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Weeds from non-flowering crops as potential contributors to oilseed rape pollination

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ABSTRACT

Pollination is essential for many crops since 70% of the world's cultivated plants depend on pollinators for their production. Floral resources within cultivated areas, especially those produced by flowering crops such as oilseed rape, are known to have a positive effect on wild pollinators. Nevertheless, little is known about the contribution of other floral resources, such as weeds within cultivated areas, in supporting wild pollinator communities and subsequent pollination services. Here, we investigate the extent to which oilseed rape pollination benefits from floral resources produced within cultivated areas, either crops or associated weeds. Based on the Müller index, we analyzed, during four pairs of consecutive years, the potential for inter-annual indirect effects received by oilseed rape through shared wild pollinators from major crops, and their associated weeds, in a typical French intensive agricultural landscape. Our results show that most of the support for oilseed rape pollinating fauna came from alternative types of floral resources than itself. We also find that weeds support oilseed rape pollination as much as flowering crops. Finally, we show that weeds growing within cereal fields have a major contribution to the support of oilseed rape pollination, exceeding the contribution of other floral resources, except oilseed rape. Our results underline that oilseed rape pollination benefits from floral resources present within cultivated fields, whatever the type of crops, including those that do not depend on pollinators for their pollination. Management practices like herbicide reduction in non-pollinator-dependent crops such as cereals are thus likely to impact the pollination of pollinator-dependent crops.

1. Introduction

Animal pollination is essential for human food production. 70% of major global food crops are affected by pollinators and these crops represent approximately 35% of annual global food production (Klein et al., 2007). Growing human demand for pollinator-dependent crops, reflected in a disproportionate increase in the area of cultivated pollinator-dependent crops since the 1960's (Aizen et al., 2008), has led to global agricultural production becoming increasingly dependent on pollinators and vulnerable to their decline. This decline, caused by several local and global drivers (Biesmeijer et al., 2006; Potts et al., 2010), impairs the ecosystem service of pollination (Garibaldi et al., 2013; Hoehn et al., 2008; Steffan-Dewenter et al., 2005).

The diet of pollinators mainly consists of pollen and nectar. In agricultural landscapes, these resources come from different sources, including hedgerows and woodlands (Timberlake et al., 2019), arable weeds (Bretagnolle and Gaba, 2015) and mass flowering crops (e.g., oilseed rape, sunflower, or alfalfa), the latter providing pulses of resource in large quantities for a short period (Westphal et al., 2003). Since the amount of collected resources is likely to affect the reproduction success of pollinators (Beyer et al., 2021; Riedinger et al., 2015; Timberlake et al., 2020; Van der Meersch et al., 2021), the availability of

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appropriate floral resources during their flight periods can influence their presence and abundance the following year. The pollination services delivered to a crop can therefore be influenced by the floral resources collected in the previous year by the crop's pollinator species. Such indirect facilitation of crop pollination services by other floral resources, flowering in the same year as crops, has been shown with the pollinating fauna of sunflowers benefiting from weeds (Carvalheiro et al., 2011), with apple orchards supporting the pollination services of strawberries (Grab et al., 2017) and might partly explain the positive effect of semi-natural habitats within farmlands on crop pollination services (Bommarco et al., 2012; Shaw et al., 2020; Woodcock et al., 2013; Andersson et al., 2014; Garibaldi et al., 2011; Holzschuh et al., 2012; Kennedy et al., 2013). However, the relative contribution of the various floral resources present in agricultural landscapes to support the pollinating fauna of pollinator-dependent crops remains unknown. Here, the various floral resources could be assimilated into the different crops or the weeds communities associated with each crop.

