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1 **Network analysis highlights increased generalisation and evenness of plant-pollinator interactions**
2 **after conservation measures**

3

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28

29 **Abstract**

30 The decline of pollinators may alter the complex system of interactions that they establish with
31 flowering plants, with potential negative consequences on both partners. Within this context,
32 network analysis may be a useful tool to study ecological properties of plant-pollinator interactions
33 and to evaluate the outcomes of conservation actions. Three conservation measures were
34 implemented within the European LIFE+ PP-ICON project to support the local pollinator
35 community of a population of the rare plant *Dictamnus albus* in a protected area near Bologna,
36 Italy. Artificial nesting sites were installed to support solitary bees, populations of native plants
37 were reinforced to increase foraging resources for pollinators, and colonies of bumblebees reared
38 from wild queens were released in the study area. In this work we evaluate the effects of these
39 conservation actions on plant-pollinator networks over a period of four years, comparing a pre-
40 (2011-2012) and a post-conservation (2013-2014) action period. The overall network generalisation
41 increased after the implementation of conservation measures and interactions were more evenly
42 distributed. Module composition significantly changed between the two periods, showing a marked
43 rewiring of interactions. *D. albus* was a module hub both before and after conservation actions, thus
44 emerging as an important node within its own module. In addition, some plant and pollinator
45 species directly targeted by conservation measures became module connectors, highlighting their
46 increased importance in linking different modules. Finally, the reinforcement of plant and pollinator
47 populations led to increased flower visitation. These results indicate that conservation actions
48 affected species both directly and indirectly and that the network of interactions has potentially
49 increased its robustness and resilience towards possible species loss. This study highlights ways in
50 which network analysis can be used to measure changes in plant-pollinator interactions in response
51 to conservation actions.

52

53 **Keywords:** bees; biodiversity conservation; community structure; modularity; population
54 reinforcement; specialization

55

56 The data analyzed during the current study are available in the Zenodo repository, PERSISTENT

57 WEB LINK TO DATASETS: <https://doi.org/10.5281/zenodo.2838952>

58

59

60 **1. Introduction**

61 An increasing number of studies highlight a generalized decline of insects at a global scale,
62 including important pollinator taxa such as butterflies, wild bees and hoverflies (e.g. Hallmann et
63 al., 2017; Ollerton et al., 2014; Powney et al., 2019; Thomas, 2016). The majority of flowering
64 plants rely on animals for their reproduction (Ollerton et al., 2011). Among them, bees are the most
65 widespread and most important pollinators (Michener, 2007). The loss of bee pollinators and of the
66 complex system of interactions that they establish with the flowering plant species upon which they
67 rely may endanger the maintenance of wild plant communities (Aguilar et al., 2006; Potts et al.,
68 2010; Thomann et al., 2013), and drive down certain ecosystem services, such as agricultural yields
69 of pollinator-dependent crops (Deguines et al., 2014). At the same time, the loss of suitable habitat
70 and foraging resources is among the main causes of bee population decline (Bates et al., 2011;
71 Biesmeijer et al., 2006; Goulson et al., 2008; Hicks et al., 2016).

72 The study of plant-pollinator networks aims to reveal the structure of the interactions between
73 partners, the mechanisms underlying such a structure, and the role of individual species within the
74 interaction network (Bascompte and Jordano, 2007; Blüthgen, 2010). The complexity of local
75 networks is linked to the dependence of interactions on the composition and space-time turnover of
76 plant and pollinator communities which, in turn, contribute to spatial and temporal differences
77 between local networks (Poisot et al., 2012). Even when species are present in a site at a given time,
78 actual interactions may not occur due to temporal mismatches, to competition or to the low
79 probability of interaction between rare species (Bartomeus et al., 2013; Basilio et al., 2006; Canard
80 et al., 2012; CaraDonna et al., 2017; Fontaine et al., 2008; Olesen et al., 2011).

81 In addition to their importance for the study of ecological and evolutionary processes, the
82 monitoring of temporal changes of mutualistic interactions and the study of structural network
83 attributes can be important tools for the assessment of conservation projects and management
84 practices (Forup and Memmott, 2005; Kaiser-Bunbury et al., 2010; Tylianakis et al., 2010) and as a
85 criterion of pollination service quality (Elle et al., 2012; Kaiser-Bunbury et al., 2017). Pollination

86 network data have already been used to make predictions and inform management decisions
87 (Carvalho et al., 2008; Larson et al., 2014), but the use of network analysis to evaluate the effects
88 of practical conservation actions has been reported only in very few cases to date (Burkle and
89 Alarcón, 2011; Forup et al., 2008; Forup and Memmott, 2005). Recently, Kaiser-Bunbury and
90 Blüthgen (2015) proposed a framework of the most suitable quantitative network metrics to
91 evaluate the outcomes of conservation actions in plant-pollinator networks. These metrics include
92 both diversity and distribution measures. Interaction evenness allows evaluating the homogeneity of
93 links in a network, while measures of specialization-generalisation highlight the level of species
94 dependency on few species (Blüthgen et al., 2006). Modularity measures how species are organized
95 into modules, i.e. link-dense regions in which species interact more strongly with each other than
96 with species in other modules (Olesen et al., 2007). Such metrics can help indirectly to understand
97 functional robustness and vulnerability of networks, reveal preferential ecological interactions
98 between species, and potentially assess the effectiveness or recommend further development of
99 conservation measures. From a conservation perspective, priority should be given to species with
100 complementary functions, while functionally redundant species could be of lower importance
101 (Blüthgen and Klein, 2011). Nevertheless, restored ecosystems can display increased diversity of
102 pollinator species, higher reproductive performance of common plants, and higher network
103 generalization, indicating increased functional redundancy (Kaiser-Bunbury et al., 2017). In
104 contrast to predictions based on simulation models that do not account for changes in the efficacy of
105 particular plant-pollinator relationships, Brosi and Briggs (2013) empirically demonstrated that
106 even a single pollinator species loss may negatively affect network robustness, reducing plant
107 reproductive success. The fragility of plant-pollinator networks to species loss can be estimated by
108 studying network organization and its effects on assemblage robustness, i.e. to what extent the
109 structure and stability of interactions deviate from a pre-existing situation or how many secondary
110 extinctions occur as a result of perturbations (Astegiano et al., 2015; Dunne et al., 2002).

