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3 Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial
4 and temporal scales

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20
21 Running title: Changing oilseed rape effect on bees and pollination success

23 **Abstract**

24 Landscape-wide mass-flowering of oilseed rape (canola; *Brassica napus*) can considerably affect
25 wild bee communities and pollination success of wild plants. We aimed to assess the impact of
26 oilseed rape on the pollination of wild plants and bee abundance during and after oilseed-rape
27 bloom, including effects on crop-noncrop spillover at landscape and adjacent field scales. We
28 focused on two shrub species (hawthorn *Crataegus* spp., dog rose *Rosa canina*) and adjacent
29 herb flowering in forest edges, connected hedges and isolated hedges. We selected 35 landscape
30 circles of 1 km radius, differing in the amount of oilseed rape; 18 of which were adjacent to
31 oilseed rape and 17 to cereal fields, and we quantified bee density via pan traps at all sites.
32 Adjacent oilseed rape positively affected fruit mass and seed number per fruit of simultaneously
33 flowering hawthorn (no effect on dog rose, which is flowering after the oilseed rape bloom). At
34 the landscape scale oilseed rape had a negative effect on bumble bee density in the hedges during
35 flowering due to dilution of pollinators per unit area and the consequently intensified
36 competition between oilseed rape and wild shrubs, but a positive effect after flowering, when
37 bees moved to the hedges, which still provided resources. In contrast, positive landscape scale
38 effects of oilseed rape were found throughout the season in forest edges, suggesting that edges
39 support nesting activity and enhanced food resources. . Our results show that oilseed rape effects
40 on bee abundances and pollination success in semi-natural habitats depend on the spatial and
41 temporal scale considered and on the habitat type, the wild plant species, and the time of crop
42 flowering. These scale-dependent positive and negative effects should be considered in
43 evaluations of landscape-scale configuration and composition of crops. Food resources provided
44 by mass-flowering crops should be most beneficial for landscape-wide enhancement of wild bee

45 populations, if semi-natural habitats are available providing (i) nesting resources and (ii)
46 continuous flowering resources during the season.

47

48 **Keywords:** bumble bee *Bombus*, *Crataegus* spp., ecosystem services, fruit set, isolation, oilseed
49 rape (canola), *Rosa* spp., scale dependency

50

51 **Introduction**

52 Pollinating insects, in particular wild bees (Hymenoptera: Apoidea), have dramatically declined
53 in the last few decades worldwide (Biesmeijer et al. 2006, Goulson et al. 2008, Potts et al. 2010,
54 Cameron et al. 2011). However, pollination of crops and wild plants is one of the most important
55 ecosystem services (Ashman et al. 2004, Klein et al. 2007, Calderone 2012). Recent estimates
56 suggest that animal-mediated pollination is required for 88% of angiosperm species and
57 influences yield of 70% of the major agricultural crop species accounting for 35% of global food
58 production (Klein et al. 2007). Causal links between extinctions of wild plant and wild pollinator
59 species have been suggested (Spira 2001, Biesmeijer et al. 2006), whereas managed honeybees
60 (*Apis mellifera*) cannot replace the functional role of wild bees (Garibaldi et al. 2013, Holzschuh
61 et al. 2012).

62 The effects of landscape configuration, annual crop rotation, and within-year changes in
63 nectar/pollen availability on pollinators and pollination are still relatively unknown (Hadley and
64 Betts 2012). As a major consequence of increasing demand for biofuel, the area of oilseed rape
65 (*Brassica napus*) in agricultural landscapes is expanding (Rowe, Street and Taylor 2009). Mass-
66 flowering oilseed rape is mainly self-pollinated, yet pollen transport by invertebrate vectors has
67 been shown to result in higher seed set and yield (Jauker et al. 2012). It attracts many insect
68 groups (Bommarco et al. 2012, Jauker et al. 2012), which might spill over to the adjacent
69 habitats (Hanley et al. 2011). However, its benefit for pollinators is questioned due to a
70 synchronized and short flowering period (Westphal et al. 2009). The dilution of pollinators per
71 area and the consequent competition for pollinators may threaten the pollination of concurrently
72 flowering wild plants (Holzschuh et al. 2011). However, flowering crops may also facilitate the
73 wild plant pollination depending on species and season (Cussans et al. 2010).

74 Here, we present the first study to quantify the changing importance of mass-flowering
75 crops for wild bees and the pollination of wild plants due to possible crop-noncrop spillover at
76 both landscape and adjacent field scales, and the importance of hedge plants (herb and shrub
77 flowers) at local habitat scale. We focused on two wild hedge shrubs — hawthorn (*Crataegus*
78 spp.) and dog rose (*Rosa* spp.), which typically grow in three habitat types with similar
79 vegetation structure but differ in how they are affected by surrounding crops: forest edges are
80 exposed with only one side to oilseed rape, connected hedges are exposed with two sides to
81 crops but they are bordered from one end by forest margins, while isolated hedges are fully
82 surrounded by crops. These landscape elements often remain the only refuges for pollinators in
83 intensively managed agricultural landscapes, providing valuable pollen and nectar resources for
84 foraging bees during the year, as well as suitable nesting habitats (Hopwood 2008, Hannon and
85 Sisk 2009).

86 We analyzed the landscape and adjacent field scale effects of oilseed rape and effects of
87 local flower resources within the hedges and forest edges on the species richness and abundance
88 of bees sampled by pan traps and on the reproductive success of the two shrubs. The fruit set,
89 fruit mass and seed number of shrubs were quantified to assess possible pollination facilitation or
90 competition by oilseed rape for pollinators. Bumble bees and other wild bee species were
91 analyzed separately, because bumble bees are usually more influenced by landscape wide effects
92 due to their larger body size and consequent larger foraging distance (Greenleaf et al. 2007;
93 Osborne et al. 2008). Other, mostly solitary wild bees are smaller, and not able to fly larger
94 distances, therefore they forage in the vicinity of their nesting sites, which make them more
95 dependent on local conditions and less sensitive to landscape-scale crop structure (Gathmann and
96 Tscharrntke 2002; Holzschuh et al. 2011). Furthermore, oilseed rape might have strong influence

97 on bumble bees as their important food resources (Westphal et al. 2003, 2009; Holzschuh et al.
98 2011).

