



**HAL**  
open science

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

Ludovic Crochard, Romain Julliard, Sabrina Gaba, Vincent Bretagnolle,  
Mathilde Baude, Colin Fontaine

► **To cite this version:**

Ludovic Crochard, Romain Julliard, Sabrina Gaba, Vincent Bretagnolle, Mathilde Baude, et al.. Weeds from non-flowering crops as potential contributors to oilseed rape pollination. Agriculture, Ecosystems & Environment, 2022, 336, pp.108026. 10.1016/j.agee.2022.108026 . hal-03684441

**HAL Id: hal-03684441**

**<https://hal.science/hal-03684441>**

Submitted on 22 Jul 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

2 Ludovic Crochard <sup>a</sup>, Romain Julliard <sup>a</sup>, Sabrina Gaba <sup>b,d</sup>, Vincent Bretagnolle <sup>c,d</sup>, Mathilde Baude<sup>e,f,\*</sup>,

3 Colin Fontaine <sup>a,\*</sup>

4 <sup>a</sup> Centre d'Ecologie et des Sciences de la Conservation, UMR 7204 MNHN-CNRS-Sorbonne Université,  
5 Muséum national d'Histoire naturelle, F-75005, Paris, France

6 <sup>b</sup> INRAE, USC 1339, Centre d'Etudes Biologiques de Chizé, F-79360 Villiers-en-Bois, France

7 <sup>c</sup> CNRS, Université de La Rochelle, UMR 7372, Centre d'Etudes Biologiques de Chizé, F-79360  
8 Beauvoir-sur-Niort, France

9 <sup>d</sup> LTSER "Zone Atelier Plaine & Val de Sèvre", CNRS, Beauvoir-sur-Niort, France

10 <sup>e</sup> Université d'Orléans, EA 1207 LBLGC, F-45067 Orléans, France

11 <sup>f</sup> Current address: Institute of Ecology and Environmental Sciences-Paris (iEES-Paris), Sorbonne  
12 Université, CNRS, IRD, INRAE, Université Paris Cité, UPEC, Paris, France

13 \* Contributed equally

14

15

16

17

18

19

20 Ludovic Crochard

21 43 rue Buffon – Campus Buffon

22 3 allée des Crapauds – Bât 135

23 CESCO – UMR 7204

24 75005 Paris

25 ludovic.crochard@edu.mnhn.fr

26 **Abstract**

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

44

45 **Keywords:** agricultural landscape, floral resources, indirect interactions, Müller index, plant-pollinator  
46 networks, wild pollinators

47 **1. Introduction**

48 Animal pollination is essential for human food production. 70% of major global food crops are affected  
49 by pollinators and these crops represent approximately 35% of annual global food production (Klein et  
50 al., 2007). Growing human demand for pollinator-dependent crops, reflected in a disproportionate  
51 increase in the area of cultivated pollinator-dependent crops since the 1960s (Aizen et al., 2008), has led  
52 to global agricultural production becoming increasingly dependent on pollinators and vulnerable to their  
53 decline. This decline, caused by several local and global drivers (Biesmeijer et al., 2006; Potts et al.,  
54 2010), impairs the ecosystem service of pollination (Garibaldi et al., 2013; Hoehn et al., 2008; Steffan-  
55 Dewenter et al., 2005).

56 The diet of pollinators mainly consists of pollen and nectar. In agricultural landscapes, these  
57 resources come from different sources, including hedgerows and woodlands (Timberlake et al., 2019),  
58 arable weeds (Bretagnolle and Gaba, 2015) and mass flowering crops (e.g., oilseed rape, sunflower, or  
59 alfalfa), the latter providing pulses of resource in large quantities for a short period (Westphal et al.,  
60 2003). Since the amount of collected resources is likely to affect the reproduction success of pollinators  
61 (Beyer et al., 2021; Riedinger et al., 2015; Timberlake et al., 2020; Van der Meersch et al., 2021), the  
62 availability of appropriate floral resources during their flight periods can influence their presence and  
63 abundance the following year. The pollination services delivered to a crop can therefore be influenced by  
64 the floral resources collected in the previous year by the crop's pollinator species. Such indirect  
65 facilitation of crop pollination services by other floral resources, flowering in the same year as crops, has  
66 been shown with the pollinating fauna of sunflowers benefiting from weeds (Carvalho et al., 2011),  
67 with apple orchards supporting the pollination services of strawberries (Grab et al., 2017) and might  
68 partly explain the positive effect of semi-natural habitats within farmlands on crop pollination services  
69 (Bommarco et al., 2012; Shaw et al., 2020; Woodcock et al., 2013; Andersson et al., 2014; Garibaldi et  
70 al., 2011; Holzschuh et al., 2012; Kennedy et al., 2013). However, the relative contribution of the various  
71 floral resources present in agricultural landscapes to support the pollinating fauna of pollinator-dependent

72 crops remains unknown. Here, the various floral resources could be assimilated into the different crops or  
73 the weeds communities associated with each crop.

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

91 We aimed to quantify the contribution of the different floral resources present in an agricultural  
92 landscape to the potential for inter-annual indirect effects received by oilseed rape. For this, we used  
93 plant-pollinator interaction data collected between 2015 and 2019 in 494 fields from the Zone Atelier  
94 Plaine & Val de Sèvre, an area located in central-western France where agricultural practices and  
95 biodiversity is monitored (Bretagnolle et al., 2018a). Oilseed rape (*Brassica napus* L.) is a flowering crop  
96 cultivated for oil that is used for human consumption and biofuel production. Despite being mainly self-  
97 pollinated, Perrot et al., (2018) showed that in our study area, insect pollination improved oilseed rape

98 yield by about 37% at the field scale. Nevertheless, there is considerable uncertainty in the estimates of  
99 this contribution with values ranging from 10 to 50%, depending on the cultivar studied or the yield  
100 parameter used (Araneda Durán et al., 2010; Bartomeus et al., 2014; Bommarco et al., 2012; Lindström et  
101 al., 2016; Stanley et al., 2013; Zou et al., 2017). In oilseed rape fields, honeybees (*Apis mellifera*) are  
102 usually found to be the most abundant flower-visiting insects (70-80%) followed by hoverflies (10-20%)  
103 and wild bees (5-10%) (Bartomeus et al., 2014; Bommarco et al., 2012; Zou et al. 2017; Perrot et al.,  
104 2018).

