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

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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
4 plants occurring in adjacent non-crop habitats. We evaluated the influence of flowering oilseed rape
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), and (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 (Carvalho et al., 2014;
39 Diekötter et al., 2010). Flowering OSR fields attract pollinators from surrounding landscapes
40 (Magrath et al., 2017; Rollin et al., 2013; Van Reeth et al., 2018; Woodcock et al., 2016) because of
41 easily accessible and highly abundant floral resources (Hoyle et al., 2007). Consequently, the
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
53 OSR landscape influences on the reproductive success of co-flowering plants seem to be dependent
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
60 can hypothesize that plant species which share similar floral traits mediating interactions with
61 pollinators are more likely influence each other (Carvalho et al., 2014; Hegland and Totland, 2005).
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.

65 In addition to landscape compositional effects, the effects of landscape configuration (i.e. the spatial
66 arrangement of habitat patches in the landscape) on pollinators and insect-pollinated plants have
67 been studied (Carré et al., 2009; Ekroos et al., 2015; Jakobsson and Ågren, 2014; Kennedy et al.,
68 2013). Kennedy *et al.* (2013) synthesized the results of 39 studies in cultivated habitats and found
69 that habitat aggregation in the landscape had the greatest influence on wild bees among the
70 configuration metrics analyzed (isolation, habitat shape and aggregation).

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

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

81 Here, we aim to assess the influence of OSR through its area and its aggregation in the landscape on
82 pollinator abundance in permanent grasslands and on the reproductive success of a co-flowering
83 wild plant functionally close to OSR. We hypothesized that the effect of OSR area both on pollinators
84 and on the reproductive success of a co-flowering wild plant can be modulated by OSR aggregation in
85 the landscape. To test these hypotheses, we simultaneously monitored the seed set of a wild plant
86 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

89 The study was carried out in 2016 in the eastern part of the “Parc Naturel Régional de Lorraine”,
90 county of Moselle, Lorraine, France (48°48'46"N, 6°43'14"E). We selected 22 similarly managed
91 permanent grasslands, which were mowed (not grazed) and fertilization never exceeded 40kg
92 nitrogen/ha/year for the last five years. Grasslands also had similar sizes (mean value \pm standard
93 deviation = 4.3 ± 1.2 ha). The mean distance between study sites was $3\,851 \pm 1\,535$ m (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 ($30.8 \pm$
96 22.4% ; min = 0%; max = 70.1%), forest ($24.7 \pm 29.0\%$; min = 0%; max = 89.0%) and permanent
97 grasslands ($21.7 \pm 13.5\%$; min = 1.2%; max = 55.0%). OSR area in the landscape was in average $6.5 \pm$
98 6.5% , ranging from 0 to 19.2%. 8 grasslands were adjacent to an OSR field whereas 14 were at least
99 280 meters away (in average = 659 ± 259 m) from an OSR field.

100 **Figure 1: (a) Study region and study areas in the “Parc Naturel Régional de Lorraine”, county of Moselle, Lorraine, France.**
101 **Black circles represent the area surrounding each permanent grassland within a 1 000m radius. (b) Seed set and bee**
102 **experiment design implemented in the centroid of each permanent grassland.** In the middle of each grassland, five
103 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
113 position). Consequently, both plants should share some pollinators, making the reproductive success
114 of *C. pratensis* particularly vulnerable to OSR (Carvalho 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
118 transect used to sample pollinators (Fig. 1). For each plant, we identified and marked one flower bud
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
123 additional flower buds were bagged in the monitored grasslands.

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

126 the number of *C. pratensis* plants surrounding each selected plant (hereafter referred to as
127 'conspecific abundance') in a 2-meter radius. Secondly, we evaluated the global floristic
128 opportunities by quantifying the number of flowers (considering all flowering species) in ten 1m²
129 quadrats randomly placed within 30 meters around plot centroid. The flower abundance in the
130 grassland was the pooled number of flowers found in the ten quadrats.

131 We harvested *C. pratensis* ripe fruits in late May. The reproductive success of *C. pratensis* in each
132 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.