111 Here we analyze the effects of conservation actions on plant-pollinator networks in a Natural Park.

112 Conservation actions were performed within the LIFE+ PP-ICON project (www.pp-icon.eu), and
113 were primarily motivated by evidence of pollination limitation on a focal plant species, *Dictamnus*
114 *albus* L. (Fisogni et al., 2016). Three main actions were implemented throughout the duration of the
115 project (four years) to support the pollinator community of *D. albus*. First, artificial nesting sites
116 were installed to facilitate colonization by solitary bees (e.g. *Osmia* spp., *Megachile* spp., *Xylocopa*
117 spp.); second, bumblebee (*Bombus terrestris*) colonies – obtained from previous captures in the
118 study area and subsequent rearing of wild queens in the laboratory – were released in the area;
119 finally, populations of native plant species that produce pollen and nectar (hereafter: bee plants)
120 were reinforced to increase the availability of foraging resources throughout the pollinators' life
121 cycle (detailed methodology may be found in the subsection 2.2 of this article and in Bortolotti et
122 al., 2016). Our objective is to evaluate the effects of these conservation measures on mutualistic
123 interactions between flowering plants and wild bees. We focus on a wild population of *D. albus* and
124 its pollinators, which include only bees (Fisogni et al., 2011, 2016), and on the flowering plants
125 found in its surrounding area. The aims of this study are to evaluate i) modifications of network
126 structural properties after the implementation of the conservation actions, ii) the effect of the
127 conservation actions on plant and pollinator species roles within the networks, and iii) the effect of
128 plant species abundance and phenology on pollinator visits.

129

130 **2. Materials and methods**

131 *2.1. Study site and focal species*

132 This study was performed within a Natura 2000 site (SCI-SPA IT4050001) in the Regional Park
133 “Parco dei Gessi Bolognesi e Calanchi dell’Abbadessa”, on the hills nearby the city of Bologna,
134 Italy (44°25'11.734" N – 11°23'56.029" E; 167 – 200 m a.s.l.). The site presents a mosaic
135 vegetation growing on clay soil, composed of xeric woods and shrubs dominated by downy oak
136 (*Quercus pubescens* Willd.) and manna ash (*Fraxinus ornus* L.) surrounded by grasslands, resulting
137 from abandoned coppice and pastures.

138 The focal species, *Dictamnus albus*, is a perennial herb that flowers from the end of April to mid-
139 May and grows at the edge between woods and grasslands and within wood clearings. Fertile
140 racemes bear several showy white and purple flowers; anthers become dehiscent prior to stigma
141 receptivity and flowers show a gender-biased nectar production towards the late female-phase
142 (Fisogni et al., 2011). Medium- to large-sized bees (Hymenoptera: Apoidea: Anthophila) are its
143 most important pollinators, and include both social (e.g., *Bombus* spp.) and solitary (e.g.,
144 *Habropoda tarsata*, *Xylocopa violacea*, *Osmia* spp.) bees; smaller bees (e.g. Halictidae, *Ceratina*
145 spp.) only rarely act as effective pollinators (Fisogni et al., 2016). *D. albus* is listed as “Least-
146 Concern” in the European Red List (Chappuis, 2014), but it is included as “Vulnerable” in several
147 national Red Lists and is locally protected throughout Europe (Schnittler and Günther, 1999).

148

149 2.2. Conservation actions

150 Three main conservation actions were implemented in the study area to favor both plants and their
151 bee pollinators. 1) Artificial nests for pollinators were provided throughout the development of the
152 study. Nest occupancy was impaired in 2011 because of colonization by ants. Solitary bees started
153 nesting in 2012, and emerged in 2013. A high number of cavities were also occupied in 2013 and
154 2014, and further more complex artificial nesting sites (i.e. bee hotels) were added in 2014 and
155 readily occupied by a variety of solitary bees (e.g. *Anthidium manicatum*, *Osmia* spp., *Megachile*
156 spp., *Xylocopa violacea*). 2) Populations of seventeen native plant species that are visited by local
157 pollinators were planted in the study area. Plants were chosen to have a flowering out of phase with
158 that of the focal species *D. albus*, to avoid competition for pollinator visitation. The majority of
159 plants successfully established few to several individuals in 2013 and 2014. 3) A total of fourteen
160 colonies of the buff-tailed bumblebee (*B. terrestris*) were reared in the laboratory starting from wild
161 queens captured in the study area, and were released in the project area in 2013 and 2014. More
162 details on methodology, materials and outcomes of these actions can be found in Bortolotti et al.
163 (2016).

164

165 2.3. *Permanent transects in the flowering community*

166 To study the links between plants and pollinators, we considered a 200 m long × 2 m wide
167 permanent transect, representative of the project area. We chose a single transect because of the
168 small area concerned by the conservation actions and because of the restricted distribution of *D.*
169 *albus* populations. Moreover, the peculiar geomorphology of the Regional Park limited additional
170 transects, because of widespread ravines and woodlands not favorable to the establishment of *D.*
171 *albus* populations. The transect was designed to cover the largest diversity of flowering plants in the
172 study site throughout the season. In addition, it included the majority of *D. albus* plants during their
173 peak of blooming and encompassed all the bee plants that were planted during the conservation
174 actions. We performed monthly pollinator surveys from March to September (7 surveys) for four
175 consecutive years (from 2011 to 2014; 28 surveys overall). The transect was walked by one
176 experienced operator at an even pace four times on survey day at fixed hours (9 and 12 AM, 3 and 6
177 PM), to cover most of the bee foraging activity period. During each transect, all individual bees that
178 visited open flowers to collect pollen or nectar were recorded, as well as the plant species visited.
179 These insects were accounted pollinators for this study purposes, regardless of their pollination
180 efficiency. Where possible, all bees were sampled by hand net and individually stored in vials
181 containing paper-tissues soaked with ethyl acetate and brought to the laboratory for taxonomic
182 determination. Some individuals left flowers before we could capture them (n = 41): in this case the
183 lowest taxonomic level recognizable by field observations (family or genus) was noted and the
184 interaction was recorded.

185

186 2.4. *Flower abundance*

187 Immediately after finishing sampling along the permanent transect, the same operator walked the
188 transect a second time to estimate the abundance of the flowering plants encountered therein. For
189 this estimation, we considered floral units such as single flowers, flower heads, spikes and umbels

190 (*sensu* Gibson et al., 2006). Based on floral units, flowering species were ranked qualitatively in
191 classes of abundance using the following categories: 1 - low abundance (solitary or sporadic floral
192 units); 2 - medium abundance (sparse floral units or small groups); 3 - high abundance (up to half of
193 the floral units in the area belonging to the species); and 4 - dominant species (more than half of the
194 floral units in the area belonging to the species).