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

114

## 115 **2. Material and methods**

### 116 **2.1 Site description and fields selection**

117           This study took place in the Long-Term Social-Ecological Research site “Zone Atelier Plaine & Val  
118 de Sèvre” located in South-West France. The study site was an area of 435km<sup>2</sup>, 87% of which was  
119 cultivated and split into 13000 fields (Bretagnolle et al., 2018a). Oilseed rape represented on average  
120 6.9% (from a minimum of 1.6% in 2019 to a maximum of 9.1% in 2016) of the cultivated area in the  
121 study site.

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

132

## 133 **2.2 Sampling method**

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

141 As we were interested in the respective roles of crops and their associated weeds, we grouped the  
142 pollinator visits into eight different types of floral resources: oilseed rape, weeds located within oilseed  
143 rape fields, sunflower, weeds within sunflower fields, alfalfa, weeds within alfalfa fields, weeds within  
144 cereal fields, and weeds within meadows (see Table B for details about the weed species list associated  
145 with each crop). As no pollinators were collected on cereal crops or grasses from meadows during the  
146 sampling period, these plants were not considered as floral resources for pollinators in our study. Each

147 year, the sampling period extended from April to August. For each crop and associated weeds, pollinators  
148 were captured during the flowering period of the crop. This sampling period extended from April to the  
149 end of May for oilseed rape, from mid-April to mid-August for alfalfa, from the end of June to mid-  
150 August for sunflower, from the end of April to the end of August for cereal, and from mid-May to mid-  
151 August for meadows.

152

### 153 **2.3 Visitation frequencies per square meter of crop fields**

154 The number of fields sampled per crop per year (Table C) was not representative of cultivated areas  
155 per crop and per year in our study site. This may result in an over- or underestimation of the effects of a  
156 floral resource relative to the area it covers in our study site. To account for that, for each crop and  
157 associated weeds, and each year, we first calculated the number of visits of each pollinator species  
158 relative to the total area of transects performed (number of the pollinator species visits per square meter).  
159 Second, variations in the sampling effort among crops and associated weeds for a given year affect the  
160 detection of the least abundant pollinator species, with an over-representation of these pollinator species  
161 in the most sampled crop fields. To avoid this bias, we defined a detectability threshold per year, which  
162 was equal to: one divided by the area sampled for the crop with the lower sampled area this year. For a  
163 given year, all pollinator species with a number of visits per square meter below this threshold were  
164 discarded from the analysis. This resulted in the exclusion of approximately 13% of individuals caught  
165 over the 5 years of our sampling (740 individuals out of 5815) corresponding to 61% of pollinator species  
166 (100 species out of 165).

167

### 168 **2.4 Potential for inter-annual indirect effect from floral resources to oilseed rape pollination**



169 We calculated the potential for inter-annual indirect effect from each floral resource to oilseed rape  
 170 via shared pollinators, from one year to the next (Fig.1, Fig.A), based on the Müller index (Müller et al.,  
 171 1999) that we adapted for the inter-annual case.

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

$$178 \quad d_{i_n,osr_{n+1}} = \sum_{k=1}^l \left( \frac{\alpha_{i_n,k} area_{i_n}}{\sum_{j=1}^m \alpha_{j_n,k} area_{j_n}} \times \frac{\alpha_{osr_{n+1},k} area_{osr_{n+1}}}{\sum_{k=1}^l \alpha_{osr_{n+1},k} area_{osr_{n+1}}} \right)$$

179 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  
 180  $n$  on oilseed rape ( $osr$ ) of the year  $n + 1$  via shared pollinators.  $\alpha_{i_n,k}$  is the number of visits of pollinators  
 181 of the species  $k$  on floral resource  $i$  the year  $n$  per unit of area of the floral resource  $i$ .  $area_{i_n}$  corresponds  
 182 to the cultivated area of the floral resource  $i$  the year  $n$ .  $m$  and  $l$  correspond to all floral resource types and  
 183 all pollinator species respectively. The first part of the equation corresponds to the proportion of floral  
 184 resource  $i$  in the diet of the pollinator species  $k$  in year  $n$ . The second part of the equation corresponds to  
 185 the proportion of pollinator visits performed by pollinator species  $k$  on oilseed rape crop in the year  $n +$   
 186  $1$ . The potential for inter-annual indirect effect of each floral resource on oilseed rape was calculated by  
 187 taking into account the area of each floral resource within the study site but also per unit area, i.e. with  
 188  $area_{i_n} = 1$ .

189 Honeybees (*Apis mellifera*) were excluded from the analysis because they should not propagate inter-  
 190 annual indirect effects in the same way as wild pollinators. Indeed, changes in honeybee abundance from  
 191 one year to the next might be more affected by beekeeping practices (e.g. winter feeding, colony

192 displacement) than by the availability of floral resources. However, we also performed the analysis  
193 including honeybees as efficient pollinators of oilseed rape. In this case, the visits made by honeybees  
194 were taken into account in the second part of the equation, depicting their contribution to the pollination  
195 of oilseed rape, but not in the first part of the equation thereby not propagating inter-annual indirect  
196 effects. This did not change the results we present next. Only the strength of the indirect effects was  
197 modified by taking into account honeybees (Fig. B).

