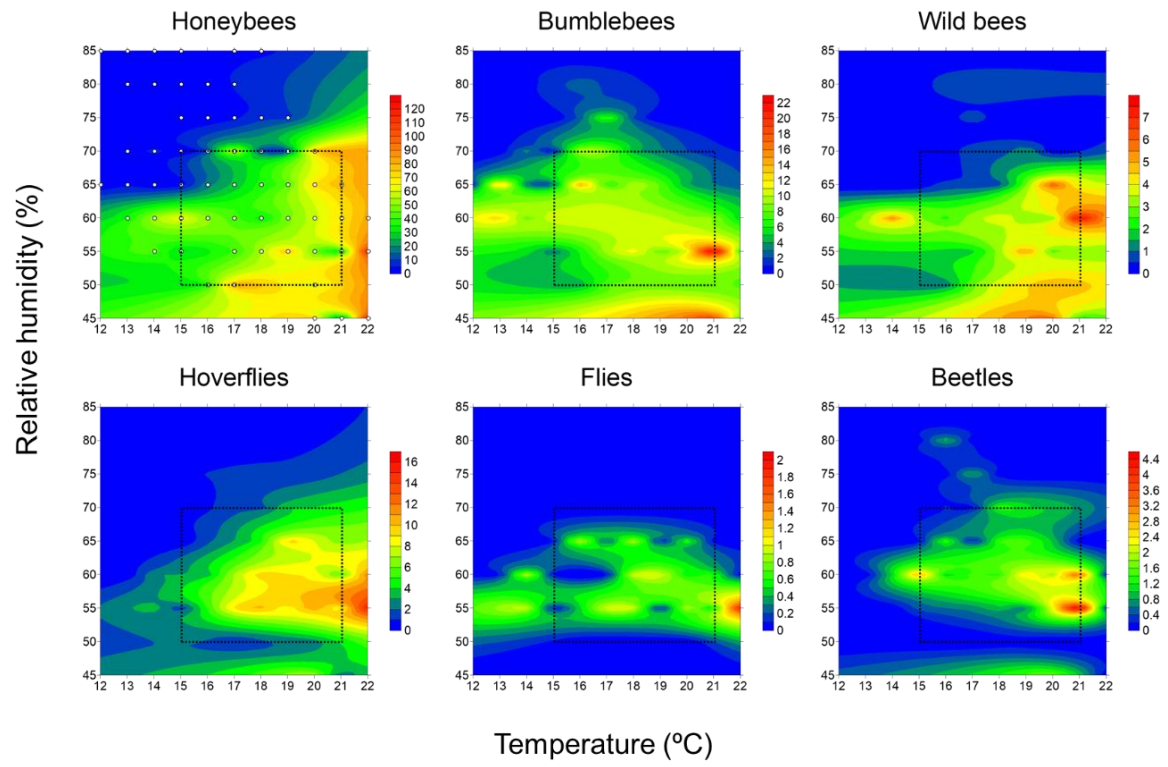


675
676
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Fig 2



679
680 **Fig 3**



681
682 **Fig 4**