

Moderate pollination limitation in some entomophilous crops of Europe

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1 **Abstract**

2 Pollination services to crops may be worsening because of declines in farmland pollinators,
3 but the consequences for yields have been uncertain. We therefore investigated pollination
4 limitation in four entomophilous crops (oilseed rape, sunflower, pears and pumpkin) by
5 quantifying the difference in harvestable mass between open-pollinated and saturation-
6 pollinated (hand-pollinated) flowers. We also examined whether pollination limitation in the
7 four crops was associated with the number of flower visits by insects. Across 105
8 commercial fields in six European countries, the average decrease in harvestable mass due to
9 pollination limitation was 2.8% (SE = 1.15). Among crops, the highest decreases were in
10 sunflowers (8%) and in one of three oilseed rape production regions (6%). We observed
11 substantial variation among crops in the numbers of insect visits received by flowers, but it
12 did not significantly correspond with the levels of pollination limitation. Our results suggest
13 that yields in these crops were not severely pollination-limited in the regions studied and that
14 other factors besides visitation by pollinators influenced the degree of pollination limitation.

15

16 Keywords: agroecology; pollinators; crop yield; landscape ecology; pollination;
17 entomophilous crops

18 **1. Introduction**

19 Crops with entomophilous flowers such as oilseeds, squash and orchard fruits are important
20 to food security and the farming economy (Losey and Vaughan, 2006). Entomophilous
21 flowers typically have showy petals and offer nectar and/or pollen to visiting insects, which
22 act as pollinators. Among insects, bees are a principal pollinator of many entomophilous
23 crops and their declines in farmland of north western Europe and eastern North America are a
24 cause of concern (Potts et al., 2016) because crop yields might become threatened by
25 pollination limitation (IPBES 2016; Dainese et al. 2019). Pollination limitation is widespread
26 among wildflowers (Wolowski et al., 2014), but its levels in many crops have been uncertain
27 (Klein et al., 2007). We therefore conducted pollen supplementation experiments in
28 commercial fields to quantify pollination limitation in some of the main entomophilous crops
29 grown in Europe.

30 We conducted experiments on four entomophilous crops from three product classes (oilseeds,
31 squash and orchard fruit) in regions of six countries (Estonia, Germany, Italy, the
32 Netherlands, Switzerland, and the United Kingdom). Specifically, we measured pollination
33 limitation and the number of insect visits received by flowers in: oilseed rape, *Brassica napus*
34 L.; sunflower, *Helianthus annuus* L.; Hokkaido pumpkin, *Cucurbita maxima* Duch.; and
35 Conference pear, *Pyrus communis* L. The objectives of our study were: (1) to determine the
36 levels of pollination limitation in various crops and regions; and (2) to examine the
37 association between the pollination limitation and the number of insect visits received by
38 flowers in crop fields.

39 **2. Methods**

40 We studied crops of oilseed rape in Estonia, Switzerland and the United Kingdom, sunflower
41 in Italy, pumpkin in Germany and pear in the Netherlands. In each of these six countries in

42 2014, we studied 18 fields in a single region with representative commercial practice, field
43 sizes and that ranged from low to high levels of semi-natural habitat for the region (Appendix
44 S1.1). The proportion of the main types of semi-natural habitat in a 1 km radius around each
45 field were mapped (Table S1.1). In each field, we quantified pollination limitation by
46 comparing the harvestable mass of pollen-saturated and open-pollinated flowers.
47 Specifically, we estimated pollen limitation as the proportional decrease in harvestable mass
48 observed in open-pollinated flowers relative to saturation-pollinated flowers:

$$49 \quad \text{pollen limitation} = 100 \times [1 - (M_{\text{open}} / M_{\text{supplemented}})] \% \quad \text{eq 1}$$

50 Focal flowers were located on plants situated along a transect perpendicular to one of the
51 field's edges and these experimental plants were located on the transect at four well-separated
52 distances (Appendix S1). To minimize the influence of the other field boundaries on
53 transects, the distance between the end of the transects and non-focal field boundaries had to
54 be at least 1.25 times the length of the transect (Bartual et al., 2018).

