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Plant-pollinator networks in semi-natural grasslands are resistant to the loss of pollinators during blooming of mass-flowering crops

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Author contributions

AH, ISD, MR, RB, HGS, SGP and MV conceived and designed the study; AH coordinated the study; MR, VR, JBW, VJW and JPGV collected field data; AM led data analysis and drafted the manuscript; IB participated in data analyses and helped draft the manuscript. All authors commented on manuscript drafts and gave final approval for publication.

Abstract

Mass-flowering crops lead to spatial redistributions of pollinators and to transient shortages within nearby semi-natural grasslands, but the impacts on plant-pollinator interactions remain largely unexplored. Here, we characterised which pollinator species are attracted by oilseed rape and how this affected the structure of plant-pollinator networks in nearby grasslands. We surveyed 177 networks from three countries (Germany, Sweden and United Kingdom) in 24 landscapes with high crop cover, and compared them to 24 landscapes with low or no oilseed rape during and after crop blooming. On average 55% of grassland pollinator species were found on the crop, which attracted 8-35% of individuals away from grasslands. However, networks in the grasslands were resistant to these reductions, since mainly abundant and highly mobile species were attracted. Nonetheless, simulations indicated that network structural changes could be triggered if >50% of individuals were attracted to the crop (a value well-above that found in our study system), which could affect community stability and resilience to further disturbance.

Introduction

Agricultural expansion and intensification are major drivers of land use change leading

to species losses across natural and semi-natural ecosystems (Foley et al. 2005). These

trends are set to continue given the constant growth in the world human population,

currently projected to reach 9.1 billion by 2050 (FAO 2009). However, major expanses

of agricultural land not only produce food, but also increasingly biofuel crops (Koh

2007). Within the EU, one of the fastest-growing biofuel crops for both energy

production and food consumption is oilseed rape (*Brassica napus* L.) (FAO 2008), for

which the area harvested has increased more than tenfold within Europe since the 1960s

to 6,715,272 ha in 2014 (FAO 2014).

Oilseed rape produces intense flushes of bright yellow insect-attractive flowers

resulting in large spatio-temporal variation in the availability of floral resources at a

landscape scale; around 525,000 plants/ha produce more than 100 flowers each during

the peak flowering which lasts about 4 weeks (Hoyle et al. 2007). This large spike in

oilseed flowering has implications for communities of native pollinators and the co-

flowering plants that rely on them (Westphal et al. 2003a, Holzschuh et al. 2013, 2016).

Recent studies have suggested that although such a mass-flowering crop can enhance

the abundance of pollinators at the landscape scale (Westphal et al. 2003b), the presence

of this attractive resource can lead to a transient dilution of floral visitors in nearby

habitats (Holzschuh et al. 2011, 2016). This dilution, caused by the attraction of

pollinators from adjacent natural habitats into flowering crops, can alter the pollinator

community composition (Diekötter et al. 2010) and reduce seed set in co-flowering wild

plants (Holzschuh et al. 2011). But the effects on the network of interactions between

the plants and their pollinators remain unexplored (Gonzalez-Varo et al. 2013), although

this understanding is essential since the structure of the plant-pollinator network can

4

76 affect community stability (Thébault and Fontaine 2010) and co-evolutionary dynamics

77 (Guimarães et al. 2011).

78 Plant-pollinator networks are generally considered to be robust to disturbance

79 (e.g., Nielsen and Totland 2014, Tiedeken and Stout 2015) given the redundancy in the

80 number of pollinator species per plant species (Memmott et al. 2004), their nested

81 structure (Bascompte et al. 2003, but see James et al. 2012), and the truncated power-

82 law distribution followed by their number of links (Jordano et al. 2003), a consequence

83 of morphological and phenological mismatching (Olesen et al. 2008, Bartomeus et al.

84 2016). However, as opposed to the way in which plant-pollinator networks disassemble

85 in response to habitat loss (i.e. with specialist or rare species disappearing first, (Fortuna

86 and Bascompte 2006, Aizen et al. 2012)), crop flowers do not attract all pollinators from

87 the surrounding area equally. Rather, only a small number of common species carry out

88 the bulk of crop pollination services (Kleijn et al. 2015). Thus, we hypothesised that

89 networks in semi-natural habitats adjacent to mass-flowering crops will primarily lose

90 common and generalist species which form the core of the network, and this could

91 affect fundamental properties of the plant-pollinator networks. In particular, we expect

92 the loss of generalist species from the network to decrease nestedness (i.e. specialist

93 species tending to interact with a subset of those that interact with more generalist

94 species) and evenness (i.e. leading to few strong interactions and many weak

95 interactions) and it might increase complementary specialization (i.e. interaction

96 exclusiveness). Such changes could be further reflected in an increase of network

97 modularity due to the loss of many links across modules performed by these generalist

98 pollinator species (Olesen et al. 2007). In a modular network, most pollinator species

99 would interact preferentially with a subset of plant species within the community

100 creating highly-connected units (or modules) with smaller probabilities of interacting

101   with plant species within other units (Olesen et al. 2007). Taken together these shifts

102   could result in less cohesive and more vulnerable networks (Bascompte et al. 2003).

103   We use a unique dataset from three European countries (Germany, Sweden and

104   UK) to examine how the proportion of an insect-dependent mass-flowering crop

105   (oilseed rape) in the landscape affects plant-pollinator networks in adjacent semi-natural

106   grasslands at two time periods: during and after crop flowering. Our study addressed the

107   following questions: (i) which species are attracted by oilseed rape flowers during peak

108   flowering and what proportion of the whole pollinator community do they represent?

109   (ii) what is the effect of such pollinator attraction on network structure in the semi-

110   natural grasslands? (iii) is there a particular level of pollinator loss that affects network

111   structure and, if so (iv) how does this level compare to the current levels of pollinator

112   reductions suffered at our study sites? We predicted that the greatest differences in

113   pollinator community composition and plant-pollinator networks would occur in

114   landscapes with high oilseed rape crop cover, during crop flowering, when generalist

115   pollinators would first move away from the grasslands, to then return after mass-

116   flowering ceases.

117 **Material and methods**

118 *Experimental design and data collection*

119   In each of three countries, Germany, Sweden and the United Kingdom, (Fig. 1a),

120   we selected 16 semi-natural grassland sites with at least one autumn sown oilseed rape

121   (OSR) field within 1 km (except in two cases where the nearest OSR field was located <

122   4 km away). Eight sites were located in landscapes with high relative cover for the

123   region of OSR (> 6%, > 11% and > 9.4 % in the case of Germany, Sweden and UK

124   respectively) while the remaining eight were located in landscapes of low cover of OSR

125 (or no cover in the two sites as mentioned above, Table S1). Within a country, sites

126 were selected to have similar geographical and land-use characteristics with differences

127 in OSR cover. At each study site we mapped the landscape within a 1 km radius

128 surrounding each site. The radius was selected to cover the majority of forage flight

129 distances and landscape-scale species responses (Steffan-Dewenter and Kuhn 2003,

130 Holzschuh et al. 2011, Hanke et al. 2014). We calculated the proportion of the surface

131 occupied by OSR and semi-natural habitats including extensively managed grasslands,

132 calcareous grasslands, shrublands or forested areas. Semi-natural habitats were selected

133 based on expert judgement to provide nesting sites, floral resources or refuges for

134 pollinators. Across all sites, the proportion of the landscape covered by the OSR ranged

135 from 0% to 42% and for semi-natural habitat from 2% to 32% (Table S1). There was a

136 low covariation between the two land-uses ($R^2 < 0.5$ in all countries).

