

# Influences of oilseed rape area and aggregation on pollinator abundance and reproductive success of a co-flowering wild plant

Colin van Reeth, Nadia Michel, Christian Bockstaller, Gaël Caro

### ▶ To cite this version:

Colin van Reeth, Nadia Michel, Christian Bockstaller, Gaël Caro. Influences of oilseed rape area and aggregation on pollinator abundance and reproductive success of a co-flowering wild plant. Agriculture, Ecosystems & Environment, 2019, 280 (280), pp.35 - 42. 10.1016/j.agee.2019.04.025 . hal-02185875

## HAL Id: hal-02185875 https://hal.science/hal-02185875

Submitted on 22 Oct 2021

**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

# Influences of oilseed rape area and aggregation on pollinator

## abundance and reproductive success of a co-flowering wild plant

Colin Van Reeth<sup>a,b</sup>, Nadia Michel<sup>a</sup>, Christian Bockstaller<sup>c</sup>, Gaël Caro<sup>a</sup>

<sup>a</sup> Laboratoire Agronomie Environnement (UMR 1121), Université de Lorraine, INRA, 2 avenue de la

forêt de Haye, 54 500 Vandœuvre-lès-Nancy, France

<sup>b</sup> Centre de Recherches sur les Ecosystèmes d'Altitude (CREA Mont-Blanc), 67 lacets du Belvédère,

74 400 Chamonix Mont-Blanc, France

<sup>c</sup> Laboratoire Agronomie Environnement (UMR 1121), INRA, Université de Lorraine, 28 rue de

Herrlisheim, 68 000 Colmar, France

Colin Van Reeth: c.v.reeth@gmail.com Nadia Michel: nadia.michel@univ-lorraine.fr Christian Bockstaller: christian.bockstaller@inra.fr Gaël Caro: gael.caro@univ-lorraine.fr

Corresponding author: Colin Van Reeth

Declarations of interest: none

#### 1 Abstract

2 Mass-flowering crops such as oilseed rape (Brassica napus) are attractive for some pollinators. 3 Consequently, flowering oilseed rape fields may compete for pollinators with co-flowering wild plants occurring in adjacent non-crop habitats. We evaluated the influence of flowering oilseed rape 4 5 through both its area and its configuration in the landscape on pollinator abundance and on the 6 reproductive success of a co-flowering wild plant functionally close to oilseed rape in surrounding 7 grasslands. We monitored the production of seeds of a pollinator-generalist plant, Cardamine 8 pratensis, and sampled pollinator communities in 22 permanent grasslands. To understand the 9 landscape effect of oilseed rape, we quantified its area and aggregation in the landscape at 1 000 m 10 around each grassland. We measured the flower abundance in the grasslands and C. pratensis 11 conspecific plant abundance to consider local influences. At the landscape scale, C. pratensis seed set 12 was unaffected by the aggregation of oilseed rape patches but it was reduced by increasing oilseed 13 rape area in the landscape. At the local scale, the conspecific plant abundance enhanced seed set 14 (i.e. facilitation effect), whereas flower abundance in the grassland reduced it (i.e. competition 15 effect). Analyses revealed a significant positive correlation between seed set and honeybee 16 abundance, but no correlation was found between seed set and solitary bee abundance. Oilseed rape 17 aggregation and the area of semi-natural habitats in the landscape had a weak negative effect on 18 honeybee abundance. Oilseed rape area had either a positive or a negative effect on solitary bee 19 abundance depending on oilseed rape aggregation in the landscape. Flowering oilseed rape can 20 either enhance or reduce the pollinator abundance and the reproductive success of wild plants 21 depending on its quantity and spatial arrangement. Guidance for plant and pollinator conservation 22 should therefore consider both landscape aspects.

23 Keywords: Mass flowering crop; Configuration; Habitat loss; Wild bees; Cardamine pratensis;
24 Pollination

25 **1. Introduction** 

26	The great majority of wild plants (87.5%) relies on animal pollination to reproduce successfully
27	(Ollerton et al., 2011). Pollinators and, consequently, the pollination success of insect-pollinated
28	plants have often been reported to be negatively influenced by agricultural intensification and
29	landscape alteration (Aguilar et al., 2006; Senapathi et al., 2017). The sensitivity of insect-pollinated
30	plants to landscape alteration depends on (i) their compatibility systems: self-incompatible plants are
31	more sensitive to landscape alteration than self-compatible plants that are capable of reproducing in
32	absence of pollinators (Aguilar et al., 2006; Aizen et al., 2002) <mark>, and</mark> (ii) their degree of pollinator
33	specialization: pollinator-specialist plants which rely on few species, may be more sensitive to
34	landscape alteration because the absence of key pollinator species cannot always be compensated
35	by the visitation of other pollinators as for pollinator-generalist plant species (Ashworth et al., 2004;
36	Morris, 2003).
37	Mass flowering crops such as oilseed rape (Brassica napus, hereafter referred to as 'OSR') have been
38	suggested to influence the interaction between wild plants and pollinators (Carvalheiro et al., 2014;
39	Diekötter et al., 2010). Flowering OSR fields attract pollinators from surrounding landscapes
40	(Magrach et al., 2017; Rollin et al., 2013; Van Reeth et al., 2018; Woodcock et al., 2016) <mark>because of</mark>
41	<mark>easily accessible and highly abundant floral resources</mark> (Hoyle et al., 2007). Consequently, <mark>the</mark>
42	abundance or density of pollinators attracted by OSR decreases in other surrounding habitats such as
43	semi-natural habitats (Holzschuh et al., 2016; Kovács-Hostyánszki et al., 2013). This attraction of bees
44	to flowering OSR fields may, in turn, have negative effects on the pollination of wild plants flowering
45	at the same time as OSR flowers in surrounding semi-natural habitats (Holzschuh et al., 2011; Stanley
46	and Stout, 2014).
47	Holzschuh et al. (2011) studied the effect of a landscape composition variable, OSR area, on the
48	reproductive success of Primula veris (Primulaceae), an OSR co-flowering grassland species. They

- 49 found a negative influence of OSR area in the landscape on *P. veris* seed set. However, the
- 50 reproductive success of *Crataegus* spp. (Rosaceae) and *Lychnis viscaria* (Caryophyllaceae), which also

51 flower during OSR flowering period, was not found to be influenced by OSR area in the landscape 52 (Ekroos et al., 2015; Kovács-Hostyánszki et al., 2013). The differences between such studies regarding OSR landscape influences on the reproductive success of co-flowering plants seem to be dependent 53 54 on plant-pollinator interactions and on how pollinators are attracted by OSR. Indeed, honeybees and 55 bumblebees are very attracted by flowering OSR fields which is less the case for solitary bees 56 (Holzschuh et al., 2016; Rollin et al., 2013). P. veris is mainly pollinated by bumblebees (Holzschuh et 57 al., 2011) whereas Crataegus spp. is a pollinator generalist species (Kovács-Hostyánszki et al., 2013). 58 Consequently, for plant species sharing pollinators with OSR, pollinator-specialist plants seem to be 59 more sensitive to the area of OSR in the landscape than pollinator-generalist species. Moreover, one can hypothesize that plant species which share similar floral traits mediating interactions with 60 pollinators are more likely influence each other (Carvalheiro et al., 2014; Hegland and Totland, 2005). 61 62 By using a generalist plant that is more closely related to oilseed rape, we explore whether a plant 63 that, due to its generalized pollination systems should be unaffected by oilseed rape, is in fact 64 affected because it is closely related to OSR.

