



HAL
open science

Pollination efficiency in farmland landscapes: exploring the relative roles of spillover, dilution and complementarity between habitats

Maxime Ragué, Vincent Bretagnolle, Olivier Martin, Thomas Perrot, Jean-Luc Gautier, Florence Carpentier, Sabrina Gaba

► To cite this version:

Maxime Ragué, Vincent Bretagnolle, Olivier Martin, Thomas Perrot, Jean-Luc Gautier, et al.. Pollination efficiency in farmland landscapes: exploring the relative roles of spillover, dilution and complementarity between habitats. *Landscape Ecology*, 2022, 37 (9), pp.2413-2433. 10.1007/s10980-022-01482-0 . hal-03738600

HAL Id: hal-03738600

<https://hal.science/hal-03738600>

Submitted on 15 Nov 2023

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.

1 **Pollination efficiency in farmland landscapes: exploring the relative roles of spillover, dilution and**
2 **complementarity between habitats**

3

4 Maxime Ragué^{1,2}, Vincent Bretagnolle^{1,3} Olivier Martin⁴, Thomas Perrot^{1,2}, Jean-Luc Gautier^{1,2}, Florence
5 Carpentier^{5,6}, Sabrina Gaba^{1,2,3}

6

7 ¹ *Centre d'Etudes Biologiques de Chizé, UMR7372, CNRS & Université de La Rochelle, F-79360 Villiers-en-Bois,*
8 *France*

9 ² *USC 1339 Centre d'Etudes Biologiques de Chizé, INRAE, 76390 Villiers-en-Bois, France*

10 ³ *LTSER « Zone Atelier Plaine & Val de Sèvre », 79360 Villiers-en-Bois, France*

11 ⁴ *BioSP, INRAE, 84914 Avignon, France*

12 ⁵ *Université Paris-Saclay, INRAE, UR MaLAGE, 78350, Jouy-en-Josas, France.*

13 ⁶ *AgroParisTech, 75005, Paris, France*

14

15

16 Corresponding author: sabrina.gaba@inrae.fr (+33 5 49 09 96 01)

17

18 Maxime Ragué (0000-0001-9100-6923)

19 Vincent Bretagnolle (0000-0002-2320-7755)

20 Thomas Perrot (0000-0003-3881-1370)

21 Florence Carpentier (0000-0001-6204-2220)

22 Sabrina Gaba (0000-0002-7145-6713)

23 **Abstract**

24 *Context* Recognized as a critical ecosystem service in farmland, pollination is threatened by the decline of
25 pollinators, notably due the homogenization of the landscape and the decline of floral resources. However, there
26 is still a limited understanding of the interplay between landscape features and the pulses of floral resources
27 provided by mass-flowering crops.

28 *Objective* The goals of this study were to (i) determine how pollination efficiency varies with the amount of
29 floral resources at field and landscape scales through the oilseed rape (OSR) flowering period and (ii) quantify the
30 magnitude of the pollination processes involved.

31 *Methods* Pollination efficiency (fruiting success) was measured using OSR plant phytometers placed in
32 grasslands, cereals and OSR fields varying in quantity of floral resources at both field and landscape scales. The
33 individual contributions of different processes to pollination were determined using a bagging experiment on plant
34 phytometers.

35 *Results* Pollination efficiency was enhanced during both the temporal period and in landscapes with a high
36 amount of OSR flowers, and semi-natural habitats as a result of higher pollinator presence. The bagging
37 experiment also supported a complementarity between habitats for pollinators, as insect-pollination in grasslands
38 and cereals was higher after OSR flowering, especially in OSR-rich landscapes, in regard to large-insect-
39 pollination.

40 *Conclusions* The floral resource availability drives insect-pollination through attraction, spillover, and spatial
41 and temporal complementarities between habitats. These results suggest that maximizing pollination efficiency in
42 farmland landscapes partly consisting of OSR fields should include a combination of habitats that provide
43 continuous floral resources.

44

45 **Key words:** Insect-pollination | Landscape composition | Semi-natural habitats | Temporal matching

46

47 **Introduction**

48 Agricultural landscapes are temporally and spatially highly dynamic mosaics of annual crops and semi-
49 natural elements. Landscape features such as crop diversity, or semi-natural habitat (SNH) surrounding fields, are
50 increasingly recognized as key factors determining biodiversity and the associated ecosystem services (Fahrig et
51 al. 2011, 2015; Martin et al. 2019; Dainese et al. 2019). However, despite the presumably strong effects of crop
52 phenology or temporal changes in land use on the availability of resources and nesting habitats for species
53 (Schellhorn et al. 2015), few studies have investigated the role of landscape features on biodiversity or ecosystem
54 services at different times, either on an annual basis or at the crop rotation level (Rusch et al. 2011; Le Féon et al.
55 2013; Vasseur et al. 2013). Maintaining pollinating insects is critical because of their key role in agroecosystem
56 functioning through the pollination of both crops and wild plants (Klein et al. 2007; Ollerton et al. 2011). Yet,
57 these insects may be particularly sensitive to temporal resource limitation since they rely exclusively on nectar and
58 pollen (Roulston and Goodell 2011), both available only for a few days in individual flowers (Rathcke and Lacey
59 1985; Elzinga et al. 2007).

60 Blooms of mass-flowering crops largely exceed the amount of floral resources provided by wild plants, and
61 are therefore highly attractive to bees (Holzschuh et al. 2011). However, this high amount of floral resources occurs
62 only during a limited period of time, a temporal pattern that may have cascading shortage effects on bees and
63 pollination over the season in agricultural landscapes (Diekötter et al. 2014; Requier et al. 2017). Given that bees
64 are optimal foragers and highly mobile organisms, temporal lags between flowering peaks either in a particular
65 field or at the landscape scale may result in a mismatch between the local number of flowers to be pollinated and
66 the number of available pollinating insects (Herbertsson et al. 2017; Fijen et al. 2019). Hence, sustaining pollinator
67 populations in agricultural landscapes requires maintaining spatial and temporal continuity of floral resources as
68 suggested by Mallinger et al. (2016). Ways to enhance the provision of complementary floral resources in space
69 and time include increasing the amount of SNH (Rollin et al. 2013) and organically farmed (OF) fields that host
70 higher density of wild plants (Requier et al. 2015; Wintermantel et al. 2019), or diversifying landscape composition
71 (Meyer et al. 2007; Petersen and Nault 2014). However, increasing the diversity of flower availability may have
72 considerable effects on pollinators and pollination. For instance, mass-flowering crops may attract pollinators from
73 surrounding SNH and/or OF fields. These movements can negatively affect wild plant species that have
74 overlapping flowering periods with crops, but at the same time may increase seed production in crops due to higher
75 pollination efficiency (Holzschuh et al. 2011). A high density of mass-flowering crops can also have potential
76 negative consequences on crop pollination (reduced seed production due to lower pollinator abundance) through
77 the dilution of available pollinators during their flowering period (Holzschuh et al. 2011, 2016).

78 While a number of studies have explored the relationships between bees and landscape features, the
79 efficiency of insect-pollination related to landscape elements while considering temporal variation in floral
80 resource availability has been little studied. This study attempted to address this gap by exploring how pollination
81 efficiency, in particular insect-pollination, varies with landscape composition both throughout the season,
82 including the flowering period of a mass-flowering crop, and afterwards. Pollination efficiency was measured with
83 a standardized metric, using the fruiting success of oilseed rape (*Brassica napus* L., OSR hereafter) plant
84 phytometers as a proxy to allow comparisons in space and time. Several studies have used crop species as plant
85 phytometers to estimate pollination efficiency: for example strawberry in SNH (Castle et al. 2019) or sunflower
86 or radish in crop fields (Bennett and Isaacs 2014; Hass et al. 2018). In the present study, OSR plant phytometers

87 were placed in three different crop types (grassland, cereal and OSR fields), in fields varying in the amount of
88 local floral resources, as well as in their surrounding landscapes, and at different times during OSR flowering
89 periods. The focal fields thus differed both in the amount and duration of floral resource availability, e.g. high
90 local floral resources in OSR fields during OSR blooming, and much lower after OSR flowering. Floral resources
91 provided by wild plants were rather constant over time and moderate in grasslands, and lower in cereal and OSR
92 fields (Frankl et al. 2005; Cole et al. 2017; Bourgeois et al. 2020).

93 The focal fields were distributed along three landscape gradients determined by the amount of SNH, OF and
94 OSR crops. The amount of floral resources around fields thus differed, with a presumably high and constant
95 availability of wildflowers in landscapes rich in OF (Hardman et al. 2016) and SNH (Cole et al. 2017), but a more
96 heterogeneous availability of floral resources in landscapes with a high level of OSR, from a very high amount
97 during OSR flowering to reduced resources outside the flowering period.

98 OSR is a mass-flowering crop that is mainly self-pollinated, however insect-pollination, involving both large
99 insects such as honeybees (Lindström et al. 2016; Perrot et al. 2018) and smaller insects such as wild bees (Zou et
100 al. 2017; Perrot et al. 2018) or to a lesser extent hoverflies (Jauker et al. 2012) also contributes to yield (Perrot et
101 al. 2018). Therefore, to disentangle the contribution of the pollination processes involved (pollination via large or
102 small insects, wind- or self-pollination), the phytometers were supplemented with a bagging experiment (using
103 bags of different mesh sizes on selected phytometer branches). When placed in OSR fields, especially during peak
104 OSR flowering, OSR phytometers were expected to show higher pollination efficiency because of higher OSR
105 pollen availability and/or higher abundance of pollinators attracted to the flowering OSR field. The bagging
106 experiment allowed differentiating between these two processes: no difference in fruiting success between control
107 flowers compared to bagged flowers (excluding insects) would suggest higher levels of OSR pollen leading to
108 higher pollination, while higher fruiting success in control flowers compared to bagged flowers would suggest a
109 higher number of insect pollinators. A lower pollination efficiency of OSR phytometers was also predicted in
110 landscapes with high amounts of OSR as compared to those with lower amounts of OSR, based on the hypothesis
111 of the dilution of insect pollinators. Similarly, a higher pollination efficiency in landscapes with high amounts of
112 SNH and OF was predicted as a result of higher pollinator abundance and attraction of insects to OSR. Finally,
113 positing complementarity between habitats, a higher pollination efficiency was predicted for OSR phytometers
114 placed in cereals and grasslands after the peak OSR flowering than during this peak, further predicting that the
115 pattern would be enhanced in OSR-rich landscapes by a spillover effect.

