1

2

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

4   and temporal scales

5

6   Anikó Kovács-Hostyánszki[1,2*], Sebastian Haenke[2], Péter Batáry[2,3], Birgit Jauker[4], András Báldi[1],

7   Teja Tscharntke[2] and Andrea Holzschuh[2,5]

8

9   [1]MTA ÖK, Lendület Ecosystem Services Research Group, Alkotmány út 2-4, H-2163 Vácrátót,

10   Hungary; [2] Agroecology, Department of Crop Sciences, Georg-August University, Grisebachstr.

11   6, D-37077 Göttingen, Germany; [3]MTA-ELTE-MTM Ecology Research Group, Budapest,

12   Hungary, Baross u. 13, H-1088 Budapest, Hungary; [4]Justus Liebig University, Department of

13   Animal Ecology, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany; and [5]University of

14   Würzburg, Department of Animal Ecology and Tropical Biology, Am Hubland, 97074

15   Würzburg, Germany

16

17   *Corresponding author: Anikó Kovács-Hostyánszki, MTA ÖK, Lendület Ecosystem Services

18   Research Group, Alkotmány út 2-4, H-2163 Vácrátót, Hungary. Tel.: +36305562595; fax: +

19   3628360110. E-mail address: kovacs.aniko@okologia.mta.hu (A. Kovács-Hostyánszki)

20

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

22

Abstract

Landscape-wide mass-flowering of oilseed rape (canola; *Brassica napus*) can considerably affect

wild bee communities and pollination success of wild plants. We aimed to assess the impact of

oilseed rape on the pollination of wild plants and bee abundance during and after oilseed-rape

bloom, including effects on crop-noncrop spillover at landscape and adjacent field scales. We

focused on two shrub species (hawthorn *Crataegus* spp., dog rose *Rosa canina*) and adjacent

herb flowering in forest edges, connected hedges and isolated hedges. We selected 35 landscape

circles of 1 km radius, differing in the amount of oilseed rape; 18 of which were adjacent to

oilseed rape and 17 to cereal fields, and we quantified bee density via pan traps at all sites.

Adjacent oilseed rape positively affected fruit mass and seed number per fruit of simultaneously

flowering hawthorn (no effect on dog rose, which is flowering after the oilseed rape bloom). At

the landscape scale oilseed rape had a negative effect on bumble bee density in the hedges during

flowering due to dilution of pollinators per unit area and the consequently intensified

competition between oilseed rape and wild shrubs, but a positive effect after flowering, when

bees moved to the hedges, which still provided resources. In contrast, positive landscape scale

effects of oilseed rape were found throughout the season in forest edges, suggesting that edges

support nesting activity and enhanced food resources. . Our results show that oilseed rape effects

on bee abundances and pollination success in semi-natural habitats depend on the spatial and

temporal scale considered and on the habitat type, the wild plant species, and the time of crop

flowering. These scale-dependent positive and negative effects should be considered in

evaluations of landscape-scale configuration and composition of crops. Food resources provided

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

50

Introduction

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

The effects of landscape configuration, annual crop rotation, and within-year changes in nectar/pollen availability on pollinators and pollination are still relatively unknown (Hadley and Betts 2012). As a major consequence of increasing demand for biofuel, the area of oilseed rape (*Brassica napus)* in agricultural landscapes is expanding (Rowe, Street and Taylor 2009). Mass-flowering oilseed rape is mainly self-pollinated, yet pollen transport by invertebrate vectors has been shown to result in higher seed set and yield (Jauker et al. 2012). It attracts many insect groups (Bommarco et al. 2012, Jauker et al. 2012), which might spill over to the adjacent habitats (Hanley et al. 2011). However, its benefit for pollinators is questioned due to a synchronized and short flowering period (Westphal et al. 2009). The dilution of pollinators per area and the consequent competition for pollinators may threaten the pollination of concurrently flowering wild plants (Holzschuh et al. 2011). However, flowering crops may also facilitate the 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   Tscharntke 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 Tscharntke 1999, Gathmann and Tscharntke 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

Bees in pan traps

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

Pollination success

The effectiveness of pollination was measured by determining fruit set of flowers and the seed
number per fruit on one individual of hawthorn and dog rose in each site. Hawthorn was
flowering in the first half of May, simultaneously with oilseed rape bloom and dog rose in the
first half of June, after oilseed rape bloom. Two branches per plant and approximately 50 flowers
per branch were marked and exposed to open pollination. To test whether insect pollination adds
to self-pollination, two branches per plant with similar numbers of marked flowers were bagged
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