142 Hoverflies and bumblebees were excluded from this study since only 5 and 33 individuals were
143 captured respectively. We split the remaining pollinator community into two groups: honeybees and
144 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
148 surrounding each grassland was described in a 1 000m buffer from vectorial data. This single spatial
149 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®, 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
161 FRAGSTATS (McGarigal et al., 2012) in each of the 22 buffers. The Aggregation Index produces a
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

174 variable 'OSR adjacency' coded as 1 when the grassland and an OSR field were contiguous or 0 in
175 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 $\log_{10}(x+1)$ -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
183 transformed with $\log_{10}(x+1)$. Full models were simplified by excluding one by one non-significant
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).

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

193 Finally, we assessed the relation between seed set and the abundance of each bee group with
194 spearman correlations.

195 We tested the multi-collinearity between predictors with Variance Inflation Factor (VIF) (Zuur et al.,
196 2009) and found no variance inflation pattern since $VIF < 2.02$. $VIF = 3$ is often considered to be a
197 threshold value (Zuur et al., 2009). Pearson correlation (r) between OSR area in the landscape and
198 OSR adjacency was relatively high (0.68) but was inferior to 0.7, the threshold value proposed by

199 Dormann *et al.* (2013). Correlations between other predictors gave $|r| < 0.32$. Spatial autocorrelation
200 was also checked for the abundance of each pollinator group and seed set using Mantel tests with 4
201 999 permutations (Dray and Dufour, 2007). No autocorrelation was found (Mantel statistics: $P > 0.17$
202 and $r < 0.14$).

203 3. Results

204 3.1. Plant and bee monitoring

205 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
209 ranged from 0 to 24 seeds per fruit (mean = 5.2 ± 2.9). Bagged flowers gave almost no seed (1 seed
210 found among all 40 bagged flowers) while we counted 199 seeds for accessible flowers located on
211 the same plant (N = 40). Therefore, we considered that *C. pratensis* has to be visited by pollinators to
212 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
215 abundance in the permanent grasslands ranged from 11 to 565 individuals (mean = 164.7 ± 144.7)
216 and honeybee abundance ranged from 0 to 32 individuals (4.5 ± 8.5).

217 3.2. Local and landscape influences

218 3.2.1. Influences on *C. pratensis* seed set

219 For the seed set model, we obtained, $R^2_{adj} = 0.26$ indicating a moderate model fit. *C. pratensis* seed
220 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
223 similar influence strength on seed set (see the Sum Sq values. in Tab. 1).

224

225 **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

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

234 3.2.2. Influences on bee abundance

235 For pollinator abundance model, we obtained, $R^2_{adj} = 0.39$ and 0.15 respectively for solitary bees and
236 honeybees. These values indicated a moderate model fit for solitary bees and a weak model fit for
237 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**
245 **solitary bee abundance.** Predictions returned by the solitary bee abundance model are shown with colored lines which
246 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_{10} 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
252 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**

255 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
258 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
260 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
262 landscape aggregation. Finally, we observed that seed set was significantly correlated to honeybee
263 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
266 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

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

275 Seed set was only marginally higher in permanent grasslands adjacent to oilseed rape fields than in
276 other grasslands. This effect, known as the 'spillover effect' (Blitzer et al., 2012), was demonstrated
277 in previous findings (Cussans et al., 2010; Kovács-Hostyánszki et al., 2013): wild plant benefited from
278 the close proximity to mass flowering crops which attracted some pollinators and enhanced, in turn,
279 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).

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

299 suggesting a competition for pollinators at the plot level (Brown and Mitchell, 2001; Caruso, 1999)
300 possibly because other grassland plant species such as *Taraxacum officinale* W. (Asteraceae) were
301 more attractive than *C. pratensis* (Fornoff et al., 2017). Some other studies found a positive effect of
302 local floral availability on pollination success (Orford et al., 2016). In conventional grasslands or field
303 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

306 Landscape composition and landscape configuration influenced differently the abundance of solitary
307 bees 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
320 competition between bee species due to spatial partitioning within a group of fields or within a field
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

323 considering only the oilseed rape area in the landscape is not enough to understand its effects and
324 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

335 We confirmed here that *C. pratensis* depends on pollinators for its seed production. In our study, the
336 abundance of honeybees was correlated with its seed set suggesting that *C. pratensis* seed set may
337 be partly driven by the visitation of honeybees in permanent grasslands during oilseed rape flowering
338 period. However, seed set, but not honeybee abundance, decreased with increasing oilseed rape
339 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;

348 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.

