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► **To cite this version:**

Claire Gay, Sabrina Gaba, Vincent Bretagnolle. The Structure of Plant–Pollinator Networks is Affected by Crop Type in a Highly Intensive Agricultural Landscape. SSRN Electronic Journal, 2023, 10.2139/ssrn.4378048 . hal-04071662

**HAL Id: hal-04071662**

**<https://hal.science/hal-04071662>**

Submitted on 19 Apr 2023

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1 **The structure of plant–pollinator networks is affected by crop**  
2 **type in a highly intensive agricultural landscape**

3

4

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12

13 **Abstract**

14 In agricultural landscapes, bipartite networks formed by pollinators and the flowers they  
15 forage on, are characterised by the presence of species managed by humans, whether  
16 honeybees (*Apis mellifera*) or crop plants. These managed species can affect the structural  
17 properties of these networks because of spatial and temporal variation in the availability of  
18 resources, and competition for these resources; for example, crop plants such as oilseed rape  
19 and sunflower produce a large number of flowers during a short blooming period. Here, we  
20 examined the structure of plant–pollinator networks in an intensive agricultural landscape, the  
21 LTSER Zone Atelier Plaine & Val de Sèvre (West of France). We compiled a six-year  
22 monitoring dataset of plant–pollinator interactions, sampling by sweep-nets along transects in  
23 the main six crop types (811 fields in total). To describe networks, we computed six metrics:  
24 connectance, nodes number, modularity, specialisation and two nestedness measures. Strong  
25 differences between crops were observed in nestedness and specialisation: in oilseed rape,

26 networks were much more nested and much less specialised than in sunflower. In addition,  
27 the link 'honeybee–crop flower' differed between the two mass-flowering crops. Honeybees  
28 and sunflowers appeared as specialist species in sunflower crops, interacting strongly and  
29 almost exclusively with each other, whereas they are usually considered highly generalist  
30 species. Indeed, sunflower pollination may be almost entirely driven by honeybees,  
31 conversely to oilseed rape crops, where the presence of wild bees and other insects tended to  
32 produce a more diversified network.

33

#### 34 **Key words**

35 Bipartite networks, Mass-flowering crops, Weeds, Honeybees, Spatio-temporal heterogeneity

36

#### 37 **Highlights**

- 38 • Honeybees and crop flowers drive the network structure in agricultural environment
- 39 • Main mass-flowering crops got very distinct network properties
- 40 • Specialisation of managed species is highly variable among mass-flowering crops

# 41 1. Introduction

42 Insect biodiversity is declining worldwide, and numerous local insect extinctions have already  
43 been documented (Habel et al., 2019). This decline has high consequences for the ecosystem  
44 services that rely upon insects, not least pollination (Frankie et al., 2009). In temperate  
45 regions, 88% of plants depend on zoogamous pollination for their reproduction (Ollerton et  
46 al., 2011) and 70% of crops depend to some extent on insect pollination (Klein et al., 2007),  
47 which improves yields of insect-pollinated crops and ensure agricultural production, as in  
48 oilseed rape (OSR; *Brassica sp.*) and sunflower (SF; *Helianthus sp.*) (Perrot et al., 2019,  
49 2018). In arable farming systems, insect pollinators forage partly – and sometimes mainly –  
50 on mass-flowering crops, but availability of these crops does not cover the entire season of the  
51 pollinators' activity (Odoux et al., 2014). Between OSR and SF blooms (the so-called 'dearth  
52 period'), the resources provided by weeds are essential for maintaining pollinators, including  
53 the honeybee *Apis mellifera* (Carvalho et al., 2011; Requier et al., 2015). Weeds and other  
54 wild plants are therefore critical for pollinators (Bretagnolle and Gaba, 2015), and contribute  
55 to their diversity and abundance at both field and landscape scales (Carvalho et al., 2011).  
56 Among insect pollinators, bees and hoverflies contain generalist species that can interact with  
57 many wild flowers (Dunn et al., 2020) or crop plants, and both improve pollination service  
58 (Garibaldi et al., 2011). Hoverflies are more resilient to agricultural modifications than bees in  
59 agricultural landscapes (Jauker et al., 2009); conversely, butterflies which also pollinate many  
60 wild plants, have been dramatically affected by agricultural intensification (Johst et al., 2006).  
61 Overall, weeds and pollinators are closely intertwined in agricultural farmland, and form  
62 ecological interaction networks, defined by a set of nodes (species) interconnected by one or  
63 more links (interactions). There is evidence that such networks have changed in structure over  
64 the last century, due to pollinator and plant community changes, with many interactions  
65 involving specialist species being lost (Mathiasson and Rehan, 2020), mostly as a result of

66 land use intensification (Ferreira et al., 2013). Indeed, the persistence of pollinators – together  
67 with the services they provide – depends on stability, hence the structure of plant–pollinator  
68 ecological networks.