116 **Materials & methods**

117 Study site

118 The study was carried out in spring from 2015 to 2019 in the Zone Atelier Plaine & Val de Sèvre (hereafter
119 ZA-PVS; Fig. 1a), a research site of 435 km² in central-western France (46°14'N 0°28'W) that is part of the Long-
120 Term Social-Ecological Research (LTSER) network. Land cover was monitored each year at the field scale by
121 field workers and recorded in a GIS database (Bretagnolle et al. 2018). The study site was dominated by annual
122 crops (almost 75% on average during the five years of study) that include more than 30 crop types. In the cultivated
123 area, the most dominant crops during the study period were cereals as wheat or barley (54%) followed by sunflower
124 (12%) and maize (12%) which flower in summer, then OSR (8%) and peas (4%). For this study, the amount of OF
125 was calculated including all organically farmed fields. These covered between 6% (2015) to 9% (2019) of the

126 cultivated area. These OF fields consisted mainly of cereals (about 50%), followed by sunflower (10%) while less
 127 than 1% were OSR fields. Grasslands were excluded because these were included in the amount of SNH, together
 128 with hedgerows and fallow and set aside land. Grasslands encompassed meadows (permanent grasslands >6 years
 129 old) and alfalfa, clover, or mixed leguminous/grass (temporary grasslands, generally <5 years old).

130

131 #Fig. 1 approximately here#

132 OSR plant phytometers

133 OSR plants were used as phytometers to measure pollination efficiency. Phytometers allow pollination
 134 efficiency to be studied independently of resource availability (e.g. water, nutrients) so that variation is only
 135 influenced by insect abundance and pollen availability (Woodcock et al. 2014; Castle et al. 2019). The fruiting
 136 success was used as a proxy of pollination efficiency. Following Jauker et al. (2012) fruiting success was measured
 137 by the ratio of pods and flowers of an OSR plant branch (Fig. 1b). Individual OSR plants were collected in
 138 cultivated fields at the end of March each year. Plants were transplanted in 3 L pots and placed in an insect-proof
 139 greenhouse to avoid any insect-pollination. Potted plants were watered as needed and no fertilizer was added. A
 140 total of 616 OSR plant phytometers were used over the study period (198 in 2015, 196 in 2016, 94 in 2017, 58 in
 141 2018 and 70 in 2019).

142 From the OSR peak flowering (the beginning of April, though this depends on the year) to post-flowering
 143 (mid-May), phytometers were placed in OSR fields (124 fields in total over the five years), cereal fields (110 fields
 144 in four years) and grasslands (46 fields in three years; Fig. 1a) for four days, corresponding to the average flowering
 145 period of an individual OSR flower (Mesquida and Renard 1981). Two plant phytometers were placed per field,
 146 one in the field core and one at the edge (Fig. 1b), to account for variation in pollinator communities between these
 147 two field compartments (i.e. small pollinators are generally more abundant at field borders; Ricketts et al. 2008;
 148 Garratt et al. 2018), and therefore potential differences in the magnitude of small insect-pollination. On each OSR
 149 phytometer, four branches of similar size and flowering stage were selected, one of which became a control branch.
 150 On this branch, open flowers were tagged with two colour rings, delineating along the branch the portion in open
 151 flower stage. After four days, the number of flowers that further opened in the field were counted and identified
 152 using another colour mark on the branch (Fig. 1b). Plants were then placed back in the insect-proof greenhouse
 153 for pod ripening. When plant phytometers reached maturity (i.e. after seed maturation), all pods on each
 154 experimental branch were collected, either under treatment or control (see below and Appendix A for details on
 155 experimental protocols). Fruiting success (in %) was obtained by counting the number of flowers that produced
 156 pods on each branch between the marks and then calculating their proportion. 12.3% of the phytometers were
 157 excluded from the study because of missing data, e.g. dead plants, broken or dried branches that did not produce
 158 pods (7.9% of fields were without data).

159 *Pollinator exclusion by bagging*

160 For each OSR phytometer, the three other branches apart from the control branch were selected for exclusion
 161 treatments. Exclusion was used to assess the relative magnitude of large and small insect-, wind-, and self-
 162 pollination (Fig. 1b) and to separate from the effects of higher pollinator abundance from effects of higher amounts
 163 of OSR pollen. The exclusion treatments consisted of covering a branch with bags of different mesh sizes

164 depending on the study target (Fig. 1b): (i) an Osmolux bag allowing air but not pollen flow (Osmolux treatment:
 165 OS) thus permitting only self-pollination, (ii) a mesh of 0.6 mm allowing only wind- or self-pollination (small
 166 mesh treatment: SM), and (iii) a mesh of 3.0 mm allowing wind-, self-pollination and pollination by small insects
 167 (small wild bees and hoverflies), with an abdomen thinner than 3 mm (large mesh treatment: LM). The absence of
 168 a bag on the control branches allowed self-, wind- and insect-pollination by small or large insects (honeybees and
 169 bumblebees with an abdomen larger than 3 mm). Self-pollination was estimated using fruiting success (in %) in
 170 the OS treatment, and was obtained exactly as in control treatment, so both were easily compared to each other.
 171 Self-pollination was expected to be high, as it is the major pollination process in OSR (Perrot et al. 2018). Given
 172 the rather minor difference between control and self-pollination (see results below), contribution of other
 173 pollination processes, i.e. insect- and wind-pollination, to fruiting success were expected to be small.
 174 Dimensionless effect sizes (varying between -1 and 1) were therefore used to compare insect- and wind-
 175 pollination. They were computed between paired treatments as the ratio of the difference in fruiting success
 176 between treatments from the sum of the paired fruiting success rates. Paired treatments included control versus
 177 SM (complete exclusion of insects) to assess the magnitude of insect-pollination (Eq.1); control versus LM
 178 (exclusion of large insects) to assess the magnitude of large insect-pollination (Eq. 2); LM versus SM to assess the
 179 magnitude of small insect-pollination (Eq. 3); and SM versus OS (exclusion of wind-pollination) to assess the
 180 magnitude of wind-pollination (Eq. 4).

$$181 \quad (\text{Eq. 1}) \text{ Insect – pollination} = \frac{\text{Fruiting success (C)} - \text{Fruiting success (SM)}}{\text{Fruiting success (C)} + \text{Fruiting success (SM)}}$$

$$182 \quad (\text{Eq. 2}) \text{ Large insect – pollination} = \frac{\text{Fruiting success (C)} - \text{Fruiting success (LM)}}{\text{Fruiting success (C)} + \text{Fruiting success (LM)}}$$

$$183 \quad (\text{Eq. 3}) \text{ Small insect – pollination} = \frac{\text{Fruiting success (LM)} - \text{Fruiting success (SM)}}{\text{Fruiting success (LM)} + \text{Fruiting success (SM)}}$$

$$184 \quad (\text{Eq. 4}) \text{ Wind – pollination} = \frac{\text{Fruiting success (SM)} - \text{Fruiting success (OS)}}{\text{Fruiting success (SM)} + \text{Fruiting success (OS)}}$$

185 Thus, for example using Eq. 2, a positive value of large insect-pollination indicated that large insects
 186 contributed to pollination, as fruiting success was higher in control treatment compared to treatment excluding
 187 large insects. A null value meant that large insects' contribution to pollination was negligible. Negative values
 188 were unexpected but were found in some situations, which may suggest that the contribution of large pollinators
 189 could be compensated by other processes (wind-, self-pollination and pollination by small pollinators) in the
 190 absence of large pollinators, and/or by pollen production increase.

191 *Four measures of OSR floral seasonality and availability in focal fields*

192 To account for spatial and temporal variation in floral resource quantity at both local and landscape scales,
 193 four measures of floral resources were derived from additional data (Fig. 1c).

194 (i) **Field Size.** Field size was used as a proxy of the quantity of available flowers at field scale, assuming that
 195 the amount of flowers was proportional to the field size, i.e. larger fields had more floral resources than smaller
 196 ones. Floral resources referred to OSR flowers in OSR fields, as wildflowers were minor compared to OSR flowers
 197 in this crop, and to wildflowers (mainly weed species) in grasslands and cereals. Previous studies in our site
 198 indicated a higher diversity and abundance of weeds in grasslands (average \pm sd: 22 ± 10 species and 308 ± 128
 199 plants/m² respectively) than in cereals (12 ± 10 and 153 ± 176) or in OSR (17 ± 4 and 153 ± 83 ; Gaba et al. 2020;
 200 Bourgeois et al. 2020). By using field size as a proxy, the quantity of flowers was assumed to depend more on the
 201 field area than on the local flower density. Indeed, in the present study, field size varied from 1.1 to 27.6 ha for

202 OSR, from 0.7 to 33.7 ha for cereals and from 0.2 to 24.1 ha for grasslands. By contrast, flower density generally
 203 varies from 6.75 to 12.75 OSR plants/m² (Momoh and Zhou 2001), from 1% to 5% of wildflower density in cereal
 204 fields (Sidemo-Holm et al. 2021), and 1% to 13% in grasslands (Hegland and Boeke 2006), i.e. five to ten times
 205 less than the variation in field size.

206 (ii) **Landscape Flower Quantity.** Floral resource quantity at the landscape scale varied with the amount of
 207 OSR, SNH and OF in the surrounding landscape at a given radius. Plant phytometers were placed along gradients
 208 of OSR flowers provided by OSR crops (%OSR), and wildflowers provided by SNH and OF (Cole et al. 2017;
 209 Sidemo-Holm et al. 2021). These were estimated in buffer zones excluding the focal fields (distances between
 210 focal field centroids and borders were 165.7 ± 58.9 m in OSR, 167.5 ± 59.4 m in cereals, and 116.7 ± 62.8 m in
 211 grasslands). For each crop type, fields were selected to maximize gradients of %OSR (min–max values in 250 m
 212 and 1000 m buffer radii: 0–55%; 0–25%), %SNH (0–72%; 0–38%) and %OF (0–76%; 0–53%). The landscape
 213 gradients were uncorrelated with crop type. The **Landscape Flower Quantity** provided by OSR, SNH and OF
 214 was estimated in buffer zones with various radii, specific for each type of pollination process and each crop type.
 215 At their respective buffer scales of maximum effect, %OSR, %SNH and %OF were then used as proxies of total
 216 floral resource availability.

