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

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Abstract

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

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

Key words

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

Highlights

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

1. Introduction

Insect biodiversity is declining worldwide, and numerous local insect extinctions have already been documented (Habel et al., 2019). This decline has high consequences for the ecosystem services that rely upon insects, not least pollination (Frankie et al., 2009). In temperate regions, 88% of plants depend on zoogamous pollination for their reproduction (Ollerton et al., 2011) and 70% of crops depend to some extent on insect pollination (Klein et al., 2007), which improves yields of insect-pollinated crops and ensure agricultural production, as in oilseed rape (OSR; *Brassica sp.*) and sunflower (SF; *Helianthus sp.*) (Perrot et al., 2019, 2018). In arable farming systems, insect pollinators forage partly – and sometimes mainly – on mass-flowering crops, but availability of these crops does not cover the entire season of the pollinators' activity (Odoux et al., 2014). Between OSR and SF blooms (the so-called 'dearth period'), the resources provided by weeds are essential for maintaining pollinators, including the honeybee *Apis mellifera* (Carvalho et al., 2011; Requier et al., 2015). Weeds and other wild plants are therefore critical for pollinators (Bretagnolle and Gaba, 2015), and contribute to their diversity and abundance at both field and landscape scales (Carvalho et al., 2011). Among insect pollinators, bees and hoverflies contain generalist species that can interact with many wild flowers (Dunn et al., 2020) or crop plants, and both improve pollination service (Garibaldi et al., 2011). Hoverflies are more resilient to agricultural modifications than bees in agricultural landscapes (Jauker et al., 2009); conversely, butterflies which also pollinate many wild plants, have been dramatically affected by agricultural intensification (Johst et al., 2006). Overall, weeds and pollinators are closely intertwined in agricultural farmland, and form ecological interaction networks, defined by a set of nodes (species) interconnected by one or more links (interactions). There is evidence that such networks have changed in structure over the last century, due to pollinator and plant community changes, with many interactions 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. Magrach 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 450km²) 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

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

2. Materials and methods

2.1. Study site

Our study site is the Long Term Socio-Ecological Research (LTSER) site ‘Zone Atelier Plaine & Val de Sèvre’, located in the Nouvelle-Aquitaine region of southwest France, south of the city of Niort (Bretagnolle et al., 2018). It covers 450 km², harbouring c. 13,000 fields. We focused on six years of survey, 2015–2020, which is one of the largest time intervals of plant–pollinator network studies (but see Chacoff et al., 2018; Petanidou et al., 2008; Ponisio et al., 2017). Each year, 100 to 220 different fields were surveyed (some fields were studied for more than one year) with a standardised protocol. Fields were selected in a stratified random process (see Bretagnolle et al. (2018) for details). From 2015–2020, the number of fields sampled per respective year were 174, 217, 195, 160, 117 and 115 (see ESM1a and 1b in Appendix A). Crop surveyed included 7% corn (*Zea mays*) and sorghum (*Sorghum bicolor*), 8% alfalfa (*Medicago sativa*), 12% meadows (temporary or permanent), 18% oilseed rape (*Brassica napus*), 22% sunflower (*Helianthus annuus*), and 33% cereal crops. Cereals included barley (*Hordeum vulgare*), durum wheat (*Triticum turgidum*), einkorn (*Triticum monococcum*), oat (*Avena sativa*), rye (*Secale cereale*), triticale (\times *Triticosecale*) and winter wheat (*Triticum aestivum*). Sampling was performed from April to August, i.e. all crops were surveyed at least once during their respective flowering periods: OSR from April–May; sunflower from July–August; alfalfa, meadows and cereals from May–June to the end of August; and corn and sorghum from July–August.

2.2. Sampling of plant–pollinator interactions

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

2.3. Statistical analyses

2.3.1. Sampling completeness and frequency distribution of degrees

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

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

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

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

data, since the number of transects per field and the number of fields sampled per crop and per year varied. We thus converted the number of interactions per transect per field into a number per hectare (ha), since each transect surveyed an area of 250 m². Next, we grouped samples per fortnight by averaging values (with standard-error, se) of interactions per ha per fortnight for each crop. Obtained values were compared with ANOVA and post-hoc Tukey tests. Data were log-transformed.