The Müller index (Müller et al., 1999) aims to quantify the potential for indirect effects from one species to another via shared interacting species. Originally developed for host-parasitoid interactions, this index has previously been used in the pollinator context to assess the potential for indirect effects among flowering plants via shared pollinators (Bergamo et al., 2017; Carvalheiro et al., 2014). For two plants and a shared pollinator, this index quantifies the potential for indirect interaction of one plant to the other and is calculated as the contribution of the first plant to the pollinator's diet multiplied by the contribution of the pollinator to the pollination of the second plant. In the context of pollination services in agricultural landscapes, summing this index over all pollinator species of a crop allow the relative contribution of the different floral resources needed to deliver pollination services to the crop to be quantified. While this index is usually calculated between co-flowering species, here we propose to address inter-annual indirect interactions from floral resources in a given year to the pollination of a crop the following year. Indeed, most insect pollinators have annual life cycles, with the floral resources available during a year influencing the abundance and composition of the pollinator community the following year. For instance, Timberlake et al. (2020) observed that farmland nectar supply during September is a strong predictor of *Bombus terrestris* colony density in the following year. Similarly, it was demonstrated that high coverage of mass flowering crops in past years could enhance wild bee densities (Beyer et al., 2021; Riedinger et al., 2015).

We aimed to quantify the contribution of the different floral resources present in an agricultural landscape to the potential for inter-annual indirect effects received by oilseed rape. For this, we used plant-pollinator interaction data collected between 2015 and 2019 in 494 fields from the Zone Atelier Plaine & Val de Sèvre, an area located in central-western France where agricultural practices and biodiversity is monitored (Bretagnolle et al., 2018a). Oilseed rape (*Brassica napus* L.) is a flowering crop cultivated for oil that is used for human consumption and biofuel production. Despite being mainly self-pollinated, Perrot et al., (2018) showed that in our study area, insect pollination improved oilseed rape yield by about 37% at the field scale. Nevertheless, there is considerable uncertainty in the estimates of this contribution with values ranging from 10% to 50%, depending on the cultivar studied or the yield parameter used (Araneda Durán et al., 2010; Bartomeus et al., 2014; Bommarco et al., 2012; Lindström et al., 2016; Stanley et al., 2013; Zou et al., 2017). In oilseed rape fields, honeybees (*Apis mellifera*) are usually found to be the most abundant flower-visiting insects (70–80%) followed by hoverflies (10–20%) and wild bees (5–10%) (Bartomeus et al., 2014; Bommarco et al., 2012; Zou et al., 2017; Perrot et al., 2018).

Using the Müller index, we compared the respective contributions of oilseed rape and the sum of the contribution of other floral resources to the potential inter-annual indirect effects received by oilseed rape, to find out whether most of the support comes from oilseed rape itself or from other resources. We then compared the contributions of weeds and crops to the effects received by oilseed rape. To know in more detail the identity of the floral resources producing the most potential for inter-annual indirect effects on oilseed rape, we further investigated the contribution of each floral resource to the potential inter-annual indirect effects received by oilseed rape. Finally, we discuss the respective contributions of cultivated areas, including crops and weeds, and semi-natural habitats to the potential inter-annual indirect effects received by oilseed rape.

2. Material and methods

2.1. Site description and fields selection

This study took place in the Long-Term Social-Ecological Research site "Zone Atelier Plaine & Val de Sèvre" located in South-West France. The study site was an area of 435 km^2, 87% of which was cultivated and split into 13,000 fields (Bretagnolle et al., 2018a). Oilseed rape represented on average 6.9% (from a minimum of 1.6% in 2019 to a maximum of 9.1% in 2016) of the cultivated area in the study site.

Each year, different fields were selected for pollinator sampling according to the method described by Bretagnolle et al. (2018a), (2018b). Within the study area, we selected each year, 40–60 landscape windows of 1 km^2, spaced at least 200 m apart, and distributed along gradients of semi-natural habitats, meadows, and organically farmed fields. We further follow the procedure described by Fahrig et al. (2011) to minimize inter-gradient correlations. These gradients were chosen because they are known to influence pollinators (Kennedy et al., 2013). Within each window, 3–4 fields growing different crops were selected for pollinator sampling, depending on the number of crops grown in the window. Here, we focused on the five main crops grown in the study site, namely: alfalfa, cereals (wheat and barley), meadows, oilseed rape and sunflower. These crops represented together approximately 70% of the area cultivated on the study site each year (Table S.A).