In addition to landscape compositional effects, the effects of landscape configuration (i.e. the spatial
arrangement of habitat patches in the landscape) on pollinators and insect-pollinated plants have
been studied (Carré et al., 2009; Ekroos et al., 2015; Jakobsson and Ågren, 2014; Kennedy et al.,
2013). Kennedy *et al.* (2013) synthetized the results of 39 studies in cultivated habitats and found
that habitat aggregation in the landscape had the greatest influence on wild bees among the
configuration metrics analyzed (isolation, habitat shape and aggregation).

While the configuration effect of OSR on wild bees and co-flowering wild plants has not been explored yet, previous analyses demonstrated negative influence of isolation from semi-natural habitats (Ekroos et al., 2015, 2013; Jakobsson and Ågren, 2014). Semi-natural habitats (hereafter referred to as 'SNH') are essential habitats for wild bees providing both nesting and feeding resources and thus greatly determine their spatial distribution in the landscape (Westrich, 1996).

Besides the effect of isolation from SNH, little is known about the configuration effect of the
landscape and especially the aggregation of resourceful patches such as OSR fields on the pollination
of insect-pollinated plants even though pollinators are known to adjust their foraging strategy to the
quantity of resources but also to its spatial distribution (Cartar and Real, 1997; Cresswell, 2000;
Kremen et al., 2007).

Here, we aim to assess the influence of OSR through its area and its aggregation in the landscape on pollinator abundance in permanent grasslands and on the reproductive success of a co-flowering wild plant functionally close to OSR. We hypothesized that the effect of OSR area both on pollinators and on the reproductive success of a co-flowering wild plant can be modulated by OSR aggregation in the landscape. To test these hypotheses, we simultaneously monitored the seed set of a wild plant species (*Cardamine pratensis*) and the abundance of pollinators in the same permanent grasslands.

- 87 **2. Material and methods**
- 88 2.1. Study region and study sites

The study was carried out in 2016 in the eastern part of the "Parc Naturel Régional de Lorraine", county of Moselle, Lorraine, France (48°48'46''N, 6°43'14''E). We selected 22 similarly managed permanent grasslands, which were mowed (not grazed) and fertilization never exceeded 40kg nitrogen/ha/year for the last five years. Grasslands also had similar sizes (mean value ± standard deviation = 4.3 ± 1.2 ha). The mean distance between study sites was 3 851 ± 1 535m (min: 2 182m;

- 94 max: 8 879m). (Figure 1).
- 95 Land use surrounding grasslands in a 1 000 m radius was mainly dominated by annual crops (30.8 ±

96 22.4%; min = 0%; max = 70.1%), forest (24.7 ± 29.0%; min = 0%; max = 89.0%) and permanent

- 97 grasslands (21.7 ± 13.5%; min = 1.2%; max = 55.0%). OSR area in the landscape was in average 6.5 ±
- 98 6.5%, ranging from 0 to 19.2%. 8 grasslands were adjacent to an OSR field whereas 14 were at least
- 280 meters away (in average =  $659 \pm 259m$ ) from an OSR field.

Figure 1: (a) Study region and study areas in the "Parc Naturel Régional de Lorraine", county of Moselle, Lorraine, France.
 Black circles represent the area surrounding each permanent grassland within a 1 000m radius. (b) Seed set and bee
 experiment design implemented in the centroid of each permanent grassland. In the middle of each grassland, five
 clusters of three pan traps (yellow, blue, white) were placed and fifteen *Cardamine pratensis* plants were selected.

104 2.2. Study plant and seed set monitoring

105 We used the herb Cardamine pratensis (Brassicaceae) to evaluate landscape effects on the 106 reproductive success of an OSR co-flowering wild plant. This plant is common in permanent 107 grasslands of Eastern France and flowers at the same time as OSR, from early-April to early-May. C. 108 pratensis is known to be highly self-incompatible and need pollination by insects such as solitary 109 bees, bumblebees, honeybees and hoverflies to produce fruits (Fitter and Peat, 1994; Kühn et al., 110 2004; Salisbury, 1965). This plant may thus suffer from a lack of pollen deposition and produce less 111 seeds when the abundance of its pollinators is low (Burd, 1994; Knight et al., 2005). C. pratensis and 112 OSR belong to the same family and have similar floral traits (flower size, flower shape, nectary position). Consequently, both plants should share some pollinators, making the reproductive success 113 114 of C. pratensis particularly vulnerable to OSR (Carvalheiro et al., 2014; Hegland and Totland, 2005). 115 For all these reasons, *C. pratensis* is a relevant plant species to evaluate OSR landscape effects. 116 We monitored the reproductive success of C. pratensis once OSR flowering had begun in mid-April. In 117 each grassland, we randomly chose 15 C. pratensis plants within a 50m zone on either side of the transect used to sample pollinators (Fig. 1). For each plant, we identified and marked one flower bud 118 119 using a short black thread. This allowed us to be sure that this bud actually flowered during OSR 120 flowering period. Among the 15 C. pratensis plants per grassland, we selected 8 plants to evaluate 121 the extent of pollinator dependence: for each of these 8 plants another flower bud was bagged with 122 a mesh bag to prevent contacts with pollinators. Altogether, 330 flower buds were marked, and 176 additional flower buds were bagged in the monitored grasslands. 123

During *C. pratensis* flowering, we measured two floristic variables in each permanent grassland to
 consider local influences. Firstly, we evaluated the potential intraspecific influences by quantifying

the number of *C. pratensis* plants surrounding each selected plant (hereafter referred to as
'conspecific abundance') in a 2-meter radius. Secondly, we evaluated the global floristic
opportunities by quantifying the number of flowers (considering all flowering species) in ten 1m<sup>2</sup>
quadrats randomly placed within 30 meters around plot centroid. The flower abundance in the
grassland was the pooled number of flowers found in the ten quadrats.