217 (iii) **Phytometer-Regional Flowering Temporal Matching.** Temporal matching between phytometer
 218 setting and regional OSR flowering in the study site that year was used to characterize the temporal lag between
 219 the flowering period of OSR and the deposition date of plant phytometers in the fields. This metric was calculated
 220 differently for plant phytometers placed in OSR fields and those placed in the other two crop types. First,
 221 generalized additive models (GAMs) was used to derive, separately for each year, the temporal dynamic of OSR
 222 flowering in the study site using % of OSR flower cover collected in OSR fields across the study site (from 0%
 223 when no OSR flowers were open in the field to 100% when OSR flowers covered the total area of the field; see
 224 Appendix B). For phytometers placed in OSR, from the fitted GAMs the period of OSR peak flowering was
 225 identified for each year as the range between the maximal estimated OSR flower cover and a relative 20%
 226 reduction of OSR flower cover. The choice of a 20% threshold was determined in order to balance the sampling
 227 dates with equal representation in both categories. The time period in days (ranging from 100 to 118 Julian days
 228 depending on the year) thus defined the peak flowering period. Phytometers placed in OSR fields during that
 229 period were considered to be placed at the peak flowering period, and those placed outside this range were
 230 considered to be placed after the peak flowering period. For phytometers placed in cereals and grasslands, a
 231 different threshold was used: a 60% reduction of OSR flower cover indicated the end of flowering (rather than
 232 20% as in OSR fields). This difference in threshold accounted for the fact that the phytometers were placed later
 233 (on average 12 days) than in OSR fields, thus balancing sample sizes between the two categories required delaying
 234 the threshold value later in the season (Appendix B).

235 (iv) **Focal Field-Regional Flowering Temporal Matching.** Temporal matching between OSR focal field
 236 flowering and OSR regional flowering in the study site for a given year referred to the temporal lag between the
 237 flowering of the focal OSR fields and the flowering of OSR at the site scale. This parameter was calculated only
 238 for plant phytometers placed in OSR fields. Here the % of OSR flower cover collected in OSR fields was used.
 239 Cumulating all data for a given year, a GAM was used to derive the deflowering pattern according to date and its
 240 intra-year variability. Using two quantiles (33% and 66%), for any given date three categories were defined based
 241 on % of flower coverage in a given focal field: OSR fields were either relatively early, i.e. below 33% deflowered

242 compared to average kinetics, relatively late (over 66%), or normal, i.e. within the range (33–66%; Appendix B).

243 Statistical analyses

244 In a first step, preliminary analyses were conducted to investigate the potential effect of the position of the
245 plant phytometers in the field (core *versus* edge). As no significant differences were detected, the two values were
246 averaged per treatment, field, and date (Appendix C). The sample size in our study was thus $n = 308$ fields.
247 Differences in pollination efficiency were then explored between crop types by using a subset of the data in which
248 all crops were investigated the same year. A linear model was used to test the effect of crop type (three levels) and
249 year (three levels in common between crops) on phytometer fruiting success. For this first set of analyses, only
250 data from the control branches were used.

251 In a second step, the effects of ‘Phytometer-Regional Flowering Temporal Matching’ and the amount of
252 floral resources at both field and landscape scales were investigated on the fruiting success of plant phytometers.
253 Again, only data from the control branches were used. Three models were built, one for each crop type, because
254 (i) ‘Phytometer-Regional Flowering Temporal Matching’ was estimated differently for phytometers in OSR fields
255 than for those in cereal fields and grasslands and (ii) the scales of influence of the landscape variables were
256 assumed to vary with the focal crop type. Fruiting success of OSR phytometers was considered as the dependent
257 variable, and ‘Field Size’, ‘Landscape Flower Quantity’ (%OSR, %SNH and %OF) and ‘Phytometer-Regional
258 Flowering Temporal Matching’ as explanatory variables. The interaction of ‘Field Size’ and ‘Landscape Flower
259 Quantity’ with ‘Phytometer-Regional Flowering Temporal Matching’ was also included (except in grasslands due
260 to a smaller sample size) as a way to identify spillover and dilution processes. Year was included as a fixed effect
261 factor with five, four and three levels respectively in OSR fields, cereal fields and grasslands to account for
262 interannual dynamics of pollinating insects (Rollin et al. 2015; Perrot et al. 2018). For phytometers placed in OSR
263 fields, the models also included ‘Focal Field-Regional Flowering Temporal Matching’ (a qualitative variable with
264 three levels), in interaction with ‘Field Size’ and ‘Phytometer-Regional Flowering Temporal Matching’. The
265 models were estimated using the ‘siland’ method (Carpentier and Martin 2021) which enables the simultaneous
266 estimation of the effect of all explanatory variables and the buffer radii of landscape variables i.e. radii of
267 ‘Landscape Flower Quantity’ (%OSR, %SNH and %OF) without any prior assumption on the spatial scales of
268 influence. The model residuals were assumed to be Gaussian (see details in Appendix D).

269 Finally, based on the bagging treatments, the variation of each pollination process (large and small insects-,
270 wind- and self-pollination) with local, temporal and landscape factors for each crop type was investigated. A total
271 of 15 linear models was built (three crop types with five pollination processes) to explore the effects of the amount
272 of floral resources in the fields and in the landscape as well as ‘Phytometer-Regional Flowering Temporal
273 Matching’. Explanatory variables were the same as those used for the study of fruiting success of the control
274 treatment. As the scale of effects of landscape features was expected to change with the pollination process, the
275 ‘siland’ method was used.

276 All the analyses were performed using R software (version 3.6.2; R Core team 2019) with the ‘siland’
277 package (Carpentier and Martin 2020), ‘car’ for Type II analyses of variance (Fox et al. 2020), ‘emmeans’ (Lenth
278 et al. 2020) for the estimations of effect sizes and ‘BSDA’ for unilateral sign tests (Arnholt and Evans 2017). For
279 each model, residual diagnostics were looked to verify for normal hypothesis (quantile-quantile plots) and
280 homoscedasticity (spread of residual did not change with predicted values; Kozak and Piepho 2018). The absence
281 of spatial autocorrelation of residuals were also confirmed with variograms visualization (Dormann et al. 2007).

282 Finally, the landscape scales of influence were ensured to be well estimated, i.e. being the global rather than the
 283 local maximum of likelihood (profile likelihood visualization) and that the metrics of landscape composition did
 284 not correlate to each other at the estimated spatial scales (see Appendix E).

285 **Results**

286 The fruiting success of the phytometer control branch (proportion of flowers producing a pod, ranging from
 287 0% to 100%) varied with crop type ($F = 10.23$; $df = 2$; $p < 0.001$). Fruiting success was higher for phytometers in
 288 OSR fields (mean \pm sd: $49\% \pm 28\%$, $n = 135$) than for phytometers in cereals ($38\% \pm 28\%$; $n = 100$) or grasslands
 289 ($36\% \pm 27\%$; $n = 43$). Year ($df = 2$; $F = 13.74$; $p < 0.001$) had also significant effects on fruiting success, but not
 290 its interaction with crop type ($df = 4$; $F = 0.16$; $p = 0.96$).

291 Factors affecting the fruiting success of OSR plant phytometers in OSR fields

292 Using ‘Field Size’ and ‘Focal Field-Regional Flowering Temporal Matching’, as two measures of floral
 293 resource availability at field scale, ‘Landscape Flower Quantity’ (measured by %SNH, %OF and %OSR) as a
 294 measure of landscape floral resource availability, and ‘Phytometer-Regional Flowering Temporal Matching’ as a
 295 measure of temporal deviation in flowering, as well as the interactions between these variables and the year (fixed
 296 effect factor), 44.3% of the variance in the fruiting success of phytometers placed in OSR fields was explained
 297 (Table 1a). Fruiting success strongly varied with year (15.2% of explained variance), ‘Phytometer-Regional
 298 Flowering Temporal Matching’ (14.0%), ‘Landscape Flower Quantity’ (8.7% cumulated for %OSR, %SNH and
 299 %OF), and the interaction between ‘Phytometer-Regional Flowering Temporal Matching’ and ‘Field Size’ (2.3%).
 300 ‘Focal Field-Regional Flowering Temporal Matching’ had no effect on fruiting success (Table 1a). Fruiting
 301 success was on average higher for phytometers in OSR fields during OSR peak flowering than after (Fig. 2a). The
 302 effect of ‘Field Size’ differed significantly between the two categories of ‘Phytometer-Regional Flowering
 303 Temporal Matching’ (Table 1a): during OSR peak flowering, fruiting success tended to decrease with ‘Field Size’,
 304 while post-peak it tended to increase (Appendix G). The fruiting success of phytometers was significantly modified
 305 by %OSR, %SNH and %OF (Table 1a): %OSR (Fig. 3a) and %SNH (Fig. 3d) had a positive effect on fruiting
 306 success while fruiting success decreased with %OF (Fig. 3g). The estimated scale of effect differed between
 307 landscape features, being small for %OSR (12 m outside the fields, meaning that considering the presence of an
 308 adjacent OSR field was enough to explain increased fruiting success in the focal field), high for %SNH (1772 m)
 309 and intermediate for %OF (210 m outside the fields).

310

311 #Fig. 2, 3 approximately here#

312 Fruiting success of OSR plant phytometers in cereal fields and grasslands

313 In cereal fields and grasslands, the statistical models explained respectively 35.8% and 54.6% of the variance
 314 in OSR phytometer fruiting success (Table 1b, c). As with phytometers in OSR fields, the fruiting success in cereal
 315 fields and grasslands varied with year, ‘Phytometer-Regional Flowering Temporal Matching’ and the amount of
 316 floral resources in the surrounding landscape; however, ‘Field Size’ had no effect (Table 1b, c). In cereals, the
 317 same pattern was observed as in OSR (Fig. 2b, Fig. 3b, e, h): fruiting success was higher during OSR flowering
 318 than after (Fig. 2b), increased with %OSR (Fig. 3b) and %SNH, but decreased with %OF, although non-

319 significantly for %SNH and %OF (Fig. 3e, h). A strikingly different pattern emerged with grasslands: as in OSR
 320 and cereals, the fruiting success of phytometers was higher during OSR flowering, though only slightly (Fig. 2c),
 321 increased with %OSR at landscape scale (Fig. 3c), but decreased with %SNH (Fig. 3f). The spatial extent of the
 322 effect of landscape differed between crop types, %OSR acted for example at higher spatial scale in grasslands (942
 323 m) than in cereals (260 m) or in OSR (12 m; Fig. 3).