137   Grassland sites were surveyed four times each year for two consecutive years

138 (2011-2012, 2012-2013 in the case of the UK). The first two surveys coincided with

139 oilseed rape flowering (April-June, 'during' period hereafter) and the second two

140 surveys when it had ceased flowering (June-August, 'after' period hereafter, Fig. 1b).

141 We used a during-after sampling design as opposed to a before-during one given the

142 low flower and pollinator counts anticipated prior to the early flowering OSR. At each

143 occasion, flower visiting bees (Hymenoptera: Apiformes) and hoverflies (Diptera:

144 Syrphidae) were surveyed at each site along two 150-m long × 1-m wide transects for

145 30 minutes, 15 minutes per transect, placed in a flower-rich part of the grassland. The

146 species of the floral visitor and the plant were recorded. Pollinators not identified to

147 species in the field were collected when possible and identified in the laboratory. In the

148 case of *Bombus terrestris* and *Bombus lucorum*, which are difficult to distinguish in the

149 field, species were grouped as *Bombus terrestris* agg. (cf. (Murray et al. 2008)). We

150 calculated flower cover for each grassland as the sum of flower units multiplied by the

151 size of these flower units and divided by transect area for every species in the transect

152 surveyed.

153   The autumn-sown OSR field site located within 1-km from each grassland site

154 was surveyed for floral visitors twice during OSR flowering within the two transects as

155 described previously but set parallel to the edge and at the interior (>25 meters from the

156 edge) of the crop. OSR fields and semi-natural grasslands were surveyed on the same

157 day for data comparability. All transect surveys were conducted in temperatures above

158 17ºC, with no rain and low wind.

159 *Pollinator community*

160   We first evaluated sampling completeness of both the pollinator community and

161 the plant-pollinator links using the Chao1 estimator of asymptotic species richness for

162 abundance data (Chao 1984), a non-parametric estimator based on the frequency of rare

163 species (or links) in the original sampling data. For each country, we first estimated the

164 richness of pollinator species and plant-pollinator links accumulated as sampling effort

165 increased up to 100% sampling coverage using package iNEXT (Hsieh et al. 2016).

166 Secondly, we calculated the proportion of pollinator species and links recorded in our

167 survey as compared to one with full sampling coverage. Thirdly, we evaluated which

168 species were shared between grasslands and the crop as well as the proportion of

169 pollinator species and individuals they represented within the grasslands out of the total

170 pollinators. In order to assess which pollinator species were attracted to the crop during

171 flowering we compared pollinator species sampled at the crop with those found in the

172 adjacent grassland at that time period. We expected pollinator species attracted to the

173 crop during flowering to decrease in abundance within grasslands surrounded by high

174   OSR covers and to return to the grasslands after crop flowering while showing no

175   changes within landscapes with low OSR covers (Fig. 1c). Thus, we expect differences

176   in the abundance of each pollinator species between both types of grasslands only

177   during OSR flowering, when pollinators from grasslands surrounded by high OSR

178   covers will be attracted to the crop. We therefore assessed which species are attracted to

179   the crop by calculating their likelihood of being attracted as: $At_i = 1 - \frac{H.dur_i}{L.dur_i}$ [Eqn.

180   1], where $H.dur_i$ and $L.dur_i$ represent pooled pollinator abundances within semi-

181   natural grasslands surrounded by high (*H*) and low (*L*) OSR proportions respectively for

182   each country during crop flowering for species *i*. This index equals 0 when $H.dur_i =$

183   $L.dur_i$ (no attraction), takes positive values up to 1 when, as hypothesized, $H.dur_i <$

184   $L.dur_i$ and negative values when $H.dur_i > L.dur_i$, which occurs for pollinator species

185   that are not attracted by the crop. In addition, for each country we evaluated the extent

186   of total pollinator attraction (*TAt*), i.e., the total share of the pollinator community

187   within grasslands surrounded by high OSR cover that is attracted towards the crop

188   during flowering. We did this by computing the proportion of all shared pollinator

189   species (*n*) found in grasslands surrounded by low OSR cover during crop flowering

190   (*L.dur*, which we consider a spatial and temporal control) that were still present in

191   grasslands surrounded by high OSR cover during the same period, when pollinators

192   were being attracted to the crop (*H.dur*), $TAt = 1 - \frac{\sum_{i=0}^{n} H.dur}{\sum_{i=0}^{n} L.dur}$ [Eqn. 2].

193   *Plant-pollinator networks*

194   To analyse how the observed changes in the pollinator community affected

195   network structure, we constructed a weighted interaction network for each 'grassland–

196   period–year' by pooling data across transects and surveys. We built quantitative

197   networks to represent the frequency of pollinator visits to plants (Fig. 1c), generating

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198   192 networks (i.e. 3 countries x [8 high OSR + 8 low OSR landscapes] $\times$ 2 periods $\times$ 2

199   years). Link density for a subset of networks (15) was too low (e.g., only one interaction

200   observed due to very low flower cover) so these were omitted from the analysis.

201   We calculated the following network-level metrics: link density, interaction

202   evenness, network-level complementary specialization ($H´_2$), modularity, and

203   nestedness. We selected these metrics because although they are weakly correlated

204   (Table S2) they reveal the diversity (i.e. link density and interaction evenness) and the

205   relative distribution of interactions (i.e. complementary specialization, nestedness, and

206   modularity) allowing for a broad understanding of flowering pulse effects on plant-

207   pollinator networks (Kaiser-Bunbury and Blüthgen 2015). These metrics are considered

208   reliable indicators of network stability and robustness to species losses (Bascompte et

209   al. 2003, Fortuna and Bascompte 2006, Bascompte and Jordano 2007, Olesen et al.

210   2007, Bastolla et al. 2009), although the role of some of them in stability is still under

211   debate (e.g., nestedness, James et al. 2012). The weighted versions of these metrics

212   were used due to the effect of matrix size, species abundances and each species´

213   quantitative importance (a function of the frequency with which it interacts with other

214   species in the network, (Kaiser-Bunbury and Blüthgen 2015)) on many of the network

215   metrics (Blüthgen et al. 2007). We estimated link density as the weighted number of

216   interactions per species, calculated as the marginal diversity of interactions per species

217   weighted by the total diversity (Bersier et al. 2002). Interaction evenness was calculated

218   following Tylianakis *et al*. (2007), where a higher number indicates a more even

219   distribution of species interactions. Complementary specialization ($H´_2$) measures the

220   deviation of interaction frequencies from a completely generalized network ($H´_2 = 0$) to

221   a completely specialized one ($H´_2 = 1$) (Blüthgen et al. 2007). Further, we calculated

222   modularity using the QuanBiMo algorithm (Dormann and Strauss 2014), where the

value represents the probability of showing more within-module than between-module interactions. This algorithm used to calculate modularity follows a stochastic approach and hence can lead to different modularity values in different runs. We thus ran the algorithm ten times and found an average difference between the first run and all subsequent runs of 0.02 only for a subset of the networks considered (N=15), while the value was consistent for the rest. Therefore, given low differences we report the results from a single run. Finally, we estimated nestedness using the weighted NODF (Nestedness based on Overlap and Decreasing Fill) metric (Almeida-Neto and Ulrich 2011), where a larger value indicates specialists have a higher tendency to interact with a perfect subset of the species that generalist species interact with.