99 We tested the following main hypotheses:

100 (i) Landscape-wide increase of oilseed rape causes reduced flower visitation and
101 reproductive output of simultaneously flowering wild plants, (shrub species in hedges and forest
102 edges).

103 (ii) Pollinator visits and reproductive success of adjacent hedge flowers increases after
104 landscape-wide oilseed rape flowering.

105 (iii) Pollinators spill over from directly neighboring oilseed rape fields into hedges and
106 forest edges, resulting in enhanced numbers of pollinators and pollination success of shrubs
107 compared to hedges and forest edges adjacent to wheat fields.

108 (iv) Increasing species richness and abundance of herb and shrub flower resources along
109 the hedges and forest edges enhances the number of flower visitors and the pollination success of
110 shrub species.

111

112 **Material and methods**

113 *Study area and design*

114 The study took place in the vicinity of the city of Göttingen (51.5°N, 9.9°E) in southern Lower
115 Saxony, Germany, in 2009 (Appendix A). The area is dominated by arable fields (2-5 ha in size
116 on average), intermingled with grasslands and remnants of deciduous forests. The most widely
117 sown crops are winter wheat and winter oilseed rape. The forests are dominated by common
118 beech (*Fagus sylvatica*), used for timber production. The agricultural matrix is characterized by
119 hedges, which are often close to or connected to forests, but can also be situated alongside arable

120 fields, isolated from forests. Most of the hedges and forest edges are managed regularly by
121 pruning (every 8-15 years). The most characteristic woody plants in hedges are blackthorn
122 (*Prunus spinosa*), hawthorn and dog rose, however, one can also find dogwood (*Cornus*
123 *sanguinea*), European ash (*Fraxinus excelsior*), common hazel (*Corylus avellana*), silver birch
124 (*Betula pendula*), elderberry (*Sambucus nigra*), European mountain ash (*Sorbus aucuparia*), etc.

125 To study the effects of habitat isolation of the semi-natural habitats (i.e. hedges) on
126 pollinators and pollination success, three different habitat types were selected, representing
127 different levels of how strongly they are embedded in the open crop landscape: forests edges
128 (n=12), hedges connected to forests (n=11) and isolated hedges (n=12) (Fig. 1). Connected
129 hedges were directly adjoined to forests. Isolated hedges were separated from forest patches,
130 with a minimum distance of 300 m representing an adequate isolation for wild bees (Steffan-
131 Dewenter and Tschardtke 1999, Gathmann and Tschardtke 2002). To consider the effects of the
132 adjacent crop fields, half of the forest edges and hedges were selected next to winter cereal
133 fields, the other half next to winter oilseed rape fields on at least one side. Length of connected
134 and isolated hedges ranged from 100 to 300 m. None of the hedges was part of a longer hedge
135 network or of green lanes with two hedges bordering dirt roads. The selected study sites had a
136 minimum distance of 300 m to each other. Hedges and forest edges had a similar species
137 composition of shrubs and trees, and were surrounded by similar landscape matrices,
138 characterized by arable fields, grasslands and forest patches. Limitations in the availability of the
139 suitable habitats precluded choosing equally oriented habitats. However, there was a random mix
140 of hedge orientation across treatments and the great majority of the samplings and observations
141 were done on the south or south-west orientated sides of the hedges and forest edges, getting the
142 highest amount of sunshine during the day.

143

144 *Bees in pan traps*

145 Bees were sampled by colored pan traps of 15 cm diameter and 10 cm depth during two one-
146 week long periods in the first part of May, and also during two one-week long periods in the
147 middle of June. Two painted white, yellow and blue pan traps, respectively, were exposed on
148 three woody posts (two traps of the same color on one post) along forest edges, connected and
149 isolated hedges, ca. 100 cm above ground level and ca. 10 m apart from each other. The traps
150 were filled with ethylene glycol-water mixture (1/4, v/v) and a small amount of detergent to
151 reduce surface tension and enhance the effectiveness of sampling. Collected bees were taken to
152 the laboratory and identified to species level. Data from the two sampling periods within a month
153 and from pan traps of different colors were pooled. May data represent the period of oilseed rape
154 flowering and June data were those collected after oilseed rape flowering. Wild bees were
155 divided into two groups: bumble bees (i.e. *Bombus* spp.) and other wild bees (all the remaining
156 species except honey bees).

157

158 *Pollination success*

159 The effectiveness of pollination was measured by determining fruit set of flowers and the seed
160 number per fruit on one individual of hawthorn and dog rose in each site. Hawthorn was
161 flowering in the first half of May, simultaneously with oilseed rape bloom and dog rose in the
162 first half of June, after oilseed rape bloom. Two branches per plant and approximately 50 flowers
163 per branch were marked and exposed to open pollination. To test whether insect pollination adds
164 to self-pollination, two branches per plant with similar numbers of marked flowers were bagged
165 with a mesh bag before the beginning of the flowering period to exclude pollinators. The bags

166 were removed after the flowering period and all mature fruits of the two bagged and the two
167 open branches were harvested in early autumn. Due to hedge cutting in the autumn three bagged
168 and three open dog rose branches were lost. The fruits were dried at 35°C for two weeks and
169 then weighed. Afterwards seeds were extracted and counted. The pollination success was
170 compared between the bagged and open branches using the following parameters: fruit set
171 (number of fruits divided by the number of flowers of the two branches per treatment), fruit mass
172 (average weight of dried fruits), seed number (average number of seeds per fruit) and aborted
173 seed number (average number of immature seeds, only important in the case of dog rose).

