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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 affect community stability (Thébault and Fontaine 2010) and co-evolutionary dynamics (Guimarães et al. 2011).

Plant-pollinator networks are generally considered to be robust to disturbance (e.g., Nielsen and Totland 2014, Tiedeken and Stout 2015) given the redundancy in the number of pollinator species per plant species (Memmott et al. 2004), their nested structure (Bascompte et al. 2003, but see James et al. 2012), and the truncated power-law distribution followed by their number of links (Jordano et al. 2003), a consequence of morphological and phenological mismatching (Olesen et al. 2008, Bartomeus et al. 2016). However, as opposed to the way in which plant-pollinator networks disassemble in response to habitat loss (i.e. with specialist or rare species disappearing first, (Fortuna and Bascompte 2006, Aizen et al. 2012)), crop flowers do not attract all pollinators from the surrounding area equally. Rather, only a small number of common species carry out the bulk of crop pollination services (Kleijn et al. 2015). Thus, we hypothesised that networks in semi-natural habitats adjacent to mass-flowering crops will primarily lose common and generalist species which form the core of the network, and this could affect fundamental properties of the plant-pollinator networks. In particular, we expect the loss of generalist species from the network to decrease nestedness (i.e. specialist species tending to interact with a subset of those that interact with more generalist species) and evenness (i.e. leading to few strong interactions and many weak interactions) and it might increase complementary specialization (i.e. interaction exclusiveness). Such changes could be further reflected in an increase of network modularity due to the loss of many links across modules performed by these generalist pollinator species (Olesen et al. 2007). In a modular network, most pollinator species would interact preferentially with a subset of plant species within the community creating highly-connected units (or modules) with smaller probabilities of interacting with plant species within other units (Olesen et al. 2007). Taken together these shifts could result in less cohesive and more vulnerable networks (Bascompte et al. 2003).

We use a unique dataset from three European countries (Germany, Sweden and UK) to examine how the proportion of an insect-dependent mass-flowering crop (oilseed rape) in the landscape affects plant-pollinator networks in adjacent semi-natural grasslands at two time periods: during and after crop flowering. Our study addressed the following questions: (i) which species are attracted by oilseed rape flowers during peak flowering and what proportion of the whole pollinator community do they represent? (ii) what is the effect of such pollinator attraction on network structure in the semi-natural grasslands? (iii) is there a particular level of pollinator loss that affects network structure and, if so (iv) how does this level compare to the current levels of pollinator reductions suffered at our study sites? We predicted that the greatest differences in pollinator community composition and plant-pollinator networks would occur in landscapes with high oilseed rape crop cover, during crop flowering, when generalist pollinators would first move away from the grasslands, to then return after mass-flowering ceases.

Material and methods

Experimental design and data collection

In each of three countries, Germany, Sweden and the United Kingdom, (Fig. 1a), we selected 16 semi-natural grassland sites with at least one autumn sown oilseed rape (OSR) field within 1 km (except in two cases where the nearest OSR field was located < 4 km away). Eight sites were located in landscapes with high relative cover for the region of OSR (> 6%, > 11% and > 9.4 % in the case of Germany, Sweden and UK respectively) while the remaining eight were located in landscapes of low cover of OSR (or no cover in the two sites as mentioned above, Table S1). Within a country, sites were selected to have similar geographical and land-use characteristics with differences in OSR cover. At each study site we mapped the landscape within a 1 km radius surrounding each site. The radius was selected to cover the majority of forage flight distances and landscape-scale species responses (Steffan-Dewenter and Kuhn 2003, Holzschuh et al. 2011, Hanke et al. 2014). We calculated the proportion of the surface occupied by OSR and semi-natural habitats including extensively managed grasslands, calcareous grasslands, shrublands or forested areas. Semi-natural habitats were selected based on expert judgement to provide nesting sites, floral resources or refuges for pollinators. Across all sites, the proportion of the landscape covered by the OSR ranged from 0% to 42% and for semi-natural habitat from 2% to 32% (Table S1). There was a low covariation between the two land-uses ($R^2 < 0.5$ in all countries).