The weighted version of these metrics can be affected by network size and the number of links, particularly in the case of complementary specialization, modularity or nestedness (Schleuning et al. 2012, 2014, Dormann and Strauss 2014). This can be problematic in comparisons of networks obtained with different sampling efforts or methodologies. In our study the weighted version of metrics is, however, unlikely to be affected due to the standardised sampling protocol and effort across all countries and hence raw values could be used. However, we additionally calculated and present corrected metrics for comparison with our raw metrics by standardising the raw values ($m_{corr} = \frac{m_{observed} - \overline{m_{null}}}{\sigma m_{null}}$) using values obtained from 1000 null model algorithms (as recommended by (Dormann and Strauss 2014) and using the Patefield and *vaznull* algorithms (Patefield 1981) in the *bipartite* package (Dormann et al. 2009) the latter with two constraints: marginal totals and connectance are both kept as in the original network to evaluate whether the changes we observe in our raw metrics are primarily driven by changes in the number of species or in network connectance.

247   Further, we calculated the following species-level metrics for pollinators to

248   evaluate whether species changed their role within the networks during OSR flowering.

249   Species-level metrics were: normalised degree, species-level specialization (d´), within-

250   module degree (z) and between-module connectivity (c), and nested rank. Normalised

251   degree represents the actual number of plant partners a pollinator has compared to the

252   total pool of potential plant partners. Species-level specialization represents a

253   standardized form of the Kullback-Leiber distance (Blüthgen et al. 2006) which

254   considers interaction frequencies whilst accounting for the diversity of partners and

255   their availability. Higher values indicate greater levels of specialization or partner

256   exclusiveness. Within-module degree (z) and between-module connectivity (c) were

257   computed using the QuanBiMo algorithm previously used to calculate modularity. Both

258   metrics were calculated as the number of links (within modules for z and between

259   modules for c, Dormann and Strauss 2014). Nested rank rearranges a network by its

260   maximal nestedness and quantifies the generalism of a given species through its rank in

261   the matrix with increasing values for more specialist or rare species (Alarcón et al.

262   2008). These network metrics at the species level (except for z and c) were calculated

263   using the *specieslevel* function in the *bipartite* package (Dormann et al. 2009).

264   *Data analyses*

265   We first evaluated whether the composition of the pollinator community

266   changed with land use type and period by creating an ordination of sites based on the

267   similarity in the pollinator community composition recorded per site using the Bray-

268   Curtis index (Magurran 2004) followed by a non-metric multidimensional scaling

269   (NMDS, Clarke and Warwick 2001). We then assessed actual differences by means of a

270   permutational multivariate analysis of variance with distance matrices between sites.

271   To evaluate whether there were changes in the plant-pollinator network structure

272   (i.e. link density, interaction evenness, complementary specialization, modularity and

273   nestedness) we used general linear mixed models (GLMMs) fitted for each country

274   separately. Plant-pollinator networks were mapped per site, period and year based on

275   pooled data from the respective two transects at each of the two surveys per site, period

276   and year. Fixed effects were the proportion of OSR and semi-natural habitats in the

277   landscape, flower cover, year, and period (during vs. after) as well as the two-way

278   interactions of period with OSR, semi-natural habitat proportion and flower cover, and

279   that of year with OSR, semi-natural habitat proportion and flower cover. Site was

280   included as a random factor to account for non-independence of the repeated sampling

281   in surveys carried out across two periods and years. All continuous variables were

282   scaled prior to fitting models.

283   We ran all combinations of models using the *dredge* function in the *MuMIn*

284   package (Bartoń 2013) and selected the best model based on the lowest second-order

285   Akaike information criterion values (AICc). If more than one plausible model existed

286   (i.e. when ΔAICc < 6 for more than one model, Burnham et al. 2011) we computed

287   average estimates for each variable across all models in which each variable was

288   retained. We did not use shrinkage when estimating the average estimates for each

289   variable, so that values were calculated only across models where the variable was

290   retained. This modelling approach was used across all analyses.

291   In another set of models, we tested the effect of period, proportion of OSR and

292   semi-natural grasslands on species-level metrics: normalized degree, species-level

293   specialization, within and between-module connectivity, and nested rank. We fitted one

294   model per species-level metric per country where all species of pollinators were

295   included. Fixed factors were the same as those included in the previous set of models.

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296   We further included the abundance of each pollinator species within a site as an

297   additional fixed factor as well as its interaction with period. GLMMs were fitted with a

298   Poisson error distribution. Site was included as a random effect in all cases. All analyses

299   were performed in the *glmmADMB* package (Skaug et al. 2012) using R version 3.0.2

300   (R Development Core Team 2011).

301   *Pollinator attraction simulation*

302   To evaluate whether an increase in OSR cover could have an impact on network

303   structure we simulated pollinator attraction using sites in low OSR landscapes during

304   OSR flowering. These sites represented our spatial control, as they were assumed to

305   harbour communities of pollinators minimally influenced by the adjacent OSR. For

306   each network we simulated the cumulative loss of shared pollinator individuals (i.e.,

307   those belonging to species that were found within grasslands as well as within the OSR

308   fields), and calculated network structure metrics for the resulting plant-pollinator

309   networks including all pollinators: those shared by grasslands and crops as well as those

310   that were never found in the crop. Each individual was given a probability of

311   disappearing from the network based on Equation 1. Negative values of attraction

312   probability, At (Fig. S3 in 13 out of 72 species, 8 out of 28 and 10 out of 58 species of

313   pollinators within Germany, Sweden and the UK), representing cases in which the

314   species was more abundant in landscapes with high covers of OSR, were given a small

315   probability of removal (0.001), while species that were never found within the crop

316   were given a probability of 0. We removed one pollinator individual at each time step

317   with no replacement and continued to remove individuals until no pollinator individuals

318   belonging to a species with an attraction probability > 0 remained in the grassland. We

319   ran 1,000 iterations and calculated average values for each network metric for each level

320   of pollinator loss (1 to N, where N is the number of shared individuals between crop and

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321 grassland). We then used segmented regression to identify for each site the threshold

322 values at which each of the response variables shifted in response to the loss of

323 pollinator individuals with package *segmented* in R version 3.0.2 (R Development Core

324 Team 2011) with the number of segments being site-dependent. Our simulations assume

325 there is no rewiring of interactions, meaning that when an individual pollinator is

326 eliminated from the network its role is not occupied by another pollinator (Kaiser-

327 Bunbury et al. 2010). The aim of this simulation was to estimate at what point network

328 metrics start to change in response to pollinator loss, and to compare this threshold of

329 pollinator loss to that currently observed in our study sites. Although most network

330 metrics are sensitive to network size (Fründ et al. 2015), the aim of this simulation

331 exercise is to compare metrics across sites, as is done for the analyses of the robustness

332 of networks to species loss (Memmott et al. 2004), and previous research shows that

333 despite an overall change in network metrics, the relative order of sites is maintained for

334 most metrics despite decreasing connectance (Bartomeus 2013). However, to control for

335 the effect of changes in network size after species removal we ran an additional

336 simulation where we calculated null-model corrected network metrics for 1,000

337 iterations following the same procedure as stated above: 1,000 null models were

338 calculated using the *vaznull* algorithm. In addition, to test whether the identity of

339 pollinator species being attracted towards the crop affected our results, in this

340 simulation pollinator individuals were removed randomly, i.e. all species (those

341 sampled within the crop as well as those that were never found there) had an equal

342 probability of being removed.

343 **Results**

344 *Pollinator community*

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345 We collected data from 177 networks, with >5,900 interaction events and including 223

346 pollinator species and 199 plant species (see Table S1 for values per site). The majority

347 of sampled pollinators were bumblebees (45.4%), followed by hoverflies (28.1%),

348 solitary bees (15.8%) and honeybees (10.6%). There was substantial variation in the

349 composition of the pollinator communities across countries (see Table S3). Flowering

350 plant species richness also varied between countries and periods. In general there were

351 more flowering plant species in the networks sampled after OSR flowering than during

352 flowering (Table S4A).

