



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

Claire Gay^{a,b,*}, Sabrina Gaba^{a,b,c}, Vincent Bretagnolle^{a,b,c}

^a UMR 7372 Centre d'Etudes Biologiques de Chizé, CNRS & La Rochelle Université, 79360 Villiers-En-Bois, France

^b USC 1339 Centre d'Etudes Biologiques de Chizé, INRAE, CNRS & La Rochelle Université, 79360 Villiers-En-Bois, France

^c LTSER "Zone Atelier Plaine & Val de Sèvre", 79360 Villiers-En-Bois, France

ARTICLE INFO

Keywords:

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

ABSTRACT

In agricultural landscapes, bipartite networks formed by pollinators and the flowers they forage on, are characterised by the presence of 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 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 a nestedness measure. We found that the degree distribution (number of partners per species in the network) fitted better to Fisher's log-series rather than Power law. Strong differences between crops were observed in nestedness and specialisation, even when accounting for the effect of sample size: 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.

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 winter 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, i.e. in May

and June in temperate farmland landscapes, there is a temporary lack of mass-flowering crop floral resources (the so-called 'dearth period') during which the resources provided by weeds are essential to bee foraging and survival (Requier et al., 2017, 2015), 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). 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 links – that involve specialist species – being lost (Mathiasson and Rehan, 2020), mostly as a result of land use intensification (Ferreira

* Corresponding author at: UMR 7372 Centre d'Etudes Biologiques de Chizé, CNRS & La Rochelle Université, 79360 Villiers-En-Bois, France.
E-mail address: clairegay.phd@gmail.com (C. Gay).

et al., 2013). Indeed, the persistence of pollinators – together with the services they provide – depends on the structure of plant–pollinator ecological networks.

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

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

In this study, we used a descriptive approach to qualify plant–pollinator networks in a highly intensive farming system, at a large spatial scale (study site of 450 km²) with data collected on six

different crop types (811 fields in total). Because our sampling effort was high, we first paid attention to two generally overlooked patterns, the effect of sample size and the degree distribution. Sampling effort has been shown to affect many network metrics, through sampling intensity and sampling bias, but also underlying species abundances (Blüthgen et al., 2007). Degree distribution is highly skewed, resulting in part from many ‘forbidden links’, the latter resulting from constraints imposed by the morphological, phenological, phylogenetic and spatial complementarity of species (Jordano, 2016): if the ecological niches of two species are incompatible, then these species cannot interact with each other. We also describe the overall visual structure of networks by seasons and crop types. Then, we investigated major features of the network, from simple network descriptors (number of nodes, connectance) to more complex ones (nestedness, modularity, specialisation), quantifying their level of variation among crop types and seasons, while accounting for sample size. We expected plant–pollinator network structure to vary seasonally because of the presence of mass-flowering crops, and the spillover or dilution effects that result from such presence. Indeed, we expected strong variations in network structure among crop types, in particular between main mass-flowering and other crops (Timberlake et al., 2019), but also between arable crops and grasslands. We further predicted a clear dominance of the managed honeybee, especially during the flower blooms of OSR and SF, which dominate landscapes when flowering. In particular, we predicted that networks would be more specialised during OSR and SF blooms than in other periods and other crops. We also predicted that networks would be more nested 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., 2018a). It covers 450 km², harbouring c. 13,000 fields. In the study site, grasslands represent about 10% of the farmed area, cereals 37%, OSR 7%, sunflower 7.5% and maize 9%, while forests cover 14% and the remaining area consist in other crops (pea, ryegrass) or urbanized areas. Surveys were conducted in farmers’ fields. Each year, 100–220 different fields were sampled (a few fields were studied for more than one year) with a standardised protocol. Fields were selected in a stratified random process: every year, 40–60 1 km² squares were randomly selected in the study site, with a stratified procedure using three gradients of landscape features (woody habitats, i.e. hedges and forest fragments, grasslands, and organic farming (Bretagnolle et al., 2018a; Crochard et al., 2022; Perrot et al., 2022)). A moving window was used to select the squares (Fahrig et al., 2011) to obtain statistically independent gradients. Within each square, we selected one field of cereal, oilseed rape, maize/sunflower, and alfalfa/meadow when they were present (resulting in three to four fields per square). Within a square, fields of different crops were 100–500 m from each other, while the squares were on average 1–3 km from each other (see, e.g., Sirami et al., 2019), avoiding the risk of generating spatial autocorrelation between sampling points (see Perrot et al., 2022). 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). 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% winter oilseed rape (*Brassica napus*), 22% sunflower (*Helianthus annuus*), and 33% cereal crops.

Cereals included barley (*Hordeum vulgare*), durum wheat (*Triticum durum*), einkorn (*Triticum monococcum*), oat (*Avena sativa*), rye (*Secale cereale*), triticale (\times *Triticosecale*) and winter wheat (*Triticum aestivum*). In the study area, alfalfa is always mowed before flowering because the quality of the leaves for goat feeding drops with flowering. Sampling was performed from April to August, i.e. all crops were surveyed at least once during their respective flowering periods: winter 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 were surveyed using transect methods, and included bees (both honeybees and wild bees), butterflies and hoverflies (Syrphidae), i.e. the three main pollinator groups in our study site. 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. Since field margins generally harbour a more diverse fauna compared to field cores, one transect was in the field margin (section between the field edge and the first seeding line, randomly selected, but starting from the road), one was in the field centre, and the last in between, at c. 25 m from the margin (except in 2015). Transects were all located within the field, and were always organized similarly (see Bretagnolle et al., 2018a, 2018b; Crochard et al., 2022; Perrot et al., 2022 for additional details). The transect always lasted 10 min each (i.e. when a bee was caught for identification, the time necessary to identification or placing the bee in a tube was not counted). Duration was measured by a hand chronometer. 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 31 °C, in sunlight – a maximum temperature of 45 °C was recorded in one specific case, but the thermometer was in full 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.