198

### 199 **3. Results**

#### 200 **3.1 Pollinators are shared among crops and weeds**

201 During the five years of our study, and after applying the detectability threshold, 5075 wild  
202 pollinators from 65 species collected from floral resources were considered in subsequent analyses.  
203 Among them, 48.9% were Diptera, 44.9% were Hymenoptera and 6.2% were Lepidoptera. Meadows  
204 were the floral resource in which the most pollinator species were caught with 31 species (Table 1).  
205 Conversely, weeds growing in oilseed rape fields were the floral resource in which the fewest pollinator  
206 species were caught with 15 species. On oilseed rape flowers, 515 insects from 25 species were sampled,  
207 of which 9 (36%) were exclusively sampled on these flowers. Weeds growing in oilseed rape fields were  
208 the floral resource that shared the most pollinator species with oilseed rape flowers, with 13 species, while  
209 alfalfa and sunflower were the floral resources sharing the least pollinator species with oilseed rape, with  
210 only 6 species. The sharing of pollinators, that we observed, between oilseed rape and other floral  
211 resources indicates that there is a potential for indirect effects from these different floral resources on  
212 oilseed rape pollination.

213

#### 214 **3.2 The support of oilseed rape pollinators is mainly provided by floral resources other than oilseed** 215 **rape**

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

224

### 225 **3.3 The support of oilseed rape pollinators provided by weeds and flowering crops is equivalent**

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

233

### 234 **3.4 The dominance of cereal fields makes cereal weeds a key resource for oilseed rape pollinating** 235 **fauna**

236 We found a significant effect of the type of floral resource on the potential for inter-annual  
237 indirect effect received by oilseed rape whatever the type of calculation: per unit area (Chisq = 26.64, df =  
238 7,  $p = 3.87e-4$ ) and accounting for the areas covered by each floral resource (Chisq = 36.514, df = 7,  $p$   
239  $< 0.0001$ ). Accounting for the areas of each floral resource, weeds growing in cereal fields ( $0.20 \pm 0.17$ )  
240 and oilseed rape ( $0.26 \pm 0.13$ ) seemed to be the floral resource producing the strongest potential for inter-  
241 annual indirect effect compared to other floral resources (Fig. 2c). The other floral resources contributed

242 approximately 3.5 times less to the pollination support of oilseed rape, except alfalfa with almost no  
243 potential for inter-annual indirect effect. Looking at the potential for inter-annual indirect effect per unit  
244 area, the pattern was different: only oilseed rape seemed to produce a higher potential for inter-annual  
245 indirect effect ( $0.26 \pm 0.09$ ) than the other floral resources (Fig. C.c). This suggests that when accounting  
246 for the areas of each floral resource, oilseed rape pollination mainly benefits from weeds growing within  
247 cereal fields and oilseed rape flowers.

#### 248 **4. Discussion**

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

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

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

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

291           One key limitation of our study is that we did not sample pollinator visits in semi-natural habitats,  
292 preventing us from quantifying their contribution. There is strong evidence that the visitation frequency of

293 flowering crops by wild pollinators and their diversity are positively linked to the proximity to semi-  
294 natural habitats (Carvalho et al., 2010; Garibaldi et al., 2011; Klein et al., 2012; Ricketts et al., 2008).  
295 In addition to nesting sites, semi-natural areas provide floral resources to wild pollinators in agricultural  
296 landscapes (Rollin et al., 2013; Woodcock et al., 2013). Therefore the strength of the potential for inter-  
297 annual indirect effects received by oilseed rape from cultivated areas could be weaker than the one we  
298 estimated here if we included the floral resources provided by these habitats in the analysis. Although  
299 nectar production from semi-natural habitats is likely to be higher than from cultivated areas (Baude et al.,  
300 2016), the area of semi-natural habitats in our study site relative to one of the crop fields suggests that the  
301 contribution of cultivated areas should remain higher than the one of semi-natural habitat (Appendix A).  
302 However, some more work is needed to compare the contribution of cultivated areas to one of semi-  
303 natural areas, for example accounting for the contribution of semi-natural habitats to other key resources,  
304 such as nesting sites (Lye et al., 2009; Nayak et al., 2015).

305 Another simplifying assumption of our approach is that all visits are considered equivalent in  
306 terms of resources for pollinators and pollination efficiency. Yet it is well known that flowers from  
307 different species differ in quantity and quality of resources they provide to pollinators (Baude et al., 2016;  
308 Pamminger et al., 2019). Even within crop species, cultivars are not equivalent in the resources they  
309 provided (Ouvrard and Jacquemart, 2019). Similarly, the pollination efficiency of one oilseed rape visit  
310 depends on the identity of the visiting species (Garibaldi et al., 2011; Jauker et al., 2012; Kremen et al.,  
311 2002; Rader et al., 2016). Accounting for such differences in our framework is possible by weighting  
312 visits by the benefit they provide but would require more data on pollination efficiency (but see:  
313 Woodcock et al., 2013) and nectar production than currently available.

## 314 **5. Conclusion**

315 Our results suggest that cultivated areas support oilseed rape pollination by wild pollinators. To  
316 promote the pollination of a given crop, it is therefore necessary to consider the whole cultivated area and  
317 not only the one where the crop of interest is grown. Our results indicate that it is also essential to  
318 promote associated weeds of crops located in the vicinity of the crop of interest. This could be an

319 interesting lever to improve pollination services. Finally, our analysis also suggests that agricultural  
320 practices favoring the presence of weed flora, even in pollinator independent crops like cereals, are  
321 beneficial for pollination services.