195

196 2.5. *Data analysis*

197 Since conservation measures were performed gradually throughout the first two years of the LIFE+
198 PP-ICON project and became established starting from the third year of the study (Bortolotti et al.,
199 2016), we assessed the effects of such measures by dividing the four years of data in two periods: a
200 pre-conservation action period (2011 – 2012), and a post-conservation action period (2013 – 2014).
201 We also aggregated two years in each period to reduce the inter-annual variability associated with
202 natural fluctuations and to have sufficiently large data sets to allow all the analyses. We evaluated
203 plant and insect species turnover by calculating the presence/absence-based Sørensen similarity
204 index (S). All analyses were performed with R ver. 3.3.2 (R Core Team, 2016), using the following
205 R packages: *igraph* (Csardi and Nepusz, 2006), *bipartite* (Dormann et al., 2008), *lme4* (Bates et al.,
206 2015), *alluvial* (Bojanowski and Edwards, 2016), and *vegan* (Oksanen et al., 2019).

207

208 2.5.1. *Network analyses*

209 Since monthly networks were small and the aim of this study was to compare the total pre- and
210 post-treatment conditions, we aggregated observations of all months in each year to obtain a more
211 exhaustive representation of the plant-pollinator interactions. We then built two two-year pollinator-
212 by-plant visit matrices (\mathbf{V}) corresponding to the pre- and post-conservation action networks. In each
213 \mathbf{V} matrix, the value in the cell at row ‘a’ and column ‘p’ represents the number of visits of pollinator
214 species ‘a’ to plant species ‘p’ in that observation period. We also analyzed pollinator-by-plant
215 incidence matrices (\mathbf{A}) in which the value of each cell is 0 or 1 and represents an absent or recorded

216 interaction, respectively ($a_{ij} = 1$ when $v_{ij} > 0$). Plant and insect phenologies (i.e. temporal changes in
217 presence/absence) were considered in further analyses (PERmutational Multivariate ANalysis Of
218 VARIance between species role and phenology, see below) to account for effects related to seasonal
219 species occurrence.

220 We calculated the connectance (C , the proportion of observed interactions over all possible
221 interactions) for both the pre- and post-conservation action networks. At the network level, we
222 calculated the specialization index (H_2') and the associated interaction evenness (E_2). H_2' is a
223 measure of the complementarity of interactions within a given network, and it ranges between 0
224 (extreme generalisation of species in the networks) and 1 (extreme specialization; Blüthgen et al.
225 2006). Interaction evenness evaluates the homogeneity of relative interaction frequencies across all
226 links in the network (Blüthgen et al., 2008). Higher evenness values reflect a more uniform
227 distribution of interactions among the species. We also calculated the specialization index (d') at the
228 species level. d' ranges between 0 and 1, with high values indicating specialization (Blüthgen,
229 2010). Both H_2' and d' are not affected much by variation in sampling effort and by the
230 incompleteness of sampled plant-pollinator interactions (Blüthgen et al., 2007).

231 To test for significant differences between pre- and post-conservation action metrics, the difference
232 between the respective indices (Δ_{observed}) was compared with that predicted by permutation-based
233 null models ($\Delta_{\text{permutation}}$). To construct the null model, we re-sampled visits involving species pairs
234 (insect and plant) after pooling all observed visits (from both pre- and post-conservation action
235 periods) together. Re-sampling kept the number of visits in each period constant, but randomly
236 shuffled the period in which each of the visit “happened” in the permuted dataset. We performed
237 10,000 permutations and compared the Δ_{observed} with the distribution of $\Delta_{\text{permutation}}$ to look for
238 significant differences (i.e. differences between pre- and post-conservation metrics that would not
239 have been predicted if visits had occurred randomly in one of the two periods).

240 We calculated network modularity (M) and module composition using the ‘cluster leading
241 eigenvector’ algorithm (Newman, 2006). To evaluate the importance of modularity in a given

242 period we compared the modularity obtained for the **A** matrices with that obtained using a
243 randomized matrix with given degrees for presence/absence interaction tables (method ‘curveball’;
244 Strona et al., 2014) with 10,000 permutations. We compared modularity values obtained in the pre-
245 and post-conservation action periods using the same permutation-based null model as described
246 above for the other network metrics. To evaluate the similarity in module composition before and
247 after conservation measures, we calculated the normalized mutual information index (NMI, Danon
248 et al., 2005) of the modular structure of interaction networks for the two periods restricted to species
249 occurring in both periods, and compared it with values obtained from randomized tables that
250 conserved the species degree distribution of the observed networks (Astegiano et al., 2017). We
251 used alluvial diagrams to show the species rearrangement among modules in the two periods
252 considered.

253 To define the role of each species with respect to network modularity, we calculated their within-
254 module degree (*z-score*) and among-module connectivity (*c-score*) values (Guimerà and Amaral,
255 2005) based on the results of the aforementioned modularity analysis with the ‘cluster leading
256 eigenvector’ algorithm. According to Olesen et al. (2007), peripheral species (i.e. specialists) have $z \leq 2.5$
257 and $c \leq 0.62$; module hubs (i.e. highly connected species within their own module) have $z >$
258 2.5 and $c \leq 0.62$; connectors (i.e. species linking several modules) have $z \leq 2.5$ and $c > 0.62$;
259 network hubs (i.e. super generalists, acting as both connectors and module hubs) have $z > 2.5$ and c
260 > 0.62 . We performed a PERMANOVA to test whether the values of the $c - z$ scores obtained for
261 both plants and insects, before and after the conservation actions, were affected by phenology (i.e.
262 the number of months in which a flowering plant or an insect species were observed).

263

264 2.5.2. *Determinants of flower visitation*

265 To assess the effects of flowering abundance, flowering phenology and conservation actions on the
266 abundance of insect flower-visits to the overall flowering community, we summed the total number
267 of visits by all bee species on all the plant species belonging to a given abundance class. The total

268 flower visits were analyzed with Generalized Linear Mixed Models (GLMMs) fit by maximum
269 likelihood with Laplace approximation and a negative binomial distribution with log-link (Bolker et
270 al., 2008). We used the plant species abundance rank (from 1 to 4), the plant phenology (i.e. the
271 number of months in which a given plant species was in bloom; min = 1, max = 7), and the
272 occurrence of conservation actions (1 = pre-conservation action period, 2 = post-conservation action
273 period) as explanatory variables. Plant abundance and phenology were considered in the models as
274 categorical variables in order to allow for non-linear relationships. We included ‘plant species’ as a
275 random factor in all models to account for inter-specific variability. We started by computing the
276 most complex model (full model with all of the abovementioned explanatory variables and their
277 interactions), and by sequentially reducing the model terms. We chose the best model by comparing
278 the Akaike Information Criteria with correction for small sample sizes (AICc) and by selecting the
279 model with the lowest AICc value (Bolker et al., 2008; Johnson and Omland, 2004).