In plant–pollinator networks, the degree distributions were shown to be best fit by the power law, a long tail distribution law (Blüthgen et al., 2007), since a significant number of nodes have many connections while most nodes in the plant–pollinator network have fewer connections. Here we compared the fit of other long tail distribution laws in order to verify that the Power Law was the best fit among those candidate distributions, and in particular used other distributions that have been used in population and community structures. 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 specific interaction subnetworks. First we built sub-datasets corresponding to the six crop categories retained: OSR, cereals, alfalfa, meadows, SF and corn–sorghum. We also split the data into three equal-length seasons (resulting in three other sub-datasets), each 45 days long: April 1st–May 20th (OSR flowering peak, characterised by high resource availability for insects and gathering data collected in OSR, cereals, alfalfa and meadows), May 21st–July 9th, characterised by a general lack of flowering crop resources available (i.e. the dearth period, with data collected in cereals, alfalfa and meadows) – 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 (gathering data collected in alfalfa, meadows, SF and corn–sorghum). Finally, we focused on the five main taxonomic groups and divided our dataset into sub-datasets corresponding to bumblebees, other social bees (including some Halictidae, e.g. *Halictus rubicundus*, *Lasioglossum pauxillum*), solitary bees, hoverflies and butterflies. We added a sixth sub-dataset corresponding to the honeybees.

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; increased connectance is expected to decrease secondary extinctions (Blüthgen et al., 2007) and improves robustness at the community level as well as stability (Thébaud and Fontaine, 2010), 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. 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.

In our study, sample sizes vary with crop type. To compare the metric values among crop types, seasons and taxonomic groups, we use the smallest sample size for the analysis by reducing the set of crops with larger sample size to this smallest sample size value. The maximum bootstrap threshold to compare the three seasons was thus 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 compared the metric values obtained at a threshold of 35 fields per group (100 groups) in the bootstrap because we had very few fields of corn–sorghum and alfalfa. We also compared four crops (OSR, SF, cereals and meadows) with 100 groups of 85 fields. Finally, we focused on the two mass-flowering crops, OSR and SF, by comparing the metric values obtained at the threshold of 165 fields.

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. We never observed two singletons (species that were sampled only once) interacting with each other, i.e. 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%, including 70 singleton species) 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 (23.0%, including 23 singleton species), 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 per crop indicated that these differences among crops (Fig. 1) could be detected even from low sample sizes (c. $n = 50$). Thus, independently of the number of sampled fields, meadows showed the highest values of node numbers, followed by alfalfa, cereals, OSR and SF (Fig. 1). Year did not affect the pattern of the accumulation curves (see ESM4 in Appendix A), although 2017 was a species-rich year regardless of the sampling effort.

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

Network structure differed strongly among crops in relation to variation of the total number of nodes, either in the repartition of interactions between the main groups of plants or between the main groups of pollinators (Fig. 3). In flowering crops, the crop flower was generally the most visited flower in the crop considered. For instance, 95.27% of pollinators visited SF plant in SF fields, and 86.07% OSR plants in OSR fields. However, this was true only for mass-flowering crops: alfalfa represented approximately a third of all visited flowers in alfalfa fields (36.12%) and corn was poorly visited in corn–sorghum fields (7.55%). In those crops, pollinators preferentially foraged on wild flowers (89.62%). Moreover, honeybees' dominance was not of the same magnitude in all crops: they were overrepresented in SF (91.95%) and OSR (76.60%), while hoverflies rather than honeybees were the most-interacting group in other crops (32.55% in corn and sorghum crops, 56.42% in cereal crops, 36.02% in alfalfa crops and 53.38% in meadows). Interestingly, when found in other crops, OSR and SF flowers showed the same interaction pattern, i.e. interacting mainly with honeybees. Moreover, hoverflies foraged more on wild flowers than did any other insect group, potentially explaining their high presence in weed-rich crops such as meadows or alfalfa. For instance, whereas the total percentage of weed visits by all pollinator groups was 63.78% in alfalfa crops, it reached 77.94% when considering only hoverfly visits.

Species with the highest degrees were not necessarily the most frequent, although species' frequency of occurrence and degree were strongly related (i.e. decreasing pattern of species degrees were concomitant with decreasing species frequencies) (see ESM6). In terms of the number of interactions, honeybees and bumblebees were most prevalent (83.72% of the total interactions number, $n = 31,089$), followed by hoverflies (8.21%, $n = 3050$), solitary bees (2.69%, $n = 998$) and butterflies (1.36%, $n = 506$). Honeybees were by far the dominant insect species (80.80% of all interactions, $n = 30,007$), the next two being *Sphaerophoria scripta* (3.80%, $n = 1412$) and *Episyrphus balteatus* (2.19%, $n = 812$), two hoverflies. However, although *S. scripta* was 20 times less abundant than honeybees in total, its number of plant partners (92) was higher than that of honeybees (75). Butterflies were far less often observed, with only 81 interactions for the most common butterfly, *Pieris rapae*. Concerning plants, SF represented 72.36% ($n = 26,871$) of the whole sample, seven times more than OSR (10.69%, $n = 3971$), and 60 times more than the most-interacting weed, *Torilis arvensis* (1.20%, $n = 446$). Therefore, the complete network was dominated by honeybees and mass-flowering crops: honeybees interacting with OSR or