322

### 323 **Acknowledgments**

324 We would like to express our thanks to Alexis Saintilan and Marilyn Roncoroni for their help to fields  
325 sampling and for insect identification. This research was funded through the ANR IMAGHO (ANR-18-  
326 CE32-0002) and the Projet ‘Pollinisateurs’ from Ministry of Ecological Transition.

327

### 328 **References**

329 Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., Klein, A.M., 2008. Long-Term Global Trends in Crop  
330 Yield and Production Reveal No Current Pollination Shortage but Increasing Pollinator  
331 Dependency. *Curr. Biol.* 18, 1572–1575. <https://doi.org/10.1016/j.cub.2008.08.066>

332 Andersson, G.K.S., Ekroos, J., Stjernman, M., Rundlöf, M., Smith, H.G., 2014. Effects of farming  
333 intensity, crop rotation and landscape heterogeneity on field bean pollination. *Agric. Ecosyst.*  
334 *Environ.* 184, 145–148. <https://doi.org/10.1016/j.agee.2013.12.002>

335 Araneda Durán, X., Breve Ulloa, R., Aguilera Carrillo, J., Lavín Contreras, J., Toneatti Bastidas, M.,  
336 2010. Evaluation of Yield Component Traits of Honeybee-Pollinated (*Apis mellifera* L.) Rapeseed  
337 Canola (*Brassica napus* L.). *Chil. J. Agric. Res.* 70, 309–314. <https://doi.org/10.4067/S0718-58392010000200014>

339 Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M.,  
340 Tscheulin, T., Roberts, S.P.M., Szentgyörgyi, H., Westphal, C., Bommarco, R., 2014.

341 Contribution of insect pollinators to crop yield and quality varies with agricultural intensification.  
342 PeerJ 2, e328. <https://doi.org/10.7717/peerj.328>

343 Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D.,  
344 Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral  
345 resources in Britain. *Nature* 530, 85–88. <https://doi.org/10.1038/nature16532>

346 Bergamo, P.J., Wolowski, M., Maruyama, P.K., Vizenin-Bugoni, J., Carvalheiro, L.G., Sazima, M.,  
347 2017. The potential indirect effects among plants via shared hummingbird pollinators are  
348 structured by phenotypic similarity. *Ecology* 98, 1849–1858. <https://doi.org/10.1002/ecy.1859>

349 Beyer, N., Gabriel, D., Westphal, C., 2021. Contrasting effects of past and present mass-flowering crop  
350 cultivation on bee pollinators shaping yield components in oilseed rape. *Agric. Ecosyst. Environ.*  
351 319, 107537. <https://doi.org/10.1016/j.agee.2021.107537>

352 Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P.,  
353 Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in  
354 Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354.  
355 <https://doi.org/10.1126/science.1127863>

356 Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and  
357 market value in oilseed rape. *Oecologia* 169, 1025–1032. [https://doi.org/10.1007/s00442-012-](https://doi.org/10.1007/s00442-012-2271-6)  
358 [2271-6](https://doi.org/10.1007/s00442-012-2271-6)

359 Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I.,  
360 Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018a. Towards sustainable and multifunctional  
361 agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER  
362 platform. *Sci. Total Environ.* 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>

363 Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I.,  
364 Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018b. Description of long-term monitoring of  
365 farmland biodiversity in a LTSER. *Data Brief* 19, 1310–1313.  
366 <https://doi.org/10.1016/j.dib.2018.05.028>



367 Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909.  
368 <https://doi.org/10.1007/s13593-015-0302-5>

369 Carvalho, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M., Bartomeus, I., Kaiser-Bunbury,  
370 C.N., Baude, M., Gomes, S.I.F., Merckx, V., Baldock, K.C.R., Bennett, A.T.D., Boada, R.,  
371 Bommarco, R., Cartar, R., Chacoff, N., Dänhardt, J., Dicks, L.V., Dormann, C.F., Ekroos, J.,  
372 Henson, K.S.E., Holzschuh, A., Junker, R.R., Lopezaraiza-Mikel, M., Memmott, J., Montero-  
373 Castaño, A., Nelson, I.L., Petanidou, T., Power, E.F., Rundlöf, M., Smith, H.G., Stout, J.C.,  
374 Temitope, K., Tschamtker, T., Tscheulin, T., Vilà, M., Kunin, W.E., 2014. The potential for  
375 indirect effects between co-flowering plants via shared pollinators depends on resource  
376 abundance, accessibility and relatedness. *Ecol. Lett.* 17, 1389–1399.  
377 <https://doi.org/10.1111/ele.12342>

378 Carvalho, L.G., Seymour, C.L., Veldtman, R., Nicolson, S.W., 2010. Pollination services decline with  
379 distance from natural habitat even in biodiversity-rich areas. *J. Appl. Ecol.* 47, 810–820.  
380 <https://doi.org/10.1111/j.1365-2664.2010.01829.x>

381 Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson,  
382 S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* 14,  
383 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>

384 Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M.,  
385 Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural  
386 landscapes. *Ecol. Lett.* 14, 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>

387 FAOSTAT [WWW Document], 2020. . Food Agric. Organ. U. S. WWW Doc. URL  
388 <http://www.fao.org/faostat/en/#data/QC> (accessed 7.15.21).

