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

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12
13 **Abstract**

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

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

34

35 **Key words**

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

37

38 **Highlights**

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

42 **1. Introduction**

43 Insect biodiversity is declining worldwide, and numerous local insect extinctions have already
44 been documented (Habel et al., 2019). This decline has high consequences for the ecosystem
45 services that rely upon insects, not least pollination (Frankie et al., 2009). In temperate regions,
46 88% of plants depend on zoogamous pollination for their reproduction (Ollerton et al., 2011)
47 and 70% of crops depend to some extent on insect pollination (Klein et al., 2007), which
48 improves yields of insect-pollinated crops and ensure agricultural production, as in winter
49 oilseed rape (OSR; *Brassica sp.*) and sunflower (SF; *Helianthus sp.*) (Perrot et al., 2019, 2018).
50 In arable farming systems, insect pollinators forage partly – and sometimes mainly – on mass-
51 flowering crops, but availability of these crops does not cover the entire season of the
52 pollinators’ activity (Odoux et al., 2014). Between OSR and SF blooms, i.e. in May and June
53 in temperate farmland landscapes, there is a temporary lack of mass-flowering crop floral
54 resources (the so-called ‘dearth period’) during which the resources provided by weeds are
55 essential to bee foraging and survival (Requier et al., 2017, 2015), including the honeybee *Apis*
56 *mellifera* (Carvalho et al., 2011; Requier et al., 2015). Weeds and other wild plants are
57 therefore critical for pollinators (Bretagnolle and Gaba, 2015), and contribute to their diversity
58 and abundance at both field and landscape scales (Carvalho et al., 2011). Overall, weeds and
59 pollinators are closely intertwined in agricultural farmland, and form ecological interaction
60 networks, defined by a set of nodes (species) interconnected by one or more links (interactions).
61 There is evidence that such networks have changed in structure over the last century, due to
62 pollinator and plant community changes, with many links – that involve specialist species –
63 being lost (Mathiasson and Rehan, 2020), mostly as a result of land use intensification (Ferreira
64 et al., 2013). Indeed, the persistence of pollinators – together with the services they provide –
65 depends on the structure of plant–pollinator ecological networks.

66 However, plant–pollinator ecological networks in agricultural landscapes present unique
67 properties: first, they harbour managed and over-abundant species such as crop plants or
68 managed honeybees (Geslin et al., 2017; Giannini et al., 2015; Rollin and Garibaldi, 2019);
69 second, they are highly dynamic in space and time (Chakraborty et al., 2021; Le Féon et al.,
70 2013; Riedinger et al., 2015). Such characteristics are expected to impact plant–pollinator
71 networks. First, farmland plant–pollinator networks are structured around managed honeybees
72 in addition to wild pollinators, and managed crops in addition to weeds (Geslin et al., 2017).
73 The effect of mass-flowering crops on the one hand, and the presence of the honeybee on the
74 other hand, can be related to ‘invasive species’ in arable systems (Geslin et al., 2017; Stanley
75 and Stout, 2014), i.e. super-generalist species that interact with multiple groups of species
76 (Giannini et al., 2015), leading to asymmetry and nestedness of the network (Ferreira et al.,
77 2013). Perhaps counterintuitively, these asymmetry and nestedness contribute to the stability
78 and the resistance of networks to land use change (Memmott et al., 2004). Links that emerge
79 from these super-abundant species may, however, come at the expense of others, leading to
80 species role shifts (Albrecht et al., 2014), or even loss of species in both plants or pollinators,
81 which should affect the structure and functioning of networks (Valido et al., 2019). For instance,
82 OSR flowers, producing both pollen and nectar, are highly visited by different types of
83 pollinators (Stanley et al., 2013). OSR can thus create a distortion in mutualistic networks and
84 has already been shown to be related to the decline of specialist long-tongued bumblebees in
85 favour of short-tongued species better adapted to its flower traits (Diekötter et al., 2010).
86 Honeybees in return may decrease wild bee richness, leading to networks with fewer links
87 (Lázaro et al., 2021). Secondly, agricultural landscapes display very high spatio-temporal
88 unpredictability (due to crop rotations), and seasonal heterogeneity (Rollin et al., 2016):
89 honeybees are present from April to September (Odoux et al., 2014), while OSR and SF, the
90 main mass-flowering crop plants, have very short flowering peaks (Bretagnolle and Gaba,

91 2015), and some wild bee species generally have a short presence within the season (e.g.
92 Andrenidae, Megachilidae; Falk and Lewington, 2015). Crop rotation and spatial heterogeneity
93 is therefore expected to affect the temporal and spatial dynamics of plant–pollinator networks
94 (Chakraborty et al., 2021).

95 There is currently a lack of descriptive information on plant–pollinator networks in farmland
96 habitats, especially at large spatial scale or over longer time-scales (Olesen et al., 2011). Indeed,
97 most studies investigated the crop compartment in relation to the semi-natural elements or its
98 plants (e.g. Magrach et al., 2018; Stanley and Stout, 2014), while few studies aimed at
99 investigating differences among crops (but see Kovács-Hostyánszki et al., 2019). This is
100 unfortunate, since crop effect was found to be the most statistically important effect in a vast
101 study of predation–prey networks in agricultural habitats (Ma et al., 2019). Indeed, descriptive
102 information is critical to understanding community stability and robustness, which are linked
103 to the number of species and the number of links between them (Carpentier et al., 2021), and
104 therefore network resilience, which relies on redundancy in the number of pollinator species
105 per plant species (Memmott et al., 2004) and network nested structure (Bascompte et al., 2003).
106 Network stability is improved by pollinator diversity (Bendel et al., 2019), nestedness and low
107 modularity, though possibly at the expense of persistence (Thébault and Fontaine, 2010). Along
108 environmental gradients from less- to more- impacted by human footprint, e.g. from natural
109 sites to monoculture farming, an increase in connectance and nestedness but a decrease in the
110 number of nodes as well as modularity were shown (Morrison et al., 2020).

111 In this study, we used a descriptive approach to qualify plant–pollinator networks in a highly
112 intensive farming system, at a large spatial scale (study site of 450km²) with data collected on
113 six different crop types (811 fields in total). Because our sampling effort was high, we first paid
114 attention to two generally overlooked patterns, the effect of sample size and the degree
115 distribution. Sampling effort has been shown to affect many network metrics, through sampling

116 intensity and sampling bias, but also underlying species abundances (Blüthgen et al., 2007).
117 Degree distribution is highly skewed, resulting in part from many ‘forbidden links’, the latter
118 resulting from constraints imposed by the morphological, phenological, phylogenetic and
119 spatial complementarity of species (Jordano, 2016): if the ecological niches of two species are
120 incompatible, then these species cannot interact with each other. We also describe the overall
121 visual structure of networks by seasons and crop types. Then, we investigated major features of
122 the network, from simple network descriptors (number of nodes, connectance) to more complex
123 ones (nestedness, modularity, specialisation), quantifying their level of variation among crop
124 types and seasons, while accounting for sample size. We expected plant–pollinator network
125 structure to vary seasonally because of the presence of mass-flowering crops, and the spillover
126 or dilution effects that result from such presence. Indeed, we expected strong variations in
127 network structure among crop types, in particular between main mass-flowering and other crops
128 (Timberlake et al., 2019), but also between arable crops and grasslands. We further predicted a
129 clear dominance of the managed honeybee, especially during the flower blooms of OSR and
130 SF, which dominate landscapes when flowering. In particular, we predicted that networks
131 would be more specialised during OSR and SF blooms than in other periods and other crops.
132 We also predicted that networks would be more nested during the blooming periods of mass-
133 flowering crops than in the dearth periods, and thus in these crops – as a result of super-
134 generalist and abundant species presence – more able to include the same partners as the
135 specialists in their spectrum of interactions.

136

137 **2. Materials and methods**

138 **2.1. Study site**

139 Our study site is the Long Term Socio-Ecological Research (LTSER) site ‘Zone Atelier Plaine
140 & Val de Sèvre’, located in the Nouvelle-Aquitaine region of southwest France, south of the

141 city of Niort (Bretagnolle et al., 2018a). It covers 450 km², harbouring c. 13,000 fields. In the
142 study site, grasslands represent about 10% of the farmed area, cereals 37%, OSR 7%, sunflower
143 7.5% and maize 9%, while forests cover 14% and the remaining area consist in other crops
144 (pea, ryegrass) or urbanized areas. Surveys were conducted in farmers' fields. Each year, 100
145 to 220 different fields were sampled (a few fields were studied for more than one year) with a
146 standardised protocol. Fields were selected in a stratified random process: every year, 40-60
147 1km² squares were randomly selected in the study site, with a stratified procedure using three
148 gradients of landscape features (woody habitats, i.e. hedges and forest fragments, grasslands,
149 and organic farming (Bretagnolle et al., 2018a; Crochard et al., 2022; Perrot et al., 2022). A
150 moving window was used to select the squares (Fahrig et al., 2011) to obtain statistically
151 independent gradients. Within each square, we selected one field of cereal, oilseed rape,
152 maize/sunflower, and alfalfa/meadow when they were present (resulting in three to four fields
153 per square). Within a square, fields of different crops were 100 to 500 m from each other, while
154 the squares were on average 1 to 3 km from each other (see, e.g., Sirami et al., 2019), avoiding
155 the risk of generating spatial autocorrelation between sampling points (see Perrot et al., 2022).
156 We focused on six years of survey, 2015–2020, which is one of the largest time intervals of
157 plant–pollinator network studies (but see Chacoff et al., 2018; Petanidou et al., 2008; Ponisio
158 et al., 2017). From 2015–2020, the number of fields sampled per respective year were 174,
159 217, 195, 160, 117 and 115 (see ESM1a and 1b in Appendix A). Crop surveyed included 7%
160 corn (*Zea mays*) and sorghum (*Sorghum bicolor*), 8% alfalfa (*Medicago sativa*), 12% meadows
161 (temporary or permanent), 18% winter oilseed rape (*Brassica napus*), 22% sunflower
162 (*Helianthus annuus*), and 33% cereal crops. Cereals included barley (*Hordeum vulgare*), durum
163 wheat (*Triticum turgidum*), einkorn (*Triticum monococcum*), oat (*Avena sativa*), rye (*Secale
164 cereale*), triticale (\times *Triticosecale*) and winter wheat (*Triticum aestivum*). In the study area,
165 alfalfa is always mowed before flowering because the quality of the leaves for goat feeding

166 drops with flowering. Sampling was performed from April to August, i.e. all crops were
167 surveyed at least once during their respective flowering periods: winter OSR from April–May;
168 sunflower from July–August; alfalfa, meadows and cereals from May–June to the end of
169 August; and corn and sorghum from July–August.