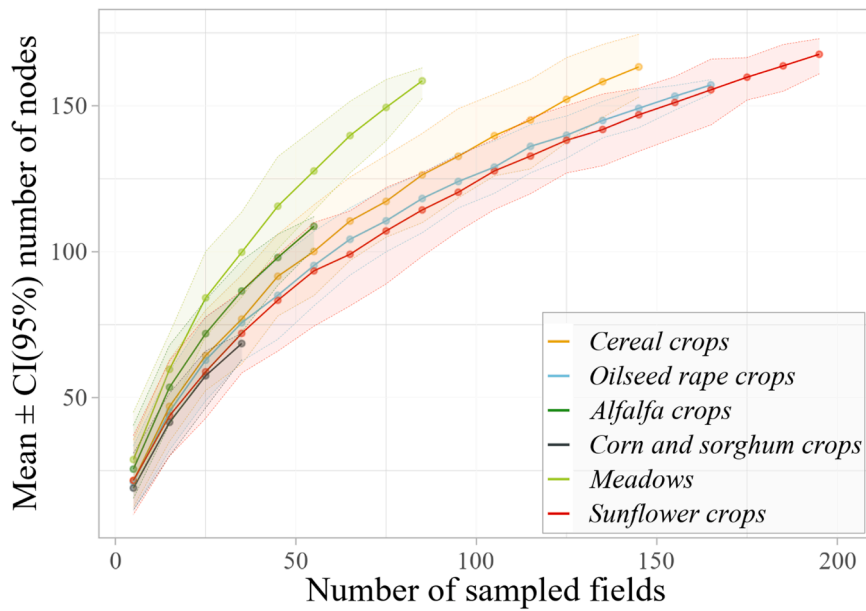


Fig. 1. Mean values of number of nodes (\pm 95% confidence intervals) for each crop, according to the number of sampled fields (x-axis). Brown points and line: cereal; Light blue points and line: oilseed rape; Dark green points and line: alfalfa; Dark blue points and line: corn and sorghum; Light green points and line: meadow; Red points and line: sunflower.

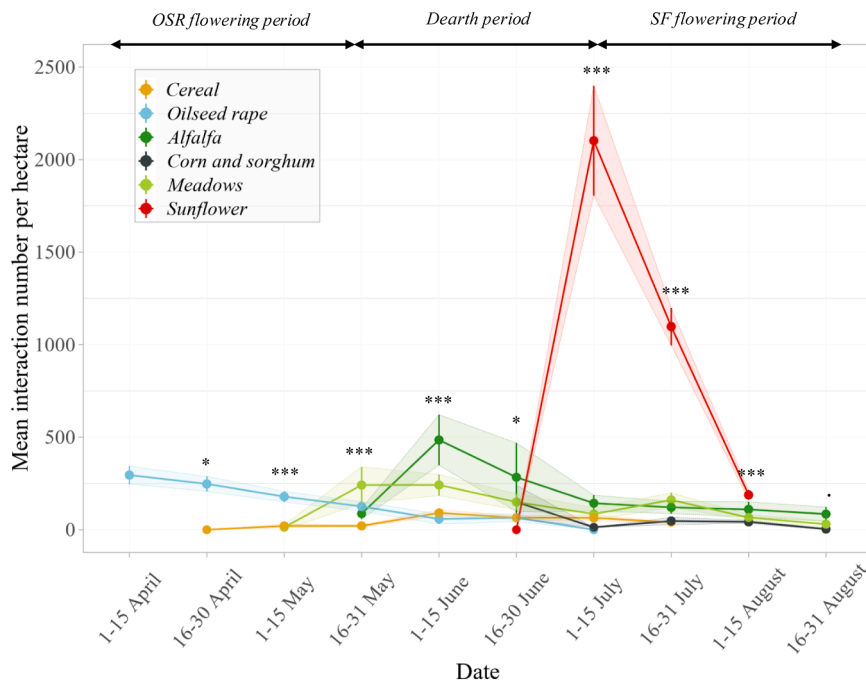


Fig. 2. Interaction number (frequency of pollinators interacting with flower) per hectare and per crop throughout the season. Data are presented as mean \pm se (standard error). Analyses of variances were run on each fortnight (two weeks aggregated) to compare crops (log+1-transformed). If p-value < 0.001 then * ** ; 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 ‘.’ Brown points and line: cereal; Light blue points and line: oilseed rape; Dark green points and line: alfalfa; Dark blue points and line: corn and sorghum; Light green points and line: meadow; Red points and line: sunflower.

SF represented 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. 4a), reaching 214 (CI_{95%}: 195–230) species when considering a sampling effort of 175 fields (see

ESM7a for details on seasons’ metric values). 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 3.0% (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