389 Gaba, S., Caneill, J., Nicolardot, B., Perronne, R., Bretagnolle, V., 2018. Crop competition in winter  
390 wheat has a higher potential than farming practices to regulate weeds. *Ecosphere* 9, e02413.  
391 <https://doi.org/10.1002/ecs2.2413>

392 Gaba, S., Gabriel, E., Chadœuf, J., Bonneau, F., Bretagnolle, V., 2016. Herbicides do not ensure for higher  
393 wheat yield, but eliminate rare plant species. *Sci. Rep.* 6, 30112.  
394 <https://doi.org/10.1038/srep30112>

395 Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A.,  
396 Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R.,  
397 Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H.,  
398 Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of  
399 pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol.*  
400 *Lett.* 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>

401 Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A.,  
402 Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V.,  
403 Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S.,  
404 Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka,  
405 K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno,  
406 M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L.,  
407 Schüepp, C., Szentgyörgyi, H., Taki, H., Tschardtke, T., Vergara, C.H., Viana, B.F., Wanger,  
408 T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops  
409 Regardless of Honey Bee Abundance. *Science* 339, 1608–1611.  
410 <https://doi.org/10.1126/science.1230200>

411 Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator  
412 competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Sci.*  
413 *Rep.* 7, 45296. <https://doi.org/10.1038/srep45296>

414 Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed  
415 metacommunity dynamics in farmland landscapes. *Proc. R. Soc. B Biol. Sci.* 282, 20150002.  
416 <https://doi.org/10.1098/rspb.2015.0002>

417 Hoehn, P., Tschardtke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee  
418 pollinators increases crop yield. *Proc. R. Soc. B Biol. Sci.* 275, 2283–2291.  
419 <https://doi.org/10.1098/rspb.2008.0405>

420 Holzschuh, A., Dormann, C.F., Tschardtke, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance  
421 wild bee abundance. *Oecologia* 172, 477–484. <https://doi.org/10.1007/s00442-012-2515-5>

422 Holzschuh, A., Dudenhöffer, J.-H., Tschardtke, T., 2012. Landscapes with wild bee habitats enhance  
423 pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153, 101–107.  
424 <https://doi.org/10.1016/j.biocon.2012.04.032>

425 Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tschardtke, T., 2007. Diversity of flower-visiting bees in  
426 cereal fields: effects of farming system, landscape composition and regional context. *J. Appl.*  
427 *Ecol.* 44, 41–49. <https://doi.org/10.1111/j.1365-2664.2006.01259.x>

428 Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees  
429 and hoverflies provided to oilseed rape. *Agric. For. Entomol.* 14, 81–87.  
430 <https://doi.org/10.1111/j.1461-9563.2011.00541.x>

431 Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R.,  
432 Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A.,  
433 Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C.,  
434 Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y.,  
435 Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M.,  
436 Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S.,  
437 Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee  
438 pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599. <https://doi.org/10.1111/ele.12082>

439 Klein, A.-M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination  
440 services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* 49, 723–732.  
441 <https://doi.org/10.1111/j.1365-2664.2012.02144.x>

442 Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C.,  
443 Tschardtke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R.*  
444 *Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>

445 Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from  
446 agricultural intensification. *Proc. Natl. Acad. Sci.* 99, 16812–16816.  
447 <https://doi.org/10.1073/pnas.262413599>

448 Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., Bommarco, R., 2016. Large-scale  
449 pollination experiment demonstrates the importance of insect pollination in winter oilseed rape.  
450 *Oecologia* 180, 759–769. <https://doi.org/10.1007/s00442-015-3517-x>

451 Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship  
452 schemes for providing foraging resources and nesting habitat for bumblebee queens  
453 (Hymenoptera: Apidae). *Biol. Conserv.* 142, 2023–2032.  
454 <https://doi.org/10.1016/j.biocon.2009.03.032>

455 Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in  
456 Sweden. *Field Crops Res.* 86, 199–209. <https://doi.org/10.1016/j.fcr.2003.08.006>

457 Müller, C.B., Adriaanse, I.C.T., Belshaw, R., Godfray, H.C.J., 1999. The structure of an aphid–parasitoid  
458 community. *J. Anim. Ecol.* 68, 346–370. <https://doi.org/10.1046/j.1365-2656.1999.00288.x>

459 Nayak, G.K., Roberts, S.P.M., Garratt, M., Breeze, T.D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis,  
460 I.N., Stirpe, M.T., Potts, S.G., 2015. Interactive effect of floral abundance and semi-natural  
461 habitats on pollinators in field beans (*Vicia faba*). *Agric. Ecosyst. Environ.* 199, 58–66.  
462 <https://doi.org/10.1016/j.agee.2014.08.016>

463 Ouvrard, P., Jacquemart, A.-L., 2019. Review of methods to investigate pollinator dependency in oilseed  
464 rape (*Brassica napus*). *Field Crops Res.* 231, 18–29. <https://doi.org/10.1016/j.fcr.2018.11.006>

465 Pamminger, T., Becker, R., Himmelreich, S., Schneider, C.W., Bergtold, M., 2019. The nectar report:  
466 quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural  
467 and non-agricultural landscapes. *PeerJ* 7, e6329. <https://doi.org/10.7717/peerj.6329>

468 Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018a. Bees increase oilseed rape  
469 yield under real field conditions. *Agric. Ecosyst. Environ.* 266, 39–48.  
470 <https://doi.org/10.1016/j.agee.2018.07.020>

471 Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018b. Bees increase oilseed rape  
472 yield under real field conditions. *Agric. Ecosyst. Environ.* 266, 39–48.  
473 <https://doi.org/10.1016/j.agee.2018.07.020>

474 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global  
475 pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.  
476 <https://doi.org/10.1016/j.tree.2010.01.007>

477 Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham,  
478 S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro,  
479 L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J.,  
480 Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein,  
481 A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M.,  
482 Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N. de O., Pisanty, G., Potts, S.G., Reemer, M.,  
483 Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C.,  
484 Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee  
485 insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146–151.  
486 <https://doi.org/10.1073/pnas.1517092112>

487 Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021. Landscape crop diversity and  
488 semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agric. Ecosyst. Environ.*  
489 306, 107189. <https://doi.org/10.1016/j.agee.2020.107189>