2.3.3. *Network structure descriptors*

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

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

2.3.4. Field selection

To calculate Chao 2 estimates and the number of interactions per hectare, we included the fields in which no insects had been observed (138 fields, 17.0%). However, to represent interaction networks and calculate metrics on aggregated fields, we only retained the fields on which at least one interaction was observed in the dataset. All analyses were run with *R software v.4.1.0* (R Core Team, 2021).

3. Results

3.1. Sampling completeness and frequency distribution of degrees

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

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

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

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

The total number of nodes varied highly among crops (165, 114, 186, 178, 161 and 75 in 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 ± 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 ($F_{5,62} = 20.16$, $p\text{-value} < 0.0001$), with significantly higher values for SF than in alfalfa (T_{HSD}
 302 $p\text{-adj} < 0.001$), meadows ($T_{\text{HSD}} p\text{-adj} < 0.001$), cereals ($T_{\text{HSD}} p\text{-adj} < 0.001$) and OSR ($T_{\text{HSD}} p\text{-}$
 303 $\text{adj} = 0.0015$).

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.

3.3. Network structure

3.3.1. Seasonal effect on network structure

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

3.3.2. Crop effect on network structure

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

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

4. Discussion

The detection of several hundreds of species in the plant–pollinator network indicates that the LTSER ZAPVS is characterised by a high diversity of species despite its intensive farming system. While the honeybee, SF and OSR are by far the species that establish most interactions, they are not necessarily those with the greatest number of interacting partners. Although OSR flower is the species with the highest degree (number of interaction partners), confirming its structuring role in the network (Diekötter et al., 2010; Stanley and Stout, 2014), it is closely followed by wild plant species, generally hosted in less-intensively managed but more diverse crops such as alfalfa or meadows. Moreover, the hoverfly *Sphaerophoria scripta* showed far more partners than honeybee, including OSR and SF flowers, suggesting that its role in the network has to be explored in more detail. *Bombus* species are also frequent visitors of SF, as Syrphidae of OSR (Jauker and Wolters, 2008). Although these are rarely studied as key species in networks, they might be strongly involved in OSR and SF pollination (Breeze et al., 2011), and could act as pollination insurance if honeybees were to decline dramatically (Sánchez-Bayo and Wyckhuys, 2019). Completeness of survey effort was, however, moderate: 65% for insects but 80% for plants 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

and Holland, 2008), they display a certain vulnerability because the sharing of partners is weak, like in the studied SF crops, but contrary to the OSR crops. Indeed, the most striking differences in networks were found between OSR and SF, both being mass-flowering crops. As expected, these two crops drove the overall behaviour of networks during their blooming season (approximately the same metrics of behaviour between the OSR crop and OSR period, and between the SF crop and SF period), although the meadows, weeds in cereals, and alfalfa were flowering at the same time. However, the OSR and SF crops' networks were somewhat opposed in some of the key metrics, hence possibly showing different network stability (Duchenne et al., 2022). The OSR network did not harbour many species, but was highly nested compared to the other crop networks, which therefore suggests it was a resilient network. Its nestedness may result from the fact that the OSR network was mostly composed of species with a high degree of generalisation (i.e. the average species specialisation was quite low in OSR crops), leading to a relatively nested structure (Fontaine et al., 2009). Thus, as the OSR network was the most nested network in our study, it was expected that the general core of species it included were generalists rather than specialists, which was indeed the case. The interaction between OSR and honeybees has a structuring effect for the network, corroborating studies that highlight OSR flower and its partners as a hub that positively influences the visitation and pollination of neighbouring wild plants, especially those with similar morphology (Thompson et al., 2021). OSR is also known to host diverse insect communities (Stanley et al., 2013), while honeybees remain one of the most efficient pollinators and, as demonstrated here, the most important partner of OSR. Conversely, SF appears less stable than OSR because it is much less nested for an equivalent diversity of species, and is composed of more specialised species, including the honeybee–SF duo, which both qualify as specialist species, interacting strongly and almost entirely with each other – a pattern that was not necessarily found in other studies (e.g. Valido et al., 2019).

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

5. Conclusion

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

Author Contributions

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

Declaration of Competing Interest

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

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Appendix A. Supporting information

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

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