69 However, plant–pollinator ecological networks in agricultural landscapes present unique  
70 properties: first, they harbour managed and over-abundant species; second, they are highly  
71 dynamic in space and time due to crop rotations. Such characteristics are expected to impact  
72 the nature and structure of plant–pollinator networks. First, farmland ecological networks are  
73 structured around managed honeybees in addition to wild pollinators, and managed crops in  
74 addition to weeds (Geslin et al., 2017). The effect of mass-flowering crops on one hand, and  
75 the presence of the honeybee on the other hand, can be related to ‘invasive species’ in arable  
76 systems (Geslin et al., 2017; Stanley and Stout, 2014), i.e. super-generalist species that  
77 interact with multiple groups of species (Giannini et al., 2015), leading to asymmetry and  
78 nestedness of the network (Ferreira et al., 2013). Perhaps counterintuitively, this asymmetry  
79 and nestedness contributes to the stability and the resistance of networks to land use change  
80 (Memmott et al., 2004). Links that emerge from these super-abundant species may, however,  
81 come at the expense of others, leading to species role shifts (Albrecht et al., 2014), or even  
82 loss of species in both plants or pollinators, which should affect the structure and functioning  
83 of networks (Valido et al., 2019). For instance, OSR flowers number c. 500,000/ha (Hoyle  
84 and Cresswell, 2007), are brightly coloured and attractive, and produce both pollen and  
85 nectar. OSR can thus create a distortion in mutualistic networks and has already been shown  
86 to be related to the decline of specialist long-tongued bumblebees in favour of short-tongued  
87 species better adapted to its flower traits (Diekötter et al., 2010). Honeybees in return may  
88 decrease wild bee richness, leading to networks with fewer links (Lázaro et al., 2021).

89 However, a decrease or even a removal of supergeneralist (key) species may destabilise the  
90 network (Kovács-Hostyánszki et al., 2019). Secondly, agricultural landscapes display very

91 high spatio-temporal unpredictability (due to crop rotations), and seasonal heterogeneity  
92 (Rollin et al., 2016): honeybees are present from April to September (Odoux et al., 2014),  
93 while OSR and SF, the main super-generalist plants, have very short flowering peaks  
94 (Bretagnolle and Gaba, 2015), and wild bees show generally have a short presence within the  
95 season. Crop rotation and spatial heterogeneity is therefore expected to affect the temporal  
96 and spatial dynamics of plant–pollinator networks (Chakraborty et al., 2021).

97 There is currently a lack of descriptive information on plant–pollinator networks in farmland  
98 habitats, especially at large spatial scale or over longer time-scales (Olesen et al., 2011).

99 Indeed, most studies investigated the crop compartment in relation to the semi-natural  
100 elements or its plants (e.g. Magrath et al., 2018; Stanley and Stout, 2014), while few studies  
101 aimed at investigating differences among crops (but see Kovács-Hostyánszki et al., 2019) and  
102 even fewer the effect of crop diversity. This is unfortunate, since crop effect was found to be  
103 the most statistically important effect in a vast study of predation–prey networks in  
104 agricultural habitats (Ma et al., 2019). Indeed, descriptive information is critical to  
105 understanding community stability and robustness, which are linked to the number of species  
106 and the number of links between them (Carpentier et al., 2021), and therefore network  
107 resilience, which relies on redundancy in the number of pollinator species per plant species  
108 (Memmott et al., 2004) and network nested structure (Bascompte et al., 2003). Network  
109 stability is improved by pollinator diversity (Bendel et al., 2019), nestedness and low  
110 modularity, though possibly at the expense of persistence (Thébault and Fontaine, 2010).

111 Along environmental gradients from less- to more- impacted by human footprint, e.g. from  
112 natural sites to monoculture farming, an increase in connectance and nestedness but a  
113 decrease in the number of nodes as well as modularity were shown (Morrison et al., 2020).

114 Increased connectance is expected to decrease secondary extinctions (Blüthgen et al., 2007)

115 and improves robustness at the community level as well as stability (Thébaud and Fontaine,  
116 2010).

117 In this study, we used a descriptive approach to qualify plant–pollinator networks in a highly  
118 intensive farming system, at a large spatial scale (study site of 450km<sup>2</sup>) with data collected on  
119 six different crop types (811 fields in total). Because our sampling effort was high, we first  
120 paid attention to two generally overlooked patterns, the effect of sample size and the degree  
121 distribution. Sampling effort has been shown to affect many network metrics, through  
122 sampling intensity and sampling bias, but also underlying species abundances (Blüthgen et  
123 al., 2007). Degree distribution is highly skewed, resulting in part from many ‘forbidden links’  
124 (Jordano, 2016). The frequency distribution of links is claimed to be best described by power-  
125 law distributions (Blüthgen, 2010), which have been shown to fit most natural networks. We  
126 also describe the overall visual structure of networks by seasons and crop types. Then, we  
127 investigated major features of the network, from simple network descriptors (number of  
128 nodes, connectance) to more complex ones (nestedness, modularity, specialisation),  
129 quantifying their level of variation among crop types and seasons, while accounting for  
130 sample size. We expected plant–pollinator network structure to vary seasonally because of the  
131 presence of mass-flowering crops, and the spillover or dilution effects that result from such  
132 presence. Indeed, we expected strong variations in network structure among crop types, in  
133 particular between mass-flowering and other crops, but also between arable crops and  
134 grasslands. We further predicted a clear dominance of the managed honeybee, especially  
135 during the flower blooms of OSR and SF, which dominate landscapes when flowering. In  
136 particular, we predicted that networks would be more specialised during OSR and SF blooms  
137 than in other periods and other crops. We also predicted that networks would be more nested  
138 during the blooming periods of mass-flowering crops than in the dearth periods, and thus in

139 these crops – as a result of super-generalist and abundant species presence – more able to  
140 include the same partners as the specialists in their spectrum of interactions.