353 We found that our survey was able to capture between 61 and 99% of the

354 pollinator species richness in our study areas as well as 41 to 52% of the plant-pollinator

355 link richness (Table S5, Fig. S1), showing values similar to those found in other studies

356 (Chacoff et al. 2012 who used Chao2 estimates).

357 We found changes in species composition across years and periods for all

358 countries sampled (Table S6, Fig. S2), while differences in the pollinator community

359 between grasslands located in areas of high and low OSR cover were only apparent in

360 the case of the UK (Table S6, Fig. S2). Most variation was explained by temporal

361 changes. Hence, the pollinator communities across sites were comparable.

362 OSR was visited by a diverse group of pollinators, representing 20.9 ± 8.3, 11.4

363 ± 5.3 and 19.9 ± 6.5 species of pollinators per site within Germany, Sweden and the UK

364 respectively. These species represented an average of 55% of pollinator species shared

365 with the adjacent semi-natural grasslands (Table S4B, Fig. S3). The group of shared

366 pollinators between the crop and the semi-natural grassland resembled closely that of

367 the pollinator community within the surveyed grasslands for each country. In Germany,

368 the pollinator community and the shared species community were both roughly evenly

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369   distributed across bumblebees, hoverflies and solitary bees (Table S3). In Sweden and

370   the UK, the community of shared pollinator were dominated by hoverflies and

371   bumblebees, respectively (Table S3). In landscapes with high OSR during flowering

372   8.1%, 26.6% and 35.3% (based on Equation 2) of pollinator individuals of species

373   shared between the crop and the grasslands were being attracted towards the crop from

374   grasslands in Germany, Sweden and the UK, respectively.

375   *Plant-pollinator networks*

376   There was a general lack of interactive effects between OSR cover and period on the

377   network structure (Table 1, Fig. 2) and large differences between countries in how

378   networks in each country respond to OSR flowering. In particular, link density

379   increased after flowering in two of the three countries surveyed (with the exception of

380   Sweden, Fig. 2 a-c) and showed a positive response to flower cover in Sweden, while

381   the opposite was true for interaction evenness across all three countries (Figs. 2 d-f). We

382   found the expected period:OSR cover interaction in the case of Sweden, where

383   complementary specialization increased during the flowering pulse in landscapes with

384   high OSR cover to decrease after. Nestedness decreased across both periods but

385   particularly so during OSR flowering (Table 1, Fig. 3b, c). In the UK, complementary

386   specialization ($H´_2$) decreased after flowering across all sites (Table 1). Modularity in

387   Germany also responded to an interactive effect between period and the proportion of

388   OSR in the landscape, increasing particularly during flowering in areas with greater

389   OSR cover. Modularity showed no changes in Sweden and decreased in the UK after

390   flowering but only in one of the years surveyed (2013). Finally, nestedness increased

391   after flowering in Germany and the UK (Table 1).

392   Our analyses with standardized metrics, corrected by using the vaznull and

393   Patefield null models, showed some slight differences although in general showed the

394   same lack of interactive effects between period and the proportion of OSR in the

395   landscape, contrary to our expectations (Tables S7-S8).

396   At the species level, changes in species roles within plant-pollinator networks

397   were solely driven by changes in species abundances and period across all sampled

398   landscapes and countries (Table 2). In general we found low values for both between

399   and within-module connectivity with only *Bombus lapidarius* acting as a network hub

400   (with $c>0.63$ and $z>2.5$, (Olesen et al. 2007), in a network in the UK, Fig. S4 a-c).

401   Nested rank, showed low values for more abundant species (i.e. generalist species)

402   across the three countries (Table 2). However, in line with our analyses of network-level

403   metrics we found no significant interaction between period and OSR cover for any of

404   the metrics evaluated.

405   *Pollinator attraction simulation*

406   The removal of pollinator individuals from grasslands belonging to species found both

407   at the OSR fields and grasslands (i.e., shared species) according to their probability of

408   being attracted towards the crop (Fig. S3) led to changes in some of the network

409   structure metrics (Fig. 4). In every case our segmented regression analyses identified

410   threshold values at which network metrics shifted in response to individual pollinator

411   loss, all of which well-exceeded current pollinator loss levels (Fig. 4). Yet pollinator

412   removal did not affect all metrics equally, nor did metrics respond in the same direction

413   across sites. Instead, changes in network structure appear highly context-dependent and

414   a function of the identity of the initial pollinator community. In particular, link density

415   tended to decrease across all countries (Fig. 4), while evenness remained rather stable

416 and showed increases and decreases in all three countries only when large proportions

417 of shared pollinator individuals moved to the crop (Fig. 4). Complementary

418 specialization showed differing responses for the different countries and sites, being the

419 metric that showed largest variability across sites. Modularity increased slightly in all

420 three countries but particularly in the UK. However, in line with other metrics it showed

421 large variation across sites (Fig. 4). Nestedness tended to decrease in all countries as

422 shared pollinator individuals were extracted from the grassland network being one of

423 the variables that most consistently responded negatively to pollinator loss (Fig. 4). A

424 comparison with a random-removal simulation with null-model corrected metrics shows

425 no major differences (other than site-specific differences) given that the pollinator

426 individuals that are attracted to OSR are also the most common, abundant species. Thus,

427 given their larger numbers they also have the greatest chances of being removed, even

428 under a random removal scenario (Fig. S5). However, we do observe differences in the

429 rate of change with thresholds for most metrics occurring at much lower levels of

430 pollinator loss for random deletions.

431 **Discussion**

432   Our analysis across three countries of plant-pollinator interaction networks in

433 semi-natural grasslands, during and after the flowering of OSR, showed that network

434 structures are robust to such spatial and temporal resource fluctuations even though the

435 crop is attracting pollinator individuals. Our results suggest that plant-pollinator

436 networks are modified primarily by temporal changes in pollinator and plant phenology.

437 Furthermore, our pollinator-removal simulations suggest that networks are relatively

438 resistant. Changes in some metrics were only apparent after ~50% of pollinator

439 individuals had disappeared, which far exceeded the loss of pollinators currently

440 observed in grasslands in the countries surveyed (~8-35%).

Pollinator community

442   The community of shared pollinator species found in the crop and the grasslands

443   matches that of the whole pollinator community in each country. These results are

444   expected for such a generalist plant as OSR, which attracts large numbers of

445   opportunistic species rather than a specialized subset of species, yet the identity and

446   impact on the pollinator community is different for each country. This is consistent with

447   our expectations, whereby mass-flowering crops primarily attract generalist species

448   (Kleijn et al. 2015) which reduce their relative abundance within adjacent semi-natural

449   grasslands, but in contrast to what is observed in relation to habitat loss (Fortuna and

450   Bascompte 2006), rare species do not seem to be directly attracted towards these crops.

451   Although OSR flowering leads to the temporary loss of some pollinator

452   individuals in grasslands, landscapes with high OSR still retain a high proportion of the

453   shared pollinators (ranging from 65% to 92% of individuals of shared species), while

454   major changes in pollinator communities are associated to temporal effects related to

455   pollinator phenologies across all landscapes. The number of flowering plant species

456   detected greatly increases in the period after flowering, suggesting that most co-

457   flowering plant species in the three countries have phenologies that do not overlap with

458   that of OSR. Thus, it is temporal shifts such as those found for flowering plants that

459   have an effect on network metrics.