490 Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-  
491 Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng', A., Viana,  
492 B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.*  
493 11, 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>

494 Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., 2015. Annual dynamics  
495 of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96, 1351–  
496 1360. <https://doi.org/10.1890/14-1124.1>

497 Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B.E., Henry, M., 2013.  
498 Differences of floral resource use between honey bees and wild bees in an intensive farming  
499 system. *Agric. Ecosyst. Environ.* 179, 78–86. <https://doi.org/10.1016/j.agee.2013.07.007>

500 Roulston, T.H., Cane, J.H., Buchmann, S.L., 2000. What Governs Protein Content of Pollen: Pollinator  
501 Preferences, Pollen–Pistil Interactions, or Phylogeny? *Ecol. Monogr.* 70, 617–643.  
502 [https://doi.org/10.1890/0012-9615\(2000\)070\[0617:WGPCOP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2)

503 Shaw, R.F., Phillips, B.B., Doyle, T., Pell, J.K., Redhead, J.W., Savage, J., Woodcock, B.A., Bullock,  
504 J.M., Osborne, J.L., 2020. Mass-flowering crops have a greater impact than semi-natural habitat  
505 on crop pollinators and pollen deposition. *Landsc. Ecol.* [https://doi.org/10.1007/s10980-019-](https://doi.org/10.1007/s10980-019-00962-0)  
506 00962-0

507 Sidemo-Holm, W., Carrié, R., Ekroos, J., Lindström, S.A.M., Smith, H.G., 2021. Reduced crop density  
508 increases floral resources to pollinators without affecting crop yield in organic and conventional  
509 fields. *J. Appl. Ecol.* 58, 1421–1430. <https://doi.org/10.1111/1365-2664.13887>

510 Stanley, D.A., Gunning, D., Stout, J.C., 2013. Pollinators and pollination of oilseed rape crops (*Brassica*  
511 *napus* L.) in Ireland: ecological and economic incentives for pollinator conservation. *J. Insect*  
512 *Conserv.* 17, 1181–1189. <https://doi.org/10.1007/s10841-013-9599-z>

513 Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at  
514 risk. *Trends Ecol. Evol.* 20, 651–652. <https://doi.org/10.1016/j.tree.2005.09.004>

515 Timberlake, T.P., Vaughan, I.P., Baude, M., Memmott, J., 2020. Bumblebee colony density on farmland  
516 is influenced by late-summer nectar supply and garden cover. *J. Appl. Ecol.* n/a.  
517 <https://doi.org/10.1111/1365-2664.13826>

518 Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals  
519 seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585–1596.  
520 <https://doi.org/10.1111/1365-2664.13403>

521 Van der Meersch, V., Billaud, O., San Cristobal, M., Vialatte, A., Porcher, E., 2021. Landscape floral  
522 resources provided by rapeseed correlate with next-year reproduction of cavity-nesting pollinators  
523 in a national participatory monitoring program. *Landsc. Ecol.* [https://doi.org/10.1007/s10980-](https://doi.org/10.1007/s10980-021-01353-0)  
524 [021-01353-0](https://doi.org/10.1007/s10980-021-01353-0)

525 Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Mass flowering crops enhance pollinator  
526 densities at a landscape scale. *Ecol. Lett.* 6, 961–965. [https://doi.org/10.1046/j.1461-](https://doi.org/10.1046/j.1461-0248.2003.00523.x)  
527 [0248.2003.00523.x](https://doi.org/10.1046/j.1461-0248.2003.00523.x)

528 Woodcock, B., Edwards, M.S.B., Redhead, J., Meek, W., Nuttall, P., Falk, S., Nowakowski, M., Pywell,  
529 R., 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural  
530 differences and diversity responses to landscape. <https://doi.org/10.1016/J.AGEE.2013.03.005>