Grassland sites were surveyed four times each year for two consecutive years (2011-2012, 2012-2013 in the case of the UK). The first two surveys coincided with oilseed rape flowering (April-June, ‘during’ period hereafter) and the second two surveys when it had ceased flowering (June-August, ‘after’ period hereafter, Fig. 1b). We used a during-after sampling design as opposed to a before-during one given the low flower and pollinator counts anticipated prior to the early flowering OSR. At each occasion, flower visiting bees (Hymenoptera: Apiformes) and hoverflies (Diptera: Syrphidae) were surveyed at each site along two 150-m long × 1-m wide transects for 30 minutes, 15 minutes per transect, placed in a flower-rich part of the grassland. The species of the floral visitor and the plant were recorded. Pollinators not identified to species in the field were collected when possible and identified in the laboratory. In the case of *Bombus terrestris* and *Bombus lucorum*, which are difficult to distinguish in the field, species were grouped as *Bombus terrestris* agg. (cf. (Murray et al. 2008)). We calculated flower cover for each grassland as the sum of flower units multiplied by the size of these flower units and divided by transect area for every species in the transect surveyed.

The autumn-sown OSR field site located within 1-km from each grassland site was surveyed for floral visitors twice during OSR flowering within the two transects as described previously but set parallel to the edge and at the interior (>25 meters from the edge) of the crop. OSR fields and semi-natural grasslands were surveyed on the same day for data comparability. All transect surveys were conducted in temperatures above 17ºC, with no rain and low wind.

Pollinator community

We first evaluated sampling completeness of both the pollinator community and the plant-pollinator links using the Chao1 estimator of asymptotic species richness for abundance data (Chao 1984), a non-parametric estimator based on the frequency of rare species (or links) in the original sampling data. For each country, we first estimated the richness of pollinator species and plant-pollinator links accumulated as sampling effort increased up to 100% sampling coverage using package iNEXT (Hsieh et al. 2016). Secondly, we calculated the proportion of pollinator species and links recorded in our survey as compared to one with full sampling coverage. Thirdly, we evaluated which species were shared between grasslands and the crop as well as the proportion of pollinator species and individuals they represented within the grasslands out of the total pollinators. In order to assess which pollinator species were attracted to the crop during flowering we compared pollinator species sampled at the crop with those found in the adjacent grassland at that time period. We expected pollinator species attracted to the crop during flowering to decrease in abundance within grasslands surrounded by high

OSR covers and to return to the grasslands after crop flowering while showing no changes within landscapes with low OSR covers (Fig. 1c). Thus, we expect differences in the abundance of each pollinator species between both types of grasslands only during OSR flowering, when pollinators from grasslands surrounded by high OSR covers will be attracted to the crop. We therefore assessed which species are attracted to the crop by calculating their likelihood of being attracted as: $At_i = 1 - \frac{H.dur_i}{L.dur_i}$ [Eqn. 1], where $H.dur_i$ and $L.dur_i$ represent pooled pollinator abundances within semi-natural grasslands surrounded by high (*H*) and low (*L*) OSR proportions respectively for each country during crop flowering for species *i*. This index equals 0 when $H.dur_i$ = $L.dur_i$ (no attraction), takes positive values up to 1 when, as hypothesized, $H.dur_i$ < $L.dur_i$ and negative values when $H.dur_i$ > $L.dur_i$, which occurs for pollinator species that are not attracted by the crop. In addition, for each country we evaluated the extent of total pollinator attraction (*TAt*), i.e., the total share of the pollinator community within grasslands surrounded by high OSR cover that is attracted towards the crop during flowering. We did this by computing the proportion of all shared pollinator species (*n*) found in grasslands surrounded by low OSR cover during crop flowering (*L.dur*, which we consider a spatial and temporal control) that were still present in grasslands surrounded by high OSR cover during the same period, when pollinators 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].

Plant-pollinator networks

To analyse how the observed changes in the pollinator community affected network structure, we constructed a weighted interaction network for each ‘grassland–period–year’ by pooling data across transects and surveys. We built quantitative networks to represent the frequency of pollinator visits to plants (Fig. 1c), generating

192 networks (i.e. 3 countries x [8 high OSR + 8 low OSR landscapes] × 2 periods × 2 years). Link density for a subset of networks (15) was too low (e.g., only one interaction observed due to very low flower cover) so these were omitted from the analysis.