460   *Plant-pollinator networks*

461   Link density increases in two of the countries, while interaction evenness

462   decreases, in the period after crop flowering across all landscapes. This suggests that

463   both pollinator and plant abundances increase, but that it is particular species of

464   generalist pollinators that increase their abundance. This increase in generalist species

465   after OSR flowering is also reflected in the increase in nestedness found in this period.

466   It is therefore not surprising that given the low levels of pollinator individual

467   losses within our surveyed sites, network metrics do not respond to OSR flowering.

468   Further, our simulation which sequentially removed pollinator individuals, suggests that

469   while some metrics are robust to the loss of these relatively common species (e.g.

470   interaction evenness), other metrics only remain relatively stable until pollinator

471   individual loss exceeds that currently faced by our surveyed grasslands (e.g. link density

472   or complementary specialization). However, in the case in which individuals were

473   removed at random we find that network metrics start to change at values of individual

474   pollinator loss that are lower than those currently found within our sites. This suggests

475   that the relative resistance of our observed networks to pollinator loss is due to the type

476   of pollinators being attracted to OSR: abundant and common species.

477   The changes observed represent a mirror image of the temporal effects observed:

478   both link density and nestedness decrease in response to the loss of these shared

479   generalist species. In addition we find that the progressive loss of shared pollinators

480   could lead to further changes if OSR cover in the landscape were to increase. Of note is

481   the effect that the loss of pollinators has on complementary specialization ($H`_2$) and

482   modularity, which although context-dependent, tend to increase with pollinator loss.

483   This increase in complementary specialization suggests that the interactions become

484   more exclusive and species more dependent on their partners, which raises the risk of

485   secondary extinctions and the vulnerability of networks to further change (Blüthgen

486   2010, Weiner et al. 2013), although it could also increase the efficiency of pollination

487   (Waser and Ollerton 2006). Correlated with the increase in complementary

488   specialization is the observed decrease in nestedness which could further reduce

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489   network stability (Bastolla et al. 2009, Thébault and Fontaine 2010, although see, James

490   et al. 2012), as well as the increase in modularity detected as more generalist connector

491   species are lost and disconnected from modules (Thébault and Fontaine 2010, Spiesman

492   and Inouye 2013). Such an increase in modularity is a consequence of disturbance also

493   observed in other plant-pollinator networks (Spiesman and Inouye 2013, although see,

494   Albrecht et al. 2014) and it can affect species persistence. It is worth noting, however,

495   that we have not included rewiring within our simulations (Kaiser-Bunbury et al. 2010)

496   - i.e. when certain pollinators are lost their function may be taken over by others - which

497   could have attenuated some of the observed effects. However, this is probably not a

498   limiting factor in our analyses because the species that are lost to the crop are generalist

499   species, whose roles might not be easily filled by the remaining pollinators. Moreover,

500   it is important to highlight that our study is restricted to diverse arable landscapes that

501   still retain semi-natural habitat cover (2-32%), such as forests or other grasslands which

502   can provide nesting sites, refuges, and feeding grounds that could potentially dilute the

503   effects of OSR on plant-pollinator networks. Finally, OSR may have long term positive

504   effects for some species ((e.g. those where attraction probability was negative due to

505   larger abundances within areas surrounded by high OSR covers, see also (Jauker et al.

506   2012)) increasing their populations at the landscape level and minimizing the impacts of

507   a temporal attraction. Most of these results based on raw network metric values hold

508   when comparing them to null models that control for network size and link density.

509   However, we also note that some of these results, albeit real and measurable, are driven

510   by the loss of species as reflected by the contrasting results of the null-corrected plant-

511   pollinator networks. This finding could be explained by the fact that the magnitude of

512   pollinator loss suffered by semi-natural grasslands adjacent to OSR fields is dwarfed by

513   the changes in both pollinator and plant communities due to phenology. However, we

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514   find the landscapes in different countries vary in their resistance to the expansion of

515   OSR, particularly if their pollinator community is composed of central place foragers

516   (those that depend on nests, e.g. bumblebees in the UK) as opposed to those dominated

517   by free-moving species whose life cycle depends less on floral resources (e.g. hoverflies

518   in Sweden). The resistance of networks to flowering pulses shows that the mismatching

519   phenology between OSR (which flowers in early spring) and wild plants makes the

520   abundance of OSR flowers complement rather than shift pollinator diets, boosting

521   pollinator communities with the extra resources. Overall, our study represents a step

522   towards understanding the effect of entomophilous crops on mutualistic plant-pollinator

523   networks. Nevertheless, we do not know which effect flowering crops have on

524   pollinator function (Ballantyne et al. 2015) or pollinator-dependent wild flower species

525   reproduction. Future studies should evaluate the effect of OSR and other mass-

526   flowering crops on seed set in wild plants with different flowering phenologies (e.g.

527   flowering synchronously with the crop vs. those flowering before or after the crop, cf.

528   (Kovács-Hostyánszki et al. 2013)).

Table 1. Confidence intervals for estimates of variables included in the averaged models (for all models with ΔAICc values < 6) for the spatial
and temporal variables affecting the network level metrics in the three countries (Germany, Sweden and the UK). Fixed factors included were
Period (during or after), OSR = oilseed rape proportion within 1km, SNH = semi-natural habitat within 1km, Year (2011 or 2012, or, 2012 or
2013 for the UK) and Flower cover. In all cases 'during' was used as the reference category for the variable period. Bold numbers indicate cases
where confidence intervals do not overlap with 0. Missing values represent variables that were not included in final selected models.

	Germany	Sweden	UK
A) Link density	**Lower CI, Upper CI**	**Lower CI, Upper CI**	**Lower CI, Upper CI**
Period	**-1.22, -0.48**	**0.02, 0.84**	**-1.75, -0.49**
Proportion OSR	-0.33, 0.08	-0.42, 0.10	**0.13, 0.73**
Proportion SNH	-0.35, 0.19	-0.31, 0.21	-0.33, 0.26
Year	-0.47, 0.26	-0.44, 0.45	-0.41, 0.80
Flower cover	-0.22, 0.25	**0.06, 0.59**	-0.31, 0.23
Period : Proportion OSR	-0.45, 0.28	-0.66, 0.13	**-1.43, -0.06**
Period : Proportion SNH	-0.07, 0.65	-0.66, 0.11	**0.04, 1.17**
Period : Flower cover	-0.13, 0.69	-0.47, 0.54	-
Year : Proportion OSR	-0.32, 0.40	-0.44, 0.55	-
Year : Proportion SNH	-	-	-
Year: Flower cover	-	-0.44, 0.42	-
B) Interaction evenness			
Period	**0.02, 0.61**	**0.04, 0.12**	**0.02, 0.21**
Proportion OSR	-0.03, 0.01	-0.03, 0.02	-0.07, 0.04
Proportion SNH	-0.04, 0.01	-0.02, 0.04	-0.08, 0.02
Year	-0.07, 0.01	-0.08, 0.00	-0.10, 0.09
Flower cover	-0.03, 0.01	-0.02, 0.03	-
Period : Proportion OSR	-0.04, 0.02	-0.07, 0.00	-0.09, 0.10
Period : Proportion SNH	-0.03, 0.04	-0.07, 0.01	-0.09, 0.10
	-0.03, 0.06		
Period: Flower cover		-0.04, 0.04	-
Year : Proportion OSR	-0.05, 0.02	-0.04, 0.04	-
Year : Proportion SNH	-0.05, 0.01	-0.02, 0.06	-
Year: Flower cover	-0.04, 0.04	-0.04, 0.04	-
C) Complementary specialization			