We harvested *C. pratensis* ripe fruits in late May. The reproductive success of *C. pratensis* in each
grassland was evaluated by calculating the mean number of seeds per fruit.

133 2.3. Pollinator monitoring

134 Pollinator sampling started when selected C. pratensis flower buds were blooming. We used pan 135 traps (ProPac, Vechta, Germany) painted with UV bright colors (Sparvar Leuchtfarbe, Spray-Color 136 GmbH, Merzenich, Germany). A cluster of three 750 mL-pan traps (blue, white and yellow) was 137 placed on a wooden stick. Five clusters were lined up in the middle of each grassland, 10 meters 138 apart from each other. Traps were positioned at vegetation height, filled with 400 mL of water and 139 three drops of an odorless and colorless dishwasher liquid. They were left active during 10 days. We 140 analyzed a total of 330 pan trap contents and summed captured individuals from the 5 pan-trap 141 clusters to evaluate pollinator abundance in each grassland.

Hoverflies and bumblebees were excluded from this study since only 5 and 33 individuals were
 captured respectively. We split the remaining pollinator community into two groups: honeybees and
 solitary bees. This last group included solitary bees, strictly speaking, but also gregarious, communal,

- 145 and social species (Michener, 2007).
- 146 2.4. Quantifying landscape composition and configuration

147 Landscape composition data were analyzed using ArcGis 10.3. (ESRI, Redlands, CA). The landscape

surrounding each grassland was described in a 1 000m buffer from vectorial data. This single spatial

scale was chosen because most foraging flights of *C. pratensis* pollinators are within this distance

150 (Haenke et al., 2014; Holzschuh et al., 2016, 2011; Steffan-Dewenter et al., 2002; Steffan-Dewenter 151 and Kuhn, 2003). Wooden areas and hedgerows were extracted from BD TOPO® (IGN) while 152 agricultural land data were obtained by field inspections during which we identified and located 153 permanent and temporary grasslands and each annual crop present in our study area. In cases where 154 the distinction between permanent and temporary grasslands was not obvious, we checked on past 155 aerial photographs of 1999 and 2009 (BD ORTHO<sup>®</sup>, IGN). With this landscape GIS database, we then 156 calculated two landscape descriptors for each buffer (excluding the grassland being sampled): the 157 area of semi-natural habitats (%SNH) and oilseed rape (%OSR) in the landscape. SNH included 158 permanent grasslands, orchard meadows, hedgerows, woodlots and forest edges (10 meters wide). 159 Landscape configuration effects of OSR were considered by measuring the aggregation of OSR fields 160 in the landscape. We calculated OSR Aggregation Index (hereafter referred to as 'OSR-AI') using FRAGSTATS (McGarigal et al., 2012) in each of the 22 buffers. The Aggregation Index produces a 161 162 quantitative value that accounts for various degrees of land use type clumpiness. OSR-AI equals 100 163 when OSR is maximally aggregated forming thus a single and compact OSR patch, while OSR-AI 164 values approach 0 when OSR is disaggregated in the landscape. Since AI is designed for raster data, 165 we calculated OSR-AI value for each buffer using a cell grid with a 100 meters resolution. We 166 attributed zero values for OSR-AI when OSR was absent in the grid assuming that OSR was maximally 167 disaggregated in this case. In order to illustrate the modulation effect of %OSR by OSR-AI, we split 168 our data set in two groups according to the median value of OSR-AI (median = 69.6): a first group of 169 grasslands with aggregated OSR patches in the landscape (N = 11, mean(OSR-AI) = 85.3 ± 11.8) and a 170 second group with more disaggregated OSR patches (N = 11, mean(OSR-AI) = 37.2 ± 30.7). 171 Previous studies found that the presence of an OSR field adjacent to a grassland influence the 172 pollinator abundance in the focal grassland (Holzschuh et al., 2011; Kovács-Hostyánszki et al., 2013). 173 Consequently, we disentangled OSR 'local' effects from OSR landscape effects by considering a

variable 'OSR adjacency' coded as 1 when the grassland and an OSR field were contiguous or 0 in
other cases.

176 2.5. Data Analysis

177 Seed set, solitary bee abundance and honeybee abundance were modelled separately as the 178 response variable (one model per response variable). Linear models (LM) were used for the 179 log<sub>10</sub>(x+1)-transformed response variables. Each model contained: %OSR, OSR-AI, %SNH, OSR 180 adjacency, flower abundance and the interaction between %OSR and OSR-AI as explanatory 181 variables. For the seed set model only, we added one predictor: C. pratensis conspecific abundance 182 to evaluate the intraspecific influences. Flower abundance and conspecific abundance were transformed with  $log_{10}(x+1)$ . Full models were simplified by excluding one by one non-significant 183 184 variables (P > 0.1 from F test) in backward stepwise selection (Holzschuh et al., 2016; Kovács-185 Hostyánszki et al., 2011; Marrec et al., 2015; Parsche et al., 2011).

We graphically controlled the homogeneity of the variance and the normal distribution of the
residuals for each model. There was no evidence of heteroscedasticity or non-normality. Then, we
calculated the sum of squares (Sum Sq) associated to each variable using likelihood ratio tests (Type
II Wald chi-squared tests) using the R-function *Anova* from the package *car* (Fox and Weisberg, 2010;
R Core Team, 2016). Sum Sq indicates the part of the variance explained by each variable and can be
used to establish a hierarchy among variables. To visualize the effects of the fitted models we used
the R-function *visreg* from the package *visreg* (Breheny and Burchett, 2016).

Finally, we assessed the relation between seed set and the abundance of each bee group withspearman correlations.

We tested the multi-collinearity between predictors with Variance Inflation Factor (VIF) (Zuur et al.,
2009) and found no variance inflation pattern since VIF < 2.02. VIF = 3 is often considered to be a</li>
threshold value (Zuur et al., 2009). Pearson correlation (r) between OSR area in the landscape and
OSR adjacency was relatively high (0.68) but was inferior to 0.7, the threshold value proposed by

Dormann *et al.* (2013). Correlations between other predictors gave |r| < 0.32. Spatial autocorrelation was also checked for the abundance of each pollinator group and seed set using Mantel tests with 4 999 permutations (Dray and Dufour, 2007). No autocorrelation was found (Mantel statistics: *P* > 0.17 and r < 0.14).