353 Other describing variables of the pollinator community than pollinator abundance may be important
354 to explain different levels of plant reproductive success (Blitzer et al., 2016; Klein et al., 2003; Orford
355 et al., 2016). Further investigation would be essential to determine the dependence of *C. pratensis*, a
356 pollinator-generalist wild plant towards pollinator abundance, pollinator taxonomical and functional
357 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.

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

373 abundance of such pollinators may increase in surrounding semi-natural habitats (Herrmann et al.,
374 2007; Kovács-Hostyánszki et al., 2013) and thus lead to an increase of wild plant reproductive success
375 at this period. However, previous findings did not find such positive effect on the reproductive
376 success of wild plants flowering after oilseed rape. To explain this absence of effect, authors
377 suggested that the spillover effect of oilseed rape on wild plant pollination is very short and
378 disappear quickly after oilseed rape flowering (Cussans et al., 2010; Diekötter et al., 2010; Ekroos et
379 al., 2015; Kovács-Hostyánszki et al., 2013).

380 Landscape configuration has rarely been studied in addition to landscape compositional effects, even
381 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
384 associated with previous findings suggested that both aspects of the landscape should be integrated
385 in future studies. Pursuing empirical research in this direction is important if we want to provide
386 useful guidance for plants and pollinators conservation in farming landscapes.