324

325 #Table 1 approximately here#

326 Pollination processes of OSR plant phytometers

327 The magnitude of the various pollination processes affecting the fruiting success of plant phytometers
 328 differed slightly between the three crop types. Self-pollination was the main pollination process of OSR
 329 phytometer whatever crop type where phytometers were set as fruiting success of the Osmolux treatment was close
 330 to fruiting success of the control treatment (Fig. 2 vs Fig. 4a). Self-pollination was however higher in OSR than in
 331 the two other crops, 41% average fruiting success compared to 49% in control (i.e., only 16% reduction compared
 332 to the control treatment). In grasslands and particularly in cereals, the reduction compared to the control was higher
 333 (Fig. 4a). Other pollination processes had therefore, overall, a small contribution, especially in OSR. Among them
 334 however, the second most dominant process of pollination was insect-pollination (Fig. 4c-e), being more important
 335 than wind-pollination, although in OSR (Fig. 4c), conversely to the other two crops (Fig. 4d, e), differences were
 336 minor. Of insects, large insects had the greatest effect in all crops, while the magnitude of small insects was greater
 337 than zero only in cereals (Fig. 4). Pollination processes also differed quite strongly according to the OSR flowering
 338 period during which the phytometer was placed, in addition to the crop in which it was placed (Fig. 4c-e). In OSR
 339 fields, higher fruiting success (Fig. 2a) in the peak flowering period resulted in significantly higher insect-
 340 pollination (Fig. 4c). In contrast, insect-pollination dramatically increased in grasslands after the OSR flowering
 341 period (Table 2c; Fig. 4e). No such marked difference was detected for insect pollination in cereals, which was
 342 high in both periods (Fig. 4d). The relative importance of wind pollination *versus* insect pollination differed
 343 between crops, with wind pollination decreasing in grasslands after the OSR flowering period while remaining
 344 similar in OSR and cereals throughout the two periods (Table 2c; Fig. 4c, d, e). Self-pollination was higher during
 345 OSR flowering than after in all crops (Fig. 4b). Supplementary analyses also showed that self-pollination linearly
 346 decreased with the Julian date (Appendix H).

347

348 #Fig. 4 approximately here#

349

350 Insect-pollination was higher than wind pollination whatever the crop and season (though not necessarily
 351 significantly, e.g. in OSR), suggesting that the abundance of pollinators, rather than the abundance of pollen, was
 352 involved in the higher observed fruiting success (Fig. 4c-e). In addition, insect-pollination often responded in the
 353 same way as fruiting success to landscape features (Fig. 3, Fig. 5). In OSR fields, insect-pollination increased with
 354 %SNH (Fig. 5a) and decreased with %OF (Fig. 5d). There was an interaction between landscape composition and
 355 ‘Phytometer-Regional Flowering Temporal Matching’ on small and large insect-pollination (Table 2a): increasing
 356 %SNH improved small insect-pollination after OSR peak flowering (Fig. 5c), while large insect-pollination was
 357 negatively related to %OF only after OSR peak flowering (Fig. 5e). The increase in fruiting success with %OSR
 358 resulted from a joint increase of insect-, wind- and self-pollination (Appendix I). However, the increase in fruiting

359 success in cereals and grasslands resulted from an increase in large insect-pollination with %OSR, although this
 360 was the case only after OSR flowering in cereals (Fig. 5g, h; Table 2b, c). Small insect-pollination also increased
 361 with %SNH in grasslands (Fig. 5i), as opposed to the pattern observed for fruiting success (Fig. 3f) and wind-
 362 pollination diminished with %SNH (Table 2c; Fig. 5j).

363 The spatial extent of the effects of landscape varied with the pollination processes, being in general lower
 364 for wind than for insect pollination (e.g. 3 m and 747 m for %OSR in OSR crops). For insects, the spatial scales
 365 of landscape features were greater for large than for small insects (e.g. 321 m and 9 m for %SNH in OSR crops).
 366 Large insect-pollination was also shown to respond at different spatial scales depending on the focal crop type, as
 367 %OSR acted on large-insect pollination at a higher spatial scale in grasslands (1442 m) than in cereals (522 m;
 368 Fig. 5g, h). Self-pollination, which was expected to be constant across the conditions, was also modified by the
 369 amount of local and landscape floral resources in OSR, cereals and grasslands (Appendix H).

370

371 #Fig. 5 & Table 2 approximately here#

372 **Discussion**

373 The results of the present study showed that fruiting success of plant phytometers placed in OSR crop was
 374 higher in OSR peak flowering period, i.e. when OSR flower resources are highest, and was improved by
 375 neighbouring OSR fields. The pulse of OSR flowers was especially attractive for small insects that lead to an
 376 increase of fruiting success in OSR crops surrounded by a high amount of SNH. A temporal spillover occurred
 377 after the period of OSR flowering and involved large insects that dispersed from OSR to grasslands and cereal
 378 crops.

379 The phytometer approach revealed high heterogeneity in fruiting success rates (used as a proxy of pollination
 380 efficiency) even within crop types, suggesting that there may be a strong spatial and temporal variation in pollen
 381 limitation in our study site. Fruiting success of the OSR phytometers (49% on average) was within the range (from
 382 31% to 75%) found in other studies on *Brassica* plant phytometers (Palmer and Zimmerman 1994; Hudewenz et
 383 al. 2014), though slightly lower than those estimated directly on OSR plants in crop fields (70%; Zou et al. 2017),
 384 including in our study site (65%; Perrot et al. 2018). Such pollination rates indicate a rather high abortion rate of
 385 flowers, i.e. from 51% in OSR fields to up to 62% and 64% in cereals and grasslands. Although other factors may
 386 also contribute to abortion, such as lack of water or nutrients that may physiologically limit plant phytometers
 387 (Marini et al. 2015), this is more likely to result, at least partly, from pollen limitation. Indeed, OSR pollen
 388 availability strongly varies between crop types (i.e. higher in OSR fields than in cereals and grassland), in the
 389 surrounding landscape of focal fields and throughout the flowering period of OSR. This lack of pollen in the air
 390 can reduce wind pollination (McCartney and Lacey 1991) at a low spatial scale, since wind-carried pollen rarely
 391 exceeds 50 m dispersion from OSR fields (Popławska et al. 2013).

392 Pollen limitation can also lower self-pollination later in the season. Lower airborne pollination may,
 393 however, be balanced out by higher insect-mediated pollination, as has been shown with radish or strawberry when
 394 used as plant phytometers in semi-natural habitats or crop fields (Hass et al. 2018; Castle et al. 2019). Pollinating
 395 insects carry pollen over long distances (Chifflet et al. 2011) and/or directly from opened flowers of plant
 396 phytometers by successively visiting different flowers (Rader et al. 2009). The bagging experiment performed in
 397 the present study confirmed that insect pollination was a major process in OSR pollination after self- and before

398 wind-pollination (Hudewenz et al. 2014; Perrot et al. 2018). The high insect-pollination rate found in cereals and
399 grasslands suggests that this pollination process may compensate for low OSR pollen availability. As expected, a
400 strong variation in the magnitude of insect-pollination was detected with the spatial and temporal conditions of the
401 focal fields under study. In our site, pollinator richness ranged from 0 to 25 species (Rollin et al. 2015) and
402 abundance from 0 to 68 individuals per 100 m² (Perrot et al. 2018). Moreover, pollinator richness and abundance
403 strongly vary across years (Perrot et al. 2018), thus directly affecting the magnitude of insect-pollination.

404 In the present study, pollination efficiency in OSR fields was higher in periods and landscapes characterized
405 by high availability of OSR flowers (Fig. 2a, 3a) in sharp contrast to predictions of the dilution hypothesis. This
406 conflicts from most previous studies, which have detected such a dilution effect, finding that increasing the amount
407 of mass-flowering crops in the landscape decreases large pollinator abundance, e.g. honeybees and bumblebees
408 (Holzschuh et al. 2016; Bänisch et al. 2020), hence decreasing pollination efficiency in these crops (Shaw et al.
409 2020) or adjacent crops (Grab et al. 2017) and grasslands (Holzschuh et al. 2011). The gradients of %OSR used
410 in the present study (from 0% to 26% in a buffer of 747 m outside OSR fields) were similar to those used in other
411 studies (e.g. from 0% to 30% in a buffer of 1000 m; Holzschuh et al. 2011), thus other factors must explain this
412 discrepancy. One possible reason may be the plant phytometer itself: dilution was found when plant phytometers
413 used was not the blooming crop (e.g. strawberry plants with the blooming of apple flowers in Grab et al., 2017),
414 or *Primula veris* with the blooming of OSR flowers (Holzschuh et al. 2011). Two other possible factors may also
415 be involved in explaining the difference with our study. First, the rich and abundant pollinator community in our
416 study site (Rollin et al. 2013; Bretagnolle et al. 2018) may avoid such a dilution effect more likely to be detected
417 in depauperate pollinator communities (Tschardt et al. 2012). Second, OSR accounted for about 8% of crops,
418 and therefore a high load of OSR pollen in the air may have balanced out any dilution of pollinator insects (Waser
419 and Price 2016; Cavallero et al. 2018). An increase in pollination efficiency with higher amount of OSR fields in
420 the landscape was also found, but at a small scale (12 m), a distance consistent with the distance at which pollen
421 disperses with wind (about 50 m; Popławska et al. 2013). Conversely, the spatial extent of the effect of %OSR on
422 insect pollination was at much larger scale (e.g. 747 m for plant phytometers in OSR fields), underlying the ability
423 of insect pollinators to forage over hundreds of metres (Greenleaf et al. 2007).

424 While the results of the present study did not support a dilution effect, patterns consistent with a reverse
425 pattern was detected, in the form of an attractive effect of the bloom of OSR flowers. During peak OSR flowering,
426 this was detected in the attraction of insects from SNH to OSR, as there was higher pollination efficiency of
427 phytometers placed in OSR fields surrounded by a high amount of SNH (Fig. 3d), particularly for small pollinators
428 (indicated by the bagging experiment; Fig. 5a, b, c). Such attraction operated at a larger scale for large pollinators
429 (321m) than for small ones (9m), in accordance with the ability of large pollinators to forage at greater distances
430 (Jackson and Fahrig 2012; Miguet et al. 2016). SNH are well-known sources of pollinators in agricultural
431 landscapes, including bees (Steffan-Dewenter et al. 2002), hoverflies (Bommarco et al. 2012) and bumblebees
432 (Hopfenmüller et al. 2014). The results of the present study thus confirm that SNH benefit wild pollinators in
433 adjacent OSR fields (Bommarco et al. 2012), hence reducing pollen limitation (Cusser et al. 2016) and increasing
434 pollination efficiency in insect-dependent crops (Bukovinszky et al. 2017; Raderschall et al. 2021) such as OSR
435 (Bartomeus et al. 2014).