2.2. Sampling method

Pollinator sampling was performed annually, from 2015 to 2019. For each selected field, flower-visiting insects were sampled using sweep nets along three 50 m long and 5 m wide transects. The three transects were positioned at the edge, 20 m from the edge and the center of the field. In 2015 however, only transects at the edge and the center of the field were carried out. The sampling effort for each transect was standardized, lasting 10 min, not counting the time needed to process captured insects. Individuals that could not be identified directly during sampling were identified in the laboratory and each captured flower-visiting insect was assigned to the plant species on which it was collected.

As we were interested in the respective roles of crops and their associated weeds, we grouped the pollinator visits into eight different types of floral resources: oilseed rape, weeds located within oilseed rape fields, sunflower, weeds within sunflower fields, alfalfa, weeds within alfalfa fields, weeds within cereal fields, and weeds within meadows (see Table S.B for details about the weed species list associated with each crop). As no pollinators were collected on cereal crops or grasses from meadows during the sampling period, these plants were not considered as floral resources for pollinators in our study. Each year, the sampling period extended from April to August. For each crop and associated weeds, pollinators were captured during the flowering period of the crop. This sampling period extended from April to the end of May for oilseed rape, from mid-April to mid-August for alfalfa, from the end of June to mid-August for sunflower, from the end of April to the end of August for cereal, and from mid-May to mid-August for meadows.

