

# 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-03684441v1

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

Pollination is essential for many crops since 70% of the world's cultivated plants depend on pollinators 27 28 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 29 known about the contribution of other floral resources, such as weeds within cultivated areas, in 30 supporting wild pollinator communities and subsequent pollination services. Here, we investigate the 31 32 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 33 consecutive years, the potential for inter-annual indirect effects received by oilseed rape through shared 34 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 much as flowering crops. Finally, we show that weeds growing within cereal fields have a major 38 contribution to the support of oilseed rape pollination, exceeding the contribution of other floral 39 40 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 41 42 on pollinators for their pollination. Management practices like herbicide reduction in non-pollinatordependent crops such as cereals are thus likely to impact the pollination of pollinator-dependent crops. 43

44

Keywords: agricultural landscape, floral resources, indirect interactions, Müller index, plant-pollinator
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 to global agricultural production becoming increasingly dependent on pollinators and vulnerable to their 52 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-Dewenter et al., 2005). 55

The diet of pollinators mainly consists of pollen and nectar. In agricultural landscapes, these 56 resources come from different sources, including hedgerows and woodlands (Timberlake et al., 2019), 57 arable weeds (Bretagnolle and Gaba, 2015) and mass flowering crops (e.g., oilseed rape, sunflower, or 58 alfalfa), the latter providing pulses of resource in large quantities for a short period (Westphal et al., 59 2003). Since the amount of collected resources is likely to affect the reproduction success of pollinators 60 (Beyer et al., 2021; Riedinger et al., 2015; Timberlake et al., 2020; Van der Meersch et al., 2021), the 61 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 facilitation of crop pollination services by other floral resources, flowering in the same year as crops, has 65 been shown with the pollinating fauna of sunflowers benefiting from weeds (Carvalheiro et al., 2011), 66 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 al., 2011; Holzschuh et al., 2012; Kennedy et al., 2013). However, the relative contribution of the various 70 71 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 orthe 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 and a shared pollinator, this index quantifies the potential for indirect interaction of one plant to the other 78 and is calculated as the contribution of the first plant to the pollinator's diet multiplied by the contribution 79 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 index is usually calculated between co-flowering species, here we propose to address inter-annual indirect 83 84 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 85 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).

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 selfpollinated, 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 105 106 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

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 435km<sup>2</sup>, 87% of which was
cultivated and split into 13000 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.

122 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 to 60 landscape 123 124 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 to influence pollinators (Kennedy et al., 2013). Within each window, 3 to 4 fields growing different crops 127 were selected for pollinator sampling, depending on the number of crops grown in the window. Here, we 128 focused on the five main crops grown in the study site, namely: alfalfa, cereals (wheat and barley), 129 130 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

Pollinator sampling was performed annually, from 2015 to 2019. For each selected field, flowervisiting insects were sampled using sweep nets along three 50m long and 5m wide transects. The three transects were positioned at the edge, 20m 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 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 midAugust for sunflower, from the end of April to the end of August for cereal, and from mid-May to midAugust 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 per crop and per year in our study site. This may result in an over- or underestimation of the effects of a 155 floral resource relative to the area it covers in our study site. To account for that, for each crop and 156 associated weeds, and each year, we first calculated the number of visits of each pollinator species 157 relative to the total area of transects performed (number of the pollinator species visits per square meter). 158 Second, variations in the sampling effort among crops and associated weeds for a given year affect the 159 detection of the least abundant pollinator species, with an over-representation of these pollinator species 160 in the most sampled crop fields. To avoid this bias, we defined a detectability threshold per year, which 161 was equal to: one divided by the area sampled for the crop with the lower sampled area this year. For a 162 163 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 164 165 over the 5 years of our sampling (740 individuals out of 5815) corresponding to 61% of pollinator species (100 species out of 165). 166

167

### 168 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.A), based on the Müller index (Müller et al.,
171 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:

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

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 179 *n* on oilseed rape (*osr*) of the year n + 1 via shared pollinators.  $\alpha_{i_n,k}$  is the number of visits of pollinators 180 of the species k on floral resource i the year n per unit of area of the floral resource i.  $area_{i_n}$  corresponds 181 to the cultivated area of the floral resource *i* the year *n*. *m* and *l* correspond to all floral resource types and 182 all pollinator species respectively. The first part of the equation corresponds to the proportion of floral 183 184 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 + 1185 1. The potential for inter-annual indirect effect of each floral resource on oilseed rape was calculated by 186 187 taking into account the area of each floral resource within the study site but also per unit area, i.e. with  $area_{i_n} = 1.$ 188

Honeybees (*Apis mellifera*) were excluded from the analysis because they should not propagate interannual 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. 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 pollinators from 65 species collected from floral resources were considered in subsequent analyses. 202 203 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). Conversely, weeds growing in oilseed rape fields were the floral resource in which the fewest pollinator 205 206 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 the floral resource that shared the most pollinator species with oilseed rape flowers, with 13 species, while 208 209 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 210 211 resources indicates that there is a potential for indirect effects from these different floral resources on 212 oilseed rape pollination.