436 Finally, a temporal spillover mechanism was found to occur later in the flowering season when insects
437 disperse from OSR fields after peak flowering to other crops and SNH, which become attractive (Fig. 4c, d, e; Fig.

438 5g). This process, already suggested, is related to the fact that pollinating insects follow the temporal pattern of
439 floral resource availability in the landscape (Mandelik et al. 2012; Bretagnolle and Gaba 2015). At a seasonal
440 scale, different habitats are therefore sequentially used, corroborating that the presence of OSR in a landscape
441 benefits pollinator diversity (Kovács-Hostyánszki et al. 2013; Diekötter et al. 2014) and pollination of wild plants
442 (Herbertsson et al. 2017) in adjacent grasslands. Such a spillover effect was also detected in cereal fields, as large
443 insect-pollination was higher in cereals surrounded by a high amount of OSR, but only after peak OSR flowering.
444 In contrast to the predictions however, a negative effect of organic farming was detected in small-bodied insects
445 whatever the OSR flowering period, and in larger insects only outside OSR flowering. This effect may result from
446 pollinator attraction to organic fields. Organically farmed cereal fields support a high diversity of wild plants
447 (Henckel et al. 2015) which are visited by both wild pollinators (Sidemo-Holm et al. 2021) and honeybees
448 (Wintermantel et al. 2019). The present study was inconclusive in regard to the possible effect of the amount of
449 floral resources at the field scale possibly because of the crude measure of local availability of floral resources
450 (field size was used as a proxy), which did not consider variation in the composition of floral resources.

451 **Conclusion**

452 The present study revealed complex and interacting mechanisms (i.e. attraction, spillover and temporal
453 complementarity between habitats) through space and time, between crops, and between crops and semi-natural
454 elements, depending on insect types. The amount of SNH in the landscape appeared to play a key role in pollination
455 efficiency: it provided pollinating insects – especially small insects – to OSR crops, with a reverse spillover effect
456 after OSR peak flowering. These results suggest that grasslands and cereals may act complementarily to OSR
457 fields in supporting insects (and hence pollination) throughout the season in a landscape. Therefore, farmland
458 landscapes that combine habitats providing nesting sites and floral resources after OSR flowering or, even better,
459 continuous flowering resources across the seasons over the entire landscape, would contribute to supporting large
460 pollinator populations and therefore improve pollination.

461 **Acknowledgements**

462 We would like to express our thanks to Marilyn Roncoroni, Alexis Saintilan, Quentin Van Hecke and
463 Anthony Stoquaert for their help with the OSR phytometer experiment and pollinator trapping and identification
464 (Marilyn Roncoroni). We also sincerely thank the farmers of the LTSER ‘Zone Atelier Plaine & Val de Sèvre’ for
465 their involvement in our research programmes. MR was supported by a PhD grant from INRAE (Metaprogram
466 SMACH) and the Nouvelle-Aquitaine region’s Birdland project. SG, TP, OM, and FC are funded by INRAE, and
467 VB by CNRS. The authors are grateful to the two anonymous reviewers whose comments greatly improved the
468 manuscript.

469 **Declarations**

470 **Funding.** This project was supported by the French Ministry of Ecology project (2017-2020 “Pollinisateurs”), the
471 ANR IMAGHO (ANR-18-CE32-0002) and the INRAE projects “ESPACE” and “INITIATE” (MP SumCrop).
472 This project also received funding from the European Union’s Horizon 2020 research and innovation programme
473 under grant agreement SHOWCASE No 862480.

474

475 **Conflicts of interest/Competing interests.** The authors declare that they have no conflict of interest.

476

477 **Availability of data and material.** The datasets generated and used for the study are available (except confidential
478 data such as landscape information) from the corresponding author on reasonable request.

479

480 **Code availability.** The code performed to analyse the dataset is available from the corresponding author on
481 reasonable request.

482

483 **Ethics approval.** Not applicable

484

485 **Consent to participate.** Not applicable

486

487 **Consent for publication.** Not applicable

488

489 **Authors' contributions.** VB and SG conceived the study and were in charge of overall direction. VB and SG
490 designed and planned the field work. JG worked in the field and in the laboratory for yield component
491 quantification with the help of TP and MR. JG entered the data. MR analysed the data. SG, FC, OM, VB, and TP
492 provided feedback and helped improve analyses. MR, SG, VB, FC, OM, and TP discussed and interpreted the
493 results. MR, SG, VB, and FC wrote the paper. TP and OM commented and helped shape the manuscript. All
494 authors approved the final version of the manuscript.

495 **Table 1:** Summary statistics of the models investigating the effects of ‘Phytometer-Regional Flowering Temporal Matching’ and floral resources in the fields (field size
 496 as a proxy) and ‘Focal Field-Regional Flowering Temporal Matching’ only for OSR fields) and in the surrounding landscapes (%OSR: % oilseed rape, %SNH: % semi-natural
 497 habitats and %OF: % organic farming) on fruiting success in the control treatment in OSR fields (a), cereal fields (b) and grasslands (c). We performed type II analyses of
 498 variance. The coefficients of determination of the three models (R^2), the variance explained by each variable (%Var; sum of squares associated to a variable divided by the total
 499 sum of squares), the degrees of freedom (df), the F-value (F) and the p-value (p) are presented. Significant values are bold. Estimations of landscape effects and scale of effects
 500 were similar without local \times landscape interactions (Appendix F).

	R^2	a. OSR				b. Cereal				c. Grassland			
		df	%Var	F	p	df	%Var	F	p	df	%Var	F	p
		44.3%				35.8%				54.6%			
Year		4	15.2	7.13	<0.001	3	18.1	6.34	<0.001	2	18.4	7.08	<0.01
Field size		1	0.0	0.07	0.79	1	0.3	0.27	0.60	1	0.5	0.35	0.56
Phytometer-Regional Flowering Temporal Matching		1	14.0	26.36	<0.001	1	7.9	8.34	<0.01	1	9.0	6.97	0.01
Focal Field-Regional Flowering Temporal Matching		2	1.1	1.00	0.37	-	-	-	-	-	-	-	-
%OSR (Landscape Flower Quantity)		1	2.9	5.45	0.02	1	4.6	4.82	0.03	1	5.6	4.31	0.05
%SNH (Landscape Flower Quantity)		1	3.0	5.65	0.02	1	0.4	0.46	0.50	1	19.1	14.73	<0.001
%OF (Landscape Flower Quantity)		1	2.8	5.32	0.02	1	2.4	2.51	0.12	1	1.7	1.29	0.26
Field size x Phytometer-Regional Flow. Temp. Matching		1	2.3	4.32	0.04	1	0.2	0.20	0.65	-	-	-	-
Focal Field-Reg. Flow. Temp. Matching x Phytometer-Reg. Flow. Temp. Matching		2	1.5	1.41	0.25	-	-	-	-	-	-	-	-
Field size x Focal Field- Reg. Flow. Temp. Matching		2	0.8	0.71	0.50	-	-	-	-	-	-	-	-
%OSR x Phytometer-Reg. Flow. Temp. Matching		1	0.1	0.26	0.61	1	0.5	0.48	0.49	-	-	-	-
%SNH x Phytometer-Reg. Flow. Temp. Matching		1	0.7	1.23	0.27	1	1.0	1.07	0.30	-	-	-	-
%OF x Phytometer-Reg. Flow. Temp. Matching		1	0.0	0.02	0.89	1	0.4	0.39	0.53	-	-	-	-

501

502 **Table 2:** Effects of ‘Phytometer-Regional Flowering Temporal Matching’ and availability of floral resources in the fields and in the surrounding landscapes (%OSR: %
 503 oilseed rape, %SNH: % semi-natural habitats and %OF: % organic farming) on the magnitude of each pollination process in (a) OSR fields, (b) cereal fields and (c) grasslands.
 504 For each of 15 models, we applied type II analyses of variance. Coefficients of determination of the models (R^2), degree of freedom (df), F-value (F) and p-value (p) for each
 505 explained variable are indicated. Significant values are in bold.