280

281 **3. Results**

282 We walked a total of 22.4 km in the 112 transects performed over the four years. We recorded a
283 total of 48 and 86 plant and pollinator species, respectively (full list of plant and pollinator species
284 in Table A.1 – Appendix A). We recorded 233 plant-pollinator interactions between 29 flowering
285 plant species and 45 bee species before the conservation actions (2011 - 2012), and 297 plant-
286 pollinator interactions between 41 flowering species and 56 bee species after the conservation
287 actions (2013 – 2014). Plant species turnover between the two periods was lower than pollinator
288 species turnover ($S = 0.31$ and $S = 0.56$, respectively).

289

290 *3.1. Network structure*

291 *3.1.1. Connectance*

292 Connectance levels were low in both the pre- ($C = 0.066$) and post-conservation action ($C = 0.061$)
293 periods, but were comparable to values found for visitation networks of similar size (e.g. $0.04 < C <$

294 0.05 in Memmott and Waser, 2002; $0.05 < C < 0.09$ in Forup and Memmott, 2005). Values of
 295 connectance did not significantly differ from each other between the two periods (Table 1).

296

297 **Table 1**

298 Descriptors of the plant-pollinator visitation networks during the pre- and post-conservation
 299 periods. Differences between connectance, specialization, evenness and modularity levels were
 300 tested using the pre- vs. post- randomization procedure described in the text.

	Pre-conservation actions (2011-2012)	Post-conservation actions (2013-2014)	Δpost - pre	<i>p</i>-value	LCI	UCI
Network level						
Connectance (<i>C</i>)	0.066	0.061	- 0.005	ns	- 0.006	- 0.001
Specialization (H_2')	0.667	0.445	- 0.222	< 0.025	- 0.204	- 0.029
Interaction evenness (E_2)	0.525	0.589	0.064	< 0.05	0.012	0.061
Modularity (<i>M</i>)	0.613	0.559	- 0.054	ns	- 0.204	- 0.010
Species level						
Plant species specialization (d_p')	0.673 ± 0.03	0.464 ± 0.04	- 0.209	< 0.025	- 0.180	- 0.033
Pollinator species specialization (d_i')	0.503 ± 0.04	0.462 ± 0.03	- 0.041	ns	- 0.128	0.014

301 Plant and pollinator species specialization indices are given as average values over all species ± SE.
 302 Lower (LCI) and upper (UCI) 95% confidence intervals obtained after randomizations are reported
 303 for each Δ value. ns = not significant.

304

305 *3.1.2. Specialization*

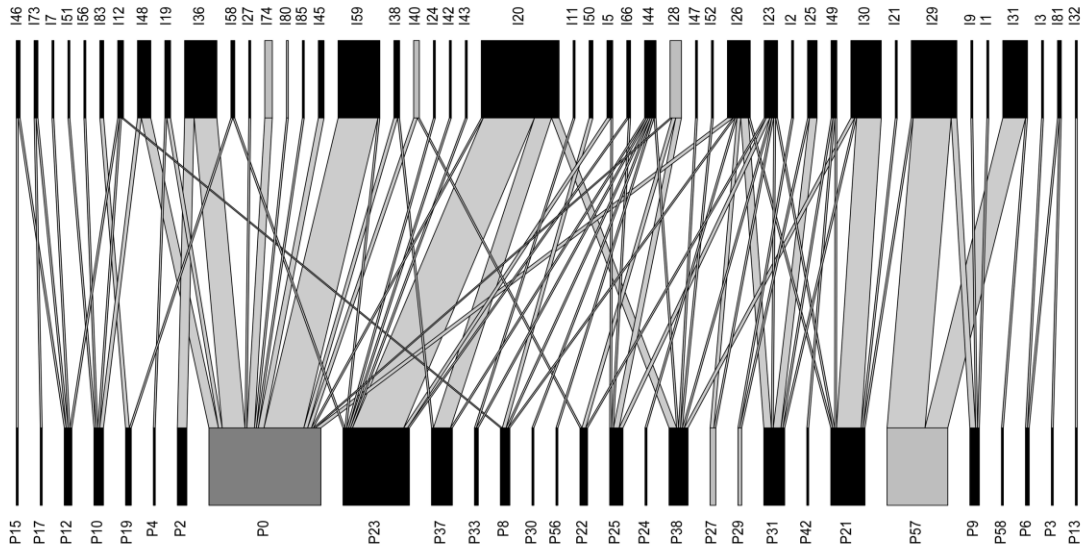
306 Specialization at the network level (H_2') significantly decreased after the conservation actions

307 ($H_2'_{pre} = 0.67$ and $H_2'_{post} = 0.45$, $p < 0.025$; Fig. 1, Table 1). Similarly, mean specialization at the
308 species level (average d_p' over all species) decreased after the conservation actions in both plant
309 ($d_p'_{pre} = 0.68 \pm 0.03$ and $d_p'_{post} = 0.46 \pm 0.04$) and pollinator species ($d_i'_{pre} = 0.50 \pm 0.04$ and $d_i'_{post} =$
310 0.46 ± 0.03), but only significantly so in plants (Table 1).