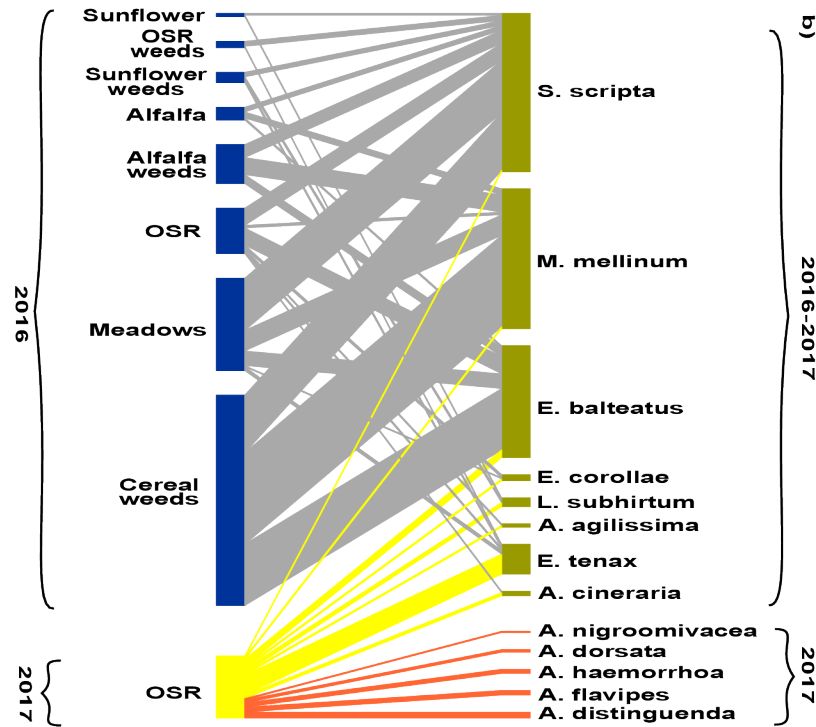
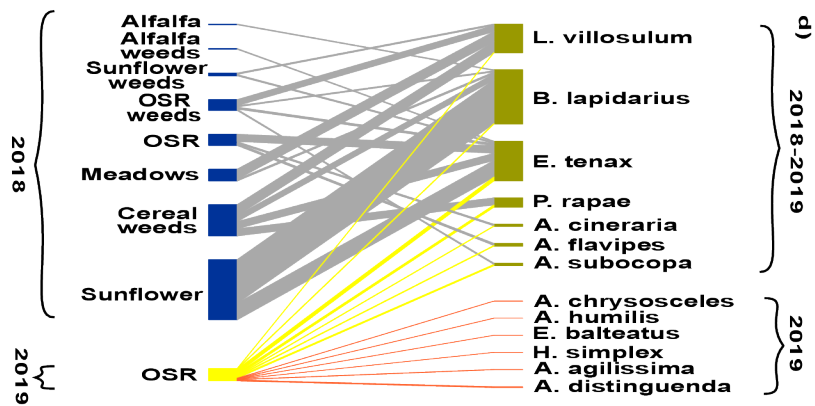
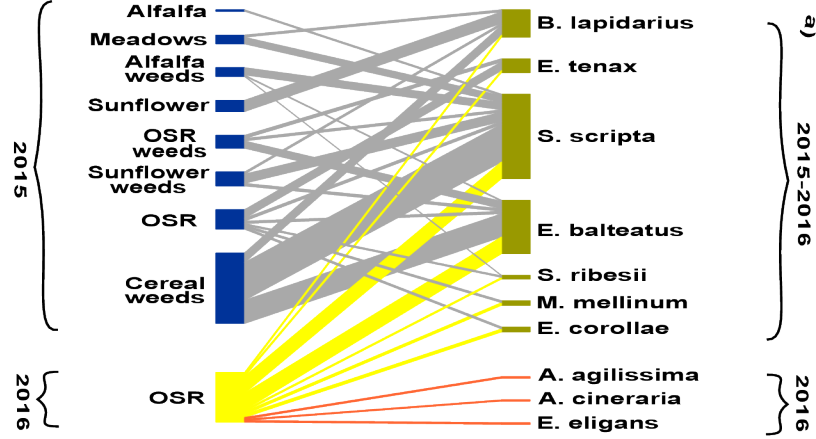
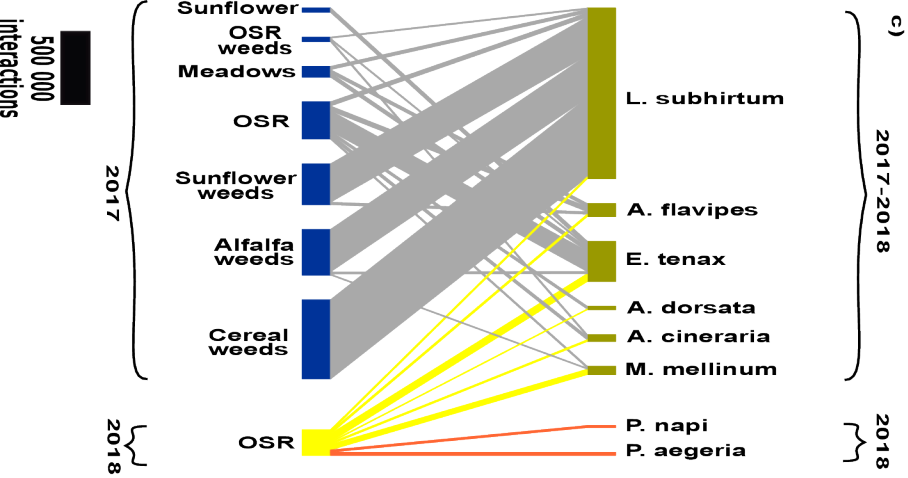
531 Zou, Y., Xiao, H., Bianchi, F.J.J.A., Jauker, F., Luo, S., van der Werf, W., 2017. Wild pollinators enhance  
532 oilseed rape yield in small-holder farming systems in China. *BMC Ecol.* 17, 6.  
533 <https://doi.org/10.1186/s12898-017-0116-1>