203 **3. Results** 

- 204 3.1. Plant and bee monitoring
- Among the 15 plants initially selected in each grassland, an average of 10 *C. pratensis* plants per
- 206 grassland remained usable for the analysis. The number of plants per site varies between 5 and 14.
- 207 The loss of one third of the selected plants was presumably due to herbivory, but we unfortunately
- 208 lack information on the animals involved. We harvested 1 178 seeds in the 22 grasslands. Seed set
- ranged from 0 to 24 seeds per fruit (mean = 5.2 ± 2.9). Bagged flowers gave almost no seed (1 seed
- found among all 40 bagged flowers) while we counted 199 seeds for accessible flowers located on
- the same plant (N = 40). Therefore, we considered that *C. pratensis* has to be visited by pollinators to
- produce seeds, as suggested previously (Fitter and Peat, 1994; Kühn et al., 2004; Salisbury, 1965).
- 213 This result suggested that pollinators play a major role in the response of *C. pratensis* seed set.
- 214 During the plant monitoring, we collected 3 623 solitary bees and 100 honeybees. Solitary bee
- abundance in the permanent grasslands ranged from 11 to 565 individuals (mean = 164.7 ± 144.7)
- and honeybee abundance ranged from 0 to 32 individuals  $(4.5 \pm 8.5)$ .
- 217 3.2. Local and landscape influences
- 218 3.2.1. Influences on *C. pratensis* seed set

For the seed set model, we obtained,  $R^2_{adj} = 0.26$  indicating a moderate model fit. *C. pratensis* seed

- set decreased significantly with %OSR and the flower abundance in grassland (Tab. 1, Fig. 2a, c).
- 221 Conversely, seed set increased with the conspecific plant abundance and was marginally higher for

222 grasslands adjacent to an OSR field than for other grasslands (Tab. 1, Fig. 2b). Selected variables had

similar influence strength on seed set (see the Sum Sq values. in Tab. 1).

224

- Table 1: Results of the seed set and pollinator models obtained after variable selection. OSR: Oilseed rape; OSR-AI:
- 226 Oilseed rape Aggregation Index; SNH: Semi-natural habitats.
- 227

Figure 2: Responses of the mean number of *Cardamine pratensis* seeds per fruit (i.e. seed set, log<sub>10</sub>(x+1) transformed) in each grassland to (a) %OSR, (b) *C. pratensis* conspecific abundance, (c) flower abundance. Predictions returned by the seed set model are shown with black lines. To test the effect of a single variable of the model on seed set, other variables were held constant (median for numeric variables and most common category for the factor variable OSR adjacency (i.e. grasslands isolated from OSR)). The grey band around the line represents the 95% confidence interval. Other statistical details are present in Table 1. Note log<sub>10</sub> scale used on x and y axis. OSR: Oilseed rape.

234 3.2.2. Influences on bee abundance

For pollinator abundance model, we obtained, R<sup>2</sup><sub>adj</sub> = 0.39 and 0.15 respectively for solitary bees and honeybees. These values indicated a moderate model fit for solitary bees and a weak model fit for honeybees.

238 Solitary bee abundance was only significantly related to %OSR, OSR-AI and their interaction term

239 (Tab. 1): %OSR had a negative effect on solitary bee abundance when OSR was aggregated whereas

240 %OSR had a positive effect on solitary bee abundance when OSR was more disaggregated in the

241 landscape (Tab. 1, Fig. 3).

242 Honeybee abundance was marginally explained by %SNH and OSR-AI (Tab. 1), whereas %OSR and

243 OSR adjacency were not found to be influencing parameters.

244 Figure 3: Interactive effect of oilseed rape area in the landscape (%OSR) and oilseed rape aggregation index (OSR-AI) on

solitary bee abundance. Predictions returned by the solitary bee abundance model are shown with colored lines which

were calculated for OSR-AI values inferior to the median = 69.6 (N = 11, red color) and for OSR-AI values superior to 69.6 (N

- 247 = 11, blue color). The color band around the line represents the 95% confidence interval. Other statistical details are
- 248 present in Table1. Note log<sub>10</sub> scale used on y axis.

249

#### 3.2.3. Linking bee abundance and C. pratensis seed set

250 We tested the relation between *C. pratensis* seed set and the abundance of each sociality bee group

251 (see Appendix 1). Spearman correlations analyses revealed a significant correlation with honeybee

- abundance (r = 0.48; P = 0.02) but no correlation was found with solitary bees (r = -0.02; P = 0.92).
- 253 These results suggested that honeybee abundance partly influenced *C. pratensis* seed set.

#### 254 **4. Discussion**

In this study, we focused on the effects of flowering oilseed rape on bee abundance and on the

256 reproductive success of *C. pratensis*, a co-flowering wild plant, in permanent grasslands. Firstly, we

257 demonstrated that *C. pratensis* is fully dependent on pollinator visits to produce seeds. Secondly, we

found that solitary bee abundance and seed set were both influenced by landscape variables,

259 whereas honeybee abundance was not. However, solitary bees and seed set had different responses

towards oilseed rape. At the landscape scale, our results showed that seed set was related to the

261 oilseed rape area, whereas solitary bees were influenced by both oilseed rape area and oilseed rape

landscape aggregation. Finally, we observed that seed set was significantly correlated to honeybee

- abundance but not to solitary bee abundance.
- 264 4.1. Local and landscape influences on seed set

265 Our results showed that the production of *C. pratensis* seeds was exclusively the result of pollinator

visitations. Seed set was mainly influenced by landscape variables, such as the area covered by mass

267 flowering crops, and by local variables, such as resources availability.

268 At the landscape scale, we found that the area of flowering oilseed rape in the landscape reduced the

269 reproductive success of *C. pratensis* as demonstrated previously with *Primula veris*, a pollinator-

270 specialist plant species (Holzschuh et al., 2011). Our study showed that pollinator-generalist plant

271 species can also be impacted by oilseed rape in the landscape, even though the mechanisms remains

272 unclear: low C. pratensis seed set observed in oilseed rape rich landscapes may be explained by a

lower deposition of conspecific pollen on the stigma of *C. pratensis* as well as a higher deposition of
heterospecific (oilseed rape) pollen (Marrero et al., 2016).

Seed set was only marginally higher in permanent grasslands adjacent to oilseed rape fields than in other grasslands. This effect, known as the 'spillover effect' (Blitzer et al., 2012), was demonstrated in previous findings (Cussans et al., 2010; Kovács-Hostyánszki et al., 2013): wild plant benefited from the close proximity to mass flowering crops which attracted some pollinators and enhanced, in turn, the visitation rate of surrounding wild plants.