	df	Insects		Large insects		Small insects		Wind		Self	
		F	p	F	p	F	p	F	p	F	p
a. OSR		$R^2 = 32.0\%$		$R^2 = 22.3\%$		$R^2 = 16.7\%$		$R^2 = 28.4\%$		$R^2 = 47.8\%$	
Year	4	2.84	0.03	1.57	0.19	0.98	0.42	5.20	<0.001	13.60	<0.001
Field size	1	2.76	0.10	0.02	0.88	1.39	0.24	2.55	0.11	0.01	0.93
Phytometer-Regional Flowering Temporal Matching	1	4.89	0.03	0.49	0.49	1.12	0.29	0.17	0.68	12.96	<0.001
Focal Field-Regional Flowering Temporal Matching	2	2.87	0.06	0.96	0.39	0.62	0.54	1.44	0.24	2.65	0.08
%OSR (Landscape Flower Quantity)	1	1.20	0.28	0.06	0.81	1.07	0.30	1.60	0.21	3.47	0.07
%SNH (Landscape Flower Quantity)	1	4.81	0.03	0.21	0.64	0.14	0.71	0.78	0.38	5.81	0.02
%OF (Landscape Flower Quantity)	1	6.65	0.01	0.85	0.36	3.71	0.06	1.50	0.22	0.36	0.55
Field size x Phytometer-Regional Flow. Temp. Matching	1	0.69	0.41	1.44	0.23	0.03	0.86	1.53	0.22	7.58	0.01
Focal Field-Reg. Flow. Temp. Matching x Phytometer-Reg. Flow. Temp. Matching	2	3.35	0.04	0.16	0.85	0.82	0.44	1.20	0.31	0.53	0.59
Field size x Focal Field- Reg. Flow. Temp. Matching	2	2.68	0.07	1.05	0.35	0.29	0.75	1.09	0.34	3.90	0.02
%OSR x Phytometer-Reg. Flow. Temp. Matching	1	3.02	0.09	1.87	0.17	3.10	0.08	0.41	0.52	1.18	0.28
%SNH x Phytometer-Reg. Flow. Temp. Matching	1	0.37	0.54	4.42	0.04	4.29	0.04	0.69	0.41	0.00	0.99
%OF x Phytometer-Reg. Flow. Temp. Matching	1	5.76	0.02	7.39	0.01	1.45	0.23	0.02	0.89	6.79	0.01
b. Cereal		$R^2 = 15.7\%$		$R^2 = 18.5\%$		$R^2 = 11.6\%$		$R^2 = 15.2\%$		$R^2 = 39.2\%$	
Year	3	1.24	0.30	0.51	0.68	0.20	0.90	0.61	0.61	10.13	<0.001
Field size	1	0.04	0.84	0.01	0.91	0.07	0.79	2.77	0.10	0.95	0.33
Phytometer-Regional Flowering Temporal Matching	1	0.11	0.74	0.02	0.89	1.13	0.29	0.94	0.34	13.06	<0.001
%OSR (Landscape Flower Quantity)	1	0.03	0.87	0.03	0.87	1.55	0.22	0.36	0.55	0.10	0.75
%SNH (Landscape Flower Quantity)	1	2.14	0.15	0.71	0.40	0.92	0.34	0.40	0.53	1.64	0.20
%OF (Landscape Flower Quantity)	1	0.17	0.68	2.69	0.11	1.95	0.17	0.20	0.65	1.10	0.30
Field size x Phytometer-Reg. Flow. Temp. Matching	1	0.09	0.77	1.09	0.30	0.16	0.69	0.30	0.58	0.02	0.88
%OSR x Phytometer-Reg. Flow. Temp. Matching	1	1.88	0.17	6.35	0.01	0.54	0.46	2.78	0.10	5.14	0.03
%SNH x Phytometer-Reg. Flow. Temp. Matching	1	1.47	0.23	1.54	0.22	0.73	0.39	1.37	0.25	2.80	0.10
%OF x Phytometer-Reg. Flow. Temp. Matching	1	1.64	0.20	0.11	0.74	0.22	0.64	3.29	0.07	3.68	0.06
c. Grassland		$R^2 = 57.4\%$		$R^2 = 56.5\%$		$R^2 = 51.4\%$		$R^2 = 42.7\%$		$R^2 = 38.4\%$	
Year	2	2.56	0.10	1.15	0.33	7.01	<0.01	3.71	0.04	2.74	0.08
Field size	1	0.04	0.85	0.49	0.49	0.23	0.64	0.15	0.70	0.42	0.52
Phytometer-Regional Flowering Temporal Matching	1	25.17	<0.001	26.54	<0.001	3.89	0.06	10.13	<0.01	0.40	0.53
%OSR (Landscape Flower Quantity)	1	1.72	0.20	10.34	<0.01	1.64	0.21	2.76	0.11	9.35	<0.01
%SNH (Landscape Flower Quantity)	1	10.38	<0.01	1.48	0.23	6.35	0.02	7.90	0.01	1.33	0.26
%OF (Landscape Flower Quantity)	1	1.88	0.18	1.34	0.26	1.90	0.18	0.34	0.56	3.73	0.06

506

507 **Fig. 1: (a)** The experimental design was set up in the LTSER Zone Atelier Plaine & Val de Sèvre, a study
 508 area situated in central western France. Oilseed rape plant phytometers were placed in OSR fields (yellow), cereal
 509 fields (grey) and grasslands (blue) from 2015 to 2019. **(b)** In each farmer's field, two OSR phytometers (circles)
 510 were placed, one at the edge and one in the core of the field. Four branches were tested, one with a control
 511 treatment, one with a large mesh treatment, one with a small mesh treatment and one with an Osmolux treatment.
 512 In OSR, the flowering sequence goes from the base to the apex. Flowers opened during the experiment were
 513 delaminated from flowers opened before or after field experiment. Pollination processes involved in each
 514 experimental treatment include in the control treatment self-pollination, wind-pollination, small insect-pollination,
 515 and large insect-pollination. **(c)** Plant phytometers were deposited in OSR, cereals or grasslands, field size was
 516 used as a proxy of the amount of floral resources at the field scale. %OSR (oilseed rape), %SNH (semi-natural
 517 habitats) and %OF (organic farming) were used to estimate 'Landscape Flower Quantity'. Information about the
 518 amount and type of floral resources provided by the habitats (focal or landscape ones) were provided based on
 519 literature (Hegland and Boeke 2006; Hardman et al. 2016; Gaba et al. 2020; Bourgeois et al. 2020; Sidemo-Holm
 520 et al. 2021): +++: flower cover > 50%, ++: flower cover > 10%, +: flower cover > 0%, 0: flower cover = 0%. The
 521 amount of flowers provided by wild plants is rather constant (Cole et al. 2017). To account for the temporal
 522 variation of OSR flower cover we developed two variables: 'Phytometer-Regional Flowering Temporal Matching'
 523 described the period of OSR flowering during which phytometers were placed in the fields (during or after OSR
 524 flowering peak) and 'Focal Field-Regional Flowering Temporal Matching' defined the temporal deviation
 525 between flowering in the OSR focal field and OSR flowering in the study site and was thus designed only for OSR
 526 fields in contrast to the other three variables.

527
 528 **Fig. 2:** Variation in OSR fruiting success with 'Phytometer-Regional Flowering Temporal Matching' in
 529 OSR (a), cereals (b) and grasslands (c). Thresholds discriminating 'Phytometer-Regional Flowering Temporal
 530 Matching' (i.e. during and after OSR flowering / flowering peak) were defined differently for phytometers in OSR
 531 fields and for phytometers placed in cereals and grasslands (see 'Methods' for details). Quantiles and means (black
 532 dots) of raw data are represented and numbers show the sample sizes. Significant differences between levels of
 533 'Phytometer-Regional Flowering Temporal Matching' are indicated by asterisks (p-value: *** < 0.001; ** < 0.01
 534 and * < 0.05). Effect sizes: fruiting success was on average greater during OSR peak flowering than after in OSR
 535 (0.21 ± 0.05 se; from Table 1a model), in cereals (0.15 ± 0.05 ; from Table 1b model) and in grasslands ($0.19 \pm$
 536 0.07 ; from Table 1c model).

537
 538 **Fig. 3:** Effect of 'Landscape Flower Quantity' on fruiting success of plant phytometers. The effects of %OSR
 539 (a, b, c), %SNH (d, e, f) and %OF (g, h, i) were quantified in buffer radii (r value in brackets) estimated by
 540 optimization of likelihood outside the OSR fields (a, d, g), cereal fields (b, e, h) and grasslands (c, f, i) in which
 541 the phytometers were placed. Dots of different shapes show raw data for each year. The lines show the adjusted
 542 relationships and the shaded area the standard error (based on models presented in Table 1). Lines in bold show
 543 significant effects (p-value < 0.05) and dotted lines non-significant effects. Effect sizes: in OSR, fruiting success
 544 increased with %OSR (mean \pm se: 0.0030 ± 0.0013 per %OSR) and %SNH (0.0126 ± 0.0057 per %SNH) and
 545 decreased with %OF (-0.0034 ± 0.0015 per %OF). Fruiting success increased with %OSR (0.0057 ± 0.0026 per
 546 %OSR) in cereals and in grasslands (0.0134 ± 0.0065 per %OSR), while it decreased with %SNH ($-0.0305 \pm$

547 0.0080 per %SNH) in grasslands.

548

549 **Fig. 4:** Fruiting success (in %) of self-pollination between crops (a, b) and effect sizes of other pollination
 550 processes in OSR fields (c), cereal fields (d) and grasslands (e) and the variation between categories of
 551 ‘Phytometer-Regional Flowering Temporal Matching’: during (orange) versus after (green) OSR flowering (peak).
 552 Significance of effect size are tested against 0, using unilateral sign tests (p-value: *** < 0.001; ** < 0.01 and *
 553 <0.05 into brackets). Asterisks (p-value: *** < 0.001; ** < 0.01 and * <0.05) also indicate significant differences
 554 between categories of ‘Phytometer-Regional Flowering Temporal Matching’ (see Table 2; c-e). Mean \pm se of raw
 555 data are presented, numbers indicate the sample sizes. Estimated effects: self-pollination was 0.11 ± 0.05 se more
 556 important during the OSR peak flowering than after in OSR fields, and 0.16 ± 0.04 (estimation from Table 2a
 557 model) greater during OSR flowering than after in cereals (from Table 2b model). Insect-pollination was $0.27 \pm$
 558 0.11 se greater during OSR peak flowering than after in OSR (from Table 2a model). Insect-pollination ($0.92 \pm$
 559 0.18) and large insect-pollination (0.88 ± 0.17) were greater after OSR flowering than during, while wind-
 560 pollination was 0.73 ± 0.23 more important during OSR flowering than after in grasslands (from Table 2c model).
 561

562 **Fig. 5:** Variation in the magnitude of pollination processes with ‘Landscape Flower Quantity’ (%OSR: %
 563 oilseed rape, %SNH: % semi-natural habitats and %OF: % organic farming) and ‘Phytometer-Regional Flowering
 564 Temporal Matching’ in OSR fields (a-f), cereals (g) and grasslands (h-j). The scale of effects was estimated by
 565 likelihood optimizations. Raw data is shown for each year, the predicted relationships are based on models
 566 presented in Table 2 (bold if a significant effect, or else dotted) and their standard errors. Black colour was used
 567 when landscape effect was independent of Phytometer-Regional Flowering Temporal Matching and green and
 568 orange colours were used for significant interaction terms.