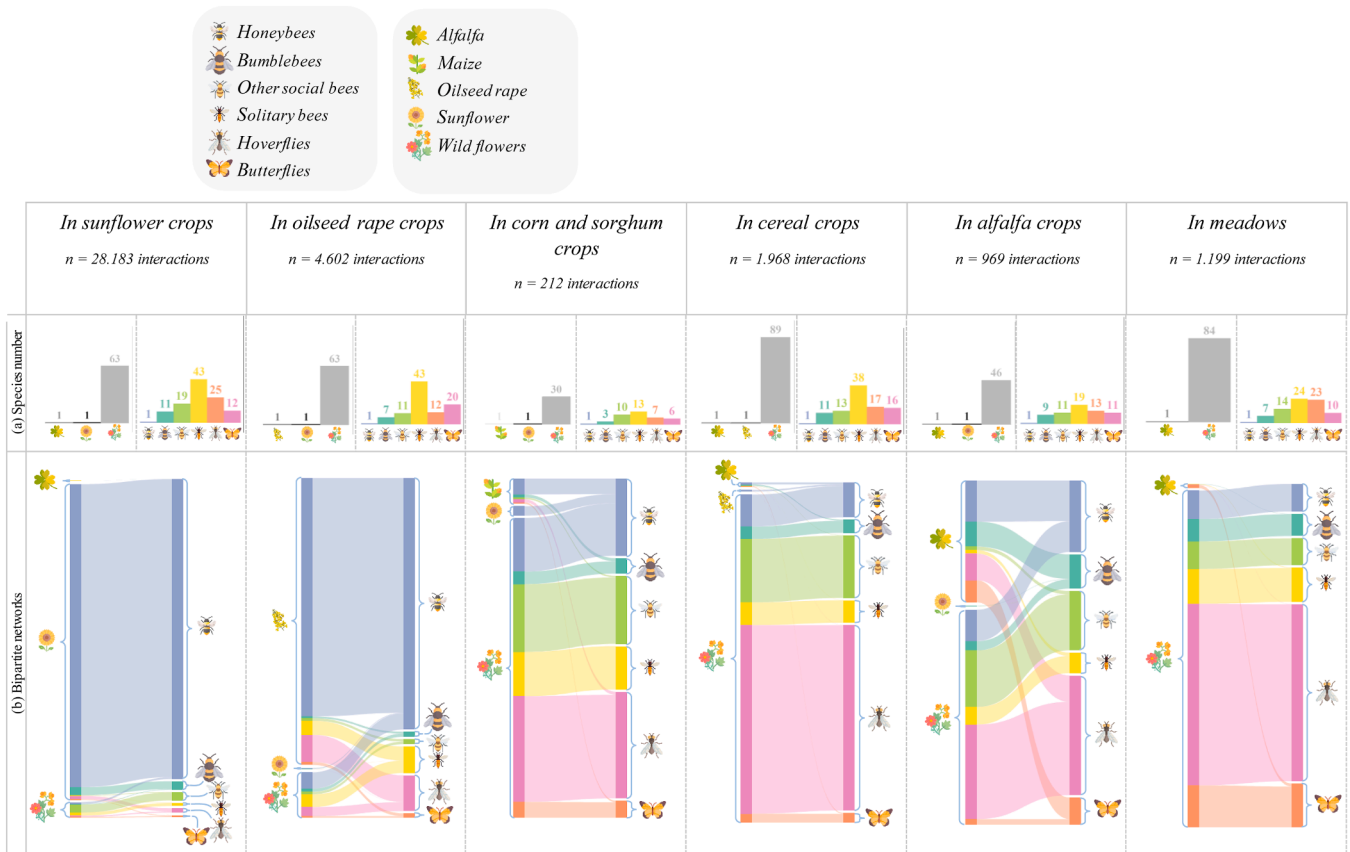


Fig. 3. (a) Histograms of species number per crop for pollinator and insect groups. Grey bars: species number of the different plant groups. Blue bar: honeybee species number; Turquoise bar: bumblebee species number; Green bar: other social bee species number; Yellow bar: solitary bee species number; Orange bar: butterfly species number; Pink bar: hoverfly species number. (b) Bipartite representations of crop networks involving the main pollinator taxonomic groups and the main plant groups. Blue path: honeybee interaction; Turquoise path: bumblebee interaction; Green path: other social bee interaction; Yellow path: solitary bee interaction; Orange path: butterfly interaction; Pink path: hoverfly interaction.

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)). 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. 4b). Although OSR blooming period was the most modular period (see above), mean modularity was almost identical whatever the crop considered, at about 0.5 (see ESM7b for details on crops' metric values). 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)).