141

## 142 **2. Materials and methods**

### 143 **2.1. Study site**

144 Our study site is the Long Term Socio-Ecological Research (LTSER) site ‘Zone Atelier  
145 Plaine & Val de Sèvre’, located in the Nouvelle-Aquitaine region of southwest France, south  
146 of the city of Niort (Bretagnolle et al., 2018). It covers 450 km<sup>2</sup>, harbouring c. 13,000 fields.  
147 We focused on six years of survey, 2015–2020, which is one of the largest time intervals of  
148 plant–pollinator network studies (but see Chacoff et al., 2018; Petanidou et al., 2008; Ponisio  
149 et al., 2017). Each year, 100 to 220 different fields were surveyed (some fields were studied  
150 for more than one year) with a standardised protocol. Fields were selected in a stratified  
151 random process (see Bretagnolle et al. (2018) for details). From 2015–2020, the number of  
152 fields sampled per respective year were 174, 217, 195, 160, 117 and 115 (see ESM1a and 1b  
153 in Appendix A). Crop surveyed included 7% corn (*Zea mays*) and sorghum (*Sorghum*  
154 *bicolor*), 8% alfalfa (*Medicago sativa*), 12% meadows (temporary or permanent), 18% oilseed  
155 rape (*Brassica napus*), 22% sunflower (*Helianthus annuus*), and 33% cereal crops. Cereals  
156 included barley (*Hordeum vulgare*), durum wheat (*Triticum turgidum*), einkorn (*Triticum*  
157 *monococcum*), oat (*Avena sativa*), rye (*Secale cereale*), triticale ( $\times$ *Triticosecale*) and winter  
158 wheat (*Triticum aestivum*). Sampling was performed from April to August, i.e. all crops were  
159 surveyed at least once during their respective flowering periods: OSR from April–May;  
160 sunflower from July–August; alfalfa, meadows and cereals from May–June to the end of  
161 August; and corn and sorghum from July–August.

162

### 163 **2.2. Sampling of plant–pollinator interactions**



164 Insects surveyed included bees (both honeybees and wild bees), butterflies and hoverflies  
165 (Syrphidae), i.e. the three main pollinator groups in the LTSER. This study site hosts a large  
166 number of pollinator species (Rollin et al., 2016). Each year, two (2015) or three (2016–2020)  
167 50 m long transects were performed per field: one in the field centre, one in the field margin  
168 (section between the field edge and the first seeding line) and the last in between, at c. 25 m  
169 from the margin (except in 2015). Field margins generally harbour a more diverse fauna  
170 compared to field cores. Transects were parallel to tram lines. For each transect, the surveyed  
171 area was a theoretical volume, 2.5 m each side, 2.5 m in front of the observer and c. 1 m  
172 above the observer's head. Surveys were conducted under calm weather conditions, i.e. sunny  
173 days with air temperatures in full sun mostly above 15°C (95% T >16°C; 12° to 45°C, in  
174 sunlight), and between 7:30 a.m. and 6:30 p.m. In 27.9% of the fields (226 of 811), two  
175 sampling sessions were conducted (early- and late-season). Each plant–pollinator interaction  
176 (i.e. an insect landing on a flower) was tallied, with both plant and pollinator being identified  
177 (pollinators being caught with a sweep-net for later identification by a professional  
178 entomologist if necessary). Transects were walked along very slowly (c. 12 s/m), for a total  
179 duration of 10 min each. The observer stopped the timer each time an insect had to be  
180 identified or captured. Butterflies were always identified by sight; however, given the time  
181 spent in flight in butterflies, all individuals crossing the sampled theoretical volume were  
182 tallied, even if not on a flower. Almost all pollinators and plants (94% and 96% respectively)  
183 were identified to species level.

184

## 185 **2.3. Statistical analyses**

### 186 *2.3.1. Sampling completeness and frequency distribution of degrees*

187 We estimated sampling completeness of plants and pollinators using the Chao estimator of  
188 asymptotic species richness (Chacoff et al., 2012), which is based on rare species (those that

189 occur only once or twice). We calculated the Chao 2 estimator using the *vegan* R package  
190 (v2.5.7; Oksanen et al., 2020) and evaluated the percentage of completion (ratio between the  
191 observed value and estimated value) of our sampling of plants and pollinators.  
192 We analysed the frequency distribution of degrees in total as well as in subnetworks (per crop  
193 and per period), testing for best-fit with *a priori* distributions, i.e. Exponential, Poisson,  
194 Weibull, Lognormal, Negative binomial, Power law and Fisher's logseries. We used the  
195 *fitdistrplus* package (Delignette-Muller and Dutang, 2015), except for the Fisher's logseries  
196 (which is not implemented in this package), which we computed. Power law was tested with  
197 the *powerLaw* package (Gillespie, 2015). Best fit was checked using the Akaike Information  
198 Criterion (AIC; Burnham et al., 2011). We fixed a threshold of 2 units' difference in AIC to  
199 select the best model among the candidate models.