55 In each field of sunflower and oilseed rape, outcross pollen was collected from at least five
56 donor flowers, mixed and applied to receptive stigmas on different plants with a soft brush.
57 In pear, a commercial pollen mix (Wellplus Co., Daejeon, Korea) was used to pollinate
58 flowers. Flowers of oilseed rape and pear were hand-pollinated with a single dose whereas in
59 sunflower the many receptive florets of each capitulum were hand-pollinated over three to
60 five occasions at two-day or three-day intervals. In oilseed rape and sunflower, we quantified
61 harvestable mass by the dry mass of mature seed produced per flower (oilseed rape) or
62 capitulum (sunflower). In pears, we quantified the mass of the fruit produced by each
63 experimental flower at the time appropriate to the commercial harvest. In Hokkaido
64 pumpkin, we estimated harvestable mass by quantifying the pollen that had accumulated on
65 stigmas of focal flowers and transforming to expected fruit mass using an experimentally

66 established pollen-fruit mass relationship (Pfister *et al.*, 2017). Each pumpkin flower
67 bloomed for only a few hours and we collected stigmas in the afternoon from senescent
68 flowers which had opened that morning before counting the pollen in a microscope
69 preparation (Pfister *et al.*, 2017). Pollination limitation of each pumpkin flower was
70 estimated by subtracting the estimated fruit mass from its maximum value, which was
71 determined by saturating pollinations (Pfister *et al.* 2017). The numbers of replicate flowers
72 (hand-pollinated, open-pollinated) in each of the 18 focal fields were: sunflower (8, 32); pear
73 (5, 5); pumpkin (0, 32); oilseed rape: Estonia (16, 96), Switzerland (8, 8) and the United
74 Kingdom (8, 8). To avoid pseudoreplication, we used the mean level of pollination limitation
75 in each field for statistical analysis.

76 **2.1 Estimating insect visits per flower**

77 We quantified pollinator visitation by estimating the overall number of insect visits received
78 by a receptive flower (Cresswell, 2008). In each field, we studied the insects visiting crop
79 flowers, including bees, syrphids and other flies, and lepidopteran species during fine weather
80 in 2014. In oilseed rape at each distance along the transect in each field, we recorded the
81 total number of flowers probed by insects over 10-minute intervals in at least two 2×2 m
82 quadrats and we also estimated the area density of flowers (i.e. flowers per m^2) for $10m^2$. We
83 thereby calculated the expected number of insect visits per receptive flower for each field by
84 assuming that flowers were receptive for $8 \text{ h d}^{-1} \times 2.7 \text{ d}$ (Bell and Cresswell, 1998).

85 Observations were made in 18 fields per country either once (United Kingdom: 14th-16th
86 April) or twice (Estonia: 16th May, 6th June; Switzerland: 22nd-24th April, 5th-6th May). In
87 sunflower (Italy), observations were made over 10 minutes in two replicate quadrats each
88 containing four capitula. Observations were made in the 18 fields twice on separate days
89 during peak bloom (capitula having >30% of florets open) between 24th June and 16th of July.
90 Based on the observed visit rates, we estimated the expected number of insect visits per

91 receptive flower by assuming that each floret in a capitulum was receptive for $8 \text{ h d}^{-1} \times 4 \text{ d}$
92 (OECD, 2005). In pumpkin, we used video cameras (Sony HDR-CX115E, Sony
93 Corporation, Tokyo, Japan) to record the activity of flower visitors. Each field was sampled
94 at each one time period on three different days in July during the flowering period, once at
95 7:00, 8:30 and 10:00 am. On each occasion, four 15-minute-long videos, one at each 2, 10, 18
96 and 26 m transect, each surveying a different female pumpkin flower. We calculated mean
97 visit rates for each field and calculated the expected number of visits received by a receptive
98 flower by assuming that it was receptive for 4 h (Pfister et al., 2017). In pear, we observed
99 clusters of approximately 500 flowers on a single branch and counted the number of insects
100 that visited it during a 10-minute period. In each field (orchard) we conducted four replicate
101 observations on one day between 2nd and 10th of April. The exact number of flowers visited
102 by each insect was not recorded but it never exceeded 10, so we estimated per-flower
103 visitation rates by assuming that insects visited either 10 flowers on the cluster or only a
104 single flower. We thereby calculated the number of visits received by a receptive flower
105 under each scenario (i.e. ‘probe-one flower’ or ‘probe-all flowers’ per cluster) by assuming
106 that the duration of a flower’s receptivity was $8 \text{ h d}^{-1} \times 6.6 \text{ d}$.