170

171 **2.2. Sampling of plant–pollinator interactions**

172 Insects were surveyed using transect methods, and included bees (both honeybees and wild
173 bees), butterflies and hoverflies (Syrphidae), i.e. the three main pollinator groups in our study
174 site. This study site hosts a large number of pollinator species (Rollin et al., 2016). Each year,
175 two (2015) or three (2016–2020) 50 m long transects were performed per field. Since field
176 margins generally harbour a more diverse fauna compared to field cores, one transect was in
177 the field margin (section between the field edge and the first seeding line, randomly selected,
178 but starting from the road), one was in the field centre, and the last in between, at c. 25 m from
179 the margin (except in 2015). Transects were all located within the field, and were always
180 organized similarly (see Bretagnolle et al., 2018a, 2018b; Crochard et al., 2022; Perrot et al.,
181 2022 for additional details). The transect always lasted 10 minutes each (i.e. when a bee was
182 caught for identification, the time necessary to identification or placing the bee in a tube was
183 not counted). Duration was measured by a hand chronometer. Transects were parallel to tram
184 lines. For each transect, the surveyed area was a theoretical volume, 2.5 m each side, 2.5 m in
185 front of the observer and c. 1 m above the observer’s head. Surveys were conducted under calm
186 weather conditions, i.e. sunny days with air temperatures in full sun mostly above 15°C (95%
187 $T > 16^\circ\text{C}$; 12° to 31°C, in sunlight – a maximum temperature of 45°C was recorded in one
188 specific case, but the thermometer was in full sunlight), and between 7:30 a.m. and 6:30 p.m. In
189 27.9% of the fields (226 of 811), two sampling sessions were conducted (early- and late-
190 season). Each plant–pollinator interaction (i.e. an insect landing on a flower) was tallied, with

191 both plant and pollinator being identified (pollinators being caught with a sweep-net for later
192 identification by a professional entomologist if necessary). Transects were walked along very
193 slowly (c. 12 s/m), for a total duration of 10 min each. The observer stopped the timer each time
194 an insect had to be identified or captured. Butterflies were always identified by sight; however,
195 given the time spent in flight in butterflies, all individuals crossing the sampled theoretical
196 volume were tallied, even if not on a flower. Almost all pollinators and plants (94% and 96%
197 respectively) were identified to species level.

198

199 **2.3. Statistical analyses**

200 *2.3.1. Sampling completeness and frequency distribution of degrees*

201 We estimated sampling completeness of plants and pollinators using the Chao estimator of
202 asymptotic species richness (Chacoff et al., 2012), which is based on rare species (those that
203 occur only once or twice). We calculated the Chao 2 estimator using the *vegan* R package
204 (v2.5.7; Oksanen et al., 2020) and evaluated the percentage of completion (ratio between the
205 observed value and estimated value) of our sampling of plants and pollinators.

206 In plant–pollinator networks, the degree distributions were shown to be best fit by the power
207 law, a long tail distribution law (Blüthgen et al., 2007), since a significant number of nodes
208 have many connections while most nodes in the plant–pollinator network have fewer
209 connections. Here we compared the fit of other long tail distribution laws in order to verify that
210 the Power Law was the best fit among those candidate distributions, and in particular used other
211 distributions that have been used in population and community structures. We analysed the
212 frequency distribution of degrees in total as well as in subnetworks (per crop and per period),
213 testing for best-fit with *a priori* distributions, i.e. Exponential, Poisson, Weibull, Lognormal,
214 Negative binomial, Power law and Fisher’s logseries. We used the *fitdistrplus* package
215 (Delignette-Muller and Dutang, 2015), except for the Fisher’s logseries (which is not

216 implemented in this package), which we computed. Power law was tested with the *powerLaw*
217 package (Gillespie, 2015). Best fit was checked using the Akaike Information Criterion (AIC;
218 Burnham et al., 2011). We fixed a threshold of 2 units' difference in AIC to select the best
219 model among the candidate models.

220

221 2.3.2. *Number of nodes and number of interactions: crop and temporal effects*

222 From floral visitation events, we constructed bipartite networks with plant and bee nodes, using
223 a visitation event as a plant–pollinator interaction. To analyse how the network structure varied
224 among crops and seasons, we built specific interaction subnetworks. First we built sub-datasets
225 corresponding to the six crop categories retained: OSR, cereals, alfalfa, meadows, SF and corn–
226 sorghum. We also split the data into three equal-length seasons (resulting in three other sub-
227 datasets), each 45 days long: April 1st–May 20th (OSR flowering peak, characterised by high
228 resource availability for insects and gathering data collected in OSR, cereals, alfalfa and
229 meadows), May 21st–July 9th, characterised by a general lack of flowering crop resources
230 available (i.e. the dearth period, with data collected in cereals, alfalfa and meadows) – when
231 honeybee colony sizes are, perhaps surprisingly, at their highest (Odoux et al., 2014) – and
232 finally, July 10th–August 22nd, corresponding to the SF flowering peak (gathering data collected
233 in alfalfa, meadows, SF and corn–sorghum). Finally, we focused on the five main taxonomic
234 groups and divided our dataset into sub-datasets corresponding to bumblebees, other social bees
235 (including some Halictidae, e.g. *Halictus rubicundus*, *Lasioglossum pauxillum*), solitary bees,
236 hoverflies and butterflies. We added a sixth sub-dataset corresponding to the honeybees.

237 To describe seasonal patterns in the number of interactions, we standardised our data, since the
238 number of transects per field and the number of fields sampled per crop and per year varied.
239 We thus converted the number of interactions per transect per field into a number per hectare
240 (ha), since each transect surveyed an area of 250 m². Next, we grouped samples per fortnight

241 by averaging values (with standard-error, se) of interactions per ha per fortnight for each crop.
242 Obtained values were compared with ANOVA and post-hoc Tukey tests. Data were log-
243 transformed.

244

245 2.3.3. *Network structure descriptors*

246 A large number of indices is available to describe network structure (see ESM2, which presents
247 their respective properties in Appendix A). We selected the following ones: number of nodes
248 (i.e. the number of species in interaction), connectance (the ratio between the number of links
249 observed and the total number of possible links; increased connectance is expected to decrease
250 secondary extinctions (Blüthgen et al., 2007) and improves robustness at the community level
251 as well as stability (Thébault and Fontaine, 2010), modularity – which gives insights into the
252 presence of subnetworks among the network (called modules, i.e. weakly interlinked subsets of
253 species that are constituted of strongly interacting species) and which was calculated using the
254 greedy Louvain algorithm method (Blondel et al., 2008) – and nestedness, described by NODF
255 (Nestedness metrics based on Overlap and Decreasing Fill; Almeida-Neto et al., 2008). The
256 latter is a property describing to what extent the partners of specialists are a subset of the
257 partners of generalists. Finally, we focused on the specialisation H_2' (standardised two-
258 dimensional Shannon entropy) – the degree of specialisation between the two levels of the entire
259 network (Blüthgen et al., 2006) – and the d' species-level specialisation measure (standardised
260 Kullback–Leibler distance, Blüthgen et al., 2006), corrected by de Manincor et al., 2020,
261 representing the degree of interaction specialisation at the species level. Network descriptors
262 were obtained using the R packages *bipartite* (Dormann et al., 2009), *igraph* (Csardi and
263 Nepusz, 2006), *NetIndices* (Kones et al., 2009) and *vegan* (Oksanen et al., 2020).
264 Some of these metrics (i.e. connectance, nestedness) are sensitive to sample or network size
265 (Dormann et al., 2009). We thus checked how indices varied with increasing numbers of

266 samples (according to periods and crops) by calculating all metrics (excluding d') with
267 increasing numbers of sampled fields. Five to 195 fields (every 10 field steps) were randomly
268 sampled (with replacement) from the overall sample. At each step (i.e. field number), 100
269 groups of fields were constituted, the six network metrics were computed and the mean and the
270 95% confidence interval (CI) were calculated.

271 In our study, sample sizes vary with crop type. To compare the metric values among crop types,
272 seasons and taxonomic groups, we use the smallest sample size for the analysis by reducing the
273 set of crops with larger sample size to this smallest sample size value. The maximum bootstrap
274 threshold to compare the three seasons was thus 175 field groups, when OSR period samples
275 stopped, but we also went up to 195 fields to compare only dearth period and sunflower period.
276 When comparing the six different crop types, we compared the metric values obtained at a
277 threshold of 35 fields per group (100 groups) in the bootstrap because we had very few fields
278 of corn–sorghum and alfalfa. We also compared four crops (OSR, SF, cereals and meadows)
279 with 100 groups of 85 fields. Finally, we focused on the two mass-flowering crops, OSR and
280 SF, by comparing the metric values obtained at the threshold of 165 fields.

281

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

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

287

288 **3. Results**

289 **3.1. Sampling completeness and frequency distribution of degrees**

290 A total of 37,133 plant–pollinator interactions were tallied over 811 fields (127 of which were
291 studied in at least two years between 2015 and 2020), occurring between 200 species of
292 pollinators foraging on 165 species of plants (including individuals that were only identified to
293 genus level). We found 96 species of solitary bees, 35 species of social bees (including the
294 honeybee *A. mellifera* and 14 species of bumblebees), 38 species of butterflies and 31 species
295 of hoverflies. A total of 758 interactions were obtained between one plant or one pollinator
296 occurring only once. We never observed two singletons (species that were sampled only once)
297 interacting with each other, i.e. no interaction was found between one plant and one pollinator
298 occurring both only once. In regard to pollinators, over the full network, 80 species (40.0%,
299 including 70 singleton species) interacted with only one plant (crop or weed), 29 species
300 (14.5%) interacted with two, while 91 species (45.5%) were more generalist (>2 plants, up to
301 92 plants). Similar values were obtained for plants, with 38 weed species interacting with only
302 one insect species (23%, including 23 singleton species), and 16 with two insect species (9.7%).
303 There were 138 fields without any observed interaction (17.0%). We caught 64.5% of
304 pollinators, and recorded 78.6% of the plant community, based on Chao 2 estimators.
305 Overall, the frequency distribution of degrees (i.e. interacting plants/pollinators) fitted better to
306 the Fisher’s log-series (see ESM3 in Appendix A) than to Lognormal ($\Delta_{AIC} = 73$) or Power laws
307 ($\Delta_{AIC} = 77$). When splitting by crop or per season, similar results were found. Differences in
308 the goodness-of-fit of Fisher’s log-series and Lognormal were, however, much lower in alfalfa
309 ($\Delta_{AIC} = 12$) and in corn and sorghum crops ($\Delta_{AIC} = 3$) than in other crops.