569 **References**

- 570 Arnholt AT, Evans B (2017) BSDA: Basic Statistics and Data Analysis. Version 1.2.0 URL [https://CRAN.R-](https://CRAN.R-project.org/package=BSDA)
571 [project.org/package=BSDA](https://CRAN.R-project.org/package=BSDA)
- 572 Bänisch S, Tschardt T, Gabriel D, Westphal C (2020) Crop pollination services: Complementary resource use by social vs
573 solitary bees facing crops with contrasting flower supply. *J Appl Ecol* n/a: <https://doi.org/10.1111/1365-2664.13777>
- 574 Bartomeus I, Potts SG, Steffan-Dewenter I, Vaissière B, Woyciechowski M, Krewenka K, Tscheulin T, Roberts S,
575 Szentgyorgyi H, Westphal C, Bommarco R (2014) Contribution of insect pollinators to crop yield and quality varies
576 with agricultural intensification. *PeerJ* 2:e328. <https://doi.org/10.7717/peerj.328>
- 577 Bennett AB, Isaacs R (2014) Landscape composition influences pollinators and pollination services in perennial biofuel
578 plantings. *Agr Ecosyst Environ* 193:1–8. <https://doi.org/10.1016/j.agee.2014.04.016>
- 579 Bommarco R, Marini L, Vaissière BE (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape.
580 *Oecol* 169:1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>
- 581 Bourgeois B, Gaba S, Plumejeaud C, Bretagnolle V (2020) Weed diversity is driven by complex interplay between multi-scale
582 dispersal and local filtering. *Proc Biol Sci* 287:20201118. <https://doi.org/10.1098/rspb.2020.1118>
583
- 584 Bretagnolle V, Berthet E, Gross N, Gauffre B, Plumejeaud C, Houte S, Badenhausser I, Monceau K, Allier F, Monestiez P,
585 Gaba S (2018) Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the
586 integrative approach of a French LTSER platform. *Sci Total Environ* 627:822–834.
587 <https://doi.org/10.1016/j.scitotenv.2018.01.142>
- 588 Bretagnolle V, Gaba S (2015) Weeds for bees? A review. *Agron Sustain Dev* 35:891–909. [https://doi.org/10.1007/s13593-015-](https://doi.org/10.1007/s13593-015-0302-5)
589 [0302-5](https://doi.org/10.1007/s13593-015-0302-5)
- 590 Bukovinszky T, Verheijen J, Zwerver S, Klopa E, Biesmeijer J, Wäckers F, Prins H, Kleijn D (2017) Exploring the relationships
591 between landscape complexity, wild bee species richness and reproduction, and pollination services along a
592 complexity gradient in the Netherlands. *Biol. Conserv* 214:312–319. <https://doi.org/10.1016/j.biocon.2017.08.027>
- 593 Carpentier, F., Martin, O., 2021. Siland a R package for estimating the spatial influence of landscape. *Sci Rep* 11, 7488.
594 <https://doi.org/10.1038/s41598-021-86900-0>
- 595 Carpentier F, Martin O (2020) siland: Spatial Influence of Landscape. Version 2.0 URL [https://CRAN.R-](https://CRAN.R-project.org/package=siland)
596 [project.org/package=siland](https://CRAN.R-project.org/package=siland)
- 597 Castle D, Grass I, Westphal C (2019) Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at
598 hedgerows in agricultural landscapes. *Agr Ecosyst Environ* 275:14–22. <https://doi.org/10.1016/j.agee.2019.01.003>
- 599 Cavallero L, Morales CL, Montero-Castaño A, Gowda JH, Aizen MA (2018) Scale-dependent effects of conspecific flower
600 availability on pollination quantity and quality in an invasive shrub. *Oecol* 188:501–513.
601 <https://doi.org/10.1007/s00442-018-4239-7>
- 602 Chifflet R, Klein EK, Lavigne C, Le Féon V, Ricrich AE, Lecomte J, Vaissière BE (2011) Spatial scale of insect-mediated
603 pollen dispersal in oilseed rape in an open agricultural landscape. *J Appl Ecol* 48:689–696.
604 <https://doi.org/10.1111/j.1365-2664.2010.01904.x>
- 605 Cole LJ, Brocklehurst S, Robertson D, Harrison W, McCracken D (2017) Exploring the interactions between resource
606 availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape.
607 *Agr Ecosyst Environ* 246:157–167. <https://doi.org/10.1016/j.agee.2017.05.007>
- 608 Cusser S, Neff JL, Jha S (2016) Natural land cover drives pollinator abundance and richness, leading to reductions in pollen
609 limitation in cotton agroecosystems. *Agr Ecosyst Environ* 226:33–42. <https://doi.org/10.1016/j.agee.2016.04.020>
- 610 Dainese M, Martin EA, Aizen MA, et al (2019) A global synthesis reveals biodiversity-mediated benefits for crop production.
611 *Sci Adv* 5:eaax0121. <https://doi.org/10.1126/sciadv.aax0121>
- 612 Diekötter T, Peter F, Jauker B, Wolters V, Jauker F (2014) Mass-flowering crops increase richness of cavity-nesting bees and
613 wasps in modern agro-ecosystems. *Glob Change Biol Bioenergy* 6:219–226. <https://doi.org/10.1111/gcbb.12080>
- 614 Dormann CF, McPherson JM, Araújo MB, et al (2007) Methods to account for spatial autocorrelation in the analysis of species

- 615 distributional data: a review. *Ecography* 30:609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- 616 Elzinga JA, Atlan A, Biere A, Gigord L, Weis A, Bernasconi G (2007) Time after time: flowering phenology and biotic
617 interactions. *Trends in Ecol Evol* 22:432–439. <https://doi.org/10.1016/j.tree.2007.05.006>
- 618 Fahrig L, Baudry J, Brotons L, Burel F, Crist T, Fuller R, Sirami C, Siriwardena C, Martin JL (2011) Functional landscape
619 heterogeneity and animal biodiversity in agricultural landscapes: Heterogeneity and biodiversity. *Ecol Lett* 14:101–
620 112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- 621 Fahrig L, Girard J, Duro D, Pasher J, Smith A, Javorek S, King D, Lindsay KF, Mitchell S, Tischendorf L (2015) Farmlands
622 with smaller crop fields have higher within-field biodiversity. *Agr Ecosyst Environ* 200:219–234.
623 <https://doi.org/10.1016/j.agee.2014.11.018>
- 624 Fijen TPM, Scheper JA, Boekelo B, Raemakers I, Kleteijn D (2019) Effects of landscape complexity on pollinators are
625 moderated by pollinators' association with mass-flowering crops. *Proc Biol Sci* 286:20190387.
626 <https://doi.org/10.1098/rspb.2019.0387>
- 627 Fox J, Weisberg S, Price B et al (2020) car: Companion to Applied Regression. Version 3.0-8URL [https://CRAN.R-](https://CRAN.R-project.org/package=car)
628 [project.org/package=car](https://CRAN.R-project.org/package=car)
- 629 Frankl R, Wanning S, Braun R (2005) Quantitative floral phenology at the landscape scale: Is a comparative spatio-temporal
630 description of “flowering landscapes” possible? *J Nat Conserv* 13:219–229.
631 <https://doi.org/10.1016/j.jnc.2004.10.002>
- 632 Gaba S, Cheviron N, Perrot T, Piutti S, Gautier JL, Bretagnolle V (2020) Weeds Enhance Multifunctionality in Arable Lands
633 in South-West of France. *Front Sustain Food Syst* 4: <https://doi.org/10.3389/fsufs.2020.00071>
- 634 Garratt MPD, Brown R, Hartfield C, Hart A, Potts SG (2018) Integrated crop pollination to buffer spatial and temporal
635 variability in pollinator activity. *Basic Appl Ecol* 32:77–85. <https://doi.org/10.1016/j.baae.2018.06.005>
- 636 Grab H, Blitzer EJ, Danforth B, Loeb G, Poveda K (2017) Temporally dependent pollinator competition and facilitation with
637 mass flowering crops affects yield in co-blooming crops. *Sci Rep* 7:45296. <https://doi.org/10.1038/srep45296>
- 638 Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecol*
639 153:589–596. <https://doi.org/10.1007/s00442-007-0752-9>
- 640 Hardman CJ, Norris K, Nevard TD, Hughes B, Potts S (2016) Delivery of floral resources and pollination services on farmland
641 under three different wildlife-friendly schemes. *Agr Ecosyst Environ* 220:142–151.
642 <https://doi.org/10.1016/j.agee.2016.01.015>
- 643 Hass AL, Kormann UG, Tschardt T, et al (2018) Landscape configurational heterogeneity by small-scale agriculture, not
644 crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc R Soc B* 285:20172242.
645 <https://doi.org/10.1098/rspb.2017.2242>
- 646 Hegland SJ, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a
647 temperate grassland community. *Ecol Entomol* 31:532–538. <https://doi.org/10.1111/j.1365-2311.2006.00812.x>
- 648 Henckel L, Börger L, Meiss H, Gaba S, Bretagnolle V (2015) Organic fields sustain weed metacommunity dynamics in
649 farmland landscapes. *Proc Biol Sci* 282:20150002. <https://doi.org/10.1098/rspb.2015.0002>
- 650 Herbertsson L, Rundlöf M, Smith HG (2017) The relation between oilseed rape and pollination of later flowering plants varies
651 across plant species and landscape contexts. *Basic Appl Ecol* 24:77–85. <https://doi.org/10.1016/j.baae.2017.08.001>
- 652 Holzschuh A, Dainese M, González-Varo JP, Mudri-Stojnic S, Riedinger V, Rundlof M, Scheper J, Wickens J, Wickens V,
653 Bommarco R, Kleijn D, Potts S, Roberts S, Smith H, Vilà M, Vujic A, Steffan-Dewenter I (2016) Mass-flowering
654 crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol Lett* 19:1228–1236.
655 <https://doi.org/10.1111/ele.12657>
- 656 Holzschuh A, Dormann CF, Tschardt T, Steffan-Dewenter I (2011) Expansion of mass-flowering crops leads to transient
657 pollinator dilution and reduced wild plant pollination. *Proc Biol Sci* 278:3444–3451.
658 <https://doi.org/10.1098/rspb.2011.0268>
- 659 Hopfenmüller S, Steffan-Dewenter I, Holzschuh A (2014) Trait-Specific Responses of Wild Bee Communities to Landscape
660 Composition, Configuration and Local Factors. *PLoS ONE* 9:e104439.