107

108 **3. Results**

109 We found a moderate but significant level of pollination limitation across 105 commercial
110 fields that produced data (mean = 2.8% of harvestable mass in supplemented flowers, SEM =
111 1.15; test $H_0: \mu = 0$ using standardized deviate on a normal distribution, $z = 2.3$, $P < 0.05$).
112 Regionally, we detected pollination limitation in sunflower crops in Italy (c. 8%) and oilseed
113 rape crops in Switzerland (c. 6%) (Fig. 2a). Western honey bees (*Apis mellifera* L.),
114 thereafter honey bees, or flies were the dominant flower visitors in all regions (Appendix S2)

115 and the number of insect visits received by flowers varied over ten thousand-fold among
116 crops and regions (Fig. 2b). We estimate that sunflower capitula and pumpkin flowers each
117 received more than 100 insect visits (principally bumblebees *Bombus* spp. and honey bees)
118 during their receptive phase (Fig 2b). By contrast, in oilseed rape it appears that less than
119 10% of flowers received even a single insect visit (Fig. 2b). The variation in insect visitation
120 did not correspond with the levels of pollination limitation (Fig. 2a).

121 **4. Discussion**

122 Our results show that the harvestable mass of individual flowers in crop fields was
123 moderately depressed by pollen limitation (mean decrease = 2.8%). This finding is probably
124 conservative because pollen supplementation overestimates pollination limitation if plants
125 divert limited resources to well-pollinated flowers (Knight et al., 2006), but resource-
126 limitation seems unlikely in well-fertilized crop fields. Therefore, our assays appear likely to
127 have quantified pollination limitation among the flowers generally and hence indicate
128 potential impacts on overall crop yields. If so, our findings suggest that the crop pollination
129 systems that we studied were underperforming only slightly despite recent bee declines in
130 some European countries (IPBES, 2016).

131

132 **4.1 The influence of crop-specific factors on pollination**

133 Among the focal crops, levels of pollination limitation were unrelated to the intensity of
134 flower visitation by insects, which suggests the influence of crop-specific factors such as the
135 pollination efficacy of the single pollinating species. We therefore discuss each crop
136 separately below.

137 **4.1.1 Sunflower**

138 Sunflower fields were intensively visited by honey bees (a capitulum apparently received
139 over 100 visits each day, on average), but the crop did not achieve full seed set. Commercial
140 cultivars of sunflower often have a high level of pollinator-dependence (Bartual et al., 2018),
141 but we speculate that pollination by honey bees was incomplete despite their high rate of
142 flower visitation because either individual bees probed only a minority of receptive florets
143 while visiting each inflorescence or their contacts with the sexual parts of the florets were not
144 fully effective.

145 **4.1.2 Oilseed rape**

146 We found little pollination limitation in winter-sown oilseed rape despite low levels of insect
147 visitation to flowers. Likewise, in field trials in the UK there was no effect on yield of
148 pollinator exclusion (Garratt et al., 2018). In contrast, insect pollination in winter-sown
149 oilseed rape in France contributed about 30% to crop yields, determined using pollinator
150 exclusion, potentially because the area had a rich wild bee community (Perrot et al., 2018).
151 Pollinators are normally scarce in the spring-flowering oilseed rape fields of northern Europe
152 where they appear to pollinate no more than two thirds of the flowers, on average (Hoyle et
153 al., 2007; Appendix S3), although was <10% in this study. Instead, pollination occurs
154 through flower-to-flower collisions among windblown plants (Hayter and Cresswell, 2006).
155 The regional differences in pollination limitation of oilseed rape may have originated from
156 the differential efficacy of this wind-facilitated pollination, which could be due to variation
157 among local plant varieties (stem flexibility) (Hudewenz et al., 2014), sowing regimes (plant
158 density) or weather (wind speeds) that affected the intensity of wind-sway by plants in the
159 crops. In spring-sown oilseed rape, which blooms in summer, rates of flower visitation by
160 insects are substantially higher than in winter-sown fields (Hayter and Cresswell, 2006).
161 Spring-sown crop varieties also show substantive levels of pollinator dependence (e.g.
162 Lindström et al., 2016).