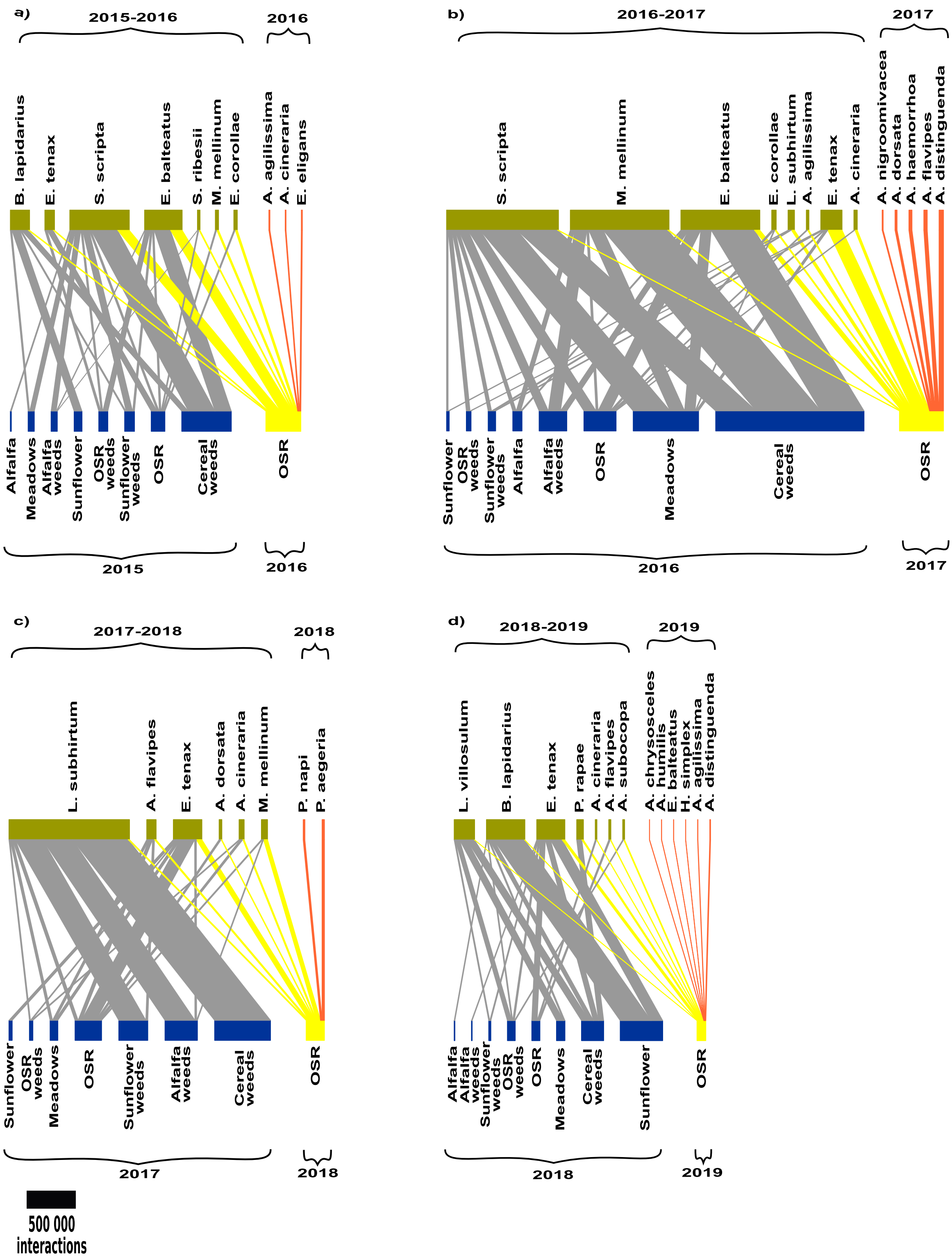

Fig. 1. Flower-visitor interaction network restricted to the pollinator species that were captured during the year n +1 on oilseed rape flowers accounting for the areas covered by each floral resource. The width of the links is proportional to the number of visits which corresponds to the intensity of the interactions between floral resources and pollinators, taking into account the areas covered by the different floral resources each year. The blue boxes correspond to the floral resource present in year n, while the green boxes correspond to the pollinators present in both year n and year n+1. The orange boxes correspond to pollinator species only present in year n+1 and the yellow box corresponds to the oilseed rape of year n+1. The grey links correspond to interactions between floral resources of year n and pollinator species of year n. The yellow links correspond to interactions of pollinators of year n+1 (already present the year n) on oilseed rape n+1. The orange links correspond to interactions between pollinator species only present in year n+1 and oilseed rape of year n+1.

2.3. Visitation frequencies per square meter of crop fields

The number of fields sampled per crop per year (Table S.C) was not representative of cultivated areas per crop and per year in our study site. This may result in an over- or underestimation of the effects of a floral resource relative to the area it covers in our study site. To account for that, for each crop and associated weeds, and each year, we first calculated the number of visits of each pollinator species relative to the total area of transects performed (number of the pollinator species visits per square meter). Second, variations in the sampling effort among crops and associated weeds for a given year affect the detection of the least abundant pollinator species, with an over-representation of these pollinator species in the most sampled crop fields. To avoid this bias, we defined a detectability threshold per year, which was equal to: one divided by the area sampled for the crop with the lower sampled area this year. For a given year, all pollinator species with a number of visits per square meter below this threshold were discarded from the analysis. This resulted in the exclusion of approximately 13% of individuals caught over the 5 years of our sampling (740 individuals out of 5815) corresponding to 61% of pollinator species (100 species out of 165).

2.4. Potential for inter-annual indirect effect from floral resources to oilseed rape pollination

We calculated the potential for inter-annual indirect effect from each floral resource to oilseed rape via shared pollinators, from one year to the next (Fig. 1, Fig. S.A), based on the Müller index (Müller et al., 1999) that we adapted for the inter-annual case.

This index is defined as the relative contribution of a floral resource in the diet of a pollinator, multiplied by the relative contribution of the pollinator in the pollination of a focal plant species (the following year, in our case). The contribution to the diet and the pollination is quantified by the number of flower visits. Summing this index over all pollinators shared between a floral resource and the focal plant gives the potential for indirect effect from the floral resource to the focal plant species. The formula is as follows:

$$d_{i_n,\ osr_{n+1}} = \sum_{k=1}^{l} \left(\frac{\alpha_{i_n,k} area_{i_n}}{\sum_{j=1}^{m} \alpha_{j_n,k} area_{j_n}} x \frac{\alpha_{osr_{n+1},k,} area_{osr_{n+1}}}{\sum_{k=1}^{l} \alpha_{osr_{n+1},k} area_{osr_{n+1}}} \right)$$