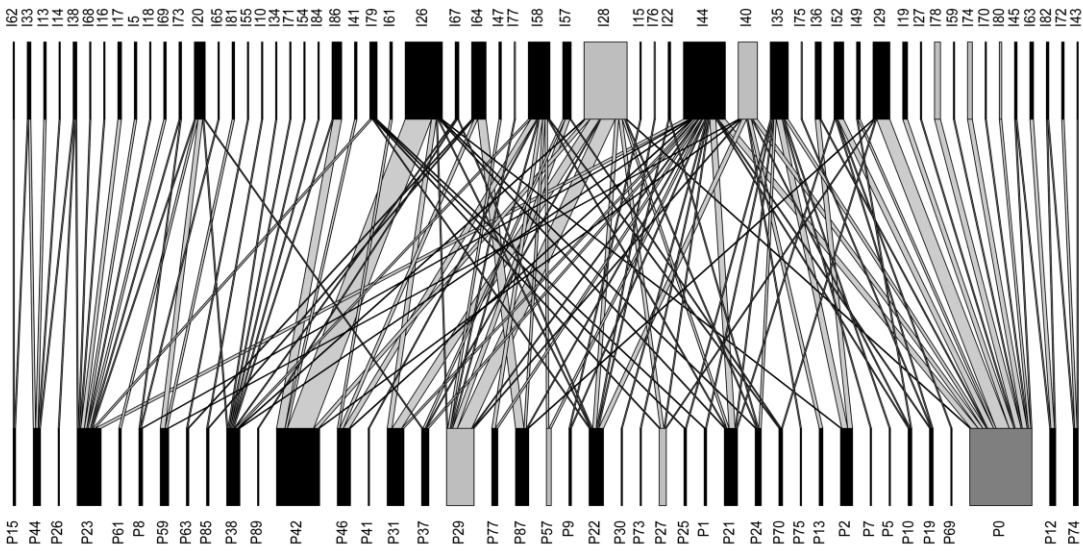
311

312 **Fig. 1.** Bipartite representation of plant-pollinator networks before and after the implementation of
313 conservation actions. Lower bars represent plant species, while higher bars represent pollinator
314 species (within each network, bar size is proportional to the number of links recorded for each
315 species). Link width (grey lines that connect plant to pollinator species) is proportional to the
316 number of observed interactions between plant and pollinator species. *Dictamnus albus* (P0; dark
317 grey), and bee plants whose populations were reinforced during conservation actions (P27 –
318 *Prunella laciniata*, P29 – *Veronica spicata*, P57 – *Cephalaria transsylvanica*; light grey) are
319 highlighted in the lower bars. Bee species that were favored by conservation actions (I28 – *Bombus*
320 *terrestris*, I40 – *Xylocopa violacea*, I74 – *Megachile circumcincta*, I78 – *Megachile centuncularis*,
321 I80 – *Osmia bicornis*; light grey) are highlighted in the higher bars. See Table A.1 in Appendix A
322 for the complete list of plant and pollinator species.

Pre-conservation actions



Post-conservation actions



323

324

325 3.1.3. Evenness

326 Interaction evenness (E_2) slightly but significantly increased from 0.53 to 0.59 ($p < 0.05$) after the
 327 implementation of the conservation actions (Fig. 1, Table 1).

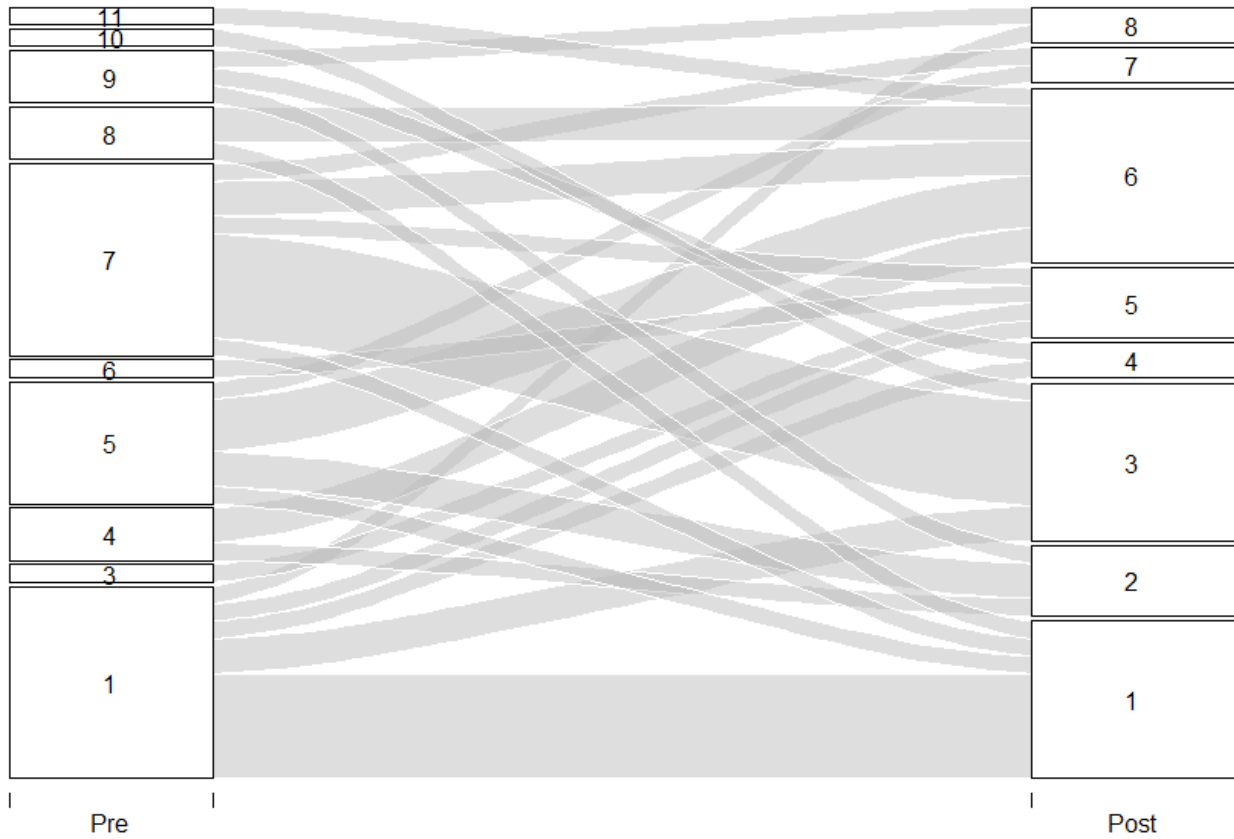
328

329 3.1.4. Modularity

330 Network modularity slightly decreased after the implementation of conservation actions, but not at a
331 significant level (Table 1). We found 11 modules and 8 modules in the pre- and post-conservation
332 action periods, respectively (species module composition is reported in Table A.2 – Appendix A).
333 Modularity was significantly higher than expected from random permutations only in the post-
334 conservation action period (‘curveball’ permutations, pre-: $p = 0.382$; post-: $p = 0.001$).
335 The normalized mutual information index quantifying the correspondence between modules in the
336 two periods was low (NMI = 0.36), and did not show significant similarity of module structure
337 between the post- and pre-conservation action periods ($p = 0.539$ for **A** matrices, tested using the
338 pre- vs. post- interaction randomization procedure). The alluvial diagram showed a significant
339 rearrangement among modules in the two periods, and highlighted that the module including *D.*
340 *albus* (module 1) was the most stable between them (Fig. 2).