Period	-0.06, 0.17	-0.16, 0.11	**0.34, 0.61**
Proportion OSR	-0.04, 0.07	-0.12, 0.08	-71.21, 85.09
Proportion SNH	-0.03, 0.09	-0.12, 0.04	-36.32, 36.99
Year	-0.01, 0.21	-0.14, 0.14	-0.24, 0.01
Flower cover	-0.05, 0.08	-0.11, 0.04	-112.22, 126.84
Period : Proportion OSR	-	**0.02, 0.26**	-0.05, 0.25
Period : Proportion SNH	-0.12, 0.10	-0.04, 0.26	-0.25, 0.00
Period: Flower cover	-0.04, 0.24	-0.11, 0.19	-0.52, 0.02
Year : Proportion OSR	-0.10, 0.11	-	-0.15, 0.06
Year : Proportion SNH	-0.07, 0.14	-0.21, 0.09	-0.12, 0.10
Year: Flower cover	-0.16, 0.07	-	-0.23, 0.14
D) Modularity			
Period	-0.12, 0.02	-0.09, 0.07	**0.02, 0.20**
Proportion OSR	-0.04, 0.06	-0.03, 0.06	-38.82, 43.66
Proportion SNH	-0.05, 0.03	-0.01, 0.09	-48.92, 55.22
Year	-0.06, 0.07	-0.02, 0.15	**-0.18, -0.01**
Flower cover	-0.03, 0.04	-0.07, 0.03	-82.72, 90.42
Period : Proportion OSR	**0.00, 0.13**	-	-0.14, 0.02
Period : Proportion SNH	-0.09, 0.06	-0.12, 0.07	-0.02, 0.14
Period: Flower cover	-0.05, 0.14	-0.15, 0.03	-0.37, 0.00
Year : Proportion OSR	-0.08, 0.06	-0.07, 0.11	-0.10, 0.06
Year : Proportion SNH	-	-0.12, 0.05	-0.10, 0.06
Year: Flower cover	-	-0.11, 0.06	-0.16, 0.12
E) Nestedness			
Period	**-0.81, -0.24**	**-1.10, -0.51**	-1.85e+05, 1.77e+05
Proportion OSR	-0.26, 0.12	**-1.29, -0.50**	-5.43, 3.37
Proportion SNH	-0.11, 0.35	-	-2.67e+02, 4.03e+02
Year	**-0.57, -0.11**	-0.15, 0.54	**2.59e-01, 1.05e+00**
Flower cover	-0.04, 0.33	**0.02, 0.51**	-1.35e+03, 7.65e+02
Period : Proportion OSR	-0.49, 0.10	**0.06, 0.73**	
Period : Proportion SNH	**0.10, 0.67**	-	
Period: Flower cover	**0.10, 0.81**	**-1.02, -0.31**	-3.53e+05, 3.67e+05
Year : Proportion OSR	-0.06, 0.41	-	-2.59e-01, 6.97e-01
Year : Proportion SNH	**-0.68, -0.17**	**-**	-3.53e-01, 1.30e-01

Year: Flower cover	-0.11, 0.45	**0.55, 1.39**	-8.65e-03, 1.02e+00

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Table 2. Confidence intervals for estimates of variables included in the averaged models (for all models with ΔAICc values < 6) for the spatial and temporal variables affecting the species level network metrics in the three countries (Germany, Sweden and the UK). In all cases 'during' was used as the reference category for the variable period. Bold numbers indicate cases where confidence intervals do not overlap with 0. Missing values represent variables that were not included in final selected models.

	Germany	Sweden	UK
A) Normalised degree	**Lower CI, Upper CI**	**Lower CI, Upper CI**	**Lower CI, Upper CI**
Period	**0.44, 1.40**	-0.02, 0.75	-0.06, 1.78
Abundance	**0.09, 0.33**	-0.02, 0.22	**0.08, 0.40**
Proportion OSR	-0.28, 0.2	-0.22, 0.21	-0.29, 0.31
Proportion SNH	-0.22, 0.24	-0.28, 0.15	-0.36, 0.26
Year	-0.35, 0.49	-0.60, 0.16	-0.57, 0.65
Period : Abundance	-1.13, 1.29	-0.14, 1.07	-2.26, 4.35
Period : Proportion OSR	-0.59, 0.27	-0.33, 0.41	-0.80, 0.60
Period: Proportion SNH	-0.50, 0.40	-0.33, 0.43	-0.70, 0.76
Year : Proportion OSR	-0.57, 0.27	-0.41, 0.40	-
Year : Proportion SNH	-0.41, 0.45	-0.42, 0.35	-0.73, 0.49
B) Species-level specialization (d´)			
Period	**-2.58, -0.15**	-0.88, 0.48	-0.21, 0.11
Abundance	**-1.40, -0.13**	-2.06, 0.23	**-0.06, 0.00**
Proportion OSR	-0.39, 0.14	-0.39, 0.30	-0.02, 0.06
Proportion SNH	-0.34, 0.17	-0.34, 0.33	-0.02, 0.05
Year	-0.41, 0.55	-0.68, 0.62	-0.08, 0.04
Period : Abundance	-3.88, 4.67	-1.75, 2.91	-0.20, 0.85
Period : Proportion OSR	-0.85, 0.94	-1.06, 0.31	-0.13, 0.05

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Period: Proportion SNH	-0.44, 1.62	-0.6, 0.68	-0.07, 0.11
Year : Proportion OSR	-0.55, 0.49	-0.97, 0.41	-0.11, 0.01
Year : Proportion SNH	-0.24, 0.70	-0.82, 0.50	-0.06, 0.06
C) Between-module connectivity (c)			
Period	-2.18, 0.31	-0.63, 0.86	-0.14, 0.19
Abundance	**0.08, 0.38**	-0.07, 0.31	**0.01, 0.05**
Proportion OSR	-0.37, 0.30	-0.40, 0.44	-0.02, 0.03
Proportion SNH	-0.35, 0.35	-0.44, 0.41	-0.02, 0.04
Year	-1.09, 0.21	-0.61, 0.94	-0.03, 0.07
Period : Abundance	-1.05, 3.30	**0.74, 2.45**	**0.00, 0.85**
Period : Proportion OSR	-0.58, 1.25	-0.78, 0.65	-0.09, 0.06
Period: Proportion SNH	-2.35, 0.64	-0.75, 0.78	-0.08, 0.01
Year : Proportion OSR	-0.61, 0.74	-1.13, 0.39	-0.03, 0.07
Year : Proportion SNH	-1.01, 0.31	-0.91, 0.71	-0.08, 0.08
D) Within-module connectivity (z)			
Period	-0.18, 0.27	-0.24, 0.04	-1.20, 0.14
Abundance	**0.15, 0.29**	-0.13, 0.00	**0.14, 0.33**
Proportion OSR	-0.08, 0.05	-0.07, 0.07	-0.11, 0.11
Proportion SNH	-0.08, 0.06	-0.08, 0.06	-0.12, 0.09
Year	-0.14, 0.12	-0.12, 0.14	-0.30, 0.11
Period : Abundance	-0.92, 0.25	**-0.74, -0.16**	**-4.23, -0.52**
Period : Proportion OSR	-0.13, 0.17	-0.13, 0.13	-0.40, 0.22
Period: Proportion SNH	-0.16, 0.18	-0.13, 0.13	-0.23, 0.44
Year : Proportion OSR	-0.16, 0.11	-	-0.26, 0.17
Year : Proportion SNH	-0.15, 0.11	-	-0.22, 0.19
E) Nested rank			
Period	-0.54, 0.42	-0.97, 0.05	-1.29, 0.93
Abundance	**-1.63, -0.66**	**-0.99, -0.04**	**-2.20, -0.39**
Proportion OSR	-0.11, 0.15	-0.19, 0.13	-0.22, 0.19
Proportion SNH	-0.10, 0.17	-0.20, 0.12	-0.23, 0.19
Year	-0.29, 0.25	-0.31, 0.28	-0.32, 0.50
Period : Abundance	-2.29, 1.66	**-3.23, -0.23**	-6.44, 4.48
Period : Proportion OSR	-0.36, 0.21	-0.34, 0.24	-0.81, 0.53