4. Discussion

The detection of several hundreds of species in the plant–pollinator

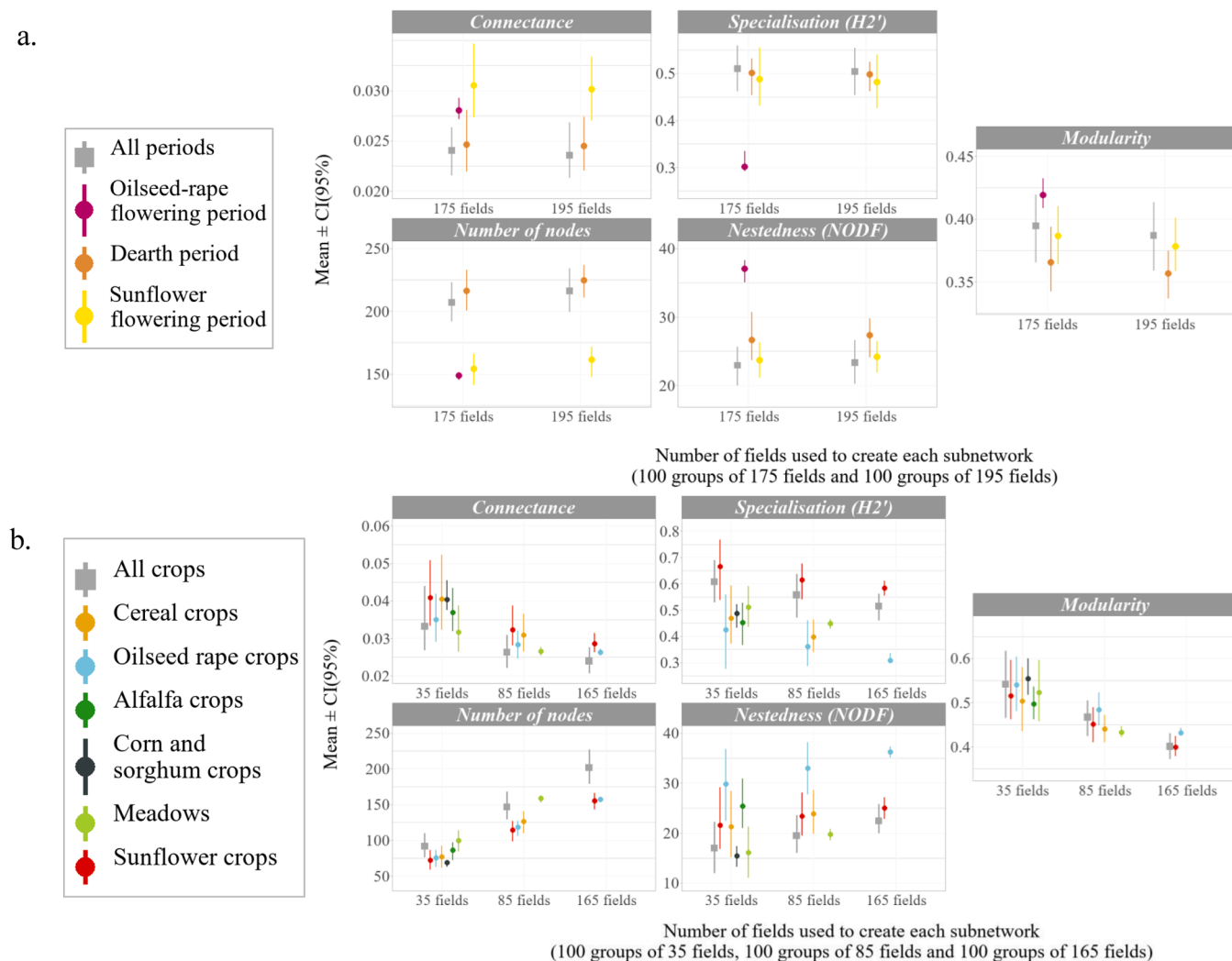


Fig. 4. Mean network metric values (\pm 95% confidence intervals) for (a) periods and (b) crops, based on the number of sampled fields (x-axis) and with a y-axis scale indicating the value of the metric. Period metrics; Grey squares: all periods; Purple points: oilseed rape flowering period; Orange points: death period; Yellow points: sunflower flowering period. Crop metrics: Grey squares: all crops; Brown points: cereal crop; Light blue points: oilseed rape crop; Dark green points: alfalfa crop; Dark blue points: corn and sorghum crop; Light green points: meadow. Red points: sunflower crop.

network indicates that our study site is characterised by a high diversity of species despite its intensive farming system. For instance, 200 pollinators' species were involved in these interactions, and Rollin (2013) had estimated a specific richness of bees in our area between 238 and 251 species in the same study site, and Munoz et al. (2020) recorded 399 weed species in this study site. 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 September) during six years. The phenology of some plants and insects being very short may explain why not all species were detected, in addition to the classic and inherently imperfect detection method. In addition, the low connectance within crops (around 2–3%) suggests that few interactions are carried out among all possible ones. These forbidden links (Jordano, 2016) could result from spatial or temporal constraints (Valdovinos, 2019). Indeed, one of our possible explanations is that each crop network corresponds to a set of different fields that belongs to different landscape entities and different sampling weeks, which generates a high community variability in terms of phenology and location. But a low connectance, i.e. high proportion of forbidden links, is in certain cases one of the indicators of destabilised networks (Landi et al., 2018). We also found that the Fisher's log-series outcome the Power law whatever the crop or season in which we considered the plant–pollinator networks. Such result is very meaningful because the Fisher's log series has been shown to fit a range of species assemblages, particularly those that have a high frequency of rare species (Magurran, 2005), and is related to the Neutral theory (Hubbell, 2001). Therefore, our results may offer alternative mechanistic explanations to the plant–pollinator topology, e.g. the higher number of low connected nodes may occur because rare

species in species assembly (either of plants or of insects) move in and out through stochastic processes such as dispersal (see Henckel et al., 2015 or Bourgeois et al., 2020 for examples in plants).

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

Occurring very abundantly during their respective flowering peaks, OSR and SF crops drive the structure of interaction networks, the other crops having little effect on these patterns. Although OSR and SF are often simply equated and grouped as 'mass-flowering crops', there are significant differences in the structure of the plant–pollinator interaction networks that are observed in both crops. Our results suggest that the honeybee and crop flower pair 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 may possibly be due to flower shape – a divergence that can be further explored with species trait approaches. Furthermore, by standardizing crop types at similar sample sizes, the comparison of the metric values between crops revealed that OSR network was highly nested compared to the other crop networks. This would suggest a higher ability of this network to cope with disturbances (i.e. resilient network) compared to corn–sorghum, cereal and even sunflower networks. OSR was already suggested to be a key crop in this study area by harbouring a high diversity (Gaba and Bretagnolle, 2021); it now appears also as an important crop for the persistence of plant–pollinator networks. Finally, our results on the best fit of degree distribution by the Fisher's log series offer other mechanistic explanations to the plant–pollinator topology that need further studies to be better understood especially in highly dynamic environment such as agricultural landscapes.

CRedit authorship contribution statement

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 & 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.

Data Availability

Data will be made available on reasonable request to breta@cebc.cnrs.fr.

Acknowledgements

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108759](https://doi.org/10.1016/j.agee.2023.108759).