341

342 **Fig. 2.** Alluvial diagram showing species rearrangement among blocks between the periods before
343 (Pre) and after (Post) the implementation of the conservation actions. *Dictamnus albus* is included
344 in module 1 in both periods. Full species module composition is reported in Table A.2 – Appendix
345 A



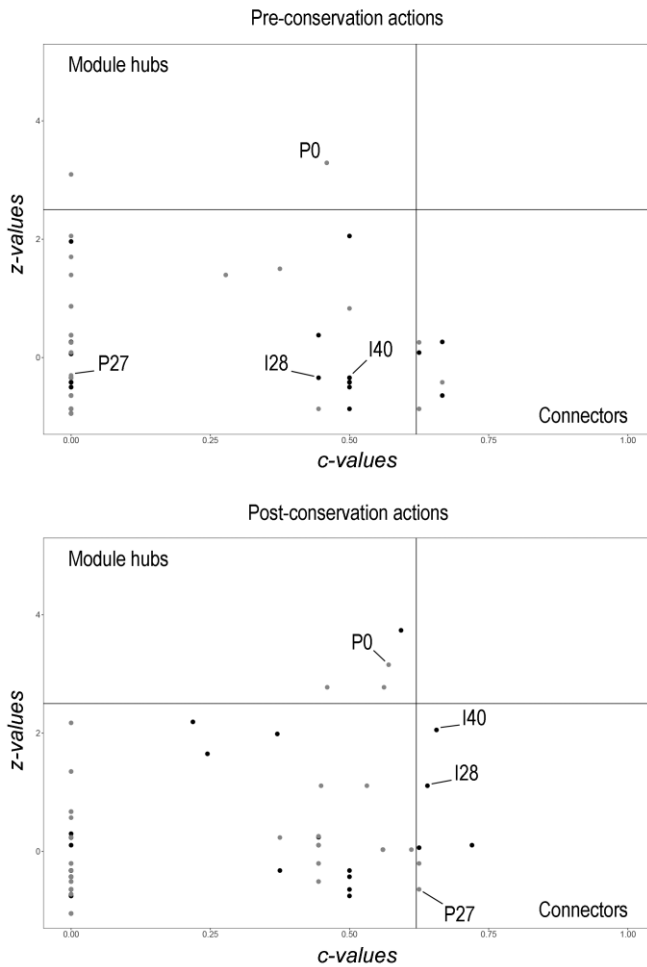
346

347

348 Regarding the role of single species within modules based on their $c - z$ scores, we found some
 349 differences in both plant and pollinator species between the two observation periods. The focal
 350 species *D. albus* was a module hub both before and after the implementation of conservation
 351 actions, while among bee plants *Prunella laciniata* became a module connector after the
 352 reinforcement of its population (Fig. 3). Concerning pollinators, *X. violacea* and *B. terrestris*
 353 became module connectors after the implementation of bee hotels and the reinforcement of their
 354 colonies, respectively (Fig. 3).

355

356 **Fig. 3.** Representation of the role of plant (grey dots) and pollinator (black dots) species in the pre-
 357 and post-conservation action periods, based on $c - z$ scores according to threshold values given by
 358 Olesen et al. (2007). A module hub is a highly connected species within its own module, while
 359 connectors are species that link several modules among them. Only species that were directly
 360 targeted by conservation actions and were either module hubs or connectors are highlighted for
 361 clarity (P0 – *Dictamnus albus*, P27 – *Prunella laciniata*; I28 – *Bombus terrestris*, I40 – *Xylocopa*
 362 *violacea*).



363

364

365 The PERMANOVA did not show significant effects of species phenology on the c - z scores of
 366 plant nor pollinator species in any of the observed periods ($F_{1,65} = 0.061$, $p = 0.526$ before the
 367 conservation actions, and $F_{1,94} = 1.529$, $p = 0.211$ after the conservation actions, based on 9999
 368 permutations).

369

370 3.2. Species targeted by conservation actions

371 We here specifically consider plant and pollinator species that were targeted by conservation
 372 actions (Table A.1 in Appendix A) and that were observed in both periods.

373 Flowers of *D. albus* were visited 59 times by 14 bee species before the conservation actions, while
 374 they were visited 52 times by 16 bee species after the conservation actions. The specialization index
 375 of *D. albus* decreased after the conservation actions ($d'_{pre} = 0.75$, $d'_{post} = 0.60$). The specialization

376 index of pollinators visiting *D. albus* was low and comparable between the two observed periods
 377 ($d'_{pre} = 0.31 \pm 0.06$, $d'_{post} = 0.28 \pm 0.04$).

378 Two bee plants (*P. laciniata* and *Veronica spicata*) received more visits by a higher number of
 379 pollinator species after the conservation actions, while *Cephalaria transsylvanica* received a lower
 380 number of visits by the same number of pollinator species after the implementation of the
 381 conservation actions (Table 2). All three plant species showed a decreased specialization index in
 382 the second study period (Table 2).

383

384 **Table 2**

385 Flowering occurrence, number of visits received by pollinators, number of bee species observed,
 386 and specialization index (d') in bee plants that flowered both before (Pre) and after (Post) the
 387 conservation actions. x symbols indicate for each species the monthly presence before (Pre) and
 388 after (Post) the conservation actions. None of these species flowered in March, April or May.

	Conservation actions	June	July	Aug	Sept	Pollinator visits	Bee species	d' plant
<i>Prunella laciniata</i>	Pre	x				3	2	0.45
	Post	x	x			7	4	0.18
<i>Veronica spicata</i>	Pre	x	x	x	x	2	2	0.77
	Post	x	x	x	x	32	10	0.46
<i>Cephalaria transsylvanica</i>	Pre			x	x	32	2	0.92
	Post			x	x	7	2	0.25

389

390 All the pollinator species that were targeted by conservation actions were more abundant after their
 391 implementation. *B. terrestris* was the most abundant visitor both before and after the reinforcement
 392 of its local population (Table 3). Among the three solitary bee species that benefited from artificial
 393 nesting sites (Bortolotti et al., 2016), *X. violacea* showed a five-fold increase in visits, *Osmia*
 394 *bicornis* more than doubled its visits and *Megachile* spp. showed a three-fold increase of visits after
 395 the conservation actions (Table 3). *B. terrestris* and *O. bicornis* showed a similar decrease of

396 specialization level in the second study period, while *X. violacea* and *Megachile* spp. showed a
 397 similar increase in the specialization level (Table 3).

398

399 **Table 3**

400 Number of flower visits and specialization index of pollinator taxa that were targeted by
 401 conservation actions.

Pollinator taxon	Total visits	Visits pre	Visits post	<i>d'</i> pre	<i>d'</i> post
<i>Bombus terrestris</i>	42	6	36	0.58	0.42
<i>Xylocopa violacea</i>	19	3	16	0.27	0.41
<i>Osmia bicornis</i>	17	5	12	0.60	0.47
<i>Megachile</i> spp.	16	4	12	0.23	0.37

402 Pre = before the conservation actions

403 Post = after the conservation actions

404

405

406 **3.3. Determinants of flower visits**

407 Plant species abundance and flowering phenology were the explanatory factors included in the best
 408 model predicting the total number of flower visits to the overall flowering community (Table 4).

409 The best fitting model was much better than the second best ($\Delta AICc = 6.85$).

410 **Table 4**

411 Model selection results examining the influence of plant species abundance and phenology, and the
 412 effect of conservation actions on flower visits by pollinators. The best model has the lowest AICc
 413 (Akaike Information Criterion corrected for small sample size) value.