280 C. pratensis seed set may be particularly influenced by oilseed rape because (i) C. pratensis obligatory 281 need pollinators for its reproduction as suggested before (Fitter and Peat, 1994; Kühn et al., 2004; 282 Salisbury, 1965) and confirmed in this study. These pollinators include some species such as 283 honeybees and short tongued bumblebees (not studied here due to scarce captures) which are 284 known to be attracted by oilseed rape mass flowering resources (Holzschuh et al., 2016; Rollin et al., 285 2013; Stanley and Stout, 2014); (ii) C. pratensis is functionally and phylogenetically close to oilseed 286 rape (both plants belong to the Brassicaceae family). Carvalheiro et al. (2014) showed that the 287 probability for two co-flowering plants to share pollinators and thus to influence each other 288 decreased with the phylogenetic distance between them. These previous findings may explain the 289 negative effect of oilseed rape area in the landscape on C. pratensis (Brassicaceae) observed in this 290 present study (close phylogenetic distance between the two co-flowering plants) as well as the 291 absence of oilseed rape effect on more phylogenetically distant species such as Crataegus spp. 292 (Rosaceae) and Lychnis viscaria (Caryophyllaceae) found in previous analyses (Ekroos et al., 2015; 293 Kovács-Hostyánszki et al., 2013).

We observed that local floristic environment also influenced *C. pratensis* seed set. The abundance of conspecific plants increased seed set illustrating a facilitation effect (Bjerknes et al., 2007) as found in Kovács-Hostyánszki *et al.* (2013): a high conspecific abundance in the very close proximity may not only attract more pollinators but may also enhance conspecific pollen deposit. In contrast, increasing flower abundance of the entire plant community in the grassland reduced *C. pratensis* seed set

- suggesting a competition for pollinators at the plot level (Brown and Mitchell, 2001; Caruso, 1999)
  possibly because other grassland plant species such as *Taraxacum officinale* W. (Asteraceae) were
  more attractive than *C. pratensis* (Fornoff et al., 2017). Some other studies found a positive effect of
  local floral availability on pollination success (Orford et al., 2016). In conventional grasslands or field
  boundaries with a low floral availability, the effects on pollination success might be positive because
- 304 pollinators concentrate into these flower patches (Rundlöf et al., 2014).
- 305 4.2. Landscape influences on pollinator abundance

Landscape composition and landscape configuration influenced differently the abundance of solitarybees and honeybees.

308 The abundance of solitary bees has often been found unrelated to mass-flowering crop area in the 309 landscape (Holzschuh et al., 2011, 2016; Kovács-Hostyánszki et al., 2013; but see Diekötter et al. 310 (2014) for cavity nesting bees). Here, we found strong but contrasted effects of oilseed rape on the 311 abundance of solitary bees (Fig. 3). When oilseed rape area increased in the landscape, solitary bee 312 abundance response differed, depending on oilseed rape aggregation: solitary bee abundance in 313 permanent grasslands decreased when %OSR increased in an aggregated configuration whereas it 314 increased when %OSR increased in a more disaggregated configuration (Fig. 3). The ability of solitary 315 bees to exploit oilseed rape resources may depend on the configuration of oilseed rape patches in 316 the landscape even though the mechanisms remain unclear. The aggregation of oilseed rape patches 317 may (i) facilitate the exploitation of oilseed rape resources by solitary bees, concentrating resources 318 in a small zone and thus limiting movements to search potential food opportunities in the landscape; 319 (ii) enhance the probability to find unvisited oilseed rape flowers and thus; (iii) reduce the competition between bee species due to spatial partitioning within a group of fields or within a field 320 321 (Calabuig, 2000). Magrach et al. (2017) showed that oilseed rape fields attract between 8 and 35% of 322 grassland individuals among which some solitary species are represented. Here we highlighted that

considering only the oilseed rape area in the landscape is not enough to understand its effects and
 must be combined with landscape configuration descriptors.

325 In our study, honeybee abundance was not significantly affected by oilseed rape landscape variables. 326 This may be due to the low number of captured individuals but also to the human choice of beehives 327 placement. Honeybees need high quantities of food for their colony and oilseed rape fields could 328 provide these resources. Thus, honeybees may concentrate into flowering oilseed rape fields rather 329 than visiting grasslands where resources availability were scarcer (Rollin et al., 2013). Consequently, 330 honeybee abundance in grassland is likely to decrease in permanent grasslands during oilseed rape 331 flowering period. Other generalist species not studied here due to scarce captures (bumblebees and 332 hoverflies) might exhibit similar dilution in the landscape (Holzschuh et al., 2016; Rollin et al., 2013;

333 Stanley and Stout, 2014) thus explaining the low number of captured individuals in grasslands.

334 4.3. Linking pollinators and *C. pratensis* seed set

We confirmed here that *C. pratensis* depends on pollinators for its seed production. In our study, the abundance of honeybees was correlated with its seed set suggesting that *C. pratensis* seed set may be partly driven by the visitation of honeybees in permanent grasslands during oilseed rape flowering period. However, seed set, but not honeybee abundance, decreased with increasing oilseed rape area in the landscape.

340 Other pollinator groups such as hoverflies, bumblebees and solitary bees are known to visit *C*.

341 *pratensis*. However, we did not find a significant correlation between solitary bee abundance and

342 seed set. This absence of correlation associated with the significant correlation found for honeybees

343 contrasted with the respective abundance of these bee groups: solitary bees were 36 times more

344 abundant than honeybees (probably because honeybees prefer to forage on highly rewarding flower

345 patches such as oilseed rape fields and are very effective in communicating their location). This may

346 be due to (i) a difference in pollination efficacy between honeybees and solitary bees even though

347 solitary bees have often been reported to pollinate as effectively as honeybees (Jauker et al., 2012;

- Javorek et al., 2002; Vicens and Bosch, 2000) and to (ii) different levels of pollination efficacy and
- 349 attraction to *C. pratensis* between solitary bees. Since we lack species-specific data on solitary bees,
- 350 it could be that total number of bees is masking the effect of few influential species. Flower visitation
- 351 data combined with pollen load measurements on bees visiting *C. pratensis* would help to conclude
- 352 which species are more important.

Other describing variables of the pollinator community than pollinator abundance may be important to explain different levels of plant reproductive success (Blitzer et al., 2016; Klein et al., 2003; Orford et al., 2016). Further investigation would be essential to determine the dependence of *C. pratensis*, a pollinator-generalist wild plant towards pollinator abundance, pollinator taxonomical and functional diversity.

358 4.4. Implications and perspectives

359 We observed that the reproductive success of C. pratensis was influenced by the environment 360 surrounding the plant, both at the local scale through the presence of wild plants and at the 361 landscape scale through the area covered by oilseed rape fields. Flowering oilseed rape area in the 362 landscape reduced seed set of C. pratensis in surrounding permanent grasslands. Consequently, the 363 attractiveness of the crop during its blooming may represent a threat at the landscape scale for both 364 pollinator-specialist (Holzschuh et al., 2011) and pollinator generalist co-flowering wild plants which 365 share similar floral traits with oilseed rape. Future studies focusing on the reproductive success of a 366 higher number of species varying in functional similarity to oilseed rape would be essential to 367 confirm the hypothesis that species closely related to oilseed rape are more likely to be influenced by 368 oilseed rape.