Where $d_{i_n,osr_{n+1}}$ is the value of the potential for the indirect effect of the floral resource i of the year n on oilseed rape (*osr*) of the year $n+1$ via shared pollinators. $\alpha_{i_n,k}$ is the number of visits of pollinators of the species k on floral resource i the year n per unit of area of the floral resource *i*. $area_{i_n}$ corresponds to the cultivated area of the floral resource i the year *n*. m and l correspond to all floral resource types and all pollinator species respectively. The first part of the equation corresponds to the proportion of floral resource i in the diet of the pollinator species k in year *n*. The second part of the equation corresponds to the proportion of pollinator visits performed by pollinator species k on oilseed rape crop in the year $n+1$. The potential for inter-annual indirect effect of each floral resource on oilseed rape was calculated by taking into account the area of each floral resource within the study site but also per unit area, i.e. with $area_{i_n} = 1$..

Honeybees *(Apis mellifera)* were excluded from the analysis because they should not propagate inter-annual indirect effects in the same way as wild pollinators. Indeed, changes in honeybee abundance from one year to the next might be more affected by beekeeping practices (e.g. winter feeding, colony displacement) than by the availability of floral resources. However, we also performed the analysis including honeybees as efficient pollinators of oilseed rape. In this case, the visits made by honeybees were taken into account in the second part of the equation, depicting their contribution to the pollination of oilseed rape, but not in the first part of the equation thereby not propagating inter-annual indirect effects. This did not change the results we present next. Only the strength of the indirect effects was modified by taking into account honeybees (Fig. S.B).

Table 1
Pollinator abundance per unit area (ha), species richness, and number of shared species with oilseed rape recorded over the 5 years of sampling for each floral resource.

Floral resource	Abundance per unit area	Species richness	Number of shared species with oilseed rape
Alfalfa	670	16	6
Weeds within alfalfa fields	1979	25	10
Weeds within cereal fields	867	19	10
Meadows	1626	31	10
Oilseed rape	707	25	
Weeds within oilseed rape fields	253	15	13
Sunflower	839	19	6
Weeds within sunflower fields	702	28	9

3. Results

3.1. Pollinators are shared among crops and weeds

During the five years of our study, and after applying the detectability threshold, 5075 wild pollinators from 65 species collected from floral resources were considered in subsequent analyses. Among them, 48.9% were Diptera, 44,9% were Hymenoptera and 6.2% were Lepidoptera. Meadows were the floral resource in which the most pollinator species were caught with 31 species (Table 1). Conversely, weeds growing in oilseed rape fields were the floral resource in which the fewest pollinator species were caught with 15 species. On oilseed rape flowers, 515 insects from 25 species were sampled, of which 9 (36%) were exclusively sampled on these flowers. Weeds growing in oilseed rape fields were the floral resource that shared the most pollinator species with oilseed rape flowers, with 13 species, while alfalfa and sunflower were the floral resources sharing the least pollinator species with oilseed rape, with only 6 species. The sharing of pollinators, that we observed, between oilseed rape and other floral resources indicates that there is a potential for indirect effects from these different floral resources on oilseed rape pollination.

3.2. The support of oilseed rape pollinators is mainly provided by floral resources other than oilseed rape

We found a significant difference when comparing the potential for inter-annual indirect effect produced by oilseed rape to the one

Table 2
Results of Student tests performed to study the difference of the potential for inter-annual indirect effects produced by oilseed rape and all other floral resources accounting for the relative areas covered by each floral resource and per unit area, and the difference of the potential for inter-annual indirect effects produced by crops and weeds accounting for the relative areas covered by each floral resource and per unit area.

Test	Scale	Df	T	P-value
Oilseed rape vs other floral resources	Accounting for the relative areas covered by each floral resource	6	2.78	0.032
Crop vs Weeds		6	-1.40	0.210
Oilseed rape vs other floral resources	Unit area	6	3.60	0.011
Crop vs Weeds		6	-1.75	0.132