Discussion

In this study we focused on the effects of flower resources on overall species richness and

abundance of bees in hedges and forest edges and pollination success of three shrub species at

three spatial scales: effects of oilseed rape at the landscape and adjacent crop field scale, and the

local scale effects of hedge plants. At the landscape scale, effects on bumble bees in hedges and

forest edges depended on whether oilseed rape was flowering at the time or had ceased flowering

and on the habitat types forest edges and hedges. At the adjacent field scale, oilseed rape had

positive effects on fruit mass and seed number per fruit in hawthorn growing in forest edges and

hedges. The abundance of local wild flowers of hedge plants enhanced the fruit set of dog rose,

particularly of conspecific flowers in the direct surrounding of the focal shrubs.

Landscape-scale effects of oilseed rape

Our study showed strong and mixed landscape-scale effects of percent area of oilseed rape fields

on bumble bees recorded in pan traps. During oilseed rape flowering in May, a higher percent

area of oilseed rape had a negative effect on bumble bee species richness and abundance in

hedges, but a positive effect in forest edges. In June, when oilseed rape had ceased flowering,

percent area of oilseed rape had a positive effect on bumble bee species and individuals in all

three habitat types (hedges and forest edges).

We suppose that the negative landscape-scale effect of oilseed rape on bumble bees in our

hedges during oilseed rape flowering is due to of the dramatically enhanced resources supplied

by mass-flowering oilseed rape. Our results suggest that the distribution of pollinators depends

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 Tscharntke 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 access 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

References

Ashman, T. L., Knight, T. M., Steets, J. A., Amarasekare, P., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mazer, S. J., Mitchell, R. J., Morgan, M. T. and Wilson W. G. 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85: 2408–2421.

Bartomeus, I., Montserrat, V. and Santamaría, L. 2008. Contrasting effects of invasive plants in plant–pollinator networks. Oecologia 155: 761–770.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. and Kunin, W. E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313: 351–354.

401   Bjerknes, A. L., Totland, O., Hegland, S. J. and Nielsen, A. 2007. Do alien plant invasions really

402   affect pollination success in native plant species? Biological Conservation 138: 1–12.

403   Bommarco, R., Marini, L. and Vaissiere, B. E. 2012. Insect pollination enhances seed yield,

404   quality, and market value in oilseed rape. Oecologia 169: 1025–1032.

405   Calderone, N. W. 2012. Insect pollinated crops, insect pollinators and US agriculture: trend

406   analysis of aggregate data for the period 1992–2009. PlosOne 7: e37235.

407   Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F. and Griswold,

408   T. L. 2011. Patterns of widespread decline in North American bumble bees. Proceedings

409   of the National Academy of Sciences Proceedings of the National Academy of Sciences

410   108: 662–667.

411   Corbet, S. A. 2000. Conserving compartments in pollination webs. Conservation Biology 14:

412   1229–1231.

413   Cussans, J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B., Osborne, J. L. 2010. Two

414   bumblebee-pollinated plant species show higher seed production when grown in gardens

415   compared to arable farmland. Plos One 5: e11753.

416   Diekötter, T., Kadoya, T., Peter, F., Wolters, V. and Jauker, F. 2010. Oilseed rape crops distort

417   plant–pollinator interactions. Journal of Applied Ecology 47: 209–214.

418   Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W. and Tscharntke, T. 2008. How does

419   plant richness affect pollinator richness and temporal stability of flower visits? Oikos

420   117: 1808–1815.

421   Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R. et al. 2013. Wild Pollinators Enhance Fruit Set

422   of Crops Regardless of Honey Bee Abundance. Science 339: 1608.

423   Gathmann, A. and Tscharntke, T. 2002. Foraging ranges of solitary bees. Journal of Animal

424   Ecology 71: 757–764.

425   Genz, A., Bretz, F., Miwa, T., Mi, X., Leisch, F., Scheipl, F. and Hothorn, T. 2010. mvtnorm:

426   Multivariate Normal and t Distributions. R package version 0.9-92. URL http://CRAN.R-

427   project.org/package=mvtnorm

428   Goulson, D., Lye, G. C. and Darvill, B. 2008. Decline and conservation of bumble bees. Annual

429   Review of Entomology 53: 191–208.

430   Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L.,

431   Darvill, B. 2010. Effects of land use at a landscape scale on bumblebee nest density and

432   survival. Journal of Applied Ecology 46: 1207–1215.

433   Greenleaf, S. S.,Williams, N. M., Winfree, R., Kremen, C. 2007. Bee foraging ranges and their

434   relationship to body size. Oecologia 153: 589–596.