We calculated the following network-level metrics: link density, interaction evenness, network-level complementary specialization (H'_2), modularity, and nestedness. We selected these metrics because although they are weakly correlated (Table S2) they reveal the diversity (i.e. link density and interaction evenness) and the relative distribution of interactions (i.e. complementary specialization, nestedness, and modularity) allowing for a broad understanding of flowering pulse effects on plant-pollinator networks (Kaiser-Bunbury and Blüthgen 2015). These metrics are considered reliable indicators of network stability and robustness to species losses (Bascompte et al. 2003, Fortuna and Bascompte 2006, Bascompte and Jordano 2007, Olesen et al. 2007, Bastolla et al. 2009), although the role of some of them in stability is still under debate (e.g., nestedness, James et al. 2012). The weighted versions of these metrics were used due to the effect of matrix size, species abundances and each species´ quantitative importance (a function of the frequency with which it interacts with other species in the network, (Kaiser-Bunbury and Blüthgen 2015)) on many of the network metrics (Blüthgen et al. 2007). We estimated link density as the weighted number of interactions per species, calculated as the marginal diversity of interactions per species weighted by the total diversity (Bersier et al. 2002). Interaction evenness was calculated following Tylianakis *et al*. (2007), where a higher number indicates a more even distribution of species interactions. Complementary specialization (H'_2) measures the deviation of interaction frequencies from a completely generalized network ($H'_2 = 0$) to a completely specialized one ($H'_2 = 1$) (Blüthgen et al. 2007). Further, we calculated 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.

Further, we calculated the following species-level metrics for pollinators to evaluate whether species changed their role within the networks during OSR flowering. Species-level metrics were: normalised degree, species-level specialization (d´), within-module degree (z) and between-module connectivity (c), and nested rank. Normalised degree represents the actual number of plant partners a pollinator has compared to the total pool of potential plant partners. Species-level specialization represents a standardized form of the Kullback-Leiber distance (Blüthgen et al. 2006) which considers interaction frequencies whilst accounting for the diversity of partners and their availability. Higher values indicate greater levels of specialization or partner exclusiveness. Within-module degree (z) and between-module connectivity (c) were computed using the QuanBiMo algorithm previously used to calculate modularity. Both metrics were calculated as the number of links (within modules for z and between modules for c, Dormann and Strauss 2014). Nested rank rearranges a network by its maximal nestedness and quantifies the generalism of a given species through its rank in the matrix with increasing values for more specialist or rare species (Alarcón et al. 2008). These network metrics at the species level (except for z and c) were calculated using the *specieslevel* function in the *bipartite* package (Dormann et al. 2009).

Data analyses

We first evaluated whether the composition of the pollinator community changed with land use type and period by creating an ordination of sites based on the similarity in the pollinator community composition recorded per site using the Bray-Curtis index (Magurran 2004) followed by a non-metric multidimensional scaling (NMDS, Clarke and Warwick 2001). We then assessed actual differences by means of a permutational multivariate analysis of variance with distance matrices between sites.

To evaluate whether there were changes in the plant-pollinator network structure (i.e. link density, interaction evenness, complementary specialization, modularity and nestedness) we used general linear mixed models (GLMMs) fitted for each country separately. Plant-pollinator networks were mapped per site, period and year based on pooled data from the respective two transects at each of the two surveys per site, period and year. Fixed effects were the proportion of OSR and semi-natural habitats in the landscape, flower cover, year, and period (during vs. after) as well as the two-way interactions of period with OSR, semi-natural habitat proportion and flower cover, and that of year with OSR, semi-natural habitat proportion and flower cover. Site was included as a random factor to account for non-independence of the repeated sampling in surveys carried out across two periods and years. All continuous variables were scaled prior to fitting models.

We ran all combinations of models using the *dredge* function in the *MuMIn* package (Bartoń 2013) and selected the best model based on the lowest second-order Akaike information criterion values (AICc). If more than one plausible model existed (i.e. when ΔAICc < 6 for more than one model, Burnham et al. 2011) we computed average estimates for each variable across all models in which each variable was retained. We did not use shrinkage when estimating the average estimates for each variable, so that values were calculated only across models where the variable was retained. This modelling approach was used across all analyses.