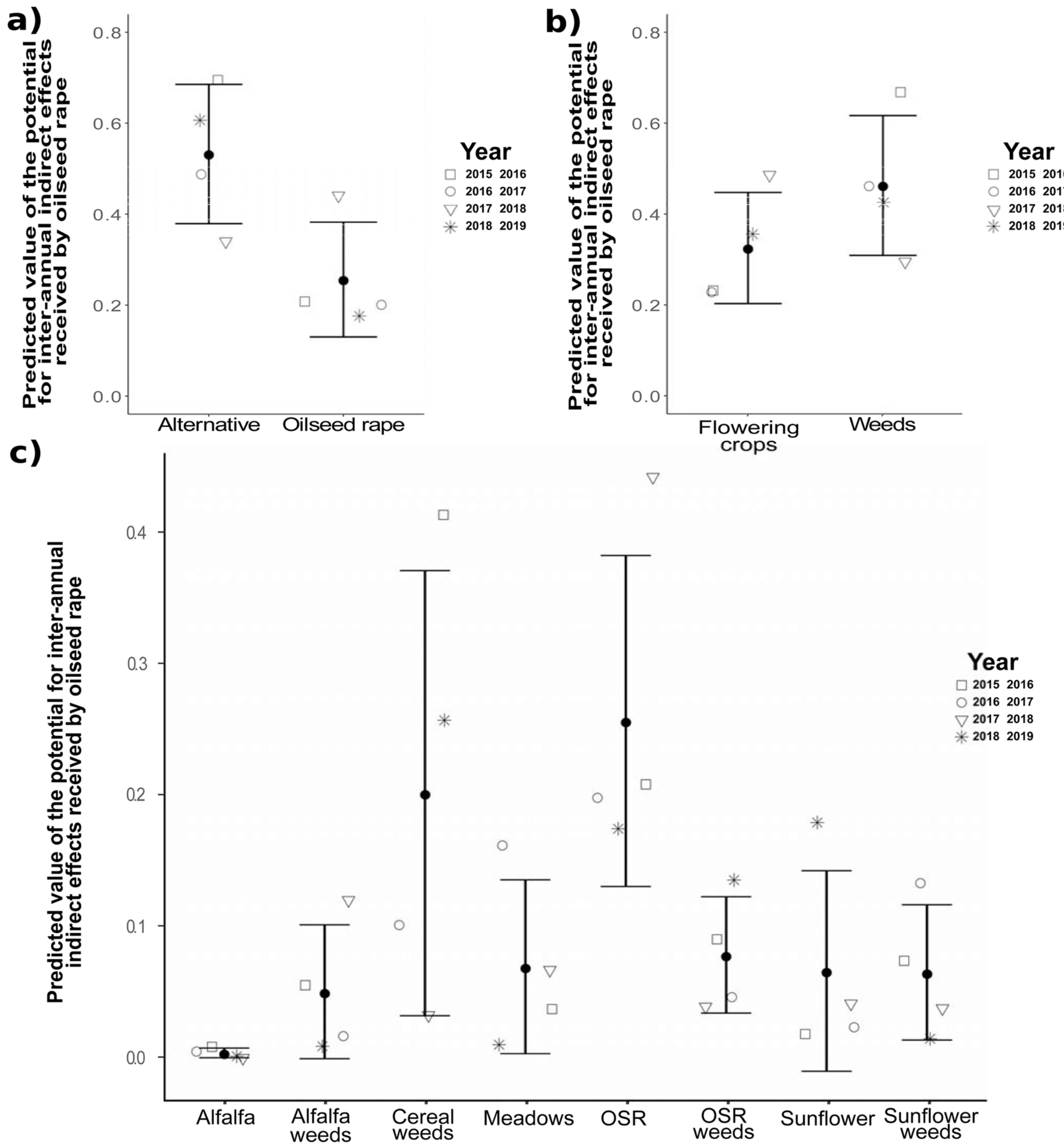

Fig. 2. Predicted values (mean ± 1 standard deviation) of the potential for inter-annual indirect effects received by oilseed rape flowers accounting for the relative areas covered by each floral resource: (a) oilseed rape alone vs the alternative types of floral resources together, (b) weeds vs crops and (c) each floral resource. The type « Alternative » corresponds to the sum of values of the potential for inter-annual indirect effects produced each year by all floral resources excepted oilseed rape. In each panel, points correspond to the predicted potential for inter-annual indirect effects calculated for each successive pair of years and the error bars to the estimated standard deviations. The different symbols correspond to the potential for inter-annual indirect effects calculated for each successive pair of years.

produced by all other floral resources taken together (Table 2). We found the same result when accounting for the areas covered by each floral resource and considering the potential for indirect interactions per unit area. Oilseed rape produced significantly less potential for inter-annual indirect effects (0.53 ± 0.15, mean ± standard deviation) than the other floral resources taken together (0.26 ± 0.13; Fig. 2a, Fig. S.C. a). This indicated that most of the support provided by floral resources within cultivated areas to the pollinating fauna of oilseed rape the following year came from alternative floral resources to oilseed rape.