Period: Proportion SNH	-0.26, 0.40	-0.23, 0.35	-0.44, 0.37
Year : Proportion OSR	-	-0.30, 0.31	-
Year : Proportion SNH	-0.27, 0.27	-0.32, 0.28	-

554

Figure Legends

556 **Figure 1.** a) Location of study sites across the three countries sampled. b) Schematic

557 representation of the study design showing the number of sites sampled at each

558 landscape type-period combination. c) Expectation in pollinator abundances during and

559 after OSR flowering in the crop and semi-natural grasslands. During flowering OSR is

560 expected to attract common and generalist species which will see their abundances

561 decrease within semi-natural grasslands surrounded by high OSR proportions. These

562 pollinators are then expected to return to the grasslands after the crop has ceased

563 flowering, while no apparent changes are expected within grasslands surrounded by low

564 OSR proportions. The change in pollinator abundance in grasslands surrounded by high

565 OSR proportions during crop blooming is reflected in lost links in the semi-natural

566 grassland plant-pollinator network.

567 **Figure 2.** Boxplots showing the effect of period (during and after oilseed rape

568 flowering, OSR) on link density and interaction evenness in nearby semi-natural

569 grasslands for the three countries. Boxes around median extend from first to third

570 quartiles. Inset in top panels shows examples of real networks for each country and

571 period. Brown filled circles represent pollinator species, and grey filled circles plant

572 species.

573 **Figure 3.** Partial residual plot showing the interactive effect between the scaled

574 proportion of oilseed rape and period on modularity in Germany and complementary

575 specialization and nestedness in Sweden.

576

577 **Figure 4.** Results of simulations showing the effect of extracting individuals belonging

578 to shared pollinator species from control sites (landscapes with low or no oilseed rape

579   cover (OSR) during oilseed rape flowering) on different network metrics for Germany

580   a)-e), Sweden f)-j) and the UK k)-o). Black dashed line indicates the mean proportion of

581   shared pollinator species that are lost in landscapes of high OSR for each country based

582   on Equation 2 (8.1%, 26.6% and 35.3% for Germany, Sweden and the UK

583   respectively). Different coloured lines indicate segmented regression fits for different

584   sites pooled across both study years. Networks in some cases were too small to compute

585   some of the metrics and are not shown in the figure. In cases where we were unable to