200

### 201 2.3.2. Number of nodes and number of interactions: crop and temporal effects

202 From floral visitation events, we constructed bipartite networks with plant and bee nodes,  
203 using a visitation event as a plant–pollinator interaction. To analyse how the network structure  
204 varied among crops and seasons, we built interaction subnetworks. Six crop categories were  
205 retained: OSR, cereals, alfalfa, meadows, SF and corn–sorghum. We also split the data into  
206 three equal-length seasons, each 45 days long: April 1<sup>st</sup>–May 20<sup>th</sup> (OSR flowering peak,  
207 characterised by high resource availability for insects), May 21<sup>st</sup>–July 9<sup>th</sup>, characterised by a  
208 general lack of flowering crop resources available (i.e. the dearth period) – when honeybee  
209 colony sizes are, perhaps surprisingly, at their highest (Odoux et al., 2014) – and finally, July  
210 10<sup>th</sup>–August 22<sup>nd</sup>, corresponding to the SF flowering peak. We also divided our dataset into  
211 six main taxonomic groups: honeybees, bumblebees, other social bees (including some  
212 *Halictidae*, e.g. *Halictus rubicundus*, *Lasioglossum pauxillum*), solitary bees, hoverflies and  
213 butterflies. To describe seasonal patterns in the number of interactions, we standardised our

214 data, since the number of transects per field and the number of fields sampled per crop and  
215 per year varied. We thus converted the number of interactions per transect per field into a  
216 number per hectare (ha), since each transect surveyed an area of 250 m<sup>2</sup>. Next, we grouped  
217 samples per fortnight by averaging values (with standard-error, se) of interactions per ha per  
218 fortnight for each crop. Obtained values were compared with ANOVA and post-hoc Tukey  
219 tests. Data were log-transformed.

220

### 221 2.3.3. *Network structure descriptors*

222 A large number of indices is available to describe network structure (see ESM2, which  
223 presents their respective properties in Appendix A). We selected the following ones: number  
224 of nodes (i.e. the number of species in interaction), connectance (the ratio between the number  
225 of links observed and the total number of possible links), modularity – which gives insights  
226 into the presence of subnetworks among the network (called modules, i.e. weakly interlinked  
227 subsets of species that are constituted of strongly interacting species) and which was  
228 calculated using the greedy Louvain algorithm method (Blondel et al., 2008) – and  
229 nestedness, described by NODF (Nestedness metrics based on Overlap and Decreasing Fill;  
230 Almeida-Neto et al., 2008). The latter is a property describing to what extent the partners of  
231 specialists are a subset of the partners of generalists. We also used WNODF (Weighted  
232 Nestedness metrics based on Overlap and Decreasing Fill; Almeida-Neto & Ulrich, 2011), the  
233 quantitative alternative to NODF that accounts for the number of similar interactions. Finally,  
234 we focused on the specialisation  $H_2'$  (standardised two-dimensional Shannon entropy) – the  
235 degree of specialisation between the two levels of the entire network (Blüthgen et al., 2006) –  
236 and the  $d'$  species-level specialisation measure (standardised Kullback–Leibler distance,  
237 Blüthgen et al., 2006), corrected by de Manincor et al. (2020), representing the degree of  
238 interaction specialisation at the species level. Network descriptors were obtained using the R

239 packages *bipartite* (Dormann et al., 2009), *igraph* (Csardi and Nepusz, 2006), *NetIndices*  
240 (Kones et al., 2009) and *vegan* (Oksanen et al., 2020).  
241 Some of these metrics (i.e. connectance, nestedness) are sensitive to sample or network size  
242 (Dormann et al., 2009). We thus checked how indices varied with increasing numbers of  
243 samples (according to periods and crops) by calculating all metrics (excluding  $d'$ ) with  
244 increasing numbers of sampled fields. Five to 195 fields (every 10 field steps) were randomly  
245 sampled (with replacement) from the overall sample. At each step (i.e. field number), 100  
246 groups of fields were constituted, the six network metrics were computed and the mean and  
247 the 95% confidence interval (CI) were calculated. The maximum bootstrap threshold to  
248 compare the three seasons was 175 field groups, when OSR period samples stopped, but we  
249 also went up to 195 fields to compare only dearth period and sunflower period. When  
250 comparing the six different crop types, we had to stop at a threshold of 35 fields per group  
251 (100 groups) in the bootstrap because we had very few fields of corn–sorghum and alfalfa. To  
252 increase the sampling effort, we had to lose crops, and were left with only four crops with 100  
253 groups of 85 fields. However, when focusing on the two mass-flowering crops, OSR and SF,  
254 we were able to analyse 100 groups of 165 fields. Therefore, the number of fields  
255 bootstrapped varied according to the crops to be compared.