435   Hadley, A. S., Betts, M. G. 2012. The effects of landscape fragmentation on pollination

436   dynamics: absence of evidence not evidence of absence. Biological Reviews 87: 526–

437   544.

438   Hanley, M. E., Franco, M., Dean, C. E., Franklin, E. L., Harris, H. R., Haynes, A. G., Rapson, S.

439   R., Rowse, G., Thomas, K. C., Waterhouse, B. R. and Knight, M. E. 2011. Increased

440   bumblebee abundance along the margins of a mass flowering crop: evidence for

441   pollinator spill-over. Oikos 11: 1618–1624.

442   Hannon, L. E. and Sisk, T. D. 2009. Hedgerows in an agri-natural landscape: Potential habitat

443   value for native bees. Biological Conservation 142: 2140–2154.

444 Herrmann, F., Westphal, C., Moritz, R. F.A. and Steffan-Dewenter, I. 2007. Genetic diversity

445   and mass resources promote colony size and forager densities of a social bee (*Bombus*

446   *pascuorum*) in agricultural landscapes. Molecular Ecology 16: 1167–1178.

447 Holzschuh, A., Dormann, C. F., Tscharntke, T. and Steffan-Dewenter, I. 2011. Expansion of

448   mass-flowering crops leads to transient pollinator dilution and reduced wild plant

449   pollination. Proceedings of the Royal Society B: Biological Sciences 278: 3444–3451.

450 Holzschuh, A., Dudenhoffer, J.-H., Tscharntke, T. 2012. Landscapes with wild bee habitats

451   enhance pollination, fruit set and yield of sweet cherry. Biological Conservation 15: 101–

452   107.

453 Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee

454   conservation. Biological Conservation 141: 2632–2640.

455 Hothorn, T., Bretz, F. and Westfall, P. 2008. Simultaneous inference in general parametric

456   models. Biometrical Journal 50: 346–363.

457 Jauker, F., Bondarenko, B., Becker, H. C. and Steffan-Dewenter, I. 2012. Pollination efficiency

458   of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology

459   14: 81–87.

460 Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C.

461   and Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world

462   crops. Proceedings of the Royal Society B: Biological Sciences 274: 303–313.

463 Lazaro, A., Lundgren, R. and Totland, Ø. 2009. Co-flowering neighbors influence the diversity

464   and identity of pollinator groups visiting plant species. Oikos 118: 691–702.

465   Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, L.

466   J., Sanderson, R. A. 2008. Bumblebee flight distances in relation to the forage landscape.

467   Journal of Animal Ecology 77: 406–415.

468   Pinheiro, J., Bates, D., DebRoy, S. and Deepayan, S. and the R Development Core Team 2010.

469   nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-97.

470   Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W. E. 2010.

471   Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution

472   25: 345–353.

473   R Development Core Team 2009. R: A language and environment for statistical computing. R

474   Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL

475   http://www.R-project.org.

476   Rand, T. A., Tylianakis, J. M. and Tscharntke, T. 2006. Spillover edge effects: the dispersal of

477   agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecology

478   Letters 9: 603–614.

479   Rowe, R. L., Street, N. R. and Taylor, G. 2009. Identifying potential environmental impacts of

480   large-scale deployment of dedicated bioenergy crops in the UK. Renewable and

481   Sustainable Energy Reviews 13: 260–279.

482   Spira, T. P. 2001. Plant-pollinator interactions: a threatened mutualism with implications for the

483   ecology and management of rare plants. Natural Areas Journal 21: 78–88.

484   Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. and Tscharntke, T. 2002. Scale-

485   dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–

486   1432.

487   Steffan-Dewenter, I. and Tscharntke, T. 1999. Effects of habitat isolation on pollinator

488   communities and seed set. Oecologia 121: 432–440.

489   Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. 2003. Mass flowering crops enhance

490   pollinator densities at a landscape scale. Ecology Letters 6: 961–965.

491   Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. 2009. Mass flowering oilseed rape

492   improves early colony growth but not sexual reproduction of bumblebees. Journal of