The effects of oilseed rape highlighted in this study were specific of the oilseed rape flowering period while its effects may be completely different at other periods, especially rapidly after oilseed rape flowering. Once oilseed rape flowering had ceased, pollinators attracted by oilseed rape move to resourceful habitats such as SNH, including grasslands (Hanley et al., 2011). Consequently,

abundance of such pollinators may increase in surrounding semi-natural habitats (Herrmann et al.,
2007; Kovács-Hostyánszki et al., 2013) and thus lead to an increase of wild plant reproductive success
at this period. However, previous findings did not find such positive effect on the reproductive
success of wild plants flowering after oilseed rape. To explain this absence of effect, authors
suggested that the spillover effect of oilseed rape on wild plant pollination is very short and
disappear quickly after oilseed rape flowering (Cussans et al., 2010; Diekötter et al., 2010; Ekroos et
al., 2015; Kovács-Hostyánszki et al., 2013).

380 Landscape configuration has rarely been studied in addition to landscape compositional effects, even

though it impacts floral, nesting and overwintering resources for bees (Hadley and Betts, 2012;

382 Kremen et al., 2007). We demonstrated that the configuration of flowering oilseed rape fields in the

383 landscape modulated the effects of oilseed rape area on solitary bee abundance. This result

associated with previous findings suggested that both aspects of the landscape should be integrated

in future studies. Pursuing empirical research in this direction is important if we want to provide

useful guidance for plants and pollinators conservation in farming landscapes.

#### 387 Acknowledgements

We are grateful to the farmers who nicely provided us access to their land. We thank Anne Vallet who helped us for hoverflies identification. We also thank Claude Gallois and Chloé Fournier who participated to the field works and Eric Van Reeth whose comments greatly improved the manuscript. This research did not receive any specific grant from funding agencies in the public,

392 commercial, or not-for-profit sectors.

393

394

395

### 397 References

398	Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat
399	fragmentation: review and synthesis through a meta-analysis. Ecol. Lett. 9, 968–980.
400	Aizen, M.A., Ashworth, L., Galetto, L., 2002. Reproductive success in fragmented habitats: do
401	compatibility systems and pollination specialization matter? J. Veg. Sci. 13, 885–892.
402	Ashworth, L., Aguilar, R., Galetto, L., Aizen, M.A., 2004. Why do pollination generalist and specialist
403	plant species show similar reproductive susceptibility to habitat fragmentation? J. Ecol. 92,
404	717–719.
405	Bjerknes, AL., Totland, O., Hegland, S.J., Nielsen, A., 2007. Do alien plant invasions really affect
406	pollination success in native plant species? Biol. Conserv. 138, 1–12.
407	https://doi.org/10.1016/j.biocon.2007.04.015
408	Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, AM., Rand, T.A., Tscharntke, T., 2012. Spillover of
409	functionally important organisms between managed and natural habitats. Agric. Ecosyst.
410	Environ. 146, 34–43. https://doi.org/10.1016/j.agee.2011.09.005
411	Blitzer, E.J., Gibbs, J., Park, M.G., Danforth, B.N., 2016. Pollination services for apple are dependent
412	on diverse wild bee communities. Agric. Ecosyst. Environ. 221, 1–7.
413	Breheny, P., Burchett, W., 2016. visreg: Visualization of regression models.
414	Brown, B.J., Mitchell, R.J., 2001. Competition for pollination: effects of pollen of an invasive plant on
415	seed set of a native congener. Oecologia 129, 43–49.
416	https://doi.org/10.1007/s004420100700
417	Burd, M., 1994. Bateman Principle and Plant Reproduction - the Role of Pollen Limitation. Bot. Rev.
418	60, 83–139. https://doi.org/10.1007/BF02856594
419	Calabuig, I., 2000. Solitary bees and bumblebees in a Danish agricultural landscape (Dissertation).
420	University of Copenhagen, Copenhagen, Denmark.
421	Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts,
422	S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin,
	18

- T., Westphal, C., Woyciechowski, M., Vaissiere, B.E., 2009. Landscape context and habitat
  type as drivers of bee diversity in European annual crops. Agric. Ecosyst. Environ. 133, 40–47.
  https://doi.org/10.1016/j.agee.2009.05.001
- 426 Cartar, R.V., Real, L.A., 1997. Habitat structure and animal movement: the behaviour of bumble bees
- 427 in uniform and random spatial resource distributions. Oecologia 112, 430–434.
- 428 https://doi.org/10.1007/s004420050329
- 429 Caruso, C.M., 1999. Pollination of Ipomopsis aggregata (Polemoniaceae): Effects of intra-vs.
- 430 interspecific competition. Am. J. Bot. 86, 663–668. https://doi.org/10.2307/2656575
- 431 Carvalheiro, L.G., Biesmeijer, J.C., Benadi, G., Fruend, J., Stang, M., Bartomeus, I., Kaiser-Bunbury,
- 432 C.N., Baude, M., Gomes, S.I.F., Merckx, V., Baldock, K.C.R., Bennett, A.T.D., Boada, R.,
- 433 Bommarco, R., Cartar, R., Chacoff, N., Danhardt, J., Dicks, L.V., Dormann, C.F., Ekroos, J.,
- 434 Henson, K.S.E., Holzschuh, A., Junker, R.R., Lopezaraiza-Mikel, M., Memmott, J., Montero-
- 435 Castano, A., Nelson, I.L., Petanidou, T., Power, E.F., Rundlof, M., Smith, H.G., Stout, J.C.,
- 436 Temitope, K., Tscharntke, T., Tscheulin, T., Vila, M., Kunin, W.E., 2014. The potential for
- 437 indirect effects between co-flowering plants via shared pollinators depends on resource
- 438 abundance, accessibility and relatedness. Ecol. Lett. 17, 1389–1399.
- 439 https://doi.org/10.1111/ele.12342
- 440 Cresswell, J.E., 2000. A comparison of bumblebees' movements in uniform and aggregated
- 441 distributions of their forage plant. Ecol. Entomol. 25, 19–25. https://doi.org/10.1046/j.1365442 2311.2000.00230.x
- 443 Cussans, J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B., Osborne, J.L., 2010. Two Bee-Pollinated
- 444 Plant Species Show Higher Seed Production when Grown in Gardens Compared to Arable
- 445 Farmland. Plos One 5, e11753. https://doi.org/10.1371/journal.pone.0011753
- 446 Diekötter, T., Kadoya, T., Peter, F., Wolters, V., Jauker, F., 2010. Oilseed rape crops distort plant-
- 447 pollinator interactions. J. Appl. Ecol. 47, 209–214. https://doi.org/10.1111/j.1365-
- 448 2664.2009.01759.x

- Dray, S., Dufour, A.-B., 2007. The ade4 package: Implementing the duality diagram for ecologists. J.
  Stat. Softw. 22, 1–20.
- 451 Ekroos, J., Jakobsson, A., Wideen, J., Herbertsson, L., Rundlof, M., Smith, H.G., 2015. Effects of
- 452 landscape composition and configuration on pollination in a native herb: a field experiment.