3.3. The support of oilseed rape pollinators provided by weeds and flowering crops is equivalent

We did not detect a significant difference between the potential for inter-annual indirect effects produced by flowering crops (0.33 ± 0.12) and the one produced by the flowering weeds growing within crop fields (0.46 ± 0.15), although there was a tendency for a higher contribution of weeds. The same results were found when considering the potential for indirect interactions per unit of area and accounting for the areas covered by each floral resource (Table 2, Fig. 2b, Fig. S.C.b). This indicated that the contribution of weeds and flowering crops to feed oilseed rape pollinating fauna was not statistically different.

3.4. The dominance of cereal fields makes cereal weeds a key resource for oilseed rape pollinating fauna

We found a significant effect of the type of floral resource on the potential for inter-annual indirect effect received by oilseed rape whatever the type of calculation: per unit area (Chisq = 26.64, df = 7, $p = 3.87e\text{-}4$) and accounting for the areas covered by each floral resource (Chisq = 36.514, df = 7, $p < 0.0001$). Accounting for the areas of each floral resource, weeds growing in cereal fields (0.20 ± 0.17) and oilseed rape (0.26 ± 0.13) seemed to be the floral resource producing the strongest potential for inter-annual indirect effect compared to other floral resources (Fig. 2c). The other floral resources contributed approximately 3.5 times less to the pollination support of oilseed rape, except alfalfa with almost no potential for inter-annual indirect effect. Looking at the potential for inter-annual indirect effect per unit area, the pattern was different: only oilseed rape seemed to produce a higher potential for inter-annual indirect effect (0.26 ± 0.09) than the other floral resources (Fig. S.C.c). This suggests that when accounting for the areas of each floral resource, oilseed rape pollination mainly benefits from weeds growing within cereal fields and oilseed rape flowers.

4. Discussion

Our analysis brings evidence that pollinators are shared among flowering crops and also among flowering crops and associated weeds. By quantifying the potential for inter-annual indirect interactions on the pollination of oilseed rape in a typical French agricultural landscape, our results further indicate that the insect-pollination of oilseed rape is mainly supported by alternative floral resources. This reflects that the main part of the diet of oilseed rape pollinators was made of floral resources other than oilseed rape in the previous year (Fig. 1). Our results thereby suggest that the pollination services of oilseed rape is affected by other flowering crops as well as arable weeds, making crop fields, flowering or not, and associated weeds potential levers for enhancing pollination services in an agricultural landscape. This is further supported by recent results showing that crop diversity may have a positive effect on the densities of some wild pollinator species (Raderschall et al., 2021).

The contribution of arable weeds that we reported is equivalent to that of flowering crops, which is in line with other studies highlighting arable weeds as important resources for wild pollinators (Bretagnolle and Gaba, 2015; Carvalheiro et al., 2011; Holzschuh et al., 2007; Rollin et al., 2013). This result is even more striking as among the considered crops here, sunflower and oilseed rape, are mass flowering crops known to provide large amounts of food resources to pollinators and to favor wild pollinators in rapeseed fields (Holzschuh et al., 2013; Westphal et al., 2003). Further, the relative contribution of weeds and flowering crops we found might underestimate weeds' contribution as we only sampled pollinator visits during the crop flowering period, and we know that weed resources are particularly needed between crop flowering peaks (Timberlake et al., 2019).