In another set of models, we tested the effect of period, proportion of OSR and semi-natural grasslands on species-level metrics: normalized degree, species-level specialization, within and between-module connectivity, and nested rank. We fitted one model per species-level metric per country where all species of pollinators were included. Fixed factors were the same as those included in the previous set of models.

We further included the abundance of each pollinator species within a site as an additional fixed factor as well as its interaction with period. GLMMs were fitted with a Poisson error distribution. Site was included as a random effect in all cases. All analyses were performed in the *glmmADMB* package (Skaug et al. 2012) using R version 3.0.2 (R Development Core Team 2011).

Pollinator attraction simulation

To evaluate whether an increase in OSR cover could have an impact on network structure we simulated pollinator attraction using sites in low OSR landscapes during OSR flowering. These sites represented our spatial control, as they were assumed to harbour communities of pollinators minimally influenced by the adjacent OSR. For each network we simulated the cumulative loss of shared pollinator individuals (i.e., those belonging to species that were found within grasslands as well as within the OSR fields), and calculated network structure metrics for the resulting plant-pollinator networks including all pollinators: those shared by grasslands and crops as well as those that were never found in the crop. Each individual was given a probability of disappearing from the network based on Equation 1. Negative values of attraction probability, *At* (Fig. S3 in 13 out of 72 species, 8 out of 28 and 10 out of 58 species of pollinators within Germany, Sweden and the UK), representing cases in which the species was more abundant in landscapes with high covers of OSR, were given a small probability of removal (0.001), while species that were never found within the crop were given a probability of 0. We removed one pollinator individual at each time step with no replacement and continued to remove individuals until no pollinator individuals belonging to a species with an attraction probability > 0 remained in the grassland. We ran 1,000 iterations and calculated average values for each network metric for each level of pollinator loss (1 to N, where N is the number of shared individuals between crop and grassland). We then used segmented regression to identify for each site the threshold values at which each of the response variables shifted in response to the loss of pollinator individuals with package *segmented* in R version 3.0.2 (R Development Core Team 2011) with the number of segments being site-dependent. Our simulations assume there is no rewiring of interactions, meaning that when an individual pollinator is eliminated from the network its role is not occupied by another pollinator (Kaiser-Bunbury et al. 2010). The aim of this simulation was to estimate at what point network metrics start to change in response to pollinator loss, and to compare this threshold of pollinator loss to that currently observed in our study sites. Although most network metrics are sensitive to network size (Fründ et al. 2015), the aim of this simulation exercise is to compare metrics across sites, as is done for the analyses of the robustness of networks to species loss (Memmott et al. 2004), and previous research shows that despite an overall change in network metrics, the relative order of sites is maintained for most metrics despite decreasing connectance (Bartomeus 2013). However, to control for the effect of changes in network size after species removal we ran an additional simulation where we calculated null-model corrected network metrics for 1,000 iterations following the same procedure as stated above: 1,000 null models were calculated using the *vaznull* algorithm. In addition, to test whether the identity of pollinator species being attracted towards the crop affected our results, in this simulation pollinator individuals were removed randomly, i.e. all species (those sampled within the crop as well as those that were never found there) had an equal probability of being removed.

Results

Pollinator community

We collected data from 177 networks, with >5,900 interaction events and including 223 pollinator species and 199 plant species (see Table S1 for values per site). The majority of sampled pollinators were bumblebees (45.4%), followed by hoverflies (28.1%), solitary bees (15.8%) and honeybees (10.6%). There was substantial variation in the composition of the pollinator communities across countries (see Table S3). Flowering plant species richness also varied between countries and periods. In general there were more flowering plant species in the networks sampled after OSR flowering than during flowering (Table S4A).

We found that our survey was able to capture between 61 and 99% of the pollinator species richness in our study areas as well as 41 to 52% of the plant-pollinator link richness (Table S5, Fig. S1), showing values similar to those found in other studies (Chacoff et al. 2012 who used Chao2 estimates).