163 **4.1.3 Pears**

164 We found that Dutch pear orchards varied in the level of pollination limitation, but with no
165 overall deficit in the region on average, perhaps because yields were buffered against low
166 numbers of pollinator visits by the capacity of pear to produce fruit by spontaneous
167 parthenocarpy (Quinet and Jacquemart, 2015).

168 **4.1.4 Pumpkin**

169 We found no evidence of pollination limitation in German pumpkin fields because the intense
170 activities of honey bees and bumble bees saturated the pollen requirements of flowers (Pfister
171 *et al.*, 2017, 2018).

172 **4.2 Strategies for sustaining and enhancing pollination**

173 The female pumpkin flowers in the fields that we studied were saturated by pollen deliveries
174 made principally by honey bees and bumble bees, which are effective pollinators of pumpkin.
175 Pollination services to these pumpkin fields can be sustained by assuring the future
176 abundance of these bees. The sunflowers in the fields that we studied were visited
177 intensively by honey bees, but nevertheless seed set was pollination-limited. The basis for
178 the pollination limitation is unclear, but potentially it could be remedied either by
179 encouraging the most effective wild insect pollinators (Blaauw and Isaacs 2014; Sutter *et al.*,
180 2018) or by reducing the pollinator-dependence of the crop, which might involve using
181 varieties with higher levels of autonomous self-pollination. In the pear orchards that we
182 studied, insects apparently visited flowers at rather marginal rates and fruit mass was
183 pollination-limited in some orchards, which suggests that some growers may benefit from
184 boosting pollinator abundance. In the studied oilseed rape fields, insects appeared to visit
185 flowers rather rarely and pollination limitation occurred in only one of three regions, which
186 suggests that the crop has low pollinator-dependence in some instances. The earliness of

187 flowering in relation to wild pollinator peak activity may limit improving winter oilseed rape
188 pollination, however, there is evidence insect pollination was higher where there was a rich
189 bee community, especially solitary bees (*Lasioglossum* spp.) (Perrot et al., 2018) and where
190 flower-rich habitats were adjacent to oilseed rape fields and levels of greening measures were
191 high (Sutter et al., 2018). In regions with low pollination potential growers may benefit from
192 using crop varieties with lower pollinator-dependence or introduce honey bees for open-
193 pollinated cultivars, as they were shown to increase yields by 11% (Lindström et al., 2015).

194

195 The proportion and types of semi-natural habitat in the landscape can influence the levels of
196 pollinators and thereby pollination (Martins et al., 2014), although the proportion of crops can
197 also be more important (Pfister et al., 2017). These studies were conducted in landscapes that
198 encompassed a range of landscape compositions to provide a representative sample of what
199 occurs. Further analyses to examine the role of landscape composition are planned.

200 Our findings indicate that pollination limitation in entomophilous crops is influenced by at
201 least two factors besides the availability of pollinator visits. First, mechanisms of non-insect
202 pollination can compensate for flower visitation by pollinators, as exemplified by the oilseed
203 rape fields in Estonia and the United Kingdom. Second, plant traits can reduce the
204 effectiveness of even high levels of pollinator activity, as exemplified by the sunflower fields
205 in Italy. Taken together, our study suggests that strategies for reducing pollination limitation
206 in crops require an integrated understanding of both pollinators and the plants that they
207 pollinate. Such knowledge will help to better target ecological intensification efforts and
208 other measures of integrated pollination management to minimize pollination limitation due
209 to shortage in suitable insect pollinators.

210

211 **5. Conclusions**

212 Overall, our study supports two main conclusions: (1) pollination limitation existed at
213 moderate although economically significant levels for some crops in Europe; and (2) the
214 levels of pollination limitation in crops did not show a clear relation with levels of in-field
215 insect activity, which suggests the importance of other factors such as the efficacy of the
216 dominant pollinator species or level of autonomous self-pollination.

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221 researchers who assisted with the field studies.