Detailing the contribution among weeds, we found that weeds growing in cereal fields made a strong contribution to the inter-annual indirect effects on oilseed rape pollination, but this pattern vanished when considering the contribution per unit area. This indicated that their contribution was mainly due to the large area cereal fields represent in our study site, though such dominance of cereal fields is representative of cultivated areas at the scale of France or Europe (FAOSTAT, 2020). This contrasts with the view that cereals fields are irrelevant to pollinators because cereals are poor resources for pollinators (Roulston et al., 2000). Our study suggests that cereal weeds can substantially contribute to the floral resources supporting the pollination fauna of oilseed rape, and thereby its pollination services. This has consequences for both our understanding of the functioning of pollination services in agricultural landscapes and also of the agricultural practices related to pollination services. For instance, practices favoring flowering weeds, by limiting herbicides, whose positive effect on yields has not been clearly demonstrated unlike their negative effect on weed flora (Gaba et al., 2016), and limiting insecticides in cereal fields might benefit pollinators (Holzschuh et al., 2007) and pollination services of other crops. Cereal organic farming could have a positive impact on the pollination services of surrounding pollinator-dependant crops, since it promotes weed diversity in cultivated fields as well as in the margins of neighboring fields, even those grown conventionally (Henckel et al., 2015). Weeds may also compete for resources with crops, potentially lowering yield (Milberg and Hallgren, 2004). If so, innovative crop management such as reduced sowing density (Sidemo-Holm et al., 2021) or sowing competitive cultivars (Gaba et al., 2018) might be promoted.

In flowering crops, we found that oilseed rape was the crop that generated the most inter-annual indirect interactions on itself, both per unit area and taking into account the areas of each floral resource. This is in accordance with previous results showing that the potential influence of one plant on another via shared pollinators increases when plants are phylogenetically close (Carvalheiro et al., 2014).

One key limitation of our study is that we did not sample pollinator visits in semi-natural habitats, preventing us from quantifying their contribution. There is strong evidence that the visitation frequency of flowering crops by wild pollinators and their diversity are positively linked to the proximity to semi-natural habitats (Carvalheiro et al., 2010; Garibaldi et al., 2011; Klein et al., 2012; Ricketts et al., 2008). In addition to nesting sites, semi-natural areas provide floral resources to wild pollinators in agricultural landscapes (Rollin et al., 2013; Woodcock et al., 2013). Therefore the strength of the potential for inter-annual indirect effects received by oilseed rape from cultivated areas could be weaker than the one we estimated here if we included the floral resources provided by these habitats in the analysis. Although nectar production from semi-natural habitats is likely to be higher than from cultivated areas (Baude et al., 2016), the area of semi-natural habitats in our study site relative to one of the crop fields suggests that the contribution of cultivated areas should remain higher than the one of semi-natural habitat (Appendix A). However, some more work is needed to compare the contribution of cultivated areas to one of semi-natural areas, for example accounting for the contribution of semi-natural habitats to other key resources, such as nesting sites (Lye et al., 2009; Nayak et al., 2015).

Another simplifying assumption of our approach is that all visits are considered equivalent in terms of resources for pollinators and pollination efficiency. Yet it is well known that flowers from different species differ in quantity and quality of resources they provide to pollinators (Baude et al., 2016; Pamminger et al., 2019). Even within crop species, cultivars are not equivalent in the resources they provided (Ouvrard and Jacquemart, 2019). Similarly, the pollination efficiency of one oilseed rape visit depends on the identity of the visiting species (Garibaldi et al., 2011; Jauker et al., 2012; Kremen et al., 2002; Rader et al., 2016). Accounting for such differences in our framework is possible by weighting visits by the benefit they provide but would require more data on pollination efficiency (but see: Woodcock et al., 2013) and nectar production than currently available.

5. Conclusion

Our results suggest that cultivated areas support oilseed rape pollination by wild pollinators. To promote the pollination of a given crop, it is therefore necessary to consider the whole cultivated area and not only the one where the crop of interest is grown. Our results indicate that it is also essential to promote associated weeds of crops located in the vicinity of the crop of interest. This could be an interesting lever to improve pollination services. Finally, our analysis also suggests that agricultural practices favoring the presence of weed flora, even in pollinator independent crops like cereals, are beneficial for pollination services.

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 doi:10.1016/j.agee.2022.108026.

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