493   Applied Ecology 46: 187–193.

494

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			
Conscpecific 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.
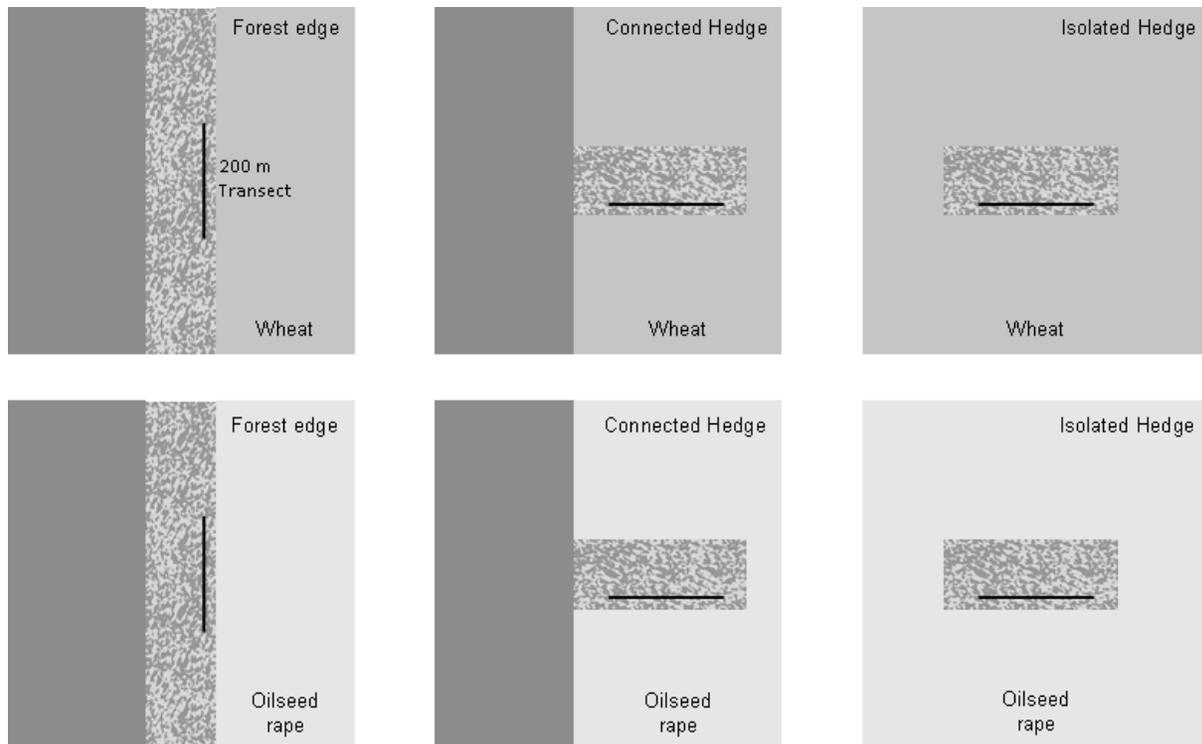
531

532

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.
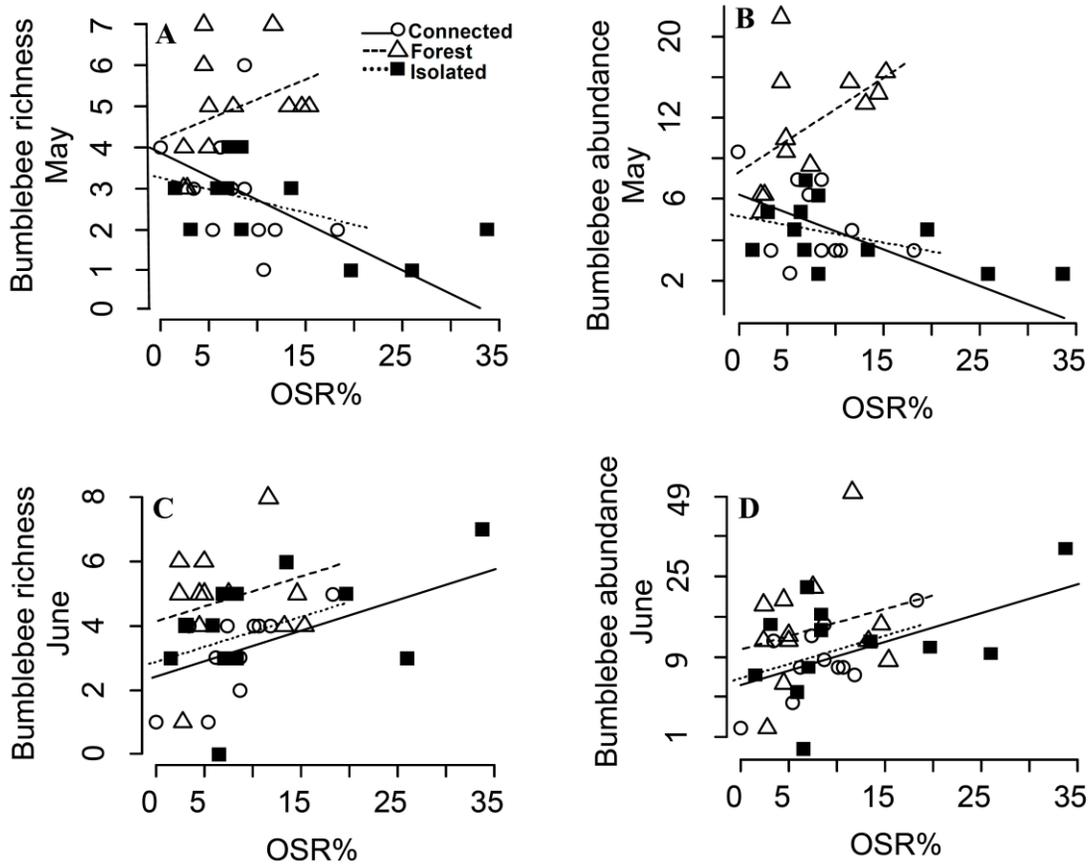
537