310

311 **3.2. Number of nodes and number of interactions: crop and temporal effects**

312 The total number of nodes varied highly among crops (165, 114, 186, 178, 161 and 75 in
313 meadows, alfalfa, cereals, SF, OSR and corn–sorghum, respectively). Accumulation curves per
314 crop indicated that these differences among crops (Fig. 1) could be detected even from low

315 sample sizes (c. $n = 50$). Thus, independently of the number of sampled fields, meadows showed
316 the highest values of node numbers, followed by alfalfa, cereals, OSR and SF (Fig. 1). Year did
317 not affect the pattern of the accumulation curves (see ESM4 in Appendix A), although 2017
318 was a species-rich year regardless of the sampling effort.

319 The number of plant–pollinator interactions, here standardised per hectare of sampling effort
320 (which can be considered as an instantaneous visitation rate per hectare), was on average
321 338.43 ± 23.19 interactions/ha (mean \pm se). This value, however, showed strong seasonal
322 variations, with most interactions occurring in early July when considering all crops, or mid-
323 June when excluding SF (Fig. 2). There were also strong variations among crops, with
324 interactions in SF being overwhelmingly dominant and driving seasonal variation. In early July,
325 we found significant differences in the average number of interactions among crops ($F_{5,62} =$
326 20.16 , p -value < 0.0001), with significantly higher values for SF than in alfalfa (T_{HSD} p -adj $<$
327 0.001), meadows (T_{HSD} p -adj < 0.001), cereals (T_{HSD} p -adj < 0.001) and OSR (T_{HSD} p -adj =
328 0.0015) (see ESM5).

329 Network structure differed strongly among crops in relation to variation of the total number of
330 nodes, either in the repartition of interactions between the main groups of plants or between the
331 main groups of pollinators (Fig. 3). In flowering crops, the crop flower was generally the most
332 visited flower in the crop considered. For instance, 95.27% of pollinators visited SF plant in SF
333 fields, and 86.07% OSR plants in OSR fields. However, this was true only for mass-flowering
334 crops: alfalfa represented approximately a third of all visited flowers in alfalfa fields (36.12%)
335 and corn was poorly visited in corn–sorghum fields (7.55%). In those crops, pollinators
336 preferentially foraged on wild flowers (89.62%). Moreover, honeybees' dominance was not of
337 the same magnitude in all crops: they were overrepresented in SF (91.95%) and OSR (76.60%),
338 while hoverflies rather than honeybees were the most-interacting group in other crops (32.55%
339 in corn and sorghum crops, 56.42% in cereal crops, 36.02% in alfalfa crops and 53.38% in

340 meadows). Interestingly, when found in other crops, OSR and SF flowers showed the same
341 interaction pattern, i.e. interacting mainly with honeybees. Moreover, hoverflies foraged more
342 on wild flowers than did any other insect group, potentially explaining their high presence in
343 weed-rich crops such as meadows or alfalfa. For instance, whereas the total percentage of weed
344 visits by all pollinator groups was 63.78% in alfalfa crops, it reached 77.94% when considering
345 only hoverfly visits.

346 Species with the highest degrees were not necessarily the most frequent, although species'
347 frequency of occurrence and degree were strongly related (i.e. decreasing pattern of species
348 degrees were concomitant with decreasing species frequencies) (see ESM6). In terms of the
349 number of interactions, honeybees and bumblebees were most prevalent (83.72% of the total
350 interactions number, n = 31,089), followed by hoverflies (8.21%, n = 3,050), solitary bees
351 (2.69%, n = 998) and butterflies (1.36%, n = 506). Honeybees were by far the dominant insect
352 species (80.80% of all interactions, n = 30,007), the next two being *Sphaerophoria scripta*
353 (3.80%, n = 1,412) and *Episyrphus balteatus* (2.19%, n = 812), two hoverflies. However,
354 although *S. scripta* was 20 times less abundant than honeybees in total, its number of plant
355 partners (92) was higher than that of honeybees (75). Butterflies were far less often observed,
356 with only 81 interactions for the most common butterfly, *Pieris rapae*. Concerning plants, SF
357 represented 72.36% (n = 26,871) of the whole sample, seven times more than OSR (10.69%, n
358 = 3,971), and 60 times more than the most-interacting weed, *Torilis arvensis* (1.20%, n = 446).
359 Therefore, the complete network was dominated by honeybees and mass-flowering crops:
360 honeybees interacting with OSR or SF represented 77.44% of all interactions.

361

362 **3.3. Network structure**

363 *3.3.1. Seasonal effect on network structure*

364 The average number of nodes during the dearth period (mid-May to early July) was similar to
365 the average number of nodes for all periods, regardless of the sampling effort (Fig. 4a), reaching
366 214 (CI_{95%}: 195–230) species when considering a sampling effort of 175 fields (see ESM7a for
367 details on seasons' metric values). The average number of species was nearly equal during SF
368 and OSR flowering blooms (154 (142–165) and 148 (146–151), respectively, in 175 fields);
369 that is to say, 1.4-times lower than during the dearth period, but with a weaker variability among
370 fields during OSR flowering. Mean connectance did not vary a lot with period, being 3% (2.6–
371 3.4) during bloom periods and 2.5% (2.2–2.8) during the dearth period in 175 fields. Mean
372 modularity was slightly higher for the OSR blooming network (0.42 (0.41–0.43)) than for other
373 periods (0.39 (0.36–0.41) in SF blooming and 0.37 (0.35–0.38) in dearth period)).
374 Specialisation of the network remained constant during dearth and SF periods when considering
375 network sizes above 100 fields (see ESM2 for details in Appendix A), but decreased much more
376 quickly in the OSR blooming period, with no overlapping 95% in CIs. This highlights that OSR
377 blooming period was represented by more generalist species than the other periods.
378 Specialisation was higher during the SF bloom and dearth periods, with average values between
379 0.49 (0.43–0.55) and 0.50 (0.46–0.52), respectively, compared to the OSR flowering bloom
380 (0.30 (0.29–0.33)). The OSR blooming period was characterised by a higher nestedness (37.2
381 (35.6–38.6) in 175 fields) than the SF blooming period (24.0 (21.3–26.9)) and dearth period
382 (27.0 (24.4–29.9)). Thus, it seems that the flowering period of the OSR was the most prone to
383 host specialist species that had partners similar to generalist species.

384

385 *3.3.2. Crop effect on network structure*

386 All crops' subnetworks were similarly poorly connected (c. 3% at a threshold of 85 fields) (Fig.
387 4b). Although OSR blooming period was the most modular period (see above), mean
388 modularity was almost identical whatever the crop considered, at about 0.5 (see ESM7b for

389 details on crops' metric values). At an equal sampling survey effort of 85 fields, modularity
390 was 0.43 (CI_{95%}: 0.39–0.47) for meadows, 0.45 (0.40–0.49) for SF and 0.48 (0.45–0.52) for
391 OSR. With a higher sampling rate (n = 165 fields), but at the cost of losing crop types in the
392 comparisons, OSR showed significant higher modularity values than SF. The two mass-
393 flowering crops' networks also had very different specialisation (H2'), showing the two most
394 extreme values among our six crops. OSR was far less specialised (0.31 (0.29–0.33) at 165
395 fields) than all other crops, while SF (0.58 (0.55–0.61)) showed the most specialised network;
396 the other crops showed intermediate values, *e.g.* 0.45 (0.43–0.47) for meadows and 0.40 (0.34–
397 0.46) for cereals at a survey effort of 85 fields. Low specialisation in OSR could be partially
398 explained by the low specialisation of the most abundant insect, the honeybee (d' = 0.27) and
399 the low specialisation of the crop flower, OSR (d' = 0.21). Indeed, in OSR, the average d' of
400 all species was 0.26 for insects (n = 97, median = 0.20) and 0.23 for plants (n = 68, median =
401 0.44), meaning that the network was lowly specialised at both trophic levels and highly driven
402 by the honeybee and OSR flower dominance. In SF, specialisation was 0.67 for SF (more than
403 three times higher than in OSR) and 0.42 for the honeybee (1.5-times higher than in OSR). SF
404 was thus highly connected to honeybees despite honeybees being slightly less specialised than
405 SF, indicating a larger partners' spectrum. The average d' of all insect species in SF was 0.41
406 (n = 109, median = 0.50) and 0.67 for plants (n = 65, median = 0.51), again reflecting the
407 preponderant roles of honeybees and SF. Nestedness (NODF) increased with sampling effort,
408 being higher in OSR than in any other crops (mean value of 29.8 (22.5–36.8) when sampling
409 effort was low, *i.e.* 35 fields), especially in meadows (16.1 (11.0–21.3)), cereals (21.3 (15.1–
410 28.4)) and SF (21.6 (16.8–29.2)), rather than in alfalfa (25.5 (21.0–30.8)). When increasing
411 sampling effort (85-field threshold), nestedness reached 33.0 (27.7–38.2) in OSR networks, *c.*
412 25% more than in cereals (23.9 (19.9–28.5)) and in SF (23.4 (19.5–28.1)).

413

414 **4. Discussion**

415 The detection of several hundreds of species in the plant–pollinator network indicates that our
416 study site is characterised by a high diversity of species despite its intensive farming system.
417 For instance, 200 pollinators’ species were involved in these interactions, and Rollin (2013)
418 had estimated a specific richness of bees in our area between 238 and 251 species in the same
419 study site, and Munoz et al. (2020) recorded 399 weed species in this study site. While the
420 honeybee, SF and OSR are by far the species that establish most interactions, they are not
421 necessarily those with the greatest number of interacting partners. Although OSR flower is the
422 species with the highest degree (number of interaction partners), confirming its structuring role
423 in the network (Diekötter et al., 2010; Stanley and Stout, 2014), it is closely followed by wild
424 plant species, generally hosted in less-intensively managed but more diverse crops such as
425 alfalfa or meadows. Moreover, the hoverfly *Sphaerophoria scripta* showed far more partners
426 than honeybee, including OSR and SF flowers, suggesting that its role in the network has to be
427 explored in more detail. *Bombus* species are also frequent visitors of SF, as Syrphidae of OSR
428 (Jauker and Wolters, 2008). Although these are rarely studied as key species in networks, they
429 might be strongly involved in OSR and SF pollination (Breeze et al., 2011), and could act as
430 pollination insurance if honeybees were to decline dramatically (Sánchez-Bayo and Wyckhuys,
431 2019).