586   find breakpoints using segmented regression, we present linear regressions instead.
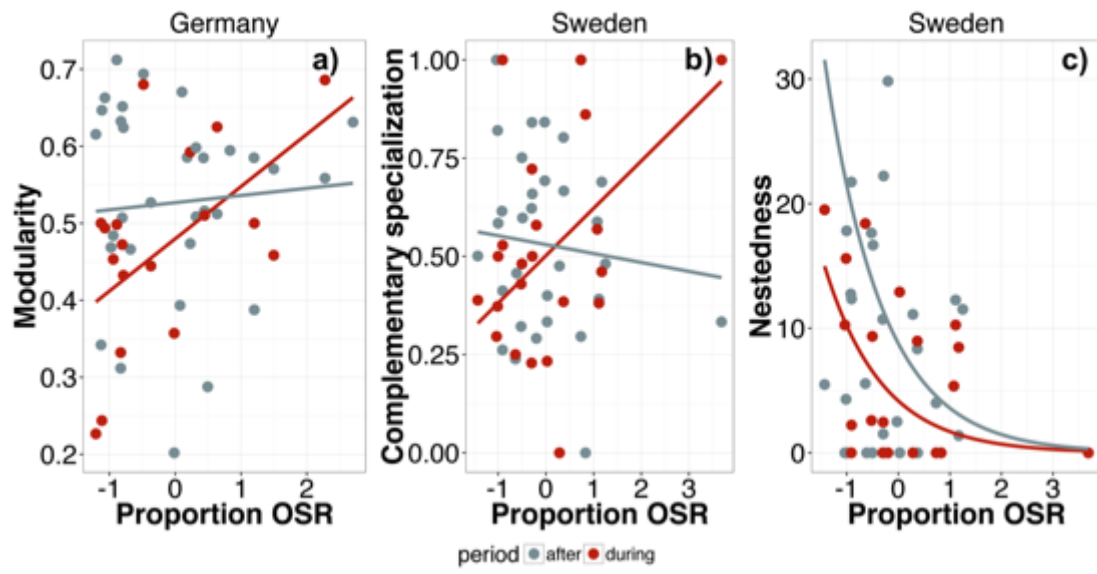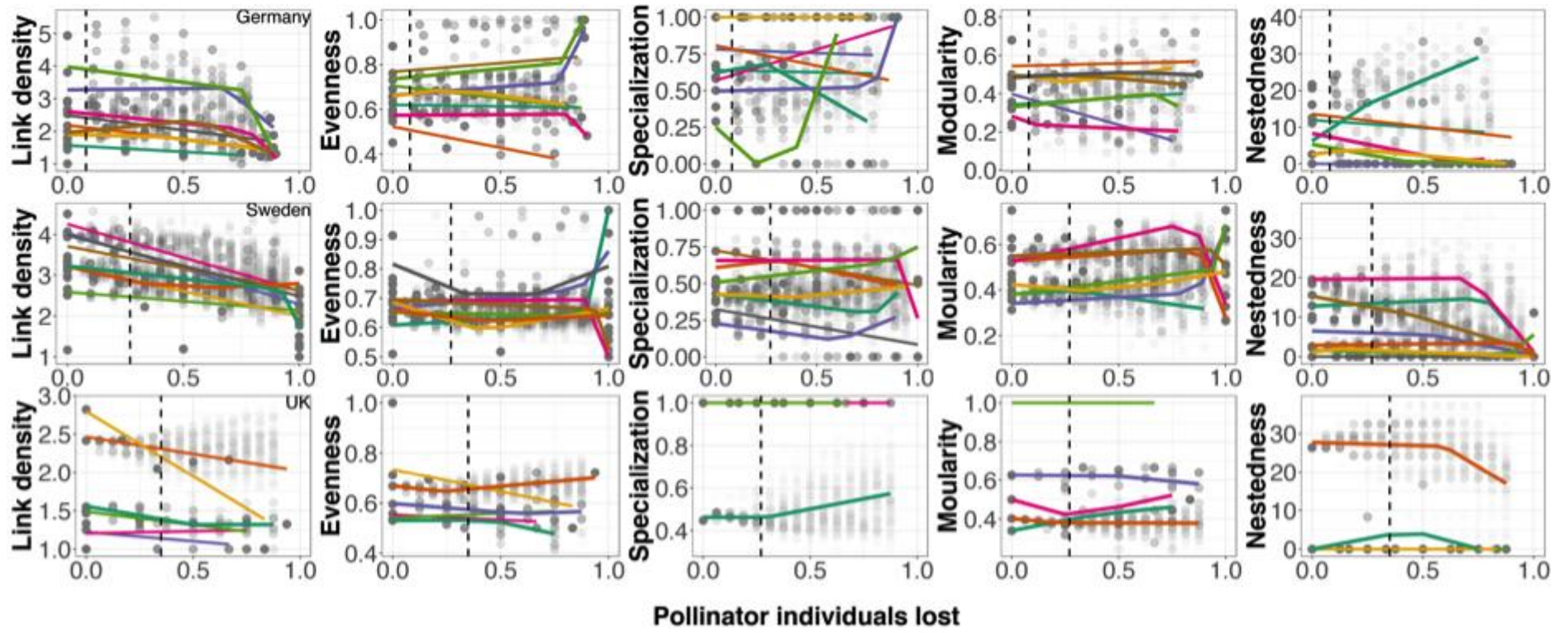
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589 **Figure 1.**
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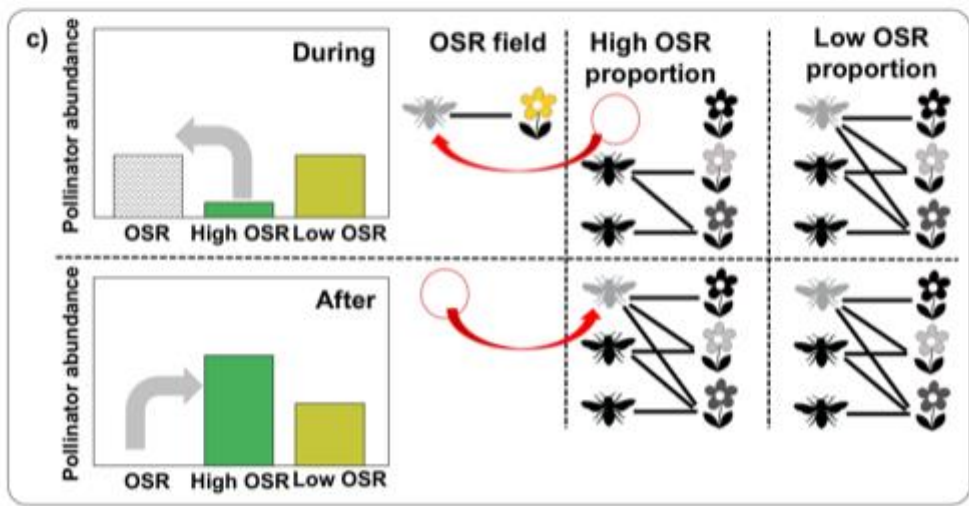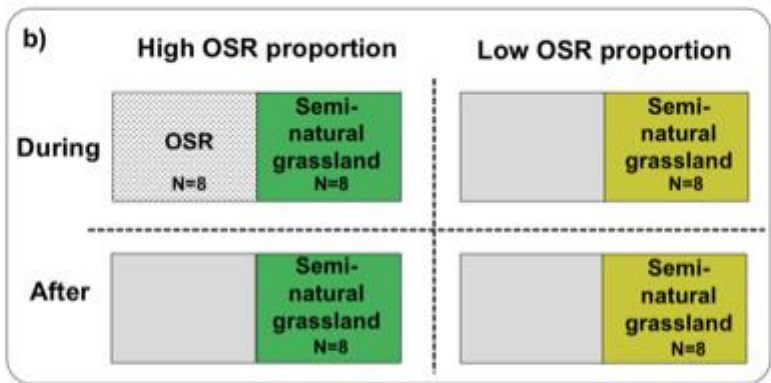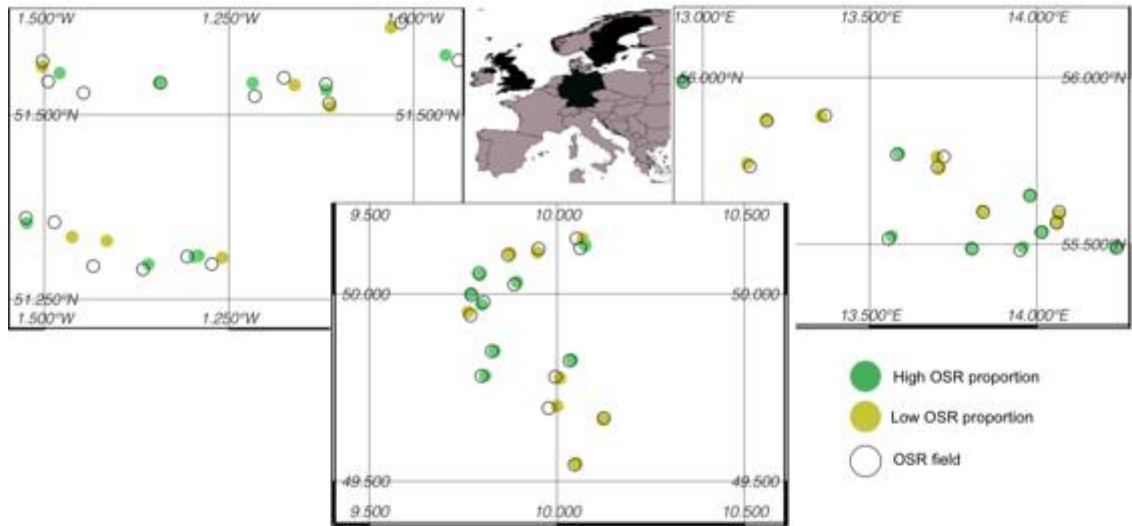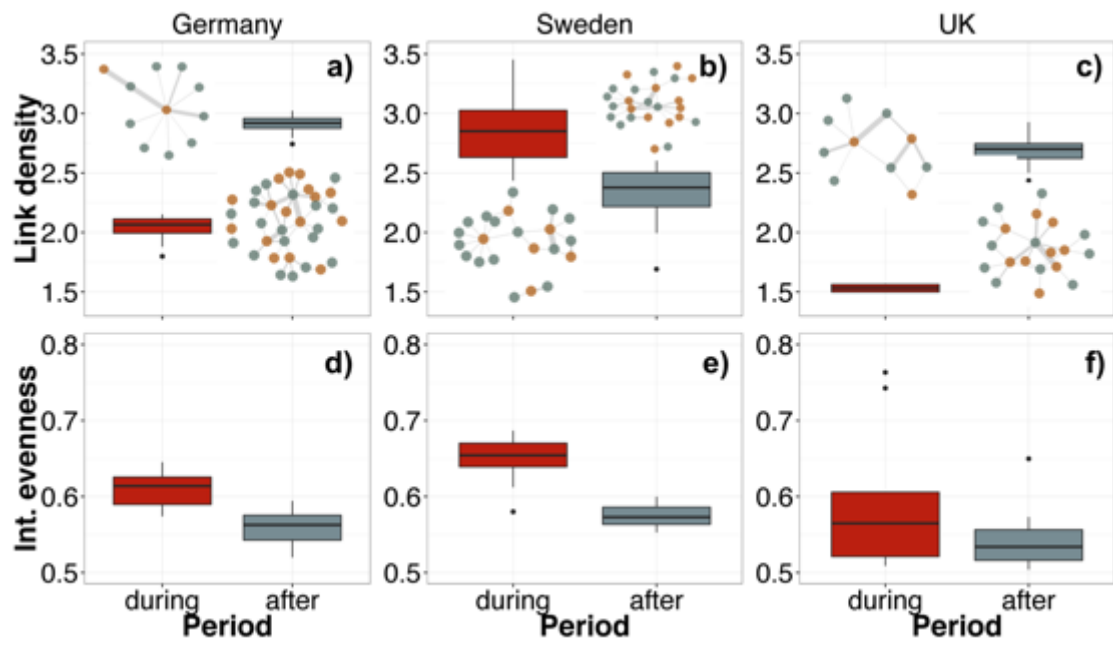
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592 **Figure 2.**
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596 **Figure 3.**

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599 **Figure 4.**

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