534

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

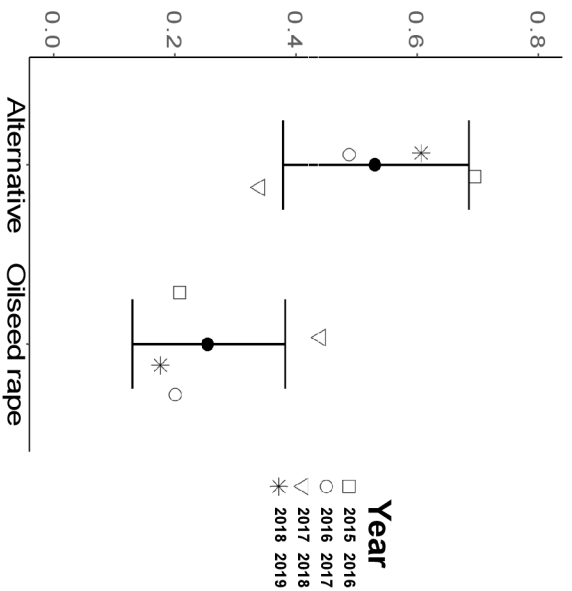
12



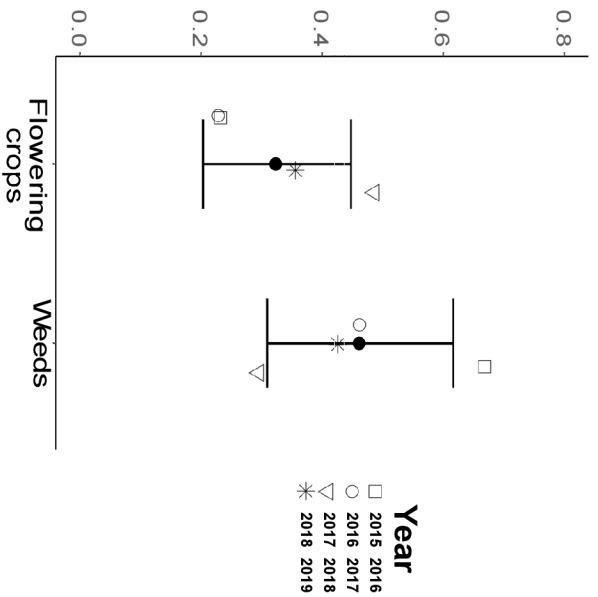


1 **Figure 2** Predicted values (mean +/- 1 standard deviation) of the potential for inter-annual indirect effects  
2 received by oilseed rape flowers accounting for the relative areas covered by each floral resource: (a)  
3 oilseed rape alone vs the alternative types of floral resources together, (b) weeds vs crops and (c) each  
4 floral resource. The type « Alternative » corresponds to the sum of values of the potential for inter-annual  
5 indirect effects produced each year by all floral resources excepted oilseed rape. In each panel, points  
6 correspond to the predicted potential for inter-annual indirect effects calculated for each successive pair of  
7 years and the error bars to the estimated standard deviations. The different symbols correspond to the  
8 potential for inter-annual indirect effects calculated for each successive pair of years.  
9

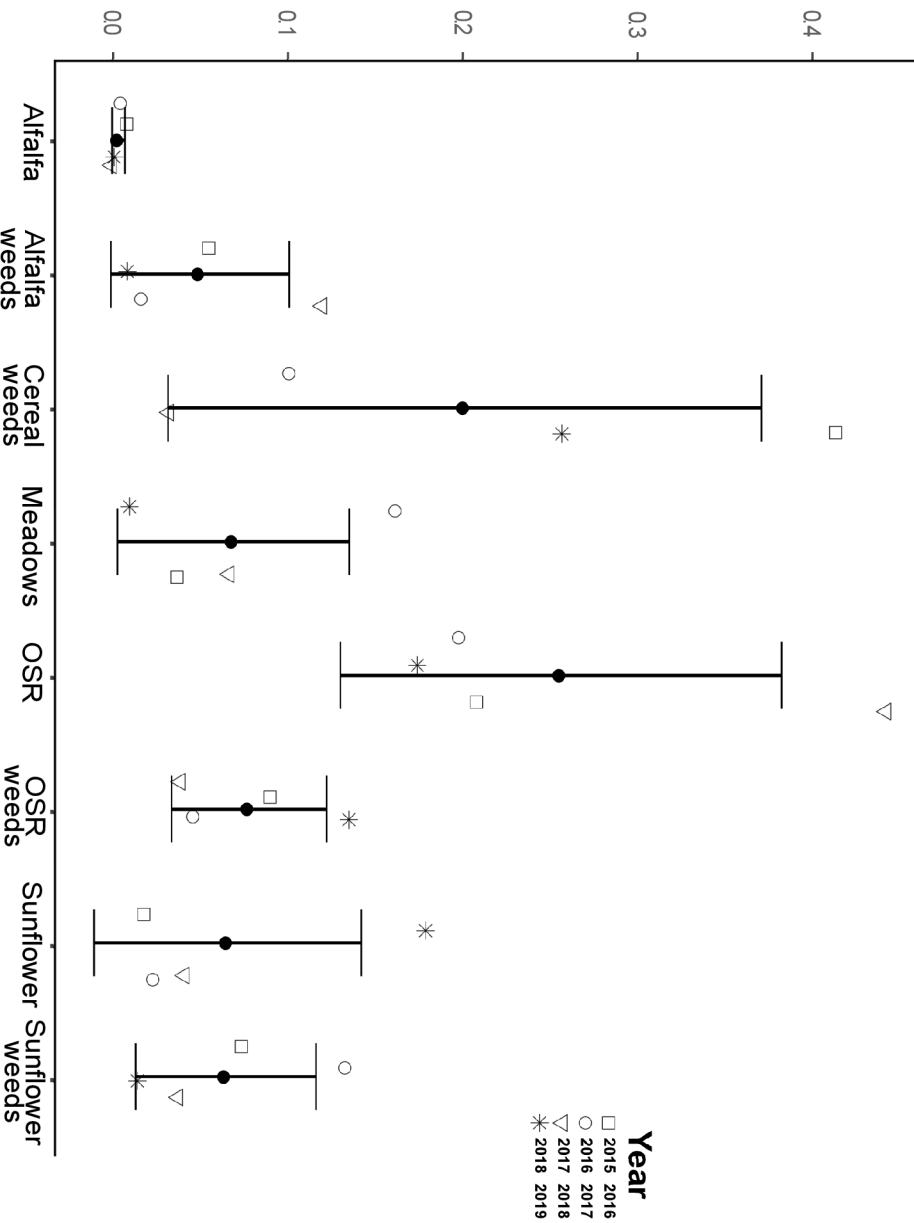
**a)** Predicted value of the potential for inter-annual indirect effects received by oilseed rape



**b)** Predicted value of the potential for inter-annual indirect effects received by oilseed rape



Predicted value of the potential for inter-annual indirect effects received by oilseed rape



**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.

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

**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.

<b>Test</b>	<b>Scale</b>	<b>Df</b>	<b>T</b>	<b>P-value</b>
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