432 Completeness of survey effort was, however, moderate: 65% for insects but 80% for plants
433 according to the Chao 2 estimator, despite our dataset covering six months (from April to
434 September) during six years. The phenology of some plants and insects being very short may
435 explain why not all species were detected, in addition to the classic and inherently imperfect
436 detection method. In addition, the low connectance within crops (around 2–3%) suggests that
437 few interactions are carried out among all possible ones. These forbidden links (Jordano, 2016)
438 could result from spatial or temporal constraints (Valdovinos, 2019). Indeed, one of our possible

439 explanations is that each crop network corresponds to a set of different fields that belongs to
440 different landscape entities and different sampling weeks, which generates a high community
441 variability in terms of phenology and location. But a low connectance, i.e. high proportion of
442 forbidden links, is in certain cases one of the indicators of destabilised networks (Landi et al.,
443 2018). We also found that the Fisher's log-series outcome the Power law whatever the crop or
444 season in which we considered the plant–pollinator networks. Such result is very meaningful
445 because the Fisher's log series has been shown to fit a range of species assemblages, particularly
446 those that have a high frequency of rare species (Magurran, 2005), and is related to the Neutral
447 theory (Hubbell, 2001). Therefore, our results may offer alternative mechanistic explanations
448 to the plant–pollinator topology, e.g. the higher number of low connected nodes may occur
449 because rare species in species assembly (either of plants or of insects) move in and out through
450 stochastic processes such as dispersal (see Henckel et al. (2015) or Bourgeois et al. (2020) for
451 examples in plants).

452 The hypothesis of the dominance of honeybee interactions with crop flowers during OSR
453 flowering and SF flowering, and not in other periods, was largely verified. Overdominance of
454 managed species may destabilise networks (Valido et al., 2019). The stability of a network can
455 be evaluated through the values of some network metrics (Thébault and Fontaine, 2010). A
456 stable bipartite mutualistic network is often a network with a high connectance and many
457 species, as well as a nested – but not very modular – network (Thébault and Fontaine, 2010).
458 In our case, connectance was always very low (<5%), whether we considered the total network
459 or the subnetworks per season or per crop. When the connectance is so low, modularity and
460 nestedness are usually positively correlated (Fortuna et al., 2010), hence a situation with a
461 nested but not modular network is unlikely, therefore possibly suggesting instability in our
462 networks. In particular, the corn–sorghum network, which is highly modular and comprises few
463 species, may show particularly low stability, though we had relatively small sample sizes.

464 Meadows were a special case, endowed with a large number of species but not very nested and
465 not very connected compared to other crops. Thus, although meadow networks appear to be
466 resilient networks thanks to the number of species they host (Okuyama and Holland, 2008),
467 they display a certain vulnerability because the sharing of partners is weak, like in the studied
468 SF crops, but contrary to the OSR crops.

469 Indeed, the most striking differences in networks were found between OSR and SF, both being
470 mass-flowering crops. As expected, these two crops drove the overall behaviour of networks
471 during their blooming season (approximately the same metrics of behaviour between the OSR
472 crop and OSR period, and between the SF crop and SF period), although the meadows, weeds
473 in cereals, and alfalfa were flowering at the same time. However, when standardizing at similar
474 sample sizes, the OSR and SF crops' networks were somewhat opposed in some of the key
475 metrics, hence possibly showing different network stability (Duchenne et al., 2022). The OSR
476 network did not harbour many species, but was highly nested compared to the other crop
477 networks, which therefore suggests it was a resilient network. Its nestedness may result from
478 the fact that the OSR network was mostly composed of species with a high degree of
479 generalisation (i.e. the average species specialisation was quite low in OSR crops), leading to a
480 relatively nested structure (Fontaine et al., 2009). Thus, as the OSR network was the most
481 nested network in our study, it was expected that the general core of species it included were
482 generalists rather than specialists, which was indeed the case. The interaction between OSR and
483 honeybees has a structuring effect for the network, corroborating studies that highlight OSR
484 flower and its partners as a hub that positively influences the visitation and pollination of
485 neighbouring wild plants, especially those with similar morphology (Thompson et al., 2021).
486 OSR is also known to host diverse insect communities (Stanley et al., 2013), while honeybees
487 remain one of the most efficient pollinators and, as demonstrated here, the most important
488 partner of OSR. Conversely, SF appears less stable than OSR because it is much less nested for

489 an equivalent diversity of species, and is composed of more specialised species, including the
490 honeybee–SF duo, which both qualify as specialist species, interacting strongly and almost
491 entirely with each other – a pattern that was not necessarily found in other studies (e.g. Valido
492 et al., 2019). Such a quasi-exclusive relationship between honeybees and SF as we found here
493 may reflect either competition within pollinators or plant communities in SF crops, or a strong
494 niche differentiation between wild and managed species. Conversely, OSR may host more
495 generalist species that interact with specialist species and therefore enhance the persistence of
496 the network (Liao et al., 2022).

497

498 **5. Conclusion**

499 Occurring very abundantly during their respective flowering peaks, OSR and SF crops drive
500 the structure of interaction networks, the other crops having little effect on these patterns.
501 Although OSR and SF are often simply equated and grouped as ‘mass-flowering crops’, there
502 are significant differences in the structure of the plant–pollinator interaction networks that are
503 observed in both crops. Our results suggest that the honeybee and crop flower pair differ
504 between OSR and SF, being an almost exclusive relationship in SF that prevents other partners
505 by competition, while allowing other modules in OSR hence increasing nestedness and
506 consequently improving network stability. This divergence may possibly result from
507 phenological difference, or may possibly be due to flower shape – a divergence that can be
508 further explored with species trait approaches. Furthermore, by standardizing crop types at
509 similar sample sizes, the comparison of the metric values between crops revealed that OSR
510 network was highly nested compared to the other crop networks. This would suggest a higher
511 ability of this network to cope with disturbances (i.e. resilient network) compared to corn-
512 sorghum, cereal and even sunflower networks. OSR was already suggested to be a key crop in
513 this study area by harbouring a high diversity (Gaba and Bretagnolle, 2021); it now appears

514 also as an important crop for the persistence of plant–pollinator networks. Finally, our results
515 on the best fit of degree distribution by the Fisher’s log series offer other mechanistic
516 explanations to the plant–pollinator topology that need further studies to be better understand
517 especially in highly dynamic environment such as agricultural landscapes.

518

519 **Author Contributions**

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

523

524 **Declaration of Competing Interest**

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

527

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537

538 **Appendix A. Supporting information**

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

540

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786 **Figure legends**

787

788 **Fig. 1**

789 Mean values of number of nodes ($\pm 95\%$ confidence intervals) for each crop, according to the number
790 of sampled fields (x-axis). Brown points and line: cereal; Light blue points and line: oilseed rape; Dark
791 green points and line: alfalfa; Dark blue points and line: corn and sorghum; Light green points and line:
792 meadow; Red points and line: sunflower.

793

794 **Fig. 2**

795 Interaction number (frequency of pollinators interacting with flower) per hectare and per crop
796 throughout the season. Data are presented as mean \pm se (standard error). Analyses of variances were run
797 on each fortnight (two weeks aggregated) to compare crops (log+1-transformed). If p-value < 0.001 then
798 ***; If $0.001 \leq$ p-value < 0.01 then **; If $0.01 \leq$ p-value < 0.05 then *; If $0.05 \leq$ p-value < 0.1 then ‘.’
799 Brown points and line: cereal; Light blue points and line: oilseed rape; Dark green points and line:
800 alfalfa; Dark blue points and line: corn and sorghum; Light green points and line: meadow; Red points
801 and line: sunflower.

802

803 **Fig. 3**

804 (a) Histograms of species number per crop for pollinator and insect groups. Grey bars: species number
805 of the different plant groups. Blue bar: honeybee species number; Turquoise bar: bumblebee species
806 number; Green bar: other social bee species number; Yellow bar: solitary bee species number; Orange
807 bar: butterfly species number; Pink bar: hoverfly species number. (b) Bipartite representations of crop
808 networks involving the main pollinator taxonomic groups and the main plant groups. Blue path:
809 honeybee interaction; Turquoise path: bumblebee interaction; Green path: other social bee interaction;
810 Yellow path: solitary bee interaction; Orange path: butterfly interaction; Pink path: hoverfly interaction.

811

812

813 **Fig. 4**

814 Mean network metric values ($\pm 95\%$ confidence intervals) for (a) periods and (b) crops, based on the
815 number of sampled fields (x-axis) and with a y-axis scale indicating the value of the metric.

816 Period metrics; Grey squares: all periods; Purple points: oilseed rape flowering period; Orange points:
817 dearth period; Yellow points: sunflower flowering period.