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.
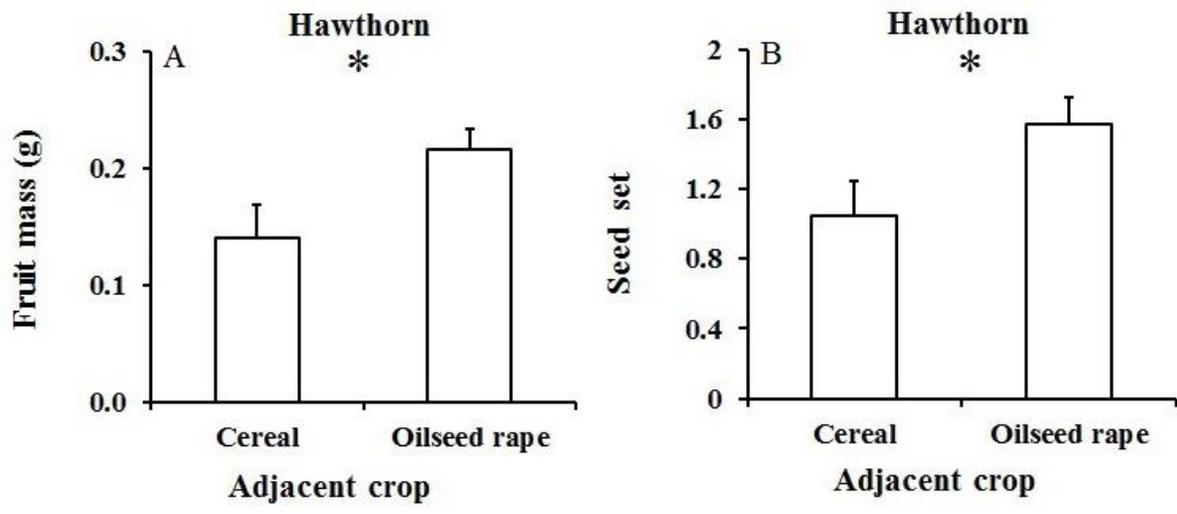
540

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

APPENDIX B. Dependent and explanatory variables of the ANCOVAs in the analyses of the two

distinct dataset.

Dataset	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	OSR% - proportion of oilseed rape in 1000 m radius
	Fruit set	Adjacent crop - oilseed rape vs. cereal
	Fruit mass	Habitat type - forest edge vs. connected hedge vs. isolated hedge
	Seed number/fruit	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		
Andrena alfkenella	1	0
Andrena angustior	0	5
Andrena bicolor	11	31
Andrena chrysosceles	19	4
Andrena cineraria	10	5
Andrena dorsata	1	0
Andrena flavipes	102	9
Andrena fucata	1	0
Andrena fulva	46	1
Andrena fulvago	0	1
Andrena gravida	17	0
Andrena haemorrhoa	232	14
Andrena helvola	77	14
Andrena jacobi	22	0
Andrena labiata	0	2
Andrena minutula	39	13
Andrena nigroaenea	324	36
Andrena nitida	74	5
Andrena proxima	5	0
Andrena strohmella	4	0
Andrena subopaca	18	20
Andrena varians	8	5
Anthophora plumipes	1	0
Chelostoma florisomne	1	0
Chelostoma rapunculi	0	3
Colletes cunicularius	2	0
Halictus confusus	0	2
Halictus langobardicus	4	1
Halictus maculatus	0	1
Halictus rubicundus	1	0
Halictus tumulorum	5	9
Heriades truncorum	0	0
Hylaeus annularis	0	1
Hylaeus communis	4	51
Hylaeus confusus	1	19

553

554

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

555

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	*P*
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 ± SE).

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

564