We found changes in species composition across years and periods for all countries sampled (Table S6, Fig. S2), while differences in the pollinator community between grasslands located in areas of high and low OSR cover were only apparent in the case of the UK (Table S6, Fig. S2). Most variation was explained by temporal changes. Hence, the pollinator communities across sites were comparable.

OSR was visited by a diverse group of pollinators, representing 20.9 ± 8.3, 11.4 ± 5.3 and 19.9 ± 6.5 species of pollinators per site within Germany, Sweden and the UK respectively. These species represented an average of 55% of pollinator species shared with the adjacent semi-natural grasslands (Table S4B, Fig. S3). The group of shared pollinators between the crop and the semi-natural grassland resembled closely that of the pollinator community within the surveyed grasslands for each country. In Germany, the pollinator community and the shared species community were both roughly evenly distributed across bumblebees, hoverflies and solitary bees (Table S3). In Sweden and the UK, the community of shared pollinator were dominated by hoverflies and bumblebees, respectively (Table S3). In landscapes with high OSR during flowering 8.1%, 26.6% and 35.3% (based on Equation 2) of pollinator individuals of species shared between the crop and the grasslands were being attracted towards the crop from grasslands in Germany, Sweden and the UK, respectively.

Plant-pollinator networks

There was a general lack of interactive effects between OSR cover and period on the network structure (Table 1, Fig. 2) and large differences between countries in how networks in each country respond to OSR flowering. In particular, link density increased after flowering in two of the three countries surveyed (with the exception of Sweden, Fig. 2 a-c) and showed a positive response to flower cover in Sweden, while the opposite was true for interaction evenness across all three countries (Figs. 2 d-f). We found the expected period:OSR cover interaction in the case of Sweden, where complementary specialization increased during the flowering pulse in landscapes with high OSR cover to decrease after. Nestedness decreased across both periods but particularly so during OSR flowering (Table 1, Fig. 3b, c). In the UK, complementary specialization (H'_2) decreased after flowering across all sites (Table 1). Modularity in Germany also responded to an interactive effect between period and the proportion of OSR in the landscape, increasing particularly during flowering in areas with greater OSR cover. Modularity showed no changes in Sweden and decreased in the UK after flowering but only in one of the years surveyed (2013). Finally, nestedness increased after flowering in Germany and the UK (Table 1).

Our analyses with standardized metrics, corrected by using the vaznull and Patefield null models, showed some slight differences although in general showed the same lack of interactive effects between period and the proportion of OSR in the landscape, contrary to our expectations (Tables S7-S8).

At the species level, changes in species roles within plant-pollinator networks were solely driven by changes in species abundances and period across all sampled landscapes and countries (Table 2). In general we found low values for both between and within-module connectivity with only *Bombus lapidarius* acting as a network hub (with $c>0.63$ and $z>2.5$, (Olesen et al. 2007), in a network in the UK, Fig. S4 a-c). Nested rank, showed low values for more abundant species (i.e. generalist species) across the three countries (Table 2). However, in line with our analyses of network-level metrics we found no significant interaction between period and OSR cover for any of the metrics evaluated.

Pollinator attraction simulation

The removal of pollinator individuals from grasslands belonging to species found both at the OSR fields and grasslands (i.e., shared species) according to their probability of being attracted towards the crop (Fig. S3) led to changes in some of the network structure metrics (Fig. 4). In every case our segmented regression analyses identified threshold values at which network metrics shifted in response to individual pollinator loss, all of which well-exceeded current pollinator loss levels (Fig. 4). Yet pollinator removal did not affect all metrics equally, nor did metrics respond in the same direction across sites. Instead, changes in network structure appear highly context-dependent and a function of the identity of the initial pollinator community. In particular, link density tended to decrease across all countries (Fig. 4), while evenness remained rather stable and showed increases and decreases in all three countries only when large proportions of shared pollinator individuals moved to the crop (Fig. 4). Complementary specialization showed differing responses for the different countries and sites, being the metric that showed largest variability across sites. Modularity increased slightly in all three countries but particularly in the UK. However, in line with other metrics it showed large variation across sites (Fig. 4). Nestedness tended to decrease in all countries as shared pollinator individuals were extracted from the grassland network being one of the variables that most consistently responded negatively to pollinator loss (Fig. 4). A comparison with a random-removal simulation with null-model corrected metrics shows no major differences (other than site-specific differences) given that the pollinator individuals that are attracted to OSR are also the most common, abundant species. Thus, given their larger numbers they also have the greatest chances of being removed, even under a random removal scenario (Fig. S5). However, we do observe differences in the rate of change with thresholds for most metrics occurring at much lower levels of pollinator loss for random deletions.