Response variable	Candidate models	(Intercept)	<i>df</i>	logLik	AICc	$\Delta AICc$	W
Flower visits	Rank, phen	-1.4330	11	-418.700	860.6	0.00	0.943
	Rank, treat, phen, phen*treat	-1.6120	15	-417.615	867.4	6.85	0.031
	Rank, treat, rank*treat, phen	-1.5100	15	-417.833	867.9	7.28	0.025
	Rank, treat, rank*treat, phen, phen*treat	-1.6160	18	-417.253	873.7	13.11	0.001
	Rank	-0.8253	6	-432.234	876.8	16.24	0.000

Rank, treat, rank*treat	-0.9921	10	-430.807	882.6	22.01	0.000
Phen	-1.0810	8	-439.378	895.4	34.80	0.000
Treat, phen, phen*treat	-1.4150	12	-436.958	899.3	38.74	0.000
	-0.2554	3	-452.966	912.0	51.44	0.000

414 Rank - plant species abundance (categorical variable), treat – occurrence of conservation actions
415 (categorical), phen - plant species phenology (categorical). *df* indicates the model degrees of
416 freedom (each model includes three degrees of freedom relative to the intercept, the residual
417 variance and the random effect), Δ AICc represents the difference of AICc values to the best model
418 and W the AICc model weights (Akaike weight).

419

420 Flower visits increased following the increase of plant abundance (Table 5). All plant species that
421 flowered for two or more months had a low and comparable positive effect on pollinator flower
422 visits, with the exception of plant species that flowered for five months which highly increased
423 flower visits (Table 5). Only two species flowered for five months (*Lotus corniculatus* and
424 *Taraxacum levigatum*). Visits increased only for *T. levigatum* and were mainly related to one bee
425 species (*Lasioglossum puncticolle*) that occurred in August 2013.

426

427 **Table 5**

428 Results of the generalized linear mixed model (GLMM) for the effect of plant abundance and
429 phenology on flower visits by pollinators.

Response variable	Factors	Estimate	Std. Error	z-value	Pr(> z)
Flower visits	Fixed effects				
	(Intercept)	-1.4332	0.3069	-4.670	3.01e-06 ***
	Rank2	0.9119	0.2926	3.117	0.00183 **
	Rank3	2.2519	0.4549	4.950	7.41e-07 ***
	Rank4	3.5813	0.7193	4.979	6.39e-07 ***
	Phen2	1.1598	0.2850	4.069	4.72e-05 ***
	Phen3	1.1077	0.5626	1.969	0.04897 *
	Phen4	1.5976	0.5626	1.930	0.05358 .

Phen5	3.5936	0.8277	3.547	0.00039 ***
Phen6	1.4221	1.3228	1.075	0.28236
Random effect	Variance	St.Dev.		
Plant species	1.923	1.387		

430 Rank – plant species abundance, from lowest (1 - intercept) to highest (4), Phen – number of
 431 months in which plant species were found in bloom (1 is the intercept). *: p -value < 0.05; **: p -
 432 value < 0.01; p -value < 0.001

433

434 **4. Discussion**

435 We analyzed the structure of plant-pollinator networks before and after the implementation of
 436 conservation measures in a natural area. We found that species generalisation increased after
 437 interventions, especially for plants, while interactions were more evenly distributed. Only the post-
 438 intervention network was significantly modular, and module composition was not congruent with
 439 that of the pre-conservation action period. *Dictamnus albus*, the focal plant of the conservation
 440 actions, was the most visited species during its flowering period and acted as an important hub
 441 within its module in both the pre- and post-conservation actions periods. *Dictamnus albus* displayed
 442 an increased generalisation level after the conservation measures. Bee plants whose populations
 443 were reinforced were generally more visited by bees and displayed an increased generalization level
 444 compared to the pre-existing situation. In their turn, bee species that were directly favored by
 445 conservation actions showed a marked increase of visits to local plants throughout the flowering
 446 season, but their generalisation levels responded heterogeneously.

447

448 *4.1. Limitations of the study*

449 The use of a low-impact sampling method, and the consequentially relatively low number of
 450 sampled pollinators and interactions, was dictated by the fact that the functionality of the study
 451 system, i.e. *Dictamnus albus* and its pollinators, is threatened by several factors and especially
 452 pollination limitation (Fisogni et al., 2016). Since the present study aimed at evaluating the effects

453 of conservation measures specifically implemented to benefit both the local plant and pollinator
454 communities (Bortolotti et al., 2016), an oversampling could have negatively affected the outcome
455 of such actions and the effort made to obtain it. The use of a standardized methodology throughout
456 the sampling seasons should guarantee the comparability of results over time. Moreover, we
457 analyzed data using robust analyses and weighted metrics to overcome as much as possible any
458 misrepresentation due to possible undersampling.

459 The conservation actions implemented aimed at supporting the pollinator fauna and increasing
460 plant-pollinator interactions in the study site. Although it is difficult to demonstrate a direct
461 relationship between the implemented actions and their effects on the local pollinator community,
462 since the observed effects could also have been unexpected consequences of conservation measures
463 (e.g. if the bee plants planted in the area attracted bees from the surroundings without actually
464 increasing the local population), expected results were accomplished. Moreover, the amelioration of
465 the local habitat quality, especially through the increase of floral resources, will probably facilitate
466 the future survival of existing bee populations and promote the establishment of new bee nests in
467 the study site (Carvell et al., 2017), with further benefits for the plant community.

468

469 4.2. *Network structure*

470 We observed a general increase of the generalisation level both in the entire network (through H_2')
471 and at the plant and pollinator species levels (through d') after the implementation of conservation
472 actions, while evenness increased during the same period, indicating a more uniform repartition of
473 visits among interaction partners. Despite these changes, connectance stayed approximately the
474 same, thus suggesting that species overall interacted with a similar number of partners but in a more
475 uniform way. This phenomenon could be interpreted in at least three, non-exclusive ways. First, the
476 addition of new plants might provide an opportunity for generalist bees to sample more uniformly
477 from the various plant species they can feed on. The conservation actions increased bee plants that
478 are suitable for a large group of pollinators and that have a non-synchronized flowering phenology

479 (Bortolotti et al., 2016), and explicitly aimed at providing sufficient resources throughout the year.
480 Second, the addition of new plants might decrease competition among bee species by expanding
481 dietary options, hence allowing some species to increase their generalisation level and, at the same
482 time, increasing the generalisation level of conservation action-focal plants and nearby plants
483 (Carvalho et al., 2014; Schleuning et al., 2012). Third, the addition of bee colonies of some of the
484 most generalist species such as *B. terrestris* (Goulson and Darvill, 2004) might also increase the
485 generalisation level of plants, since more plant species would thus be visited by the measure-
486 targeted bee species. The significant increase of plant species generalisation after conservation
487 management suggests that the local plant community should be less prone to negative effects
488 connected to pollinator loss, because of increased functional redundancy (Memmott et al., 2004;
489 Walker, 1995). Similarly, the increased generalisation of pollinators should buffer possible losses of
490 flowering plants (Kaiser-Bunbury et al., 2010). In addition, we could expect positive effects of the
491 increased plant and pollinator diversity, since high species diversity and the opportunism (i.e. high
492 levels of generalism) of species interactions may further increase network resilience to phenological
493 shifts or species loss (Bartomeus et al., 2013; Burkle and Alarcón, 2011).