174

175 *Vegetation and landscape parameters*

176 Transects of 200 m length (if possible) were assigned in all habitat types along the hedges and
177 forest edges (Fig. 1). The overall number of herb flowers along the transects was assessed once
178 per pan trap sampling period, four times in total. Flower density was assessed along the transects
179 by estimating the number of flower heads at species level in the (h)edges and the adjacent grassy
180 herbaceous margin of maximum 0.5 m width (only one side of the hedges, for pan trap data
181 analyses on that side of the hedge, where traps were exposed, for flower visitor data analyses on
182 the shrubs from the sunny side of the hedge, where samples were taken). Data from the two
183 consecutive sampling periods within a month were pooled, taking the average number of
184 flowers. During the flowering of hawthorn and dog rose shrubs the following flower data were
185 assessed: abundance of conspecific flowers in the observed 2*2 m patch, and the pooled number
186 of herb flowers. Flower species richness and the number/cover of blossoms are suitable proxies
187 of foraging resources of bees (e.g. Ebeling et al. 2008).

188 Landscape parameters were measured within a 1000 m radius around each site based on
189 official digital thematic maps (ATKIS DTK 50) and mapping of the arable fields (based on
190 Steffan-Dewenter et al. 2002). We calculated the percent area of oilseed rape fields (OSR%) and
191 the percent area of non-crop habitats excluding forest interiors (i.e. grasslands and 10 m wide
192 forest boundaries). The percent area of non-crop habitats was significantly related to habitat type
193 (Anova: $df=32$, $F=3.91$, $p=0.03$), with lower values around the connected (Tukey post-hoc: $t=-$
194 2.15 , $p=0.095$) and higher around the isolated hedges (Tukey post-hoc: $t=2.61$, $p=0.035$) than
195 around forest edges. Therefore we decided not to include this landscape parameter in the models.
196 OSR% was not significantly related to the adjacent crop type (Anova: $df=33$, $F=2.48$, $p=0.125$).
197

198 *Statistics*

199 First, we used ANCOVAs to test which predictors affected the pollinators recorded in the pan
200 traps samples. In the models of the pan-trap analyses, response variables were the species
201 richness and the abundance of bumble bees and of other wild bees. Predictors in all full models
202 were adjacent crop type (oilseed rape vs. cereal), habitat type (forest edge vs. connected hedge
203 vs. isolated hedge) along with the proportion of oilseed rape in 1000 m radius and total flower
204 abundance (number of herb flowers along the 200 m transect) included as covariates. Pan trap
205 data were tested separately for May and June. Abundance data were square root transformed to
206 reach normal residual distribution.

207 Second, we assessed the reproductive success of hawthorn and dog rose. Reproductive
208 success was measured as fruit set, fruit mass, seed number or number of aborted seeds (only in
209 case of dog rose), which were used as response variables in the following analyses. T-tests for
210 paired samples were used to assess the effect of open pollination vs. self-pollination of bagged

211 flowers on reproductive success. ANCOVAs were used to test the effect of the predictors OSR%,
212 adjacent crop, habitat type, total flower abundance and conspecific flower abundance in the
213 patch on the reproductive success of open-pollinated flowers. Fruit set values of hawthorn were
214 arcsine-transformed to reach normal residual distribution.

215 In all the above-mentioned analyses, two-way interactions were tested between habitat
216 type and adjacent crop type, habitat type and OSR%, respectively. Non-significant variables
217 ($p > 0.05$ from F-test) were excluded in backward stepwise selection, except being part of a
218 significant interaction. Multivariate comparisons by means of Tukey contrasts were performed
219 between habitat types. Analyses were performed using the nlme (Pinheiro et al. 2010), stats (R
220 Development Core Team 2009), multcomp (Hothorn et al. 2008) and mvtnorm (Genz et al.
221 2010) packages of R 2.10.1 software. An overview on all the described ANCOVA models is
222 provided in Appendix B.

223

224 **Results**

225 *Bees in pan traps*

226 Pan traps sampled 235 individuals of 11 bumble bee species and 1315 individuals of 51 other
227 wild bee species in May, and 421 individuals of 11 bumble bee species and 1117 individuals of
228 45 other wild bee species in June (Appendix C). The most abundant bumble bee species were
229 *Bombus lapidarius*, *B. pascuorum*, *B. pratorum*, and *B. terrestris* agg. in both May and June. The
230 oilseed rape fields in the landscape (OSR%) had contrasting effects on bumble bees in May
231 (during rape flowering) compared to June (after rape flowering). There was a significant
232 interaction between the effects of OSR% and habitat type on bumble bee abundance in May, and
233 a marginally significant interaction for bumble bee species richness in May (Table 1). Bumble

234 bee abundance and species richness increased with increasing OSR% in the forest edges, and
235 decreased with increasing OSR% in connected and isolated hedges (Fig. 2). Both species
236 richness and abundance of bumble bees were higher in forest edges than in connected and
237 isolated hedges in May, with differences being small for low OSR% and large for high OSR%.
238 In June, species richness of bumble bees was also higher in forest edges than in the connected
239 hedges ($t=2.784$, $p=0.024$), while the isolated hedges did not differ from the other two habitat
240 types (Fig. 2). In June, OSR% had a positive effect on species richness and abundance of bumble
241 bees in all habitat types. We found no significant difference in the abundance of bumble bees
242 between the habitats in June.

243 Species richness and abundance of other wild bees were not found to be influenced by
244 any of the tested variables. The adjacent crop had no effect on the bees sampled by pan traps.

245

246 *Pollination success*

247 The fruit set, fruit mass and seed number per fruit of hawthorn were significantly higher for open
248 than for bagged branches (Appendix D, E). There was no difference in fruit set of dog rose
249 between the two treatments, however, higher fruit mass, more seeds and less aborted seeds were
250 found in fruits from open than from bagged branches (Appendix D, E).