- 661 <https://doi.org/10.1371/journal.pone.0104439>
- 662 Hudewenz A, Pufal G, Böggeholz A-L, Klein A-M (2014) Cross-pollination benefits differ among oilseed rape varieties. *J Agric*
663 *Sci* 152:770–778. <https://doi.org/10.1017/S0021859613000440>
- 664 Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? *Landsc Ecol* 27:929–941.
665 <https://doi.org/10.1007/s10980-012-9757-9>
- 666 Jauker F, Bondarenko B, Becker HC, Steffan-Dewenter I (2012) Pollination efficiency of wild bees and hoverflies provided to
667 oilseed rape. *Agri Fo Entomol* 14:81–87. <https://doi.org/10.1111/j.1461-9563.2011.00541.x>
- 668 Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham S, Kremen C, Tscharntke T (2007) Importance of
669 pollinators in changing landscapes for world crops. *Proc Biol Sci* 274:303–313.
670 <https://doi.org/10.1098/rspb.2006.3721>
- 671 Knapp EE, Goedde MA, Rice KJ (2001) Pollen-limited reproduction in blue oak: implications for wind pollination in
672 fragmented populations. *Oecol* 128:48–55. <https://doi.org/10.1007/s004420000623>
- 673 Kovács-Hostyánszki A, Haenke S, Batáry P, Jauker B, Báldi A, Tscharntke T, Holzschuh A (2013) Contrasting effects of mass-
674 flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecol Appl* 23:1938–1946.
675 <https://doi.org/10.1890/12-2012.1>
- 676 Kozak M, Piepho H-P (2018) What’s normal anyway? Residual plots are more telling than significance tests when checking
677 ANOVA assumptions. *J Agron Crop Sci* 204:86–98. <https://doi.org/10.1111/jac.12220>
- 678 Kremen C, Williams NM, Aizen MA, Barbara Gemmill-Herren, LeBuhn G, Minckley R, Packer L, Potts S, Roulston T,
679 Steffan-Dewenter I, Vázquez D, Winfree R, Adams L, Crone E, Greenleaf S, Keitt T, Klein AM, Regetz J, Ricketts
680 T (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the
681 effects of land-use change. *Ecol Lett* 10:299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>
- 682 Le Féon V, Burel F, Chifflet R, Henry M, Ricroch A, Vaissière B, Baudry J (2013) Solitary bee abundance and species richness
683 in dynamic agricultural landscapes. *Agr Ecosyst Environ* 166:94–101. <https://doi.org/10.1016/j.agee.2011.06.020>
- 684 Lenth R, Singmann H, Love J, Buerkner P, Herve M (2020) emmeans: Estimated Marginal Means, aka Least-Squares Means.
685 Version 1.4.6 URL <https://CRAN.R-project.org/package=emmeans>
- 686 Lindström SAM, Herbertsson L, Rundlöf M, Bommarco R, Smith H (2016) Experimental evidence that honeybees depress
687 wild insect densities in a flowering crop. *Proc Biol Sci* 283:20161641. <https://doi.org/10.1098/rspb.2016.1641>
- 688 Mallinger RE, Gibbs J, Gratton C (2016) Diverse landscapes have a higher abundance and species richness of spring wild bees
689 by providing complementary floral resources over bees’ foraging periods. *Landsc Ecol* 31:1523–1535.
690 <https://doi.org/10.1007/s10980-015-0332-z>
- 691 Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. *Ecol*
692 *App* 22:1535–1546. <https://doi.org/10.1890/11-1299.1>
- 693 Marini L, Tamburini G, Petrucco-Toffolo E, Lindström SAM (2015) Crop management modifies the benefits of insect
694 pollination in oilseed rape. *Agr Ecosyst Environ* 207:61–66. <https://doi.org/10.1016/j.agee.2015.03.027>
- 695 Martin EA, Dainese M, Clough Y et al (2019) The interplay of landscape composition and configuration: new pathways to
696 manage functional biodiversity and agroecosystem services across Europe. *Ecol Lett* 22:1083–1094.
697 <https://doi.org/10.1111/ele.13265>
- 698 McCartney HA, Lacey ME (1991) Wind dispersal of pollen from crops of oilseed rape (*Brassica napus* L.). *J Aerosol Sci* 22:
699 467–477. [https://doi.org/10.1016/0021-8502\(91\)90005-3](https://doi.org/10.1016/0021-8502(91)90005-3)
- 700 Mesquida J, Renard M (1981) Pollinisation du colza d’hiver mâle-fertile et mâle-stérile (*Brassica napus* L var. *oleifera* Metzger)
701 par l’abeille domestique (*Apis M. mellifica* L.). Effets sur la phénologie et le rendement. *Apidologie* 12:345–362.
702 <https://doi.org/10.1051/apido:19810404>
- 703 Meyer B, Gaebele V, Steffan-Dewenter I (2007) Patch Size and Landscape Effects on Pollinators and Seed Set of the Horseshoe
704 Vetch, *Hippocrepis comosa*, in an Agricultural Landscape of Central Europe. *Entomol Gen* 173–185.
705 <https://doi.org/10.1127/entom.gen/30/2007/173>

- 706 Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on
707 species? *Landsc Ecol* 31:1177–1194. <https://doi.org/10.1007/s10980-015-0314-1>
- 708 Momoh EJJ, Zhou W (2001) Growth and Yield Responses to Plant Density and Stage of Transplanting in Winter Oilseed Rape
709 (*Brassica napus* L.). *J Agron Crop Sci* 186:253–259. <https://doi.org/10.1046/j.1439-037x.2001.00476.x>
- 710 Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
711 <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- 712 Palmer TM, Zimmerman M (1994) Pollen Competition and Sporophyte Fitness in *Brassica campestris*: Does Intense Pollen
713 Competition Result in Individuals with Better Pollen? *Oikos* 69:80–86. <https://doi.org/10.2307/3545286>
- 714 Perrot T, Gaba S, Roncoroni M, Gautier JL, Bretagnolle V (2018) Bees increase oilseed rape yield under real field conditions.
715 *Agr Ecosyst Environ* 266:39–48. <https://doi.org/10.1016/j.agee.2018.07.020>
- 716 Petersen JD, Nault BA (2014) Landscape diversity moderates the effects of bee visitation frequency to flowers on crop
717 production. *J Appl Ecol* 51:1347–1356. <https://doi.org/10.1111/1365-2664.12287>
- 718 Popławska W, Liersch A, Jędrzycka M, Wielebski F, Bartkowiak-Broda I (2013) Wind-mediated pollen dispersal of oilseed
719 rape - an estimation using pollen traps. *Geography*
- 720 R Core team (2019) A language and environment for statistical computing. Version 3.6.2. R Foundation for Statistical
721 Computing, Vienna, Austria
- 722 Rader R, Howlett BG, Cunningham SA, Westcott DA, Newstrom-Lloyd LE, Walker MK, Teulon D, Edwards W (2009)
723 Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *J Appl*
724 *Ecol* 46:1080–1087. <https://doi.org/10.1111/j.1365-2664.2009.01700.x>
- 725 Raderschall CA, Bommarco R, Lindström SAM, Lundin O (2021) Landscape crop diversity and semi-natural habitat affect
726 crop pollinators, pollination benefit and yield. *Agr Ecosyst Environ* 306:107189.
727 <https://doi.org/10.1016/j.agee.2020.107189>
- 728 Ratheke B, Lacey EP (1985) Phenological Patterns of Terrestrial Plants. *Annu. Rev Ecol Evol Syst* 16:179–214.
729 <https://doi.org/10.1146/annurev.es.16.110185.001143>
- 730 Requier F, Odoux J-F, Henry M, Bretagnolle V (2017) The carry-over effects of pollen shortage decrease the survival of
731 honeybee colonies in farmlands. *J Appl Ecol* 54:1161–1170. <https://doi.org/10.1111/1365-2664.12836>
- 732 Requier F, Odoux J-F, Tamic T, Nathalie Moreau, Henry M, Decourtye A, Bretagnolle V (2015) Honey bee diet in intensive
733 farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecol Appl* 25:881–890.
734 <https://doi.org/10.1890/14-1011.1>
- 735 Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham S, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf S, Klein
736 AM, Mayfield M, Morandin L, Ochieng L, Viana B (2008) Landscape effects on crop pollination services: are there
737 general patterns? *Ecol Lett* 11:499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- 738 Rollin O, Bretagnolle V, Decourtye A, Aptel J, Michele N, Vaissière B, Henry M (2013) Differences of floral resource use
739 between honey bees and wild bees in an intensive farming system. *Agr Ecosyst Environ* 179:78–86.
740 <https://doi.org/10.1016/j.agee.2013.07.007>
- 741 Rollin O, Bretagnolle V, Fortel L, Guilbaud L, Henry M (2015) Habitat, spatial and temporal drivers of diversity patterns in a
742 wild bee assemblage. *Biodivers Conserv* 24:1195–1214. <https://doi.org/10.1007/s10531-014-0852-x>
- 743 Roulston T, Goodell K (2011) The Role of Resources and Risks in Regulating Wild Bee Populations. *Annu Rev Entomol*
744 56:293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- 745 Rusch A, Valantin-Morison M, Sarthou J-P, Roger-Estrade J (2011) Multi-scale effects of landscape complexity and crop
746 management on pollen beetle parasitism rate. *Landsc Ecol* 26:473–486. <https://doi.org/10.1007/s10980-011-9573-7>
- 747 Schellhorn NA, Gagic V, Bommarco R (2015) Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol*
748 *Evol* 30:524–530. <https://doi.org/10.1016/j.tree.2015.06.007>
- 749 Shaw RF, Phillips BB, Doyle T, Pell J, Redhead J, Savage J, Woodcock B, Bullock J, Osborne J (2020) Mass-flowering crops
750 have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. *Landsc Ecol* 35:513–527.

- 751 <https://doi.org/10.1007/s10980-019-00962-0>
- 752 Sidemo-Holm W, Carrié R, Ekroos J, Lindström SAM, Smith HG (2021) Reduced crop density increases floral resources to
753 pollinators without affecting crop yield in organic and conventional fields. *J Appl Ecol* 1365-2664.13887.
754 <https://doi.org/10.1111/1365-2664.13887>
- 755 Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tschamtkke T (2002) Scale-Dependent Effects of Landscape Context
756 on Three Pollinator Guilds. *Ecol* 83:1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083](https://doi.org/10.1890/0012-9658(2002)083)
- 757 Tschamtkke T, Tylianakis JM, Rand TA, et al (2012) Landscape moderation of biodiversity patterns and processes - eight
758 hypotheses. *Biol Rev* 87:661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- 759 Vasseur C, Joannon A, Aviron S, Burel F, Meynard JM, Baudry J (2013) The cropping systems mosaic: How does the hidden
760 heterogeneity of agricultural landscapes drive arthropod populations? *Agr Ecosyst Environ* 166:3–14.
761 <https://doi.org/10.1016/j.agee.2012.08.013>
- 762 Waser NM, Price MV (2016) Drought, pollen and nectar availability, and pollination success. *Ecology* 97:1400–1409.
763 <https://doi.org/10.1890/15-1423.1>
- 764 Wintermantel D, Odoux J, Chadœuf J, Bretagnolle V (2019) Organic farming positively affects honeybee colonies in a flower-
765 poor period in agricultural landscapes. *J Appl Ecol* 1365-2664.13447. <https://doi.org/10.1111/1365-2664.13447>
- 766 Woodcock TS, Pekkola LJ, Dawson C, Gadallah F, Kevan P (2014) Development of a Pollination Service Measurement (PSM)
767 method using potted plant phytometry. *Environ Monit Assess* 186:5041–5057. <https://doi.org/10.1007/s10661-014-3758-x>
- 769 Zou Y, Xiao H, Bianchi FJJA, Jauker F, Luo S, Van der Werf W (2017) Wild pollinators enhance oilseed rape yield in small-
770 holder farming systems in China. *BMC Ecol* 17:6. <https://doi.org/10.1186/s12898-017-0116-1>