256

#### 257 *2.3.4. Field selection*

258 To calculate Chao 2 estimates and the number of interactions per hectare, we included the  
259 fields in which no insects had been observed (138 fields, 17.0%). However, to represent  
260 interaction networks and calculate metrics on aggregated fields, we only retained the fields on  
261 which at least one interaction was observed in the dataset.

262 All analyses were run with *R software v.4.1.0* (R Core Team, 2021).

263

## 264 **3. Results**

### 265 **3.1. Sampling completeness and frequency distribution of degrees**

266 A total of 37,133 plant–pollinator interactions were tallied over 811 fields (127 of which were  
267 studied in at least two years between 2015 and 2020), occurring between 200 species of  
268 pollinators foraging on 165 species of plants (including individuals that were only identified  
269 to genus level). We found 96 species of solitary bees, 35 species of social bees (including the  
270 honeybee *A. mellifera* and 14 species of bumblebees), 38 species of butterflies and 31 species  
271 of hoverflies. A total of 758 interactions were obtained between one plant or one pollinator  
272 occurring only once. No interaction was found between one plant and one pollinator occurring  
273 both only once. In regard to pollinators, over the full network, 80 species (40.0%) interacted  
274 with only one plant (crop or weed), 29 species (14.5%) interacted with two, while 91 species  
275 (45.5%) were more generalist (>2 plants, up to 92 plants). Similar values were obtained for  
276 plants, with 38 weed species interacting with only one insect species (23%), and 16 with two  
277 insect species (9.7%). There were 138 fields without any observed interaction (17.0%). We  
278 caught 64.5% of pollinators, and recorded 78.6% of the plant community, based on Chao 2  
279 estimators.

280 Overall, the frequency distribution of degrees (i.e. interacting plants/pollinators) fitted better  
281 to the Fisher’s log-series (see ESM3 in Appendix A) than to Lognormal ( $\Delta_{AIC} = 73$ ) or Power  
282 laws ( $\Delta_{AIC} = 77$ ). When splitting by crop or per season, similar results were found.

283 Differences in the goodness-of-fit of Fisher’s log-series and Lognormal were, however, much  
284 lower in alfalfa ( $\Delta_{AIC} = 12$ ) and in corn and sorghum crops ( $\Delta_{AIC} = 3$ ) than in other crops.

285

### 286 **3.2. Number of nodes and number of interactions: crop and temporal effects**

287 The total number of nodes varied highly among crops (165, 114, 186, 178, 161 and 75 in  
288 meadows, alfalfa, cereals, SF, OSR and corn–sorghum, respectively). Accumulation curves

289 per crop indicated that these differences among crops (Fig. 1) could be detected even from  
290 low sample sizes (c.  $n = 50$ ). Thus, independently of the number of sampled fields, meadows  
291 showed the highest values of node numbers, followed by alfalfa, cereals, OSR and SF (Fig.  
292 1). Year did not affect the pattern of the accumulation curves (see ESM4 in Appendix A),  
293 although 2017 was a species-rich year regardless of the sampling effort.

294 The number of plant–pollinator interactions, here standardised per hectare of sampling effort  
295 (which can be considered as an instantaneous visitation rate per hectare), was on average  
296  $338.43 \pm 23.19$  interactions/ha (mean  $\pm$  se). This value, however, showed strong seasonal  
297 variations, with most interactions occurring in early July when considering all crops, or mid-  
298 June when excluding SF (Fig. 2). There were also strong variations among crops, with  
299 interactions in SF being overwhelmingly dominant and driving seasonal variation. In early  
300 July, we found significant differences in the average number of interactions among crops  
301 ( $F_{5,62} = 20.16$ ,  $p$ -value  $< 0.0001$ ), with significantly higher values for SF than in alfalfa ( $T_{HSD}$   
302  $p$ -adj  $< 0.001$ ), meadows ( $T_{HSD}$   $p$ -adj  $< 0.001$ ), cereals ( $T_{HSD}$   $p$ -adj  $< 0.001$ ) and OSR ( $T_{HSD}$   $p$ -  
303 adj = 0.0015).