251 The fruit mass and seed number per fruit of hawthorn were higher next to oilseed rape
252 fields than next to cereal fields (Table 2; Fig. 3a, b). The seed number per fruit of dog rose was
253 slightly higher in connected than in isolated hedges (Tukey; $t=-2.37$, $p=0.061$); the forest edges
254 did not differ from the other two habitat types (Tukey; forest edge-connected hedge: $t=-2.05$,
255 $p=0.119$; forest edge-isolated hedge: $t=-0.27$, $p=0.959$). Fruit set of dog rose was positively
256 related to the number of dog rose flowers in the observed patch.

257

258 **Discussion**

259 In this study we focused on the effects of flower resources on overall species richness and
260 abundance of bees in hedges and forest edges and pollination success of three shrub species at
261 three spatial scales: effects of oilseed rape at the landscape and adjacent crop field scale, and the
262 local scale effects of hedge plants. At the landscape scale, effects on bumble bees in hedges and
263 forest edges depended on whether oilseed rape was flowering at the time or had ceased flowering
264 and on the habitat types forest edges and hedges. At the adjacent field scale, oilseed rape had
265 positive effects on fruit mass and seed number per fruit in hawthorn growing in forest edges and
266 hedges. The abundance of local wild flowers of hedge plants enhanced the fruit set of dog rose,
267 particularly of conspecific flowers in the direct surrounding of the focal shrubs.

268

269 *Landscape-scale effects of oilseed rape*

270 Our study showed strong and mixed landscape-scale effects of percent area of oilseed rape fields
271 on bumble bees recorded in pan traps. During oilseed rape flowering in May, a higher percent
272 area of oilseed rape had a negative effect on bumble bee species richness and abundance in
273 hedges, but a positive effect in forest edges. In June, when oilseed rape had ceased flowering,
274 percent area of oilseed rape had a positive effect on bumble bee species and individuals in all
275 three habitat types (hedges and forest edges).

276 We suppose that the negative landscape-scale effect of oilseed rape on bumble bees in our
277 hedges during oilseed rape flowering is due to of the dramatically enhanced resources supplied
278 by mass-flowering oilseed rape. Our results suggest that the distribution of pollinators depends
279 on the amount of oilseed rape in bloom: in landscapes with high amounts of oilseed rape,

280 pollinator abundances per area hedge decline because pollinators are attracted to the oilseed rape
281 fields. Thus, our results suggest that competition between oilseed rape and wild shrubs is higher
282 in landscapes with high amounts of oilseed rape. Bumble bee abundance declined in oilseed rape
283 fields, when the percent area of oilseed rape was high at the landscape scale during oilseed rape
284 flowering (Holzschuh et al. 2011). Here, we show that competition for bumble bee pollinators
285 results in a transient decline in visitation to flowers or captures in pan traps in semi-natural
286 habitats like hedges, when oilseed rape is flowering.

287 In contrast to hedges, bumble bee abundance in forest edges increased with increasing
288 percent area of oilseed rape in the landscape, and was generally higher in forest edges than in
289 hedges. Forest edges might provide more extended nesting and foraging habitat compared to
290 hedges. An increased abundance of bumble bees in forest edges surrounded by high percent area
291 of oilseed rape suggests increased nesting activity and enhanced growth of new colonies due to
292 the increased availability of nectar and pollen resources in the landscape (Westphal et al. 2009).

293 After oilseed rape flowering, species richness and abundance of bumble bees in both the
294 hedges and forest edges were positively affected by percent area of oilseed rape in the landscape.
295 Semi-natural habitats represent continuous foraging resources for bumble bees when flowering
296 crops are not available (Corbet 2000), resulting in spillover and concentration of bumble bees in
297 the semi-natural habitat patches. Our result corresponds with former studies, which showed great
298 benefits of mass-flowering crops, especially oilseed rape, in terms of subsequent bumble bee
299 densities in semi-natural habitats (Westphal et al. 2003, Herrmann et al. 2007, Diekötter et al.
300 2010, Goulson et al. 2010), deviating from the general assumption that social wild bees do not
301 profit from annual crops because of the short flowering time (Corbet 2000).

302 In contrast to bumble bees, we did not find a landscape-wide oilseed rape effect on the
303 species richness and abundance of other wild bees. Other wild bee species, most of them of
304 smaller body size, forage in the vicinity of their nesting sites, being more dependent on local
305 conditions and less sensitive to landscape-scale crop structure (Gathmann and Tschardtke 2002).
306 Therefore, solitary bees are more likely to be influenced by intermediate-scale oilseed rape
307 effects, showing increased diversity and abundance in semi-natural grasslands adjacent to oilseed
308 rape fields (Holzschuh et al. 2011).

309

310 *Effects of oilseed rape at the adjacent field scale*

311 The fruit mass and the seed number per fruit of hawthorn were higher adjacent to oilseed rape
312 fields than next to cereal fields. Hawthorn was flowering simultaneously with oilseed rape,
313 therefore the adjacent flowering oilseed rape fields might have had a facilitation effect on the
314 reproductive success of hawthorn. Hanley et al. (2011) described higher bumble bee visitation
315 rate to wild flowers in field margins next to mass-flowering bean fields than adjacent to wheat,
316 suggesting that mass-flowering crops facilitate pollinator spillover into adjacent semi-natural
317 habitats during their flowering. However, Hanley et al. (2011) did not study the effects of
318 pollinators on plant reproduction. Our study supports Cussans et al. (2010) finding positive local
319 effects of oilseed rape during its flowering on the reproductive success of a simultaneously
320 flowering wild plant species. Adjacent oilseed rape in flower might have served as a highly
321 attractive magnet plant as it is known from abundantly flowering invasive plants, which can also
322 facilitate the visitation and pollination of neighboring native plants by attracting high numbers of
323 pollinators (Bartomeus et al. 2008).