494 The modules identified in the pre- and post-conservation action networks, restricted to species
495 found in both periods, were not congruent. The lack of congruence in module composition
496 indicates that significant interaction rewiring occurred between species belonging to different pre-
497 conservation action modules. Temporal rewiring of interactions is generally high in natural
498 communities, and is mainly driven by species phenology, abundance and behavior (Burkle and
499 Alarcón, 2011; CaraDonna et al., 2017). It is not possible to determine whether the changes
500 highlighted by our results are due to natural fluctuations or to the conservation actions, or to an
501 interaction between the two. The augmentation of both pollinators and bee plants can have
502 influenced the patterns of floral visitation and the consequent arrangement of their interactions.
503 However, *Dictamnus albus* was included in the same module both before and after the conservation
504 actions. Moreover, this module was the most stable of all modules with regard to species

505 composition between the two periods. The analysis of c-z scores highlighted the species that
506 became more central (i.e. connectors) and the species that were more important within their own
507 module (i.e. hubs) following conservation actions. Two bee species (*B. terrestris* and *X. violacea*)
508 and one plant species (*P. laciniata*) that were favored by conservation management became module
509 connectors. Both *B. terrestris* and *X. violacea* are large-sized generalist species which could visit
510 several flowering species for nectar or pollen (Goulson and Darvill, 2004; Vicidomini, 1995), thus
511 connecting plants that may belong to different modules. Similarly, *P. laciniata* was visited by
512 several solitary and social bee species that belonged to different modules. *Dictamnus albus* was a
513 module hub in both periods, highlighting its primary role within its own module (Olesen et al.,
514 2007). Connector species potentially play an important role for the resilience of the network,
515 because their loss would increase modularity and therefore the fragmentation of the network
516 (Dupont and Olesen, 2009; Olesen et al., 2007), while the loss of module hubs could lead to less
517 densely connected modules (Memmott et al., 2004). The fact that *D. albus* was a module hub in a
518 relatively stable module indicates that, during its short flowering period, it plays an important role
519 not only by hosting several pollinator species, but also in ensuring the stability of the interactions
520 that occur between those species included within its own module.

521

522 4.3. *Species targeted by conservation actions*

523 The increased generalisation in the overall network after the conservation actions was partly shaped
524 by the higher generalisation observed in species directly targeted by conservation actions. Overall,
525 these plants were visited more and by a higher number of pollinator species, highlighting their
526 central role for the pollinator community as suitable foraging resources. This was particularly
527 evident for *P. laciniata*, which became a module connector after the reinforcement of its population.
528 *Dictamnus albus*, the focal plant of conservation strategy, was a key flowering species for the local
529 community: it was the most abundant species during its blooming period (end of April – mid May)
530 and attracted the majority (species and abundance) of pollinators (Fisogni et al., 2018, 2016).

531 Following the interventions, its degree of specialization within the network decreased. At the same
532 time, pollinators that visited *D. albus* were highly generalist both before and after the conservation
533 actions. Despite possible negative effects on plant reproductive fitness (e.g. lower pollination
534 efficiency, pollen discounting), the more diverse community of pollinators of *D. albus* should
535 guarantee an “insurance” against a possible reduction in pollination efficiency by single groups of
536 pollinators.

537

538 4.4. *Plant abundance and phenology*

539 More abundant plant species received more visits than less abundant ones. Increasing the number
540 and abundance of bee plants in the study site therefore likely had a general positive effect by
541 supporting the local pollinator community, or by attracting nearby pollinators. The importance of
542 plant abundance and diversity in attracting pollinators has been highlighted in other studies
543 (Ghazoul, 2006; Knight, 2003; Norfolk et al., 2015). Moreover, the spatial clustering of bee plants
544 (Bortolotti et al., 2016) may have increased their potential for attracting bees, whose vision relies
545 more on patches of plants than on sparse single individuals (Giurfa and Leherer, 2001). However,
546 since we cannot separate the effect of increased plant abundance from increased pollinator
547 availability through the implementation of nesting sites and bumblebee colonies, it is likely that a
548 higher availability of pollinators also contributed to the higher number of flower visits observed.
549 Indeed, both conservation actions were carried out at the same time with the aim to increase the
550 probability of having more flower visits.

551 We found that plant species that flowered for more than one month generally received more visits
552 than species with a very short phenology. Longer plant phenologies can increase the probability of
553 interaction with pollinators because of an increase in overlap with the flight period of a larger
554 number of species (de Manincor et al., 2019; Olesen et al., 2011, 2008). Nevertheless, the increase
555 in flower visits was comparable between species that flowered for two or more months, indicating a
556 weak effect of flowering length on the number of visits received. The higher visits observed for *T.*

557 *levigatum* were more likely linked to a sampling effect or to the pollinator phenology (e.g. our
558 sampling occurred during the flight peak of *L. puncticolle* in that particular year) than to its longer
559 (five months) flowering period.

560

561

562 **5. Conclusions**

563 In this work we used a network approach to analyze the effects of conservation actions carried out
564 in a protected area for the safeguard of the rare plant *D. albus* and its bee pollinators. Network
565 structure showed a general increase of more evenly distributed plant-pollinator interactions and
566 higher species generalisation after conservation measures, with potential positive effects on the
567 pollinator community. However, the analysis of modules showed a significant rewiring of plant
568 pollinator interactions among species that were present in both periods. *Dictamnus albus* did not
569 change its importance within the network after the implementation of conservation actions: during
570 its relatively low flowering period it was visited by most bees sampled in the study area and it was
571 an important hub connecting several species within its own module, likely playing an important role
572 in its stability. Finally, the simultaneous habitat amelioration through bee plants reinforcement and
573 increased pollinator availability through the placement of artificial nesting sites and bumblebee
574 colonies led to increased flower visitation.

575

576 **Author contribution**

577 MG, AF and LB conceived the study. AF, NdM, GB, LB and MG performed field work. MQ
578 identified bees. AF, NdM and FM analyzed data. AF wrote the article with input from FM and MG.
579 All authors discussed and commented on the article.

580

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