304 Network structure differed strongly among crops in relation to variation of the total number of  
305 nodes, either in the repartition of interactions between the main groups of plants or between  
306 the main groups of pollinators (Fig. 3). In flowering crops, the crop flower was generally the  
307 most visited flower in the crop considered. For instance, 95.27% of pollinators visited SF  
308 plant in SF fields, and 86.07% OSR plants in OSR fields. However, this was true only for  
309 mass-flowering crops: alfalfa represented approximately a third of all visited flowers in alfalfa  
310 fields (36.12%) and corn was poorly visited in corn–sorghum fields (7.55%). In those crops,  
311 pollinators preferentially foraged on wild flowers (89.62%). Moreover, honeybees’  
312 dominance was not of the same magnitude in all crops: they were overrepresented in SF  
313 (91.95%) and OSR (76.60%), while hoverflies rather than honeybees were the most-

314 interacting group in other crops (32.55% in corn and sorghum crops, 56.42% in cereal crops,  
315 36.02% in alfalfa crops and 53.38% in meadows). Interestingly, when found in other crops,  
316 OSR and SF flowers showed the same interaction pattern, i.e. interacting mainly with  
317 honeybees. Moreover, hoverflies foraged more on wild flowers than did any other insect  
318 group, potentially explaining their high presence in weed-rich crops such as meadows or  
319 alfalfa. For instance, whereas the total percentage of weed visits by all pollinator groups was  
320 63.78% in alfalfa crops, it reached 77.94% when considering only hoverfly visits.

321 The overall pattern of the network is depicted on Fig. 4, which represents standardised  
322 interactions between pollinators and plants according to their degree (i.e. number of  
323 interaction partners). Species with the highest degrees were not necessarily the most frequent,  
324 although species' frequency of occurrence and degree were strongly related (i.e. decreasing  
325 pattern of species degrees were concomitant with decreasing species frequencies) (Fig. 4). In  
326 terms of the number of interactions, honeybees and bumblebees were most prevalent (83.72%  
327 of the total interactions number,  $n = 31,089$ ), followed by hoverflies (8.21%,  $n = 3,050$ ),  
328 solitary bees (2.69%,  $n = 998$ ) and butterflies (1.36%,  $n = 506$ ). Honeybees were by far the  
329 dominant insect species (80.80% of all interactions,  $n = 30,007$ ), the next two being  
330 *Sphaerophoria scripta* (3.80%,  $n = 1,412$ ) and *Episyrphus balteatus* (2.19%,  $n = 812$ ), two  
331 hoverflies. However, although *S. scripta* was found 20 fewer times than honeybees in total, its  
332 number of plant partners (92) was higher than that of honeybees (75). Butterflies were far less  
333 often observed, with only 81 interactions for the most common butterfly, *Pieris rapae*.

334 Concerning plants, SF represented 72.36% ( $n = 26,871$ ) of the whole sample, seven times  
335 more than OSR (10.69%,  $n = 3,971$ ), and 60 times more than the most-interacting weed,  
336 *Torilis arvensis* (1.20%,  $n = 446$ ). Therefore, the complete network was dominated by  
337 honeybees and mass-flowering crops: honeybees interacting with OSR or SF represented  
338 77.44% of all interactions.

339

### 340 **3.3. Network structure**

#### 341 *3.3.1. Seasonal effect on network structure*

342 The average number of nodes during the dearth period (mid-May to early July) was similar to  
343 the average number of nodes for all periods, regardless of the sampling effort (Fig. 5a),  
344 reaching 214 (CI<sub>95%</sub>: 195–230) species when considering a sampling effort of 175 fields. The  
345 average number of species was nearly equal during SF and OSR flowering blooms (154 (142–  
346 165) and 148 (146–151), respectively, in 175 fields); that is to say, 1.4-times lower than  
347 during the dearth period, but with a weaker variability among fields during OSR flowering.  
348 Mean connectance did not vary a lot with period, being 3% (2.6–3.4) during bloom periods  
349 and 2.5% (2.2–2.8) during the dearth period in 175 fields. Mean modularity was slightly  
350 higher for the OSR blooming network (0.42 (0.41–0.43)) than for other periods (0.39 (0.36–  
351 0.41) in SF blooming and 0.37 (0.35–0.38) in dearth period)). Specialisation of the network  
352 remained constant during dearth and SF periods when considering network sizes above 100  
353 fields (see ESM2 for details in Appendix A), but decreased much more quickly in the OSR  
354 blooming period, with no overlapping 95% in CIs. This highlights that OSR blooming period  
355 was represented by more generalist species than the other periods. Specialisation was higher  
356 during the SF bloom and dearth periods, with average values between 0.49 (0.43–0.55) and  
357 0.50 (0.46–0.52), respectively, compared to the OSR flowering bloom (0.30 (0.29–0.33)). The  
358 OSR blooming period was characterised by a higher nestedness (37.2 (35.6–38.6) in 175  
359 fields) than the SF blooming period (24.0 (21.3–26.9)) and dearth period (27.0 (24.4–29.9)).  
360 Similar patterns were observed when using weighted NODF: 14.8 (12.7–16.8) during the  
361 dearth period, 13.3 (11.8–15.0) during the SF blooming period, and 21.9 (20.6–23.1) during  
362 the OSR blooming period. Thus, it seems that the flowering period of the OSR was the most  
363 prone to host specialist species that had partners similar to generalist species.