References

- Albrecht, M., Padrón, B., Bartomeus, I., Traveset, A., 2014. Consequences of plant invasions on compartmentalization and species' roles in plant–pollinator networks. *Proc. R. Soc. B* 281, 20140773. <https://doi.org/10.1098/rspb.2014.0773>.
- Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1227–1239. <https://doi.org/10.1111/j.0030-1299.2008.16644.x>.
- Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* 100, 9383–9387. <https://doi.org/10.1073/pnas.1633576100>.
- Bendel, C.R., Kral-O'Brien, K.C., Hovick, T.J., Limb, R.F., Harmon, J.P., 2019. Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition. *Ecosphere* 10, 1–14. <https://doi.org/10.1002/ecs2.2569>.
- Blondel, V.D., Guillaume, J.-L., Lambiotte, R., Lefebvre, E., 2008. Fast unfolding of communities in large networks. *J. Stat. Mech.: Theory Exp.* 2008, P10008. <https://doi.org/10.1088/1742-5468/2008/10/P10008>.
- Blüthgen, Nico, Menzel, F., Blüthgen, Nils, 2006. Measuring specialization in species interaction networks. *BMC Ecol.* 6, 1–12. <https://doi.org/10.1186/1472-6785-6-9>.
- Blüthgen, Nico, Menzel, F., Hovestadt, T., Fiala, B., Blüthgen, Nils, 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Curr. Biol.* 17, 341–346. <https://doi.org/10.1016/j.cub.2006.12.039>.
- Bourgeois, B., Gaba, S., Plumejeaud, C., Bretagnolle, V., 2020. Weed diversity is driven by complex interplay between multi-scale dispersal and local filtering. *Proc. R. Soc. B: Biol. Sci.* 287, 20201118. <https://doi.org/10.1098/rspb.2020.1118>.
- Breeze, T.D., Bailey, A.P., Balcombe, K.G., Potts, S.G., 2011. Pollination services in the UK: how important are honeybees? *Agric., Ecosyst. Environ.* 142, 137–143. <https://doi.org/10.1016/j.agee.2011.03.020>.
- Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909. <https://doi.org/10.1007/s13593-015-0302-5>.
- Bretagnolle, V., Berthet, E., Gross, N., Gaufrre, B., Plumejeaud, C., Houte, S., Badenhaußer, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018a. Towards sustainable and multifunctional agriculture in farmland landscapes: lessons from the integrative approach of a French LTSEr platform. *Sci. Total Environ.* 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>.
- Bretagnolle, V., Berthet, E., Gross, N., Gaufrre, B., Plumejeaud, C., Houte, S., Badenhaußer, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018b. Description of long-term monitoring of farmland biodiversity in a LTSEr. *Data Brief.* 19, 1310–1313. <https://doi.org/10.1016/j.dib.2018.05.028>.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Socio* 65, 23–35. <https://doi.org/10.1007/s00265-010-1029-6>.
- Carpentier, C., Barabás, G., Spaak, J.W., De Laender, F., 2021. Reinterpreting the relationship between number of species and number of links connects community structure and stability. *Nat. Ecol. Evol.* 5, 1102–1109. <https://doi.org/10.1038/s41559-021-01468-2>.
- Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity: weeds maximize nature benefits to crops. *Ecol. Lett.* 14, 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>.
- Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J., Padrón, B., 2012. Evaluating sampling completeness in a desert plant–pollinator network: sampling a plant–pollinator network. *J. Anim. Ecol.* 81, 190–200. <https://doi.org/10.1111/j.1365-2656.2011.01883.x>.
- Chacoff, N.P., Resasco, J., Vázquez, D.P., 2018. Interaction frequency, network position, and the temporal persistence of interactions in a plant–pollinator network. *Ecology* 99, 21–28. <https://doi.org/10.1002/ecy.2063>.
- Chakraborty, P., Chatterjee, S., Smith, B.M., Basu, P., 2021. Seasonal dynamics of plant pollinator networks in agricultural landscapes: how important is connector species identity in the network? *Oecologia* 196, 825–837. <https://doi.org/10.1007/s00442-021-04975-y>.
- Crochard, L., Julliard, R., Gaba, S., Bretagnolle, V., Baude, M., Fontaine, C., 2022. Weeds from non-flowering crops as potential contributors to oilseed rape pollination. *Agric., Ecosyst. Environ.* 336, 108026. <https://doi.org/10.1016/j.agee.2022.108026>.
- Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. *Inter. Complex Syst.* 1695.
- Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: an R package for fitting distributions. *J. Stat. Softw.* 64. <https://doi.org/10.18637/jss.v064.i04>.
- Diekötter, T., Kadoya, T., Peter, F., Wolters, V., Jauker, F., 2010. Oilseed rape crops distort plant–pollinator interactions. *J. Appl. Ecol.* 47, 209–214. <https://doi.org/10.1111/j.1365-2664.2009.01759.x>.
- Dormann, C.F., Frund, J., Blüthgen, N., Gruber, B., 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *TOECOL* 2, 7–24. <https://doi.org/10.2174/1874213000902010007>.
- Duchenne, F., Wüest, R.O., Graham, C.H., 2022. Seasonal structure of interactions enhances multidimensional stability of mutualistic networks. *Proc. R. Soc. B: Biol. Sci.* 289. <https://doi.org/10.1098/rspb.2022.0064>.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes: heterogeneity and biodiversity. *Ecol. Lett.* 14, 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>.