453 Oecologia 179, 509–518. https://doi.org/10.1007/s00442-015-3370-y

- 454 Ekroos, J., Rundlof, M., Smith, H.G., 2013. Trait-dependent responses of flower-visiting insects to
- 455 distance to semi-natural grasslands and landscape heterogeneity. Landsc. Ecol. 28, 1283–
- 456 1292. https://doi.org/10.1007/s10980-013-9864-2
- 457 Fitter, A.H., Peat, H.J., 1994. The Ecological Flora Database. J. Ecol. 82, 415–425.
- 458 https://doi.org/10.2307/2261309
- 459 Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017.
- 460 Functional flower traits and their diversity drive pollinator visitation. Oikos [In Press].
  461 https://doi.org/10.1111/oik.03869
- 462 Fox, J., Weisberg, S., 2010. An R Companion to Applied Regression, 2nd Edition. ed. Sage, Thousand
  463 Oaks.
- 464 Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics:
- 465 absence of evidence not evidence of absence. Biol. Rev. 87, 526–544.
- 466 Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tscharntke, T., Holzschuh, A.,
- 467 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. J.
  468 Appl. Ecol. 51, 505–513.
- 469 Hanley, M.E., Franco, M., Dean, C.E., Franklin, E.L., Harris, H.R., Haynes, A.G., Rapson, S.R., Rowse, G.,
- 470 Thomas, K.C., Waterhouse, B.R., Knight, M.E., 2011. Increased bumblebee abundance along
- 471 the margins of a mass flowering crop: evidence for pollinator spill-over. Oikos 120, 1618–
- 472 1624. https://doi.org/10.1111/j.1600-0706.2011.19233.x

- Hegland, S.J., Totland, O., 2005. Relationships between species' floral traits and pollinator visitation
  in a temperate grassland. Oecologia 145, 586–594. https://doi.org/10.1007/s00442-0050165-6
- 476 Herrmann, F., Westphal, C., Moritz, R.F.A., Steffan-Dewenter, I., 2007. Genetic diversity and mass
- 477 resources promote colony size and forager densities of a social bee (Bombus pascuorum) in
- 478 agricultural landscapes. Mol. Ecol. 16, 1167–1178. https://doi.org/10.1111/j.1365-

479 294X.2007.03226.x

480 Holzschuh, A., Dainese, M., Gonzalez-Varo, J.P., Mudri-Stojnic, S., Riedinger, V., Rundlof, M., Scheper,

481 J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith,

- 482 H.G., Vila, M., Vujic, A., Steffan-Dewenter, I., 2016. Mass-flowering crops dilute pollinator
- 483 abundance in agricultural landscapes across Europe. Ecol. Lett. 19, 1228–1236.
- 484 https://doi.org/10.1111/ele.12657
- Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering
   crops leads to transient pollinator dilution and reduced wild plant pollination. Proc. R. Soc. B-

487 Biol. Sci. 278, 3444–3451. https://doi.org/10.1098/rspb.2011.0268

- 488 Hoyle, M., Hayter, K., Cresswell, J.E., 2007. Effect of pollinator abundance on self-fertilization and
- 489 gene flow: Application to GM canola. Ecol. Appl. 17, 2123–2135. https://doi.org/10.1890/06490 1972.1
- Jakobsson, A., Ågren, J., 2014. Distance to semi-natural grassland influences seed production of
   insect-pollinated herbs. Oecologia 175, 199–208. https://doi.org/10.1007/s00442-014-2904-
- 493

z

- 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.

496 https://doi.org/10.1111/j.1461-9563.2011.00541.x

Javorek, S.K., Mackenzie, K.E., Vander Kloet, S.P., 2002. Comparative pollination effectiveness among
bees (Hymenoptera : Apoidea) on lowbush blueberry (Ericaceae : Vaccinium angustifolium).

- 499 Ann. Entomol. Soc. Am. 95, 345–351. https://doi.org/10.1603/0013-
- 500 8746(2002)095[0345:CPEABH]2.0.CO;2
- 501 Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R.,
- 502 Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A.,
- 503 Danforth, B.N., Dudenhoeffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C.,
- 504 Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y.,
- 505 Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlof, M.,
- 506 Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S.,
- 507 Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee
- 508 pollinators in agroecosystems. Ecol. Lett. 16, 584–599. https://doi.org/10.1111/ele.12082
- Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003. Fruit set of highland coffee increases with the
   diversity of pollinating bees. Proc. R. Soc. B-Biol. Sci. 270, 955–961.
- 511 https://doi.org/10.1098/rspb.2002.2306
- 512 Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston,
- 513 M.O., Mitchell, R.J., Ashman, T.L., 2005. Pollen limitation of plant reproduction: Pattern and
- process, in: Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto,
  pp. 467–497.
- 516 Kovács-Hostyánszki, A., Batary, P., Baldi, A., 2011. Local and landscape effects on bee communities of

517 Hungarian winter cereal fields. Agric. For. Entomol. 13, 59–66.

518 https://doi.org/10.1111/j.1461-9563.2010.00498.x

- 519 Kovács-Hostyánszki, A., Haenke, S., Batary, P., Jauker, B., Baldi, A., Tscharntke, T., Holzschuh, A.,
- 520 2013. Contrasting effects of mass-flowering crops on bee pollination of hedge plants at
- 521 different spatial and temporal scales. Ecol. Appl. 23, 1938–1946. https://doi.org/10.1890/12-
- 522 2012.1
- 523 Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L.,
- 524 Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone,