324 Considering the functionally adequate spatial scale and further differences between
325 pollinator guilds, however, is important to assess the effects of oilseed rape on the reproduction
326 success of co-flowering plants. In contrast to the positive field scale effects of oilseed rape on
327 directly adjacent hawthorn, Holzschuh et al. (2011) found a negative landscape-scale effect of
328 oilseed rape on cowslip (*Primula veris*). During mass flowering, oilseed rape might have positive
329 (magnet) effect on pollinator abundance and pollination success at adjacent field scale, but
330 negative (competition) effect at the landscape scale. Whether pollinators and pollinator-
331 dependent plants are influenced on the adjacent field or the landscape scales, might depend on
332 the mobility of the pollinators. Therefore, wild plant species like cowslip, which are mainly
333 pollinated by large mobile bumble bees, might be affected at landscape scales, while plant
334 species like hawthorn, which are also frequently visited by small solitary bees, are rather affected
335 at smaller scales.

336 We found higher fruit mass, more seeds and fewer aborted seeds in fruits from open than
337 from bagged branches, however, the higher abundance of pollinators in hedges and forest edges
338 adjacent to oilseed rape fields did not translate to increased fruit and/or seed production of dog
339 rose. Spillover of arthropods subsidized by a managed agricultural land to the adjacent semi-
340 natural habitats has already been described in the case of insect natural enemies (Rand et al.
341 2006) and pollinators (Hanley et al. 2011). However, a positive effect on pollinators of a wild
342 plant flowering after the mass-flowering crop has not been described yet. Hanley et al. (2011)
343 compared bumble bee activity along hedgerow transects adjacent to mass-flowering field bean
344 and wheat fields, but they found no difference two weeks after bean flowering.

345

346 *Local effects of hedge plant flowers*

347 The conspecific flower abundance had a positive effect on the fruit set of dog rose, which might
348 be attributed to the increased flower-visitation by the higher abundance of flower-visiting
349 insects. The higher number of flowers and the amount of available pollen might increase fruit
350 set, showing a facilitation effect (Bjerknes et al. 2007). However, differences in pollinator
351 generalization levels and the prevalence of main pollinators result in species-specific response of
352 the focal shrub species to the co-flowering neighborhood (Lazaro et al. 2009). The self-
353 compatible flowers of dog rose set fruits even without pollinators, while the self-incompatible
354 flowers of hawthorn set no fruits without insect pollination.

355

356 **Conclusion**

357 We conclude that considering the right scale is important when effects of mass-flowering crops
358 on pollinators and pollination success of wild plants are evaluated. At the landscape scale,
359 flowering of oilseed rape resulted in a lower number of bumble bees in the hedges. However, at
360 the adjacent field scale, pollinators show crop-noncrop spillover. Our results on hawthorn
361 suggest that the consequent higher number of bees might increase the pollination success of wild
362 plants in the neighborhood hedges and forest edges. However, this has to be tested for further
363 plant species. After the flowering of oilseed rape, the value of wild flower resources in hedges
364 and forest edges for foraging bees increases as demonstrated by their general spillover from the
365 oilseed rape fields and increase in these still flower-rich semi-natural habitats.

366 The total area planted in oilseed rape has considerably increased due to the increased
367 demand for bioenergy. Understanding the effects of this mass-flowering crop on biodiversity is
368 therefore critical. Given the potential impacts of oilseed rape on co-flowering wild plants high
369 amounts of mass-flowering fields in the landscape around nature reserves are critical for the

370 conservation of wild species. Future agri-environmental management should consider the pros
371 and cons in evaluations of landscape-scale configuration and composition of crops. Food
372 resources provided by mass-flowering crops should be most beneficial for landscape-wide
373 enhancement of wild bee populations, if semi-natural habitats are available providing (i) nesting
374 resources and (ii) continuous flowering resources during the season. The enhancement of the
375 diversity of flowering plants is recommended due to reasonable hedge management in the form
376 of diverse shrub communities and wide grassy margins along the hedges and forest edges.
377

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389

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495

496 **Supplemental Material**

497

498 Appendix A. Location of the sample sites using Google Earth.

499

500 Appendix B. Dependent and explanatory variables of the ANCOVAs in the analyses.

501

502 Appendix C. The abundance of bumblebee and other wild bee species sampled by pan traps.

503

504 Appendix D. Results of the paired t-tests on the effects of treatment (bagged vs. open branches)
505 on the different parameters of pollination success of hawthorn *Crataegus* spp. and dog rose *Rosa*
506 *canina* flowers.

507

508 Appendix E. Different parameters of pollination success on the bagged branches and flowers
509 open for pollinator insects on hawthorn *Crataegus* spp. and dog rose *Rosa canina* shrubs.

510 TABLE 1. Local and landscape scale effects on species richness and abundance of bumblebees
 511 and other wild bees in forest edges, connected and isolated hedges in May and June 2009,
 512 according to the final ANCOVA models after backward selection. Explanatory variables of the
 513 full model were: OSR% - percent area of oilseed rape fields in 1000 m radius, Adjacent crop -
 514 oilseed rape vs. cereal, Habitat type - forest edge vs. connected hedge vs. isolated hedge, Total
 515 flower abundance - number of herb flowers along the 200 m transect. (NS: no significant effect).

	df	F	P
May			
Species richness			
Bumble bees			
OSR%	31	5.21	0.029
Habitat	31	10.98	<0.001
OSR%*Habitat	31	2.53	0.097
Other wild bees			NS
Abundance			
Bumble bees			
OSR%	31	3.05	0.090
Habitat	31	19.00	<0.001
OSR%*Habitat	29	4.87	0.015
Other wild bees			NS
June			
Species richness			
Bumble bees			
OSR%	31	5.43	0.026
Habitat	31	4.14	0.025
Other wild bees			NS
Abundance			
Bumble bees			
OSR%	32	5.23	0.029
Other wild bees			NS