818 Crop metrics; Grey squares: all crops; Brown points: cereal crop; Light blue points: oilseed rape crop;

819 Dark green points: alfalfa crop; Dark blue points: corn and sorghum crop; Light green points: meadow.

820 Red points: sunflower crop.

Figures

Figure 1

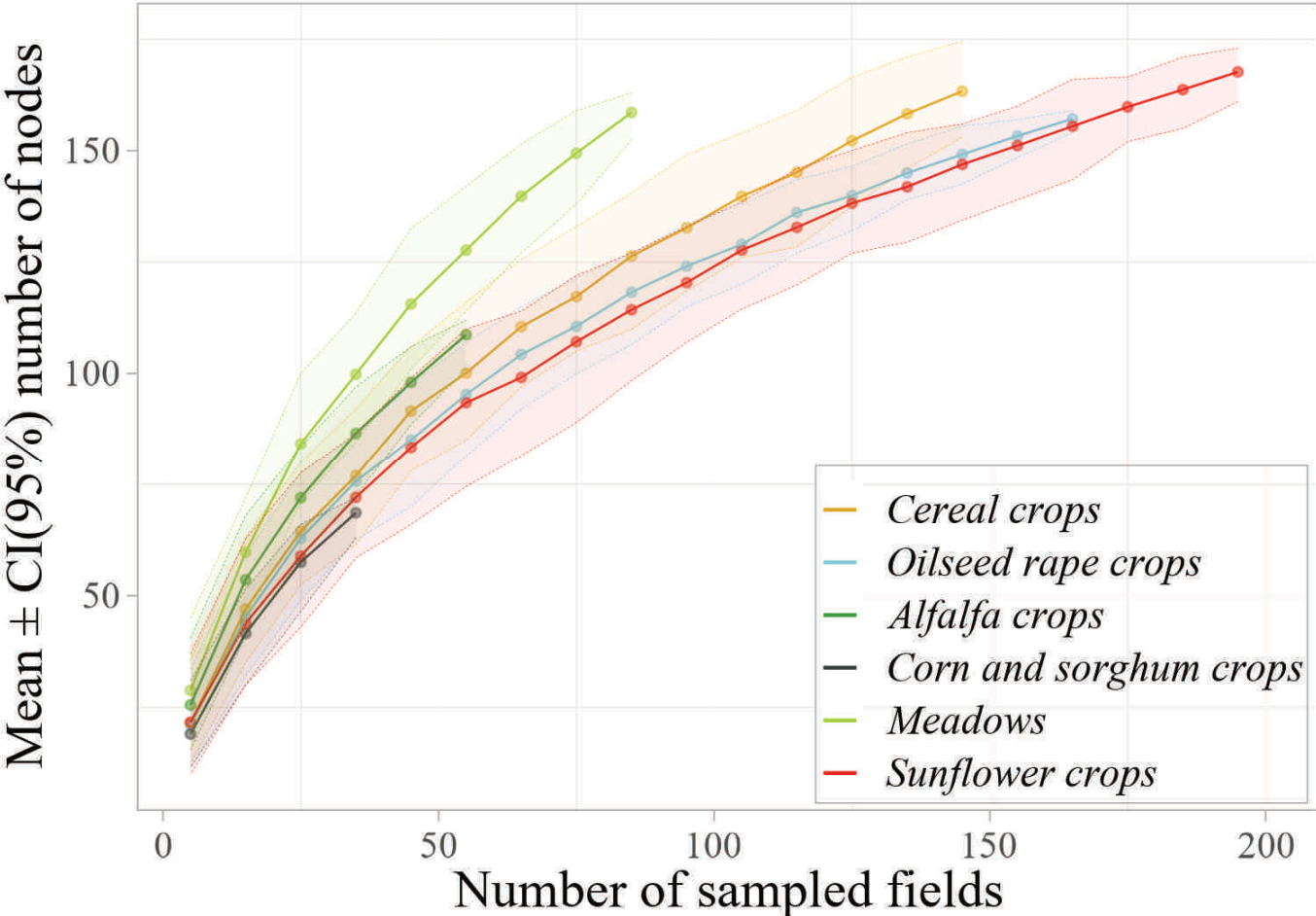


Figure 2

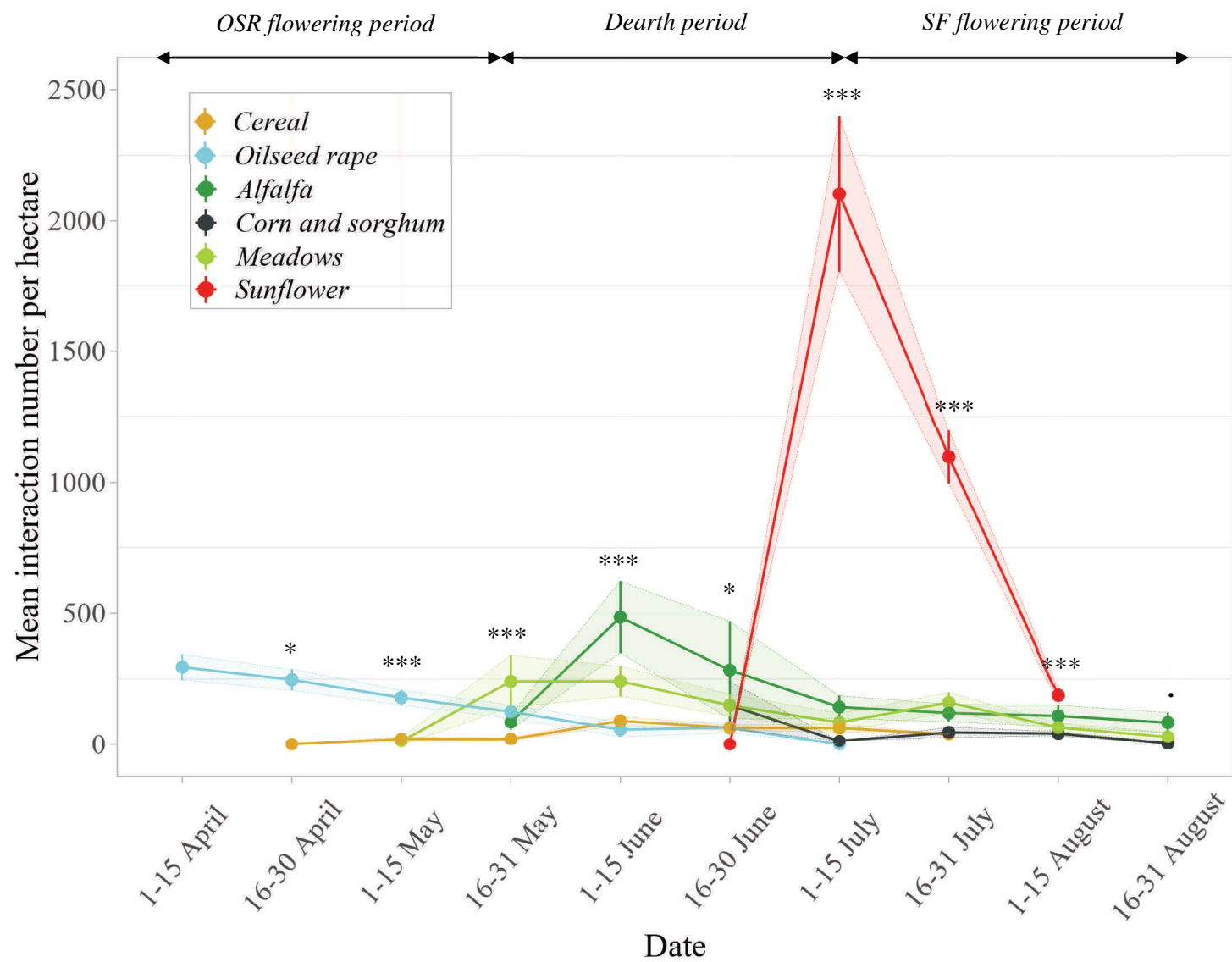


Figure 3

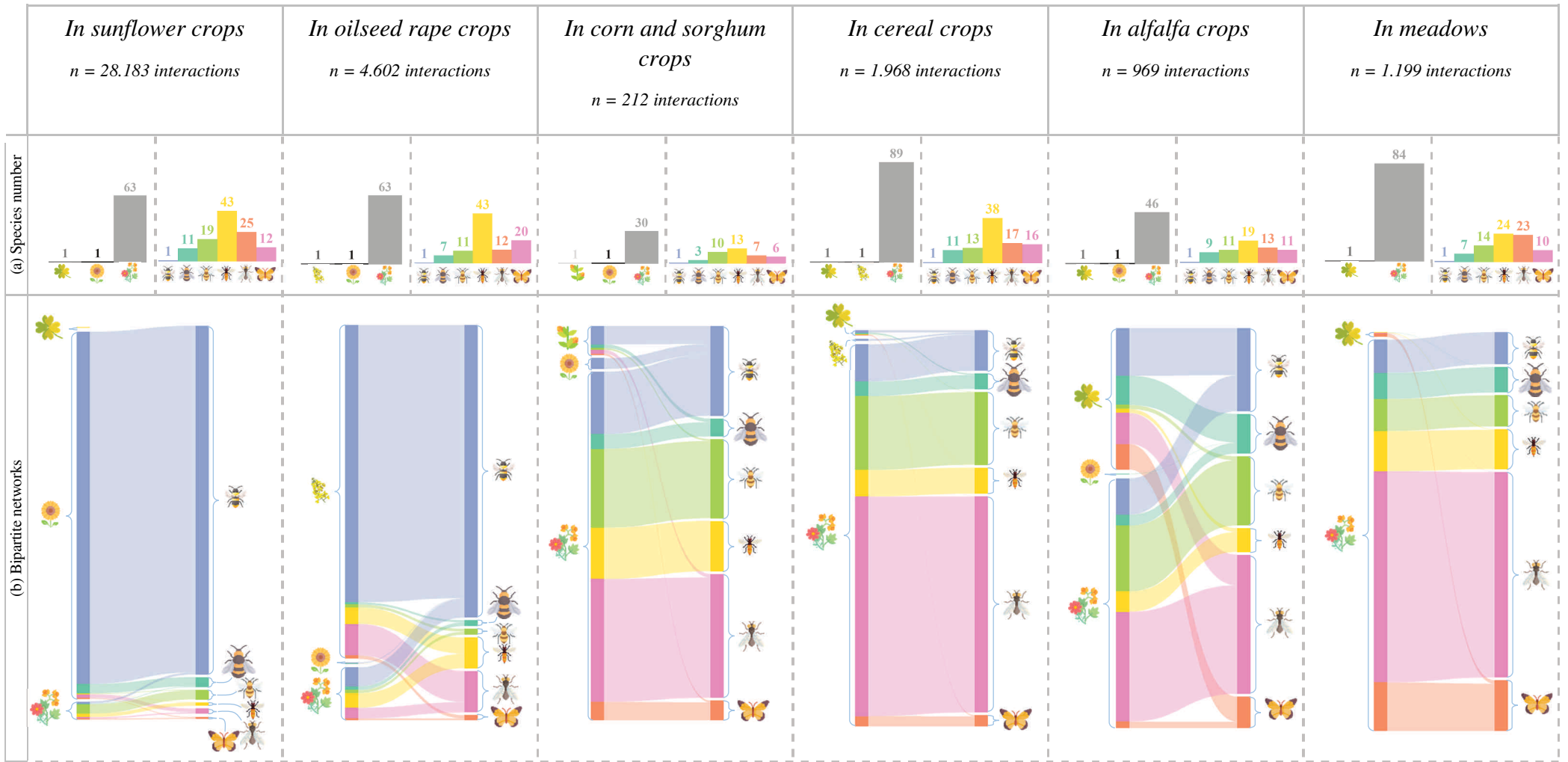
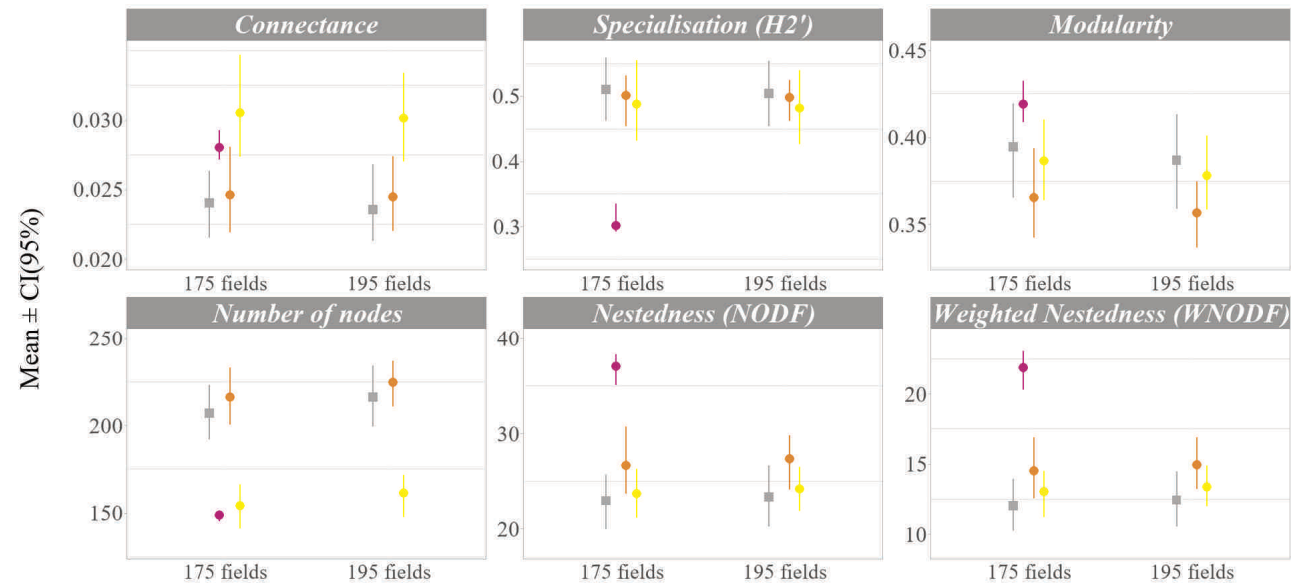
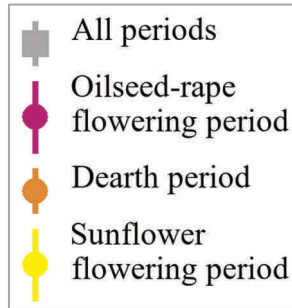