- Falk, S.J., Lewington, R., 2015. *Field Guide to the Bees of Great Britain and Ireland, First ed.* Bloomsbury British Wildlife Field Guides. British Wildlife Publishing, London.
- Ferreira, P.A., Boscolo, D., Viana, B.F., 2013. What do we know about the effects of landscape changes on plant–pollinator interaction networks? *Ecol. Indic.* 31, 35–40. <https://doi.org/10.1016/j.ecolind.2012.07.025>.
- Fontaine, C., Thébault, E., Dajoz, I., 2009. Are insect pollinators more generalist than insect herbivores? *Proc. R. Soc. B: Biol. Sci.* 276, 3027–3033. <https://doi.org/10.1098/rspb.2009.0635>.
- Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., Poulin, R., Bascompte, J., 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? *J. Anim. Ecol.* 79, 811–817. <https://doi.org/10.1111/j.1365-2656.2010.01688.x>.
- Frankie, G.W., Thorp, R.W., Hernandez, J., Rizzardi, M., Ertter, B., Pawelek, J.C., Witt, S.L., Schindler, M., Coville, R., Wojcik, V.A., 2009. Native bees are a rich natural resource in urban California gardens. *Calif. Agric.* 63, 113–120. <https://doi.org/10.3733/ca.v063n03p113>.
- Gaba, S., Bretagnolle, V., 2021. Designing multifunctional and resilient agricultural landscapes: lessons from long-term monitoring of biodiversity and land use. In: Hurford, C., Wilson, P., Storkey, J. (Eds.), *The Changing Status of Arable Habitats in Europe*. Springer International Publishing, Cham, pp. 203–224. https://doi.org/10.1007/978-3-030-59875-4_14.
- Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E., Vereecken, N.J., 2017. Massively introduced managed species and their consequences for plant–pollinator interactions. *Adv. Ecol. Res.* 57, 147–199. <https://doi.org/10.1016/bs.aecr.2016.10.007>.
- Giannini, T.C., Garibaldi, L.A., Acosta, A.L., Silva, J.S., Maia, K.P., Saraiva, A.M., Guimarães, P.R., Kleinert, A.M.P., 2015. Native and non-native supergeneralist bee species have different effects on plant–bee networks. *PLoS One* 10, e0137198. <https://doi.org/10.1371/journal.pone.0137198>.
- Gillespie, C.S., 2015. Fitting heavy tailed distributions: The powerLaw package. *J. Stat. Soft.* 64. <https://doi.org/10.18637/jss.v064.i02>.
- Habel, J.C., Ulrich, W., Biburger, N., Seibold, S., Schmitt, T., 2019. Agricultural intensification drives butterfly decline. *Insect Conserv. Divers.* 12343. <https://doi.org/10.1111/icad.12343>.
- Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed metacommunity dynamics in farmland landscapes. *Proc. R. Soc. B: Biol. Sci.* 282, 20150002. <https://doi.org/10.1098/rspb.2015.0002>.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press.
- Jauker, F., Wolters, V., 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156, 819–823. <https://doi.org/10.1007/s00442-008-1034-x>.
- Jordano, P., 2016. Sampling networks of ecological interactions. *Funct. Ecol.* 30, 1883–1893. <https://doi.org/10.1111/1365-2435.12763>.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kones, J.K., Soetaert, K., Van Oevelen, D., Owino, J., 2009. Are network indices robust indicators of food web functioning? a Monte Carlo approach. *Ecol. Model.* 370–382. <https://doi.org/10.1016/j.ecolmodel.2008.10.012>.
- Kovács-Hostyánszki, A., Földesi, R., Báldi, A., Endrédi, A., Jordán, F., 2019. The vulnerability of plant–pollinator communities to honeybee decline: a comparative network analysis in different habitat types. *Ecol. Indic.* 97, 35–50. <https://doi.org/10.1016/j.ecolind.2018.09.047>.
- Landi, P., Minoarivelo, H.O., Brännström, Å., Hui, C., Dieckmann, U., 2018. Complexity and stability of ecological networks: a review of the theory. *Popul. Ecol.* 60, 319–345. <https://doi.org/10.1007/s10144-018-0628-3>.
- Lázaro, A., Müller, A., Ebmer, A.W., Dathe, H.H., Scheuchl, E., Schwarz, M., Risch, S., Pauly, A., Devalez, J., Tscheulin, T., Gómez-Martínez, C., Papas, E., Pickering, J., Waser, N.M., Petanidou, T., 2021. Impacts of beekeeping on wild bee diversity and pollination networks in the Aegean Archipelago. *Ecography* 44, 1353–1365. <https://doi.org/10.1111/ecog.05553>.
- Le Féon, V., Burel, F., Chifflet, R., Henry, M., Ricroch, A., Vaissière, B.E., Baudry, J., 2013. Solitary bee abundance and species richness in dynamic agricultural landscapes. *Agric., Ecosyst. Environ.* 166, 94–101. <https://doi.org/10.1016/j.agee.2011.06.020>.
- Liao, J., Bearup, D., Strona, G., 2022. A patch-dynamic metacommunity perspective on the persistence of mutualistic and antagonistic. *Ecology* 103. <https://doi.org/10.1002/ecy.3686>.
- Ma, A., Lu, X., Gray, C., Raybould, A., Tamadoni-Nezhad, A., Woodward, G., Bohan, D.A., 2019. Ecological networks reveal resilience of agro-ecosystems to changes in farming management. *Nat. Ecol. Evol.* 3, 260–264. <https://doi.org/10.1038/s41559-018-0757-2>.
- Magrath, A., Holzschuh, A., Bartomeus, I., Riedinger, V., Roberts, S.P.M., Rundlof, M., Vujic, A., Wickens, J.B., Wickens, V.J., Bommarco, R., Gonzalez-Varo, J.P., Potts, S.G., Smith, H.G., Steffan-Dewenter, I., Vila, M., 2018. Plant–pollinator networks in semi-natural grasslands are resistant to the loss of pollinators during blooming of mass-flowering crops. *Ecography* 41, 62–74. <https://doi.org/10.1111/ecog.02847>.