Discussion

Our analysis across three countries of plant-pollinator interaction networks in semi-natural grasslands, during and after the flowering of OSR, showed that network structures are robust to such spatial and temporal resource fluctuations even though the crop is attracting pollinator individuals. Our results suggest that plant-pollinator networks are modified primarily by temporal changes in pollinator and plant phenology. Furthermore, our pollinator-removal simulations suggest that networks are relatively resistant. Changes in some metrics were only apparent after ~50% of pollinator individuals had disappeared, which far exceeded the loss of pollinators currently observed in grasslands in the countries surveyed (~8-35%).

Pollinator community

The community of shared pollinator species found in the crop and the grasslands matches that of the whole pollinator community in each country. These results are expected for such a generalist plant as OSR, which attracts large numbers of opportunistic species rather than a specialized subset of species, yet the identity and impact on the pollinator community is different for each country. This is consistent with our expectations, whereby mass-flowering crops primarily attract generalist species (Kleijn et al. 2015) which reduce their relative abundance within adjacent semi-natural grasslands, but in contrast to what is observed in relation to habitat loss (Fortuna and Bascompte 2006), rare species do not seem to be directly attracted towards these crops.

Although OSR flowering leads to the temporary loss of some pollinator individuals in grasslands, landscapes with high OSR still retain a high proportion of the shared pollinators (ranging from 65% to 92% of individuals of shared species), while major changes in pollinator communities are associated to temporal effects related to pollinator phenologies across all landscapes. The number of flowering plant species detected greatly increases in the period after flowering, suggesting that most co-flowering plant species in the three countries have phenologies that do not overlap with that of OSR. Thus, it is temporal shifts such as those found for flowering plants that have an effect on network metrics.

Plant-pollinator networks

Link density increases in two of the countries, while interaction evenness decreases, in the period after crop flowering across all landscapes. This suggests that both pollinator and plant abundances increase, but that it is particular species of generalist pollinators that increase their abundance. This increase in generalist species after OSR flowering is also reflected in the increase in nestedness found in this period.

It is therefore not surprising that given the low levels of pollinator individual losses within our surveyed sites, network metrics do not respond to OSR flowering. Further, our simulation which sequentially removed pollinator individuals, suggests that while some metrics are robust to the loss of these relatively common species (e.g. interaction evenness), other metrics only remain relatively stable until pollinator individual loss exceeds that currently faced by our surveyed grasslands (e.g. link density or complementary specialization). However, in the case in which individuals were removed at random we find that network metrics start to change at values of individual pollinator loss that are lower than those currently found within our sites. This suggests that the relative resistance of our observed networks to pollinator loss is due to the type of pollinators being attracted to OSR: abundant and common species.

The changes observed represent a mirror image of the temporal effects observed: both link density and nestedness decrease in response to the loss of these shared generalist species. In addition we find that the progressive loss of shared pollinators could lead to further changes if OSR cover in the landscape were to increase. Of note is the effect that the loss of pollinators has on complementary specialization ($H`_2$) and modularity, which although context-dependent, tend to increase with pollinator loss. This increase in complementary specialization suggests that the interactions become more exclusive and species more dependent on their partners, which raises the risk of secondary extinctions and the vulnerability of networks to further change (Blüthgen 2010, Weiner et al. 2013), although it could also increase the efficiency of pollination (Waser and Ollerton 2006). Correlated with the increase in complementary specialization is the observed decrease in nestedness which could further reduce network stability (Bastolla et al. 2009, Thébault and Fontaine 2010, although see, James et al. 2012), as well as the increase in modularity detected as more generalist connector species are lost and disconnected from modules (Thébault and Fontaine 2010, Spiesman and