213

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

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 ( $0.26 \pm 0.09$ ) than the other floral resources (Fig. 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.

#### 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 is affected by other flowering crops as well as arable weeds, making crop fields, flowering or not, and 255 256 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 flowering crops known to provide large amounts of food resources to pollinators and to favor wild 263 pollinators in rapeseed fields (Holzschuh et al., 2013; Westphal et al., 2003). Further, the relative 264 contribution of weeds and flowering crops we found might underestimate weeds' contribution as we only 265 266 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). 267

268 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 269 270 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 for pollinators (Roulston et al., 2000). Our study suggests that cereal weeds can substantially contribute to 274 275 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. Cereal organic farming could have a positive impact on the pollination services of surrounding pollinator-281 dependant crops, since it promotes weed diversity in cultivated fields as well as in the margins of 282 283 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.

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

293 flowering crops by wild pollinators and their diversity are positively linked to the proximity to semi-294 natural habitats (Carvalheiro 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., 2016), the area of semi-natural habitats in our study site relative to one of the crop fields suggests that the 300 301 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 terms of resources for pollinators and pollination efficiency. Yet it is well known that flowers from 306 different species differ in quantity and quality of resources they provide to pollinators (Baude et al., 2016; 307 308 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

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.

322

### 323 Acknowledgments

- 324 We would like to express our thanks to Alexis Saintilan and Marylin 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-
338	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.,
- Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral
  resources in Britain. Nature 530, 85–88. https://doi.org/10.1038/nature16532
- Bergamo, P.J., Wolowski, M., Maruyama, P.K., Vizentin-Bugoni, J., Carvalheiro, L.G., Sazima, M.,
  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
- Beyer, N., Gabriel, D., Westphal, C., 2021. Contrasting effects of past and present mass-flowering crop
  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
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P.,
  Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in
  Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. Science 313, 351–354.
- 355 https://doi.org/10.1126/science.1127863
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and
  market value in oilseed rape. Oecologia 169, 1025–1032. https://doi.org/10.1007/s00442-0122271-6
- 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
- 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 Carvalheiro, 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., Tscharntke, 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
- abundance, accessibility and relatedness. Ecol. Lett. 17, 1389–1399.
- 377 https://doi.org/10.1111/ele.12342
- Carvalheiro, L.G., Seymour, C.L., Veldtman, R., Nicolson, S.W., 2010. Pollination services decline with
  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 Carvalheiro, 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
- 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., Bonneu, F., Bretagnolle, V., 2016. Herbicides do not ensure for higher wheat yield, but eliminate rare plant species. Sci. Rep. 6, 30112. 393 394 https://doi.org/10.1038/srep30112 395 Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., 396 Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., 397 Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of 398 pollination services decreases with isolation from natural areas despite honey bee visits. Ecol. 399 400 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., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., 402 403 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, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, 405 M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., 406 407 Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, 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 Regardless of Honey Bee Abundance. Science 339, 1608–1611. 409 https://doi.org/10.1126/science.1230200 410 Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator 411 competition and facilitation with mass flowering crops affects yield in co-blooming crops. Sci. 412 Rep. 7, 45296. https://doi.org/10.1038/srep45296 413 Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed 414 415 metacommunity dynamics in farmland landscapes. Proc. R. Soc. B Biol. Sci. 282, 20150002. https://doi.org/10.1098/rspb.2015.0002 416
  - 17

- 417 Hoehn, P., Tscharntke, 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
- Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance
  wild bee abundance. Oecologia 172, 477–484. https://doi.org/10.1007/s00442-012-2515-5
- Holzschuh, A., Dudenhöffer, J.-H., Tscharntke, T., 2012. Landscapes with wild bee habitats enhance
  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., Tscharntke, 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

- Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees
  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
- 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.,
- 443Tscharntke, 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
- Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in
  Sweden. Field Crops Res. 86, 199–209. https://doi.org/10.1016/j.fcr.2003.08.006
- Müller, C.B., Adriaanse, I.C.T., Belshaw, R., Godfray, H.C.J., 1999. The structure of an aphid–parasitoid
  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

- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018a. Bees increase oilseed rape
  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
- Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021. Landscape crop diversity and
  semi-natural habitat affect crop pollinators, pollination benefit and yield. Agric. Ecosyst. Environ.
  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
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-
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-
524	021-01353-0
525	Westphal, C., Steffan-Dewenter, I., Tscharntke, 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-
527	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	

Figure 1 Flower-visitor interaction network restricted to the pollinator species that were captured during 1 2 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 3 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 year *n*. The yellow links correspond to interactions of pollinators of year n+1 (already present the year *n*) 9 on oilseed rape n+1. The orange links correspond to interactions between pollinator species only present 10 in year n+1 and oilseed rape of year n+1. 11







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.



**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

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