- Magurran, A.E., 2005. Species abundance distributions: pattern or process? *Funct. Ecol.* 19, 177–181. <https://doi.org/10.1111/j.0269-8463.2005.00930.x>.
- de Manincor, N., Hautekèete, N., Mazoyer, C., Moreau, P., Piquot, Y., Schatz, B., Schmitt, E., Zélazny, M., Massol, F., 2020. How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based representations of the same networks. *Acta Oecologica* 105, 103551. <https://doi.org/10.1016/j.actao.2020.103551>.
- Mathiasson, M.E., Rehan, S.M., 2020. Wild bee declines linked to plant-pollinator network changes and plant species introductions. *Insect Conserv. Divers.* 13, 595–605. <https://doi.org/10.1111/icad.12429>.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B* 271, 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>.
- Morrison, B.M.L., Brosi, B.J., Dirzo, R., 2020. Agricultural intensification drives changes in hybrid network robustness by modifying network structure. *Ecol. Lett.* 23, 359–369. <https://doi.org/10.1111/ele.13440>.
- Munoz, F., Fried, G., Armengot, L., Bourgeois, B., Bretagnolle, V., Chadouef, J., Mahaut, L., Plumejeaud, C., Storkey, J., Violle, C., Gaba, S., 2020. Ecological specialization and rarity of arable weeds: insights from a comprehensive survey in France. *Plants* 9, 824. <https://doi.org/10.3390/plants9070824>.
- Odoux, J.-F., Aupinel, P., Gateff, S., Requier, F., Henry, M., Bretagnolle, V., 2014. ECOBEE: a tool for long-term honey bee colony monitoring at the landscape scale in West European intensive agroecosystems. *J. Apic. Res.* 53, 57–66. <https://doi.org/10.3896/IBRA.1.53.1.05>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. *vegan: Community Ecology Package*. R package version 2.5–7. (<https://CRAN.R-project.org/package=vegan>).
- Okuyama, T., Holland, J.N., 2008. Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.* 11, 208–216. <https://doi.org/10.1111/j.1461-0248.2007.01137.x>.
- Olesen, J.M., Stefanescu, C., Traveset, A., 2011. Strong, long-term temporal dynamics of an ecological network. *PLoS ONE* 6, e26455. <https://doi.org/10.1371/journal.pone.0026455>.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018. Bees increase oilseed rape yield under real field conditions. *Agric., Ecosyst. Environ.* 266, 39–48. <https://doi.org/10.1016/j.agee.2018.07.020>.
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Saintilan, A., Bretagnolle, V., 2019. Experimental quantification of insect pollination on sunflower yield, reconciling plant and field scale estimates. *Basic Appl. Ecol.* 34, 75–84. <https://doi.org/10.1016/j.baee.2018.09.005>.
- Perrot, T., Bretagnolle, V., Gaba, S., 2022. Environmentally friendly landscape management improves oilseed rape yields by increasing pollinators and reducing pests. *J. Appl. Ecol.* 59, 1825–1836. <https://doi.org/10.1111/1365-2664.14190>.
- Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P., Pantis, J.D., 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization: high plasticity in plant-pollinator networks. *Ecol. Lett.* 11, 564–575. <https://doi.org/10.1111/j.1461-0248.2008.01170.x>.
- Ponisio, L.C., Gaiarsa, M.P., Kremen, C., 2017. Opportunistic attachment assembles plant-pollinator networks. *Ecol. Lett.* 20, 1261–1272. <https://doi.org/10.1111/ele.12821>.
- R Core Team, 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (URL). (<https://www.R-project.org/>).
- Requier, F., Odoux, J.-F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., Bretagnolle, V., 2015. Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecol. Appl.* 25, 881–890. <https://doi.org/10.1890/14-1011.1>.
- Requier, F., Odoux, J.-F., Henry, M., Bretagnolle, V., 2017. The carry-over effects of pollen shortage decrease the survival of honeybee colonies in farmlands. *J. Appl. Ecol.* 54, 1161–1170. <https://doi.org/10.1111/1365-2664.12836>.
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., 2015. Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96, 1351–1360. <https://doi.org/10.1890/14-1124.1>.
- Rollin, O., 2013. *Etude multi-échelle du patron de diversité des abeilles et utilisation des ressources fleuries dans un agrosystème intensif*. Université d'Avignon, Avignon.
- Rollin, O., Garibaldi, L.A., 2019. Impacts of honeybee density on crop yield: a meta-analysis. *J. Appl. Ecol.* 56, 1152–1163. <https://doi.org/10.1111/1365-2664.13355>.
- Rollin, O., Benelli, G., Benvenuti, S., Decourtye, A., Wratten, S.D., Canale, A., Desneux, N., 2016. Weed-insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review. *Agron. Sustain. Dev.* 36, 8. <https://doi.org/10.1007/s13593-015-0342-x>.
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>.
- Sirami, C., Gross, N., Bailod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguët, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-García, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tschamtké, T., Bretagnolle, V., Siriwardena, G., Quin, A., Brotons, L., Martin, J.-L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.* 116, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>.
- Stanley, D.A., Stout, J.C., 2014. Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination. *Plant Ecol.* 215, 315–325. <https://doi.org/10.1007/s11258-014-0301-7>.
- Stanley, D.A., Gunning, D., Stout, J.C., 2013. Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: ecological and economic incentives for pollinator conservation. *J. Insect Conserv.* 17, 1181–1189. <https://doi.org/10.1007/s10841-013-9599-z>.
- Thébault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856. <https://doi.org/10.1126/science.1188321>.
- Thompson, A., Ștefan, V., Knight, T.M., 2021. Oilseed rape shares abundant and generalized pollinators with its co-flowering plant species. *Insects* 12, 1096. <https://doi.org/10.3390/insects12121096>.
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585–1596. <https://doi.org/10.1111/1365-2664.13403>.
- Valdovinos, F.S., 2019. Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.* 22, 1517–1534. <https://doi.org/10.1111/ele.13279>.
- Valido, A., Rodríguez-Rodríguez, M.C., Jordano, P., 2019. Honeybees disrupt the structure and functionality of plant-pollinator networks. *Sci. Rep.* 9, 4711. <https://doi.org/10.1038/s41598-019-41271-5>.