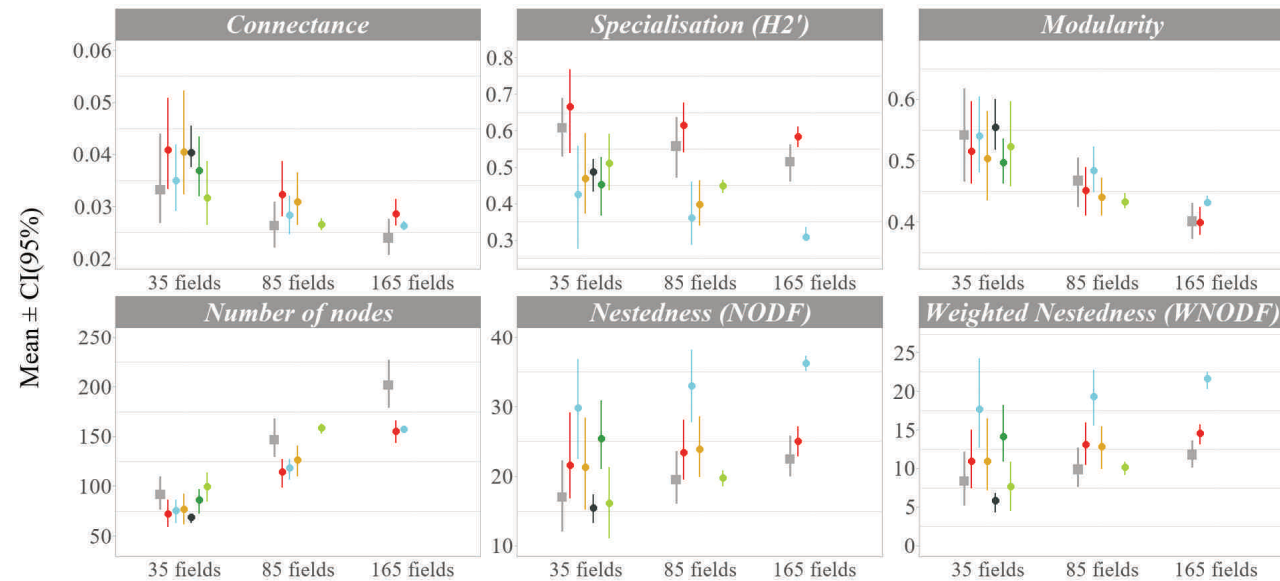
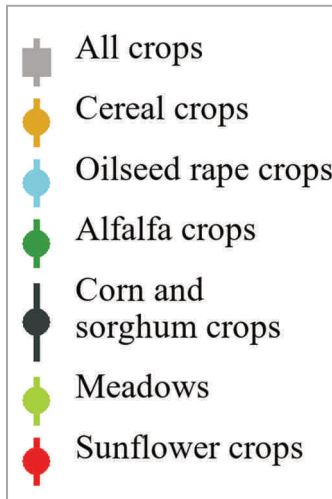
Figure 4

a.



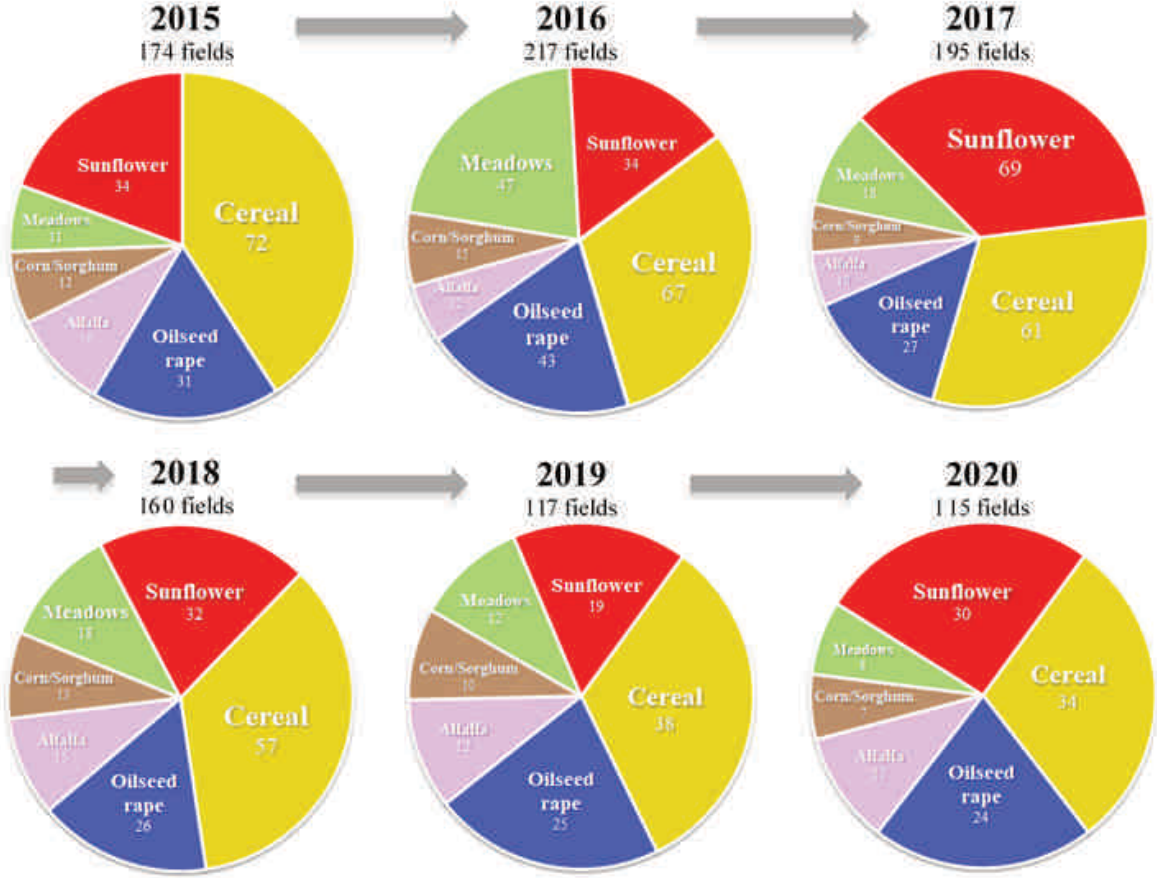
Number of fields used to create each subnetwork
(100 groups of 175 fields and 100 groups of 195 fields)

b.



Number of fields used to create each subnetwork
(100 groups of 35 fields, 100 groups of 85 fields and 100 groups of 165 fields)

Supplementary materials



Supplementary material 1a

Number of sampled fields per year and per crop, for 6 years of data.

Red: sunflower crop; Brown: corn and sorghum crop; Yellow: cereal crop; Blue: oilseed rape crop; Pink: alfalfa crop; Green: meadows.

Supplementary material 1b

Number of sampled fields per year and per crop, for 6 years of data.