222 **Datasets**

223 Data used in this study is available at the Open Research Exeter archive,
224 <https://ore.exeter.ac.uk/repository/handle/#####>

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289
290

291 SUPPLEMENTAL INFORMATION

292

Crop (country)	Mean field area ha (SD)	mean % cover of SNH (SD)	Distance from boundary of sampling locations along transects (m)
oilseed rape (EE)	26 (21)	38 (15)	2, 25, 50, 75
oilseed rape (UK)	14 (6)	14 (7)	2, 25, 48, 71
oilseed rape (CH)	2 (0.7)	28 (13)	2, 9, 17, 25
sunflower (IT)	6 (4)	42 (19)	2, 16, 30, 44
pumpkin (DE)	3 (3)	23 (14)	2,10, 18, 26
pears (NL)	2 (1)	10 (6)	3, 11, 19, 27

299

300 Table S1.2. Sizes of focal fields of the four crops, mean proportion of semi-natural
301 habitat (SNH) in surrounding landscapes (from 4 habitats in S1.1), which included a
302 circular area of 1 km radius around each focal field and sampling locations along
303 transects. There were 18 focal fields in each country. CH = Switzerland; DE =
304 Germany; EE = Estonia; IT = Italy; NL = The Netherlands; UK = United Kingdom.

305

306 APPENDIX S2: Taxonomic breakdown of the insect faunas of focal entomophilous
 307 crops.

Crop ↓	Flower visits by taxon (% of total)							Visits observed	hours
	A.m.	<i>Bombus</i>	Solitary bees	Flies	Syrphids	Lepid.	Non-bee hymenopt.		
Sunflower IT	98.0	0.9	1.0	0.0	0.1	0.0		3428	85
Pumpkin DE	69.9	24.1	5.6	0.0	0.4			2254	54
Pear NL	75.7	6.7	0.0	1.0	16.3	0.3		387	11
OSR (CH)	95.5	1.0	1.0	1.5	0.9	0.0	0.1	36295	48
OSR (EE)	33.7	5.5	11.9	48.8				991	48
OSR (UK)	8.3	10.1	11.9	58.3	10.1	0.7	0.7	278	48

308

309 Table S2.1. Relative contributions (%) of insect taxa to the total number of flower
 310 visits recorded during observations of in-field quadrats in each crop and region.

311 OSR = oilseed rape.

312 CH = Switzerland; DE = Germany; EE = Estonia; IT = Italy; NL = The Netherlands;
 313 UK = United Kingdom.

314 A.m. = *Apis mellifera*; *Bombus* = *Bombus* spp.; Flies = all dipterans except syrphid
 315 flies; Lepid. = Lepidoptera; Non-bee hymenopt. = non-bee hymenoptera (principally
 316 wasps).

317 Visits = the total number of flower visits recorded (note: the magnitudes of these are
 318 not comparable across regions because of the different quadrat sizes and flower
 319 densities – see instead Fig. 1b).

320 Hours = the total number of hours of observation made in each region.

321

322 APPENDIX S3: Estimating the number of insect visits received by a receptive flower
323 in a canola field in Northern Europe.

324 We can estimate the number of insect visits received by a receptive flower, V , by
325 quantifying each of the parameters in the following relationship (Cresswell 2008):

$$326 \quad V = \frac{B}{F} \cdot \frac{L}{H} \quad \text{Eq. S5.1}$$

327 where B_i denotes the area density of flower-visiting insects in the field (insects m^{-2}), F
328 denotes the area density of the crop's flowers in the field (flowers m^{-2}), L denotes the
329 receptive lifetime of a flower (hours), and H (hours) denotes the elapsed time
330 between successive flower visits by individual insects (i.e. duration of inter-flower
331 travel + duration of handling time per probe).

332 Thus, L/H quantifies the number of visits that a flower could receive if a single insect
333 concentrated on it exclusively and B/F quantifies the number of insects per flower,
334 which is a cardinal indicator of pollinating intensity (Pleasants 1981).

335 *Solution for spring-flowering canola*

336 A survey of 60 sites across the United Kingdom (Hoyle et al. 2007) recorded one bee
337 per 77 m^2 including both honey bees and bumble bees, i.e. $B = 0.013$.

338 Typical flower densities are c. $1000 \text{ flowers m}^{-2}$ (Hayter & Cresswell, 2006), i.e. $F =$
339 1000

340 Foraging rates of honey bees and bumble bees are no more than 0.32 flowers
341 visited sec^{-1} (Hayter & Cresswell 2006), i.e. $H = 9 \times 10^{-4} \text{ h}$.

342 Assume each flower is receptive for five days (8 h each day), i.e. $L = 40 \text{ h}$.

343 Hence, $B/F = 1.3 \times 10^{-5}$ and $L/H = 46080$, i.e. $V = 0.6$.

344 Since $V < 1$, its value is the proportion of flowers that receive a single visit.

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