364

### 365 3.3.2. Crop effect on network structure

366 All crops' subnetworks were similarly poorly connected (c. 3% at a threshold of 85 fields)  
367 (Fig. 5b). Although OSR blooming period was the most modular period (see above), mean  
368 modularity was almost identical whatever the crop considered, at about 0.5. At an equal  
369 sampling survey effort of 85 fields, modularity was 0.43 (CI<sub>95%</sub>: 0.39–0.47) for meadows,  
370 0.45 (0.40–0.49) for SF and 0.48 (0.45–0.52) for OSR. With a higher sampling rate (n = 165  
371 fields), but at the cost of losing crop types in the comparisons, OSR showed significant higher  
372 modularity values than SF. The two mass-flowering crops' networks also had very different  
373 specialisation (H2'), showing the two most extreme values among our six crops. OSR was far  
374 less specialised (0.31 (0.29–0.33) at 165 fields) than all other crops, while SF (0.58 (0.55–  
375 0.61)) showed the most specialised network; the other crops showed intermediate values, e.g.  
376 0.45 (0.43–0.47) for meadows and 0.40 (0.34–0.46) for cereals at a survey effort of 85 fields.  
377 Low specialisation in OSR could be partially explained by the low specialisation of the most  
378 abundant insect, the honeybee (d' = 0.27) and the low specialisation of the crop flower, OSR  
379 (d' = 0.21). Indeed, in OSR, the average d' of all species was 0.26 for insects (n = 97, median  
380 = 0.20) and 0.23 for plants (n = 68, median = 0.44), meaning that the network was lowly  
381 specialised at both trophic levels and highly driven by the honeybee and OSR flower  
382 dominance. In SF, specialisation was 0.67 for SF (more than three times higher than in OSR)  
383 and 0.42 for the honeybee (1.5-times higher than in OSR). SF was thus highly connected to  
384 honeybees despite honeybees being slightly less specialised than SF, indicating a larger  
385 partners' spectrum. The average d' of all insect species in SF was 0.41 (n = 109, median =  
386 0.50) and 0.67 for plants (n = 65, median = 0.51), again reflecting the preponderant roles of  
387 honeybees and SF. Nestedness (NODF) increased with sampling effort, being higher in OSR  
388 than in any other crops (mean value of 29.8 (22.5–36.8) when sampling effort was low, i.e. 35

389 fields), especially in meadows (16.1 (11.0–21.3)), cereals (21.3 (15.1–28.4)) and SF (21.6  
390 (16.8–29.2)), rather than in alfalfa (25.5 (21.0–30.8)). When increasing sampling effort (85-  
391 field threshold), nestedness reached 33.0 (27.7–38.2) in OSR networks, c. 25% more than in  
392 cereals (23.9 (19.9–28.5)) and in SF (23.4 (19.5–28.1)). Weighted NODF average values  
393 showed similar patterns: SF reached a WNODF mean value of 14.5 (13.1–15.7) when  
394 considering a threshold of 165 fields, whereas OSR networks peaked on average at 21.6  
395 (20.3–22.5).

396

#### 397 **4. Discussion**

398 The detection of several hundreds of species in the plant–pollinator network indicates that the  
399 LTSER ZAPVS is characterised by a high diversity of species despite its intensive farming  
400 system. While the honeybee, SF and OSR are by far the species that establish most  
401 interactions, they are not necessarily those with the greatest number of interacting partners.  
402 Although OSR flower is the species with the highest degree (number of interaction partners),  
403 confirming its structuring role in the network (Diekötter et al., 2010; Stanley and Stout, 2014),  
404 it is closely followed by wild plant species, generally hosted in less-intensively managed but  
405 more diverse crops such as alfalfa or meadows. Moreover, the hoverfly *Sphaerophoria scripta*  
406 showed far more partners than honeybee, including OSR and SF flowers, suggesting that its  
407 role in the network has to be explored in more detail. *Bombus* species are also frequent  
408 visitors of SF, as Syrphidae of OSR (Jauker and Wolters, 2008). Although these are rarely  
409 studied as key species in networks, they might be strongly involved in OSR and SF  
410 pollination (Breeze et al., 2011), and could act as pollination insurance if honeybees were to  
411 decline dramatically (Sánchez-Bayo and Wyckhuys, 2019).

412 Completeness of survey effort was, however, moderate: 65% for insects but 80% for plants  
413 according to the Chao 2 estimator, despite our dataset covering six months (from April to

414 September) and six years. The phenology of some plants and insects being very short may  
415 explain why not all species were detected, in addition to the classic and inherently imperfect  
416 detection method. In addition, the low connectance within crops (around 2–3%) suggests that  
417 few interactions are carried out among all possible ones. These forbidden links (Jordano,  
418 2016) could result from spatial or temporal constraints (Valdovinos, 2019). Indeed, one of our  
419 possible explanations is that each crop network corresponds to a set of different fields that  
420 belongs to different landscape entities and different sampling weeks, which generates a high  
421 community variability in terms of phenology and location. But a low connectance, i.e. high  
422 proportion of forbidden links, is in certain cases one of the indicators of destabilised networks  
423 (Landi et al., 2018).