	<i>2015</i>	<i>2016</i>	<i>2017</i>	<i>2018</i>	<i>2019</i>	<i>2020</i>	Total	
Number of sampled crop fields	Cereal	70	65	61	57	38	34	325
	Oilseed rape	30	45	27	26	26	24	178
	Alfalfa	16	11	10	14	13	12	76
	Corn/Sorghum	12	17	9	13	10	7	68
	Meadows	12	46	19	18	11	8	114
	Sunflower	34	33	69	32	19	30	217
	Total	174	217	195	160	117	115	978
Number of sampled period fields	Oilseed rape flowering period	31	59	35	27	29	32	218
	Dearth period	76	108	81	61	40	28	389
	Sunflower flowering period	67	50	79	72	48	55	371
	Total	174	217	195	160	117	115	978

Supplementary material 2

Description of metrics used in the subnetwork analyses and species-level analyses.

	Definition	Type of targeted data	Value range	Interpretation	Observations on network size and composition	R package used
<i>Number of nodes</i>	The number of species in the interaction network (one node is equal to one species of plant or pollinator)	Occurrence	2 to high numbers	The higher the number of nodes, the more species there are interacting in the network	-	NetIndices (Kones et al., 2009)
<i>Connectance</i>	Ratio between the number of links performed, i.e. performed interactions, and the number of possible links	Occurrence	0 to 100	The higher the connectance, the more potential interactions in the network are actually realised	Decrease with network size (Blüthgen et al., 2007)	NetIndices (Kones et al., 2009)
<i>Modularity</i>	Property that explores to what extent the network is constituted of weakly interlinked subsets of species (modules), which nevertheless are internally constituted of strongly interacting species; thus, it seeks to detect sub-communities among our groups	Occurrence	0 to 1	The higher the modularity, the more closely the module's species are related to each other; better than they are with the species of other modules	Greedy Louvain algorithm method (Blondel et al., 2008) more performant on various network sizes (Aynaud et al., 2013)	igraph (Csardi and Nepusz, 2006)
<i>NODF</i>	<i>(Nestedness metrics based on Overlap and Decreasing Fill)</i> Property that explores to what extent the partners of specialists are a subset of the partners of generalists (Almeida-Neto et al., 2008)	Occurrence	0 to 100	The higher the nestedness, the more the partners of a species of a given degree are a subset of the partners of species of higher degree	Underestimated in case of pool of same degree species (Staniczenko et al., 2013) and negatively correlated with network size (Payrató-Borràs et al. 2020)	vegan (Oksanen et al., 2020)
<i>WNODF</i>	<i>(Weighted Nestedness metrics based on Overlap and Decreasing Fill)</i> Quantitative alternative to NODF, built for quantitative networks (Almeida-Neto and Ulrich, 2011)	Abundance	0 to 100	See NODF section	-	vegan (Oksanen et al., 2020)
<i>H₂'</i>	<i>(Standardised two-dimensional Shannon entropy)</i> Degree of specialisation between two parties in the entire network (Blüthgen et al., 2006)	Abundance	0 to 1	The higher the H ₂ ', the fewer interaction frequencies are evenly distributed	Independent of network size (Blüthgen et al., 2007)	bipartite (Dormann et al., 2009)
<i>d'</i>	<i>(Standardised Kullback-Leibler distance)</i> Degree of interaction specialisation at the species level (Blüthgen et al., 2006)	Abundance	0 to 1	The higher the d', the more specialised the species	Not applicable (species-level metric)	bipartite (Dormann et al., 2009) corrected by De Manincor (2019)

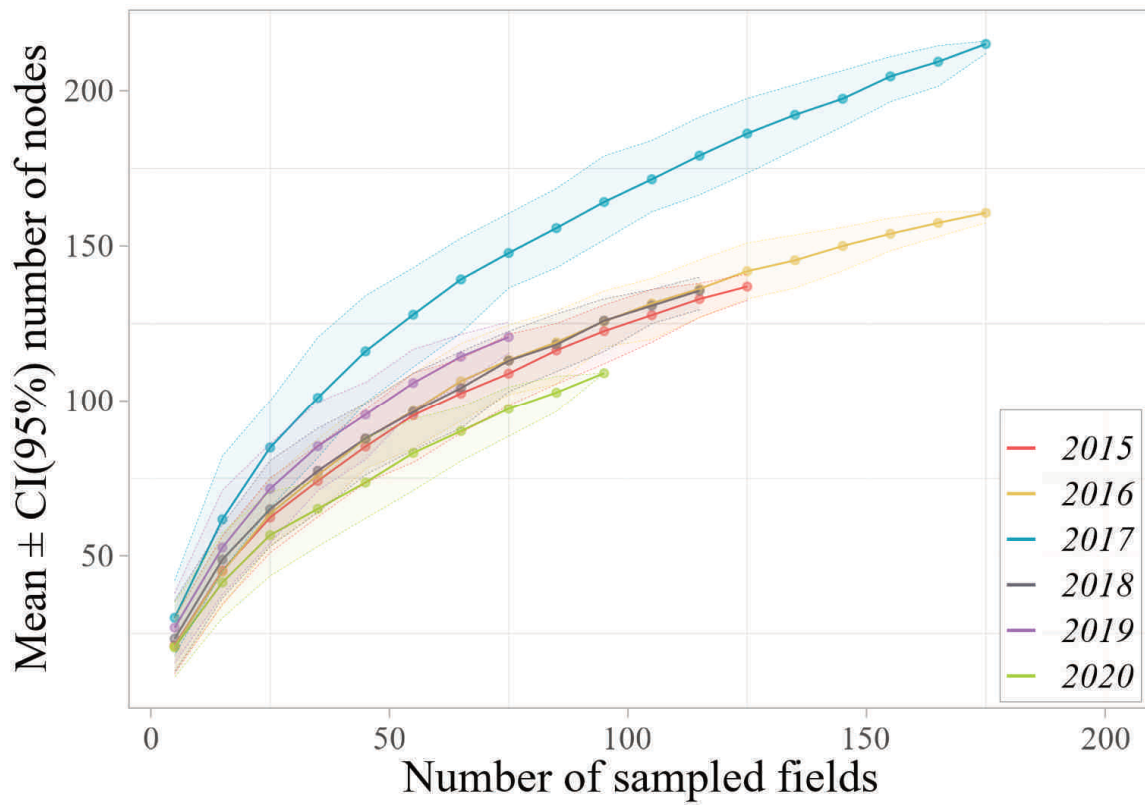
Additional references (not included in the manuscript):

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Supplementary material 3

Most likely degree distribution laws for each subnetwork (crop, period) and for the total network (six years, six crops, all species). When laws are bolded, the degree distribution of the considered group follows this law and the second-best one is rejected ($\Delta_{AIC} > 2$). In other cases, the second-best law cannot be dismissed.

	Degree distribution	
	Best law	Next-best law
Cereal	Fisher's logseries (AIC=871)	Lognormal (AIC=897)
Oilseed rape	Fisher's logseries (AIC=691)	Powerlaw (AIC=708)
Alfalfa	Fisher's logseries (AIC=465)	Powerlaw (AIC=477)
Corn/Sorghum	Fisher's logseries (AIC=270)	Lognormal (AIC=273)
Meadows	Fisher's logseries (AIC=739)	Lognormal (AIC=760)
Sunflower	Fisher's logseries (AIC=802)	Powerlaw (AIC=823)
Oilseed rape bloom	Fisher's logseries (AIC=651)	Lognormal (AIC=667)
Dearth period	Fisher's logseries (AIC=1317)	Powerlaw (AIC=1355)
Sunflower bloom	Fisher's logseries (AIC=982)	Powerlaw (AIC=1016)
Total	Fisher's logseries (AIC=2096)	Lognormal (AIC=2169)



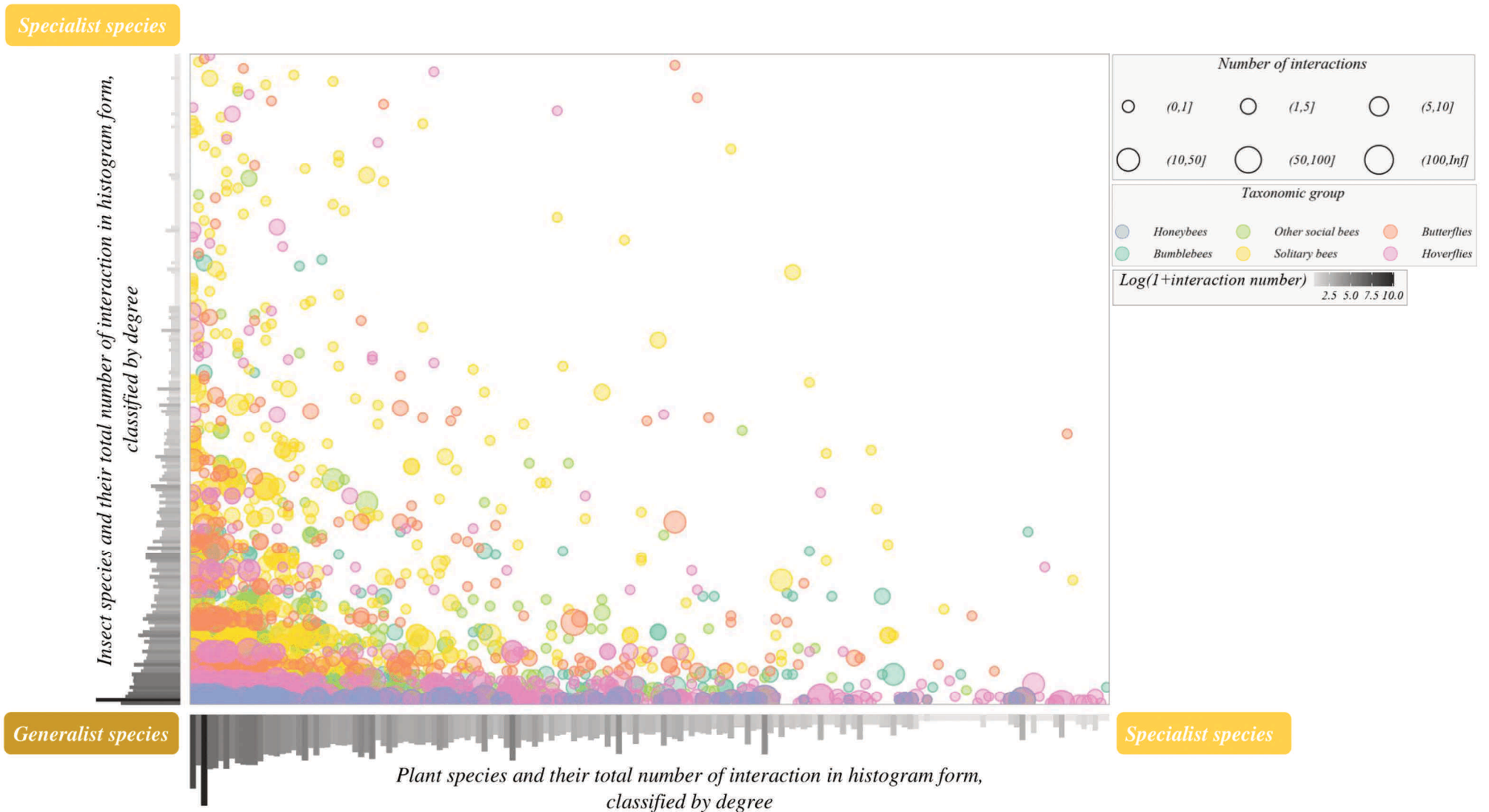
Supplementary material 4

Mean values of number of nodes ($\pm 95\%$ confidence intervals) for years, based on the number of sampled fields (x-axis). Red points and line: 2015; Yellow points and line: 2016; Blue points and line: 2017; Brown points and line: 2018; Purple points and line: 2019; Green points and line: 2020.