516

517

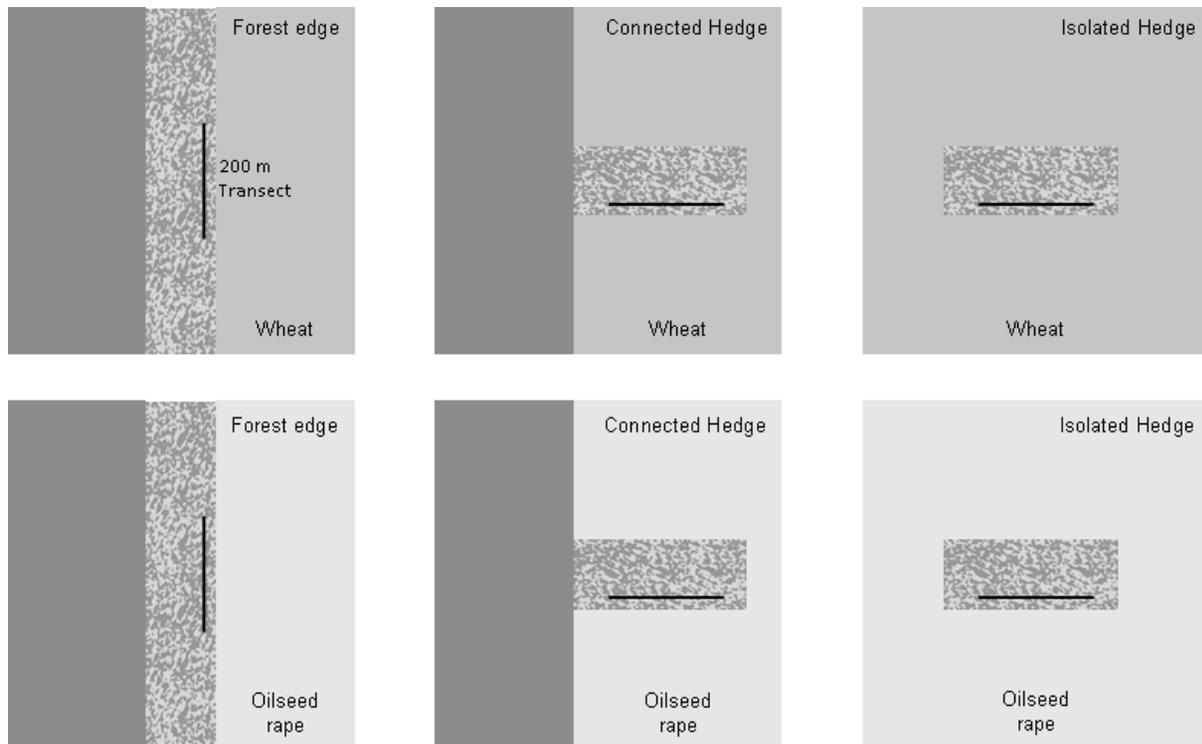
518 TABLE 2. Final ANCOVA models on the different parameters of pollination success of hawthorn
 519 and dog rose flowers available to pollinators in forest edges, connected and isolated hedges.
 520 Explanatory variables of the full model were: OSR% - percent area of oilseed rape fields in 1000
 521 m radius, Adjacent crop - oilseed rape vs. cereal, Habitat type - forest edge vs. connected hedge
 522 vs. isolated hedge, Total flower abundance - number of herb flowers along the 200 m transect,
 523 Conspecific flower abundance (patch) - abundance of conspecific flowers in the observation
 524 patch. (NS: no significant effect).

	df	F	P
Hawthorn			
Fruit set			NS
Fruit mass			
Adjacent crop type (OSR>cereal)	33	5.41	0.026
Seed number/fruit			
Adjacent crop type (OSR>cereal)	33	4.26	0.047
Dog rose			
Fruit set			
Conspecific flower abundance (patch)	30	8.35	0.007
Fruit mass			NS
Seed number/fruit			
Habitat	29	3.34	0.049
Aborted seed number/fruit			NS

525

526

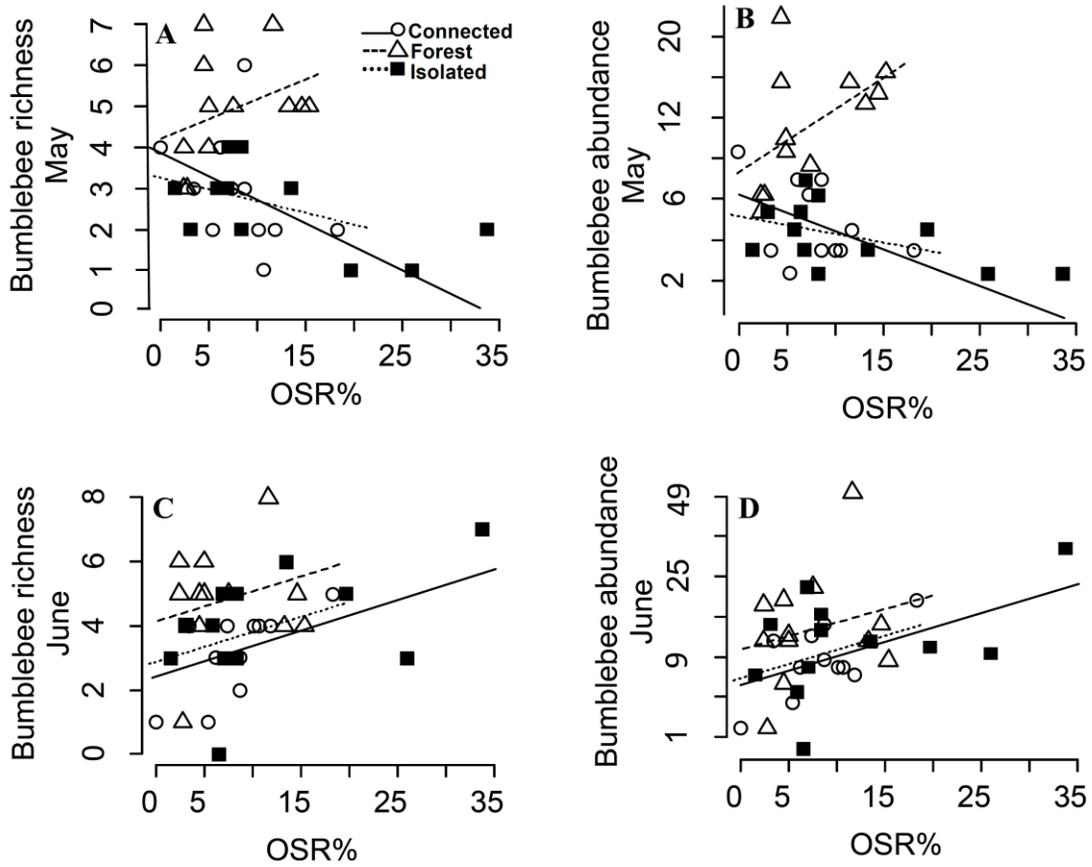
527 FIG. 1. The study design: spatial arrangement of the forest edges (left), connected (middle), and
528 isolated hedges (right). Dark gray=forest, dotted gray=study site, light gray=landscape matrix:
529 wheat (top) or oilseed rape (bottom). Flowering plants were assessed along a 200-m-transect in
530 each study site.