525	E.E., Greenleaf, S.S., Keitt, T.H., Klein, AM., Regetz, J., Ricketts, T.H., 2007. Pollination and
526	other ecosystem services produced by mobile organisms: a conceptual framework for the
527	effects of land-use change. Ecol. Lett. 10, 299–314. https://doi.org/10.1111/j.1461-
528	0248.2007.01018.x
529	Kühn, I., Durka, W., Klotz, S., 2004. BiolFlor - a new plant-trait database as a tool for plant invasion
530	ecology. Divers. Distrib. 10, 363–365. https://doi.org/10.1111/j.1366-9516.2004.00106.x
531	Magrach, A., Holzschuh, A., Bartomeus, I., Riedinger, V., Roberts, S.P., Rundlöf, M., Vujić, A., Wickens,
532	J.B., Wickens, V.J., Bommarco, R., Gonzalez-Varo, J.P., Potts, S.G., Smith, H.G., Steffan-
533	Dewenter, I., Vilà, M., 2017. Plant–pollinator networks in semi-natural grasslands are
534	resistant to the loss of pollinators during blooming of mass-flowering crops. Ecography 40, 1–
535	13.
536	Marrec, R., Badenhausser, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N., Gauffre, B., 2015.
537	Crop succession and habitat preferences drive the distribution and abundance of carabid
538	beetles in an agricultural landscape. Agric. Ecosyst. Environ. 199, 282–289.
539	Marrero, H.J., Medan, D., Zarlaysky, G.E., Torretta, J.P., 2016. Agricultural land management
540	negatively affects pollination service in Pampean agro-ecosystems. Agric. Ecosyst. Environ.
541	218, 28–32. https://doi.org/10.1016/j.agee.2015.10.024
542	McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS: Spatial Pattern Analysis Program for
543	Categorical and Continuous Maps. Amherst, Massachusetts.
544	Michener, C.D., 2007. The Bees of the World, 2nd Revised Edition. ed. Johns Hopkins University
545	Press, Baltimore.
546	Morris, W.F., 2003. Which mutualists are most essential? Buffering of plant reproduction against the
547	extinction of pollinators, in: The Importance of Species: Perspectives on Expendability and
548	Triage. Peter Kareiva and Simon A. Levin, Princeton, pp. 260–280.
549	Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals?
550	Oikos 120, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

551	Orford, K.A., Murray, P.J., Vaughan, I.P., Memmott, J., 2016. Modest enhancements to conventional
552	grassland diversity improve the provision of pollination services. J. Appl. Ecol. 53, 906–915.
553	https://doi.org/10.1111/1365-2664.12608

- Parsche, S., Fruend, J., Tscharntke, T., 2011. Experimental environmental change and mutualistic vs.
- 555 antagonistic plant flower-visitor interactions. Perspect. Plant Ecol. Evol. Syst. 13, 27–35.
- 556 https://doi.org/10.1016/j.ppees.2010.12.001
- R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for
   Statistical Computing, Vienna, Austria.
- Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissiere, B.E., Henry, M., 2013.
- 560 Differences of floral resource use between honey bees and wild bees in an intensive farming
- 561 system. Agric. Ecosyst. Environ. 179, 78–86. https://doi.org/10.1016/j.agee.2013.07.007
- 562 Rundlöf, M., Persson, A.S., Smith, H.G., Bommarco, R., 2014. Late-season mass-flowering red clover
- 563 increases bumble bee queen and male densities. Biol. Conserv. 172, 138–145.
- 564 https://doi.org/10.1016/j.biocon.2014.02.027
- 565 Salisbury, E., 1965. Reproduction of Cardamine Pratensis L and Cardamine Palustris Peterman
- 566 Particularly in Relation to Their Specialized Foliar Vivipary and Its Deflexion of Constraints of
- 567 Natural Selection. Proc. R. Soc. Ser. B-Biol. Sci. 163, 321–342.
- 568 https://doi.org/10.1098/rspb.1965.0072
- 569 Senapathi, D., Goddard, M.A., Kunin, W.E., Baldock, K.C.R., 2017. Landscape impacts on pollinator
- 570 communities in temperate systems: evidence and knowledge gaps. Funct. Ecol. 31, 26–37.
- 571 https://doi.org/10.1111/1365-2435.12809
- 572 Stanley, D.A., Stout, J.C., 2014. Pollinator sharing between mass-flowering oilseed rape and co-
- 573 flowering wild plants: implications for wild plant pollination. Plant Ecol. 215, 315–325.
- 574 https://doi.org/10.1007/s11258-014-0301-7
- 575 Steffan-Dewenter, I., Kuhn, A., 2003. Honeybee foraging in differentially structured landscapes. Proc.
- 576 R. Soc. B-Biol. Sci. 270, 569–575. https://doi.org/10.1098/rspb.2002.2292

- 577 Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent
- 578 effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.

579 https://doi.org/10.2307/3071954

- 580 Van Reeth, C., Michel, N., Bockstaller, C., Caro, G., 2018. Current and previous spatial distributions of
- 581 oilseed rape fields influence the abundance and the body size of a solitary wild bee, Andrena
- 582 cineraria, in permanent grasslands. PLOS ONE 13, e0197684.
- 583 https://doi.org/10.1371/journal.pone.0197684
- Vicens, N., Bosch, J., 2000. Pollinating efficacy of Osmia cornuta and Apis mellifera (Hymenoptera:

585 Megachilidae, Apidae) on 'red Delicious' apple. Environ. Entomol. 29, 235–240.

586 Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial

587 habitats, in: Linnean Society Symposium Series. Academic Press Limited, pp. 1–16.

- 588 Woodcock, B.A., Isaac, N.J.B., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A., Pywell, R.F., 2016.
- 589 Impacts of neonicotinoid use on long-term population changes in wild bees in England. Nat.
- 590 Commun. 7, 12459. https://doi.org/10.1038/ncomms12459
- 591 Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and
- 592 extensions in ecology with R, Statistics for Biology and Health. Springer, New York.
- 593
- 594
- 595
- 596
- 597
- 598

599

### 601 Appendix

- 602 Appendix 1: Relation between (a) honeybee abundance and *C. pratensis* seed set, (b) solitary bee abundance and *C.*
- 603 pratensis seed set. Pollinator abundances and seed set were log10(x+1) transformed.







	df	Sum Sq	Estimate	t value	P
Seed Set					
%OSR	1	0.32	-0.027	-2.63	0.017
$log_{10}$ (flower abundance +1)	1	0.26	-0.256	-2.37	0.030
log <sub>10</sub> (conspecific abundance +1)	1	0.23	0.290	2.23	0.040
OSR adjacency - Yes	1	0.14	0.236	1.77	0.095
Solitary bees					
%OSR	1	0.25	0.205	3.26	0.004
OSR-AI	1	0.30	0.006	2.61	0.018
%OSR:OSR-AI	1	1.03	-0.003	-3.04	0.007
Honeybees					
OSR-AI	1	0.80	-0.006	-1.91	0.071
%SNH	1	0.67	-0.013	-1.75	0.096