424 The hypothesis of the dominance of honeybee interactions with crop flowers during OSR  
425 flowering and SF flowering, and not in other periods, was largely verified. Overdominance of  
426 managed species may destabilise networks (Valido et al., 2019). The stability of a network  
427 can be evaluated through the values of some network metrics (Thébault and Fontaine, 2010).  
428 A stable bipartite mutualistic network is often a network with a high connectance and many  
429 species, as well as a nested – but not very modular – network (Thébault and Fontaine, 2010).  
430 In our case, connectance was always very low (<5%), whether we considered the total  
431 network or the subnetworks per season or per crop. When the connectance is so low,  
432 modularity and nestedness are usually positively correlated (Fortuna et al., 2010), hence a  
433 situation with a nested but not modular network is unlikely, therefore possibly suggesting  
434 instability in our networks. In particular, the corn–sorghum network, which is highly modular  
435 and comprises few species, may show particularly low stability, though we had relatively  
436 small sample sizes. Meadows were a special case, endowed with a large number of species  
437 but not very nested and not very connected compared to other crops. Thus, although meadow  
438 networks appear to be resilient networks thanks to the number of species they host (Okuyama

439 and Holland, 2008), they display a certain vulnerability because the sharing of partners is  
440 weak, like in the studied SF crops, but contrary to the OSR crops.

441 Indeed, the most striking differences in networks were found between OSR and SF, both  
442 being mass-flowering crops. As expected, these two crops drove the overall behaviour of  
443 networks during their blooming season (approximately the same metrics of behaviour  
444 between the OSR crop and OSR period, and between the SF crop and SF period), although the  
445 meadows, weeds in cereals, and alfalfa were flowering at the same time. However, the OSR  
446 and SF crops' networks were somewhat opposed in some of the key metrics, hence possibly  
447 showing different network stability (Duchenne et al., 2022). The OSR network did not  
448 harbour many species, but was highly nested compared to the other crop networks, which  
449 therefore suggests it was a resilient network. Its nestedness may result from the fact that the  
450 OSR network was mostly composed of species with a high degree of generalisation (i.e. the  
451 average species specialisation was quite low in OSR crops), leading to a relatively nested  
452 structure (Fontaine et al., 2009). Thus, as the OSR network was the most nested network in  
453 our study, it was expected that the general core of species it included were generalists rather  
454 than specialists, which was indeed the case. The interaction between OSR and honeybees has  
455 a structuring effect for the network, corroborating studies that highlight OSR flower and its  
456 partners as a hub that positively influences the visitation and pollination of neighbouring wild  
457 plants, especially those with similar morphology (Thompson et al., 2021). OSR is also known  
458 to host diverse insect communities (Stanley et al., 2013), while honeybees remain one of the  
459 most efficient pollinators and, as demonstrated here, the most important partner of OSR.

460 Conversely, SF appears less stable than OSR because it is much less nested for an equivalent  
461 diversity of species, and is composed of more specialised species, including the honeybee–SF  
462 duo, which both qualify as specialist species, interacting strongly and almost entirely with  
463 each other – a pattern that was not necessarily found in other studies (e.g. Valido et al., 2019).

464 Such a quasi-exclusive relationship between honeybees and SF as we found here may reflect  
465 either competition within pollinators or plant communities in SF crops, or a strong niche  
466 differentiation between wild and managed species. Conversely, OSR may host more  
467 generalist species that interact with specialist species and therefore enhance the persistence of  
468 the network (Liao et al., 2022).

469

## 470 **5. Conclusion**

471 Our results suggest that the honeybee and crop flower pair may differ between OSR and SF,  
472 being an almost exclusive relationship in SF that prevents other partners by competition,  
473 while allowing other modules in OSR hence increasing nestedness and consequently  
474 improving network stability. This divergence may possibly result from phenological  
475 difference, or as a consequence of flower shape – a divergence that can be further explored  
476 with species trait approaches.

477

## 478 **Author Contributions**

479 Conceptualisation, V.B. and S.G.; Methodology, C.G., V.B. and S.G.; Formal Analysis, C.G.;  
480 Writing-Original Draft Preparation, C.G., S.G. and V.B; Writing-Review and Editing, C.G.,  
481 S.G. and V.B. All authors have read and agreed to the published version of the manuscript.

482

## 483 **Declaration of Competing Interest**

484 The authors declare that they have no known competing financial interests or personal  
485 relationships that could have appeared to influence the work reported in this paper.

486

## 487 **Acknowledgements**

488 We thank in particular Jean-Luc Gautier, Alexis Saintilan and Marilyn Roncoroni for the  
489 monitoring, sampling and identification of the pollinator' data. We also thank the farmers of  
490 the LTSER 'Zone Atelier Plaine & Val de Sèvre' involved in the research program. CG  
491 received funding for her PhD grant from the project SHOWCASE (SHOWCASing synergies  
492 between agriculture, biodiversity and ecosystem services to help farmers capitalising on  
493 native biodiversity) within the European Union's Horizon 2020 Research and Innovation  
494 Programme under grant agreement N° 862480. This study was supported by the 'Programme  
495 Pollinisateurs' (2015–2020) funded by the Ministère de l'Ecologie et de l'Environnement.

496

#### 497 **Appendix A. Supporting information**

498 Supplementary data associated with this article can be found in the online version at [...]

499

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