531

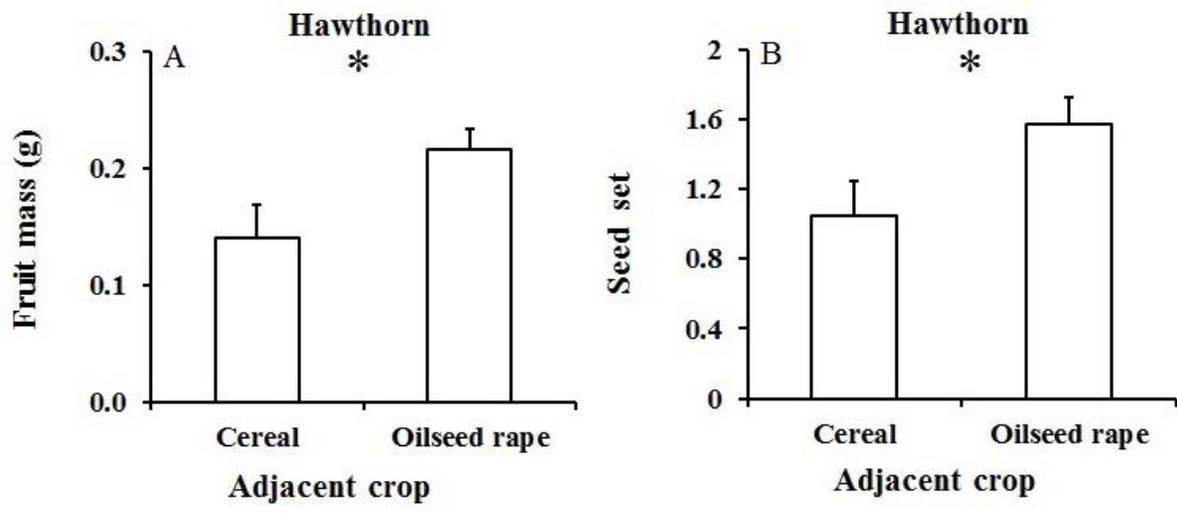
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533 Fig. 2. Results from ANCOVA models for (A) species richness and (B) abundance of
 534 bumblebees in forest edges, connected and isolated hedges in May 2009 and (C) species richness
 535 and (D) abundance of bumblebees in June 2009 in relation to percentage of the area in a 1000 m
 536 radius that is oilseed rape fields.



537

538 FIG. 3. The (A) seed number per fruit and (B) fruit mass of hawthorn in relation to crop type
539 (oilseed rape vs. wheat). Stars indicate significant differences.



540

541

542 APPENDIX A. Location of the sample sites around the city Göttingen, using Google Earth. The
543 study sites are indicated by yellow lines (F: forest edge, C: connected hedge, I: isolated hedge;
544 numbers indicate the serial number of the study site).

545

546 APPENDIX B. Dependent and explanatory variables of the ANCOVAs in the analyses of the two
 547 distinct dataset.

Datas et	Dependent variables	Explanatory variables of the ANCOVAs
Pantraps		
May		
	Bumble bee species richness	OSR% - proportion of oilseed rape in 1000 m radius
	Other wild bee species richness	Adjacent crop - oilseed rape vs. cereal
	Bumble bee abundance	Habitat type - forest edge vs. connected hedge vs. isolated hedge
	Other wild bee abundance	Total flower abundance - number of herb flowers along the 200 m transect
June		
	Bumble bee species richness	
	Other wild bee species richness	
	Bumble bee abundance	
	Other wild bee abundance	
Pollination success		
Hawthorn		
	Fruit set	OSR% - proportion of oilseed rape in 1000 m radius
	Fruit mass	Adjacent crop - oilseed rape vs. cereal
	Seed number/fruit	Habitat type - forest edge vs. connected hedge vs. isolated hedge
		Total flower abundance - number of herb flowers along the 200 m transect

Hip

Conspecific flower abundance (patch) - abundance of conspecific flowers in the observation patch

Fruit set

Fruit mass

Seed number/fruit

Aborted seed
number/fruit

548

549

550 APPENDIX C. The abundance of bumblebees and other wild bees sampled by pan traps in May
 551 and June 2009 in the studied forest edges, connected and isolated hedges. (*Bombus terrestris*
 552 agg. includes *Bombus terrestris* and *B. lucorum*.)