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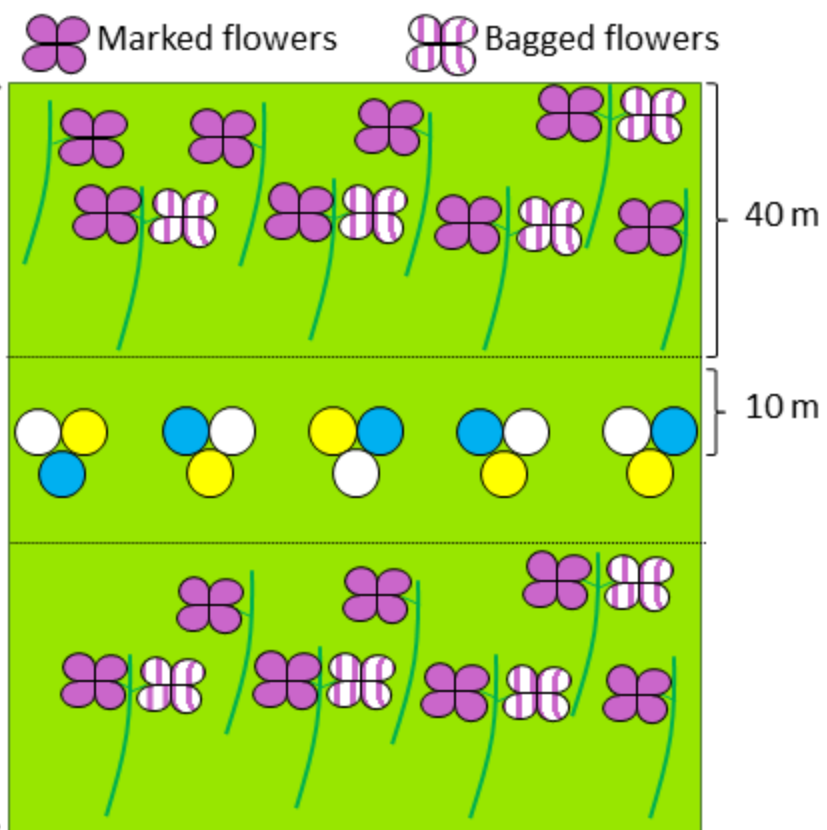
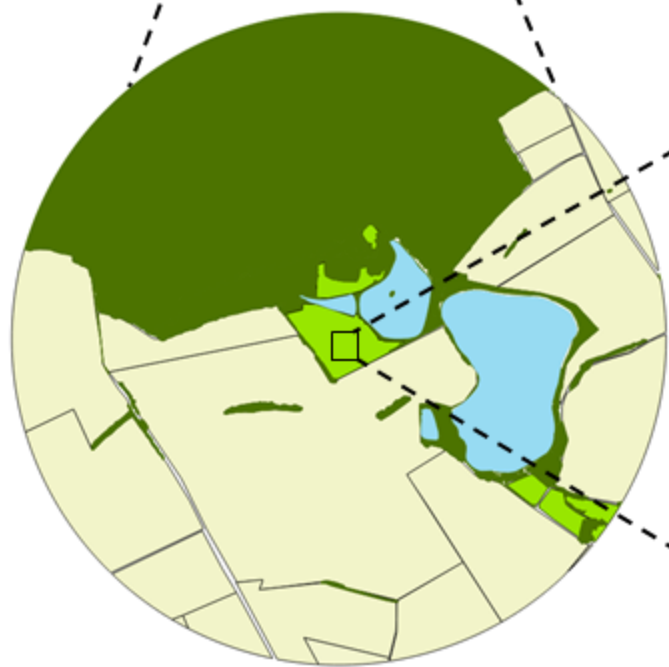
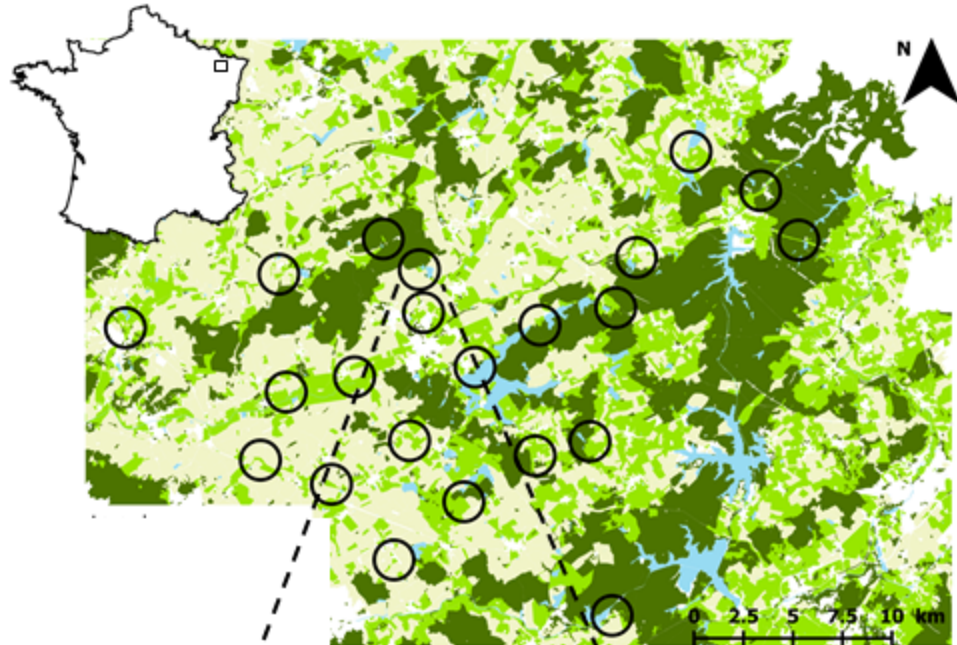
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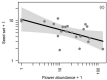
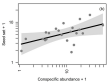
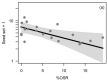
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601 **Appendix**

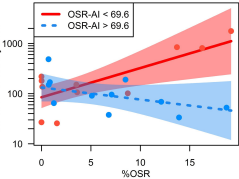
602 **Appendix 1: Relation between (a) honeybee abundance and *C. pratensis* seed set, (b) solitary bee abundance and *C.***

603 ***pratensis* seed set. Pollinator abundances and seed set were $\log_{10}(x+1)$ transformed.**





Abundance of solitary bees + 1



	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 ₁₀ (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