Supplementary material 5

Statistical tests' results for the differences in the number of interactions per fortnight.

Fortnight	ANOVA P-value	F-value	df	Tukey HSD test results				
				Compared crops	Difference in the observed means	Lower end point of the interval	Upper end point of the interval	P-value adjusted
1-15 April								
16-30 April	0.010	6.945	1	OSR-cereal	4.596	1.115	8.077	0.010
1-15 May	0.000	8.916	2	meadows-cereal	-0.207	-3.539	3.124	0.988
				OSR-cereal	2.19	0.852	3.528	0.001
				OSR-meadows	2.397	-0.720	5.514	0.165
16-31 May	0.000	18.180	3	alfalfa-cereal	2.967	0.088	5.847	0.041
				meadows-cereal	3.078	1.610	4.546	0.000
				OSR-cereal	2.343	1.247	3.439	0.000
				meadows-alfalfa	0.111	-3.022	3.244	1,000
				OSR-alfalfa	-0.625	-3.601	2.352	0.947
				OSR-meadows	-0.735	-2.387	0.916	0.653
				alfalfa-cereal	2.502	0.881	4.124	0.001
1-15 June	0.000	9.096	3	meadows-cereal	1.597	0.543	2.651	0.001
				OSR-cereal	0.743	-2.241	3.727	0.916
				meadows-alfalfa	-0.905	-2.691	0.881	0.553
				OSR-alfalfa	-1.759	-5.074	1.555	0.514
				OSR-meadows	-0.854	-3.931	2.222	0.888
16-30 June	0.018	2.833	5	alfalfa-cereal	1.377	-0.880	3.634	0.495
				corn-cereal	2.247	-2.164	6.658	0.684
				meadows-cereal	1.379	-0.052	2.810	0.066
				SF-cereal	-2.551	-8.765	3.663	0.844
				OSR-cereal	0.947	-1.310	3.204	0.831
				corn-alfalfa	0.870	-4.022	5.763	0.996
				meadows-alfalfa	0.003	-2.552	2.558	1,000
				SF-alfalfa	-3.928	-10.492	2.637	0.517
				OSR-alfalfa	-0.429	-3.524	2.665	0.999
				meadows-corn	-0.868	-5.438	3.703	0.994
				SF-corn	-4.798	-12.378	2.782	0.452
				OSR-corn	-1.300	-6.192	3.593	0.973
				SF-meadows	-3.930	-10.258	2.398	0.474
				OSR-meadows	-0.432	-2.987	2.123	0.997
1-15 July	0.000	20.160	5	OSR-SF	3.498	-3.066	10.063	0.641
				corn-cereal	-0.441	-5.688	4.807	1,000
				meadows-cereal	-0.292	-2.639	2.055	0.999
				SF-cereal	4.114	2.523	5.705	0,000
				OSR-cereal	-3.103	-8.351	2.144	0.512
				corn-alfalfa	-1.149	-6.526	4.228	0.988
				meadows-alfalfa	-1,000	-3.623	1.624	0.871
				SF-alfalfa	3.406	1.430	5.383	0,000
				OSR-alfalfa	-3.811	-9.188	1.566	0.309
				meadows-corn	0.149	-5.271	5.569	1,000
				SF-corn	4.555	-0.583	9.692	0.111
				OSR-corn	-2.663	-9.832	4.507	0.883
				SF-meadows	4.406	2.316	6.495	0,000
				OSR-meadows	-2.812	-8.231	2.608	0.649
OSR-SF	-7.217	-12.355	-2.080	0.001				
16-31 July	0.000	23.380	4	alfalfa-cereal	0.436	-4.543	5.414	0.999
				corn-cereal	-1.667	-6.684	3.351	0.891
				meadows-cereal	0.722	-4.285	5.730	0.995
				SF-cereal	2.354	-2.518	7.226	0.674
				corn-alfalfa	-2.102	-3.762	-0.443	0.005
				meadows-alfalfa	0.287	-1.343	1.916	0.989
				SF-alfalfa	1.918	0.770	3.066	0,000
				meadows-corn	2.389	0.643	4.135	0.002
				SF-corn	4.021	2.712	5.329	0,000
1-15 August	0.000	6.966	3	SF-meadows	1.631	0.361	2.901	0.005
				corn-alfalfa	-0.576	-1.845	0.693	0.642
				meadows-alfalfa	-0.175	-1.56	1.210	0.988
				SF-alfalfa	0.926	-0.213	2.066	0.155
				meadows-corn	0.401	-0.812	1.614	0.827
16-31 August	0.098	2.657	2	SF-corn	1.502	0.580	2.425	0,000
				SF-meadows	1.101	0.024	2.179	0.043
				corn-alfalfa	-2.626	-5.671	0.419	0.098
				meadows-alfalfa	-1.420	-3.882	1.042	0.327
meadows-corn	1.206	-1.897	4.309	0.591				



Supplementary material 6

Interaction number (i.e. each time insect in foraging behaviour was observed on a flower) between main types of pollinator groups (y-axis) and plant species (x-axis), with histograms of the number of interactions per species (log+1 transformed data) ranging from highest species degrees to lowest species degrees (light grey to dark grey). Point size: number of interactions category, from zero to infinity. Blue points: honeybees; Turquoise points: bumblebees; Green points: other social bees; Yellow points: solitary bees; Orange points: butterflies; Pink points: hoverflies.

alfalfa	NODF	35	25.464	21.009	30.845
corn	NODF	35	15.416	13.262	17.395
meadows	NODF	35	16.109	11.013	21.321
SF	NODF	35	21.632	16.831	29.198
cereal	Number of nodes	35	76.910	61.475	92.050
OSR	Number of nodes	35	75.670	62.475	86.050
alfalfa	Number of nodes	35	86.540	72.425	97.000
corn	Number of nodes	35	68.560	63.000	72.000
meadows	Number of nodes	35	99.840	84.475	113.575
SF	Number of nodes	35	72.040	58.475	86.525
cereal	WNODF	35	10.945	7.185	16.473
OSR	WNODF	35	17.664	12.643	24.251
alfalfa	WNODF	35	14.100	10.862	18.201
corn	WNODF	35	5.890	4.316	6.842
meadows	WNODF	35	7.642	4.458	10.863
SF	WNODF	35	10.978	7.401	15.026
cereal	connectance	85	0.031	0.026	0.037
OSR	connectance	85	0.028	0.025	0.032
alfalfa	connectance	85			
corn	connectance	85			
meadows	connectance	85	0.026	0.025	0.028
SF	connectance	85	0.032	0.028	0.039
cereal	H2'	85	0.398	0.340	0.464
OSR	H2'	85	0.361	0.286	0.461
alfalfa	H2'	85			
corn	H2'	85			
meadows	H2'	85	0.449	0.430	0.466
SF	H2'	85	0.614	0.540	0.677
cereal	modularity	85	0.440	0.410	0.472
OSR	modularity	85	0.484	0.448	0.523
alfalfa	modularity	85			
corn	modularity	85			
meadows	modularity	85	0.433	0.421	0.446
SF	modularity	85	0.451	0.410	0.489
cereal	NODF	85	23.921	19.887	28.543
OSR	NODF	85	32.970	27.731	38.166
alfalfa	NODF	85			
corn	NODF	85			
meadows	NODF	85	19.741	18.502	20.840
SF	NODF	85	23.359	19.501	28.113
cereal	Number of nodes	85	126.350	109.950	140.525
OSR	Number of nodes	85	118.250	106.475	127.000
alfalfa	Number of nodes	85			
corn	Number of nodes	85			
meadows	Number of nodes	85	158.570	152.475	163.000
SF	Number of nodes	85	114.320	98.425	127.050
cereal	WNODF	85	12.820	9.886	15.469
OSR	WNODF	85	19.299	15.480	22.719
alfalfa	WNODF	85			
corn	WNODF	85			
meadows	WNODF	85	10.198	9.152	10.869
SF	WNODF	85	13.117	10.459	15.925
cereal	connectance	165			
OSR	connectance	165	0.026	0.025	0.027
alfalfa	connectance	165			
corn	connectance	165			
meadows	connectance	165			
SF	connectance	165	0.029	0.026	0.031
cereal	H2'	165			
OSR	H2'	165	0.309	0.297	0.337
alfalfa	H2'	165			
corn	H2'	165			
meadows	H2'	165			
SF	H2'	165	0.584	0.554	0.611
cereal	modularity	165			
OSR	modularity	165	0.432	0.425	0.442

alfalfa	modularity	165			
corn	modularity	165			
meadows	modularity	165			
SF	modularity	165	0.399	0.378	0.424
cereal	NODF	165			
OSR	NODF	165	36.270	35.066	37.303
alfalfa	NODF	165			
corn	NODF	165			
meadows	NODF	165			
SF	NODF	165	24.993	22.848	27.134
cereal	Number of nodes	165			
OSR	Number of nodes	165	157.160	154.000	159.000
alfalfa	Number of nodes	165			
corn	Number of nodes	165			
meadows	Number of nodes	165			
SF	Number of nodes	165	155.490	143.475	166.000
cereal	WNODF	165			
OSR	WNODF	165	21.633	20.266	22.522
alfalfa	WNODF	165			
corn	WNODF	165			
meadows	WNODF	165			
SF	WNODF	165	14.534	13.118	15.674