Species	Abundance	
	May	June
Other wild bees		
<i>Andrena alfenella</i>	1	0
<i>Andrena angustior</i>	0	5
<i>Andrena bicolor</i>	11	31
<i>Andrena chrysoseles</i>	19	4
<i>Andrena cineraria</i>	10	5
<i>Andrena dorsata</i>	1	0
<i>Andrena flavipes</i>	102	9
<i>Andrena fucata</i>	1	0
<i>Andrena fulva</i>	46	1
<i>Andrena fulvago</i>	0	1
<i>Andrena gravida</i>	17	0
<i>Andrena haemorrhoa</i>	232	14
<i>Andrena helvola</i>	77	14
<i>Andrena jacobi</i>	22	0
<i>Andrena labiata</i>	0	2
<i>Andrena minutula</i>	39	13
<i>Andrena nigroaenea</i>	324	36
<i>Andrena nitida</i>	74	5
<i>Andrena proxima</i>	5	0
<i>Andrena stromella</i>	4	0
<i>Andrena subopaca</i>	18	20
<i>Andrena varians</i>	8	5
<i>Anthophora plumipes</i>	1	0
<i>Chelostoma florisomme</i>	1	0
<i>Chelostoma rapunculi</i>	0	3
<i>Colletes cunicularius</i>	2	0
<i>Halictus confusus</i>	0	2
<i>Halictus langobardicus</i>	4	1
<i>Halictus maculatus</i>	0	1
<i>Halictus rubicundus</i>	1	0
<i>Halictus tumulorum</i>	5	9
<i>Heriades truncorum</i>	0	0
<i>Hylaeus annularis</i>	0	1
<i>Hylaeus communis</i>	4	51
<i>Hylaeus confusus</i>	1	19

553

554

<i>Lasioglossum albipes</i>	3	9
<i>Lasioglossum calceatum</i>	21	46
<i>Lasioglossum fulvicorne</i>	1	2
<i>Lasioglossum laticeps</i>	0	344
<i>Lasioglossum leucozonium</i>	0	1
<i>Lasioglossum morio</i>	12	105
<i>Lasioglossum nitidiusculum</i>	0	2
<i>Lasioglossum parvulum</i>	2	0
<i>Lasioglossum pauxillum</i>	42	321
<i>Lasioglossum pygmaeum patulum</i>	1	0
<i>Lasioglossum rufitarse</i>	0	0
<i>Lasioglossum villosulum</i>	0	1
<i>Nomada alboguttata</i>	1	0
<i>Nomada fabriciana</i>	6	0
<i>Nomada flavoguttata</i>	29	3
<i>Nomada flava</i>	6	0
<i>Nomada fucata</i>	7	1
<i>Nomada fulvicornis</i>	0	0
<i>Nomada leucophthalma</i>	1	0
<i>Nomada marshamella</i>	2	0
<i>Nomada moeschleri</i>	1	0
<i>Nomada panzeri</i>	30	2
<i>Nomada ruficornis</i>	6	0
<i>Nomada succincta</i>	5	0
<i>Osmia bicolor</i>	61	10
<i>Osmia brevicornis</i>	1	2
<i>Osmia caerulescens</i>	2	0
<i>Osmia leaiana</i>	0	1
<i>Osmia leucomelana</i>	0	3
<i>Osmia pilicornis</i>	1	0
<i>Osmia rufa</i>	40	1
<i>Panurgus calcaratus</i>	0	1
<i>Sphecodes ephippius</i>	4	1
<i>Sphecodes geofrellus</i>	0	1
<i>Sphecodes hyalinatus</i>	0	7
<i>Stelis ornatula</i>	0	1
Bumblebees		
<i>Bombus (Psithyrus) bohemicus</i>	6	3
<i>Bombus (Psithyrus) campestris</i>	4	10
<i>Bombus (Psithyrus) rupestris</i>	1	0
<i>Bombus (Psithyrus) vestalis</i>	12	9
<i>Bombus hortorum</i>	17	13
<i>Bombus hypnorum</i>	1	9
<i>Bombus lapidarius</i>	40	57
<i>Bombus pascuorum</i>	58	55
<i>Bombus pratorum</i>	50	69
<i>Bombus soroeensis</i>	0	1
<i>Bombus sylvarum</i>	3	14
<i>Bombus terrestris</i> agg.	43	181

556 APPENDIX D. Results of the paired t-tests on the effects of treatment (bagged vs. open branches)
 557 on the different parameters of pollination success of hawthorn *Crataegus* spp. and dog rose *Rosa*
 558 *canina* flowers in forest edges, connected and isolated hedges.

	df	t	<i>P</i>
Hawthorn			
Fruitset (no. fruit/flower)	34	-3.5	0.001
Fruitmass per fruit	34	-5.5	<0.001
Average seed number	34	-6	<0.001
Dog rose			
Fruitset (no. fruit/flower)	30	0.41	0.679
Fruitmass per fruit	30	-2.5	0.018
Average seed number	30	-3.7	<0.001
Aborted seed number	30	3.85	<0.001

559

560

561 APPENDIX E. Different parameters of pollination success on the bagged branches and flowers
 562 open for pollinator insects on hawthorn *Crataegus* spp. and dog rose *Rosa canina* shrubs (mean
 563 \pm SE).

	Hawthorn		Dog rose	
	Bagged	Open	Bagged	Open
Fruit set	0.01 \pm 0.00	0.17 \pm 0.05	0.42 \pm 0.04	0.39 \pm 0.03
Fruit mass	0.06 \pm 0.02	0.18 \pm 0.02	0.64 \pm 0.04	0.71 \pm 0.04
Seed set	0.34 \pm 0.10	1.31 \pm 0.13	15.11 \pm 0.90	18.12 \pm 0.88
Aborted seed set			9.51 \pm 0.73	7.41 \pm 0.62
564 Seed mass	0.02 \pm 0.01	0.07 \pm 0.01	0.02 \pm 0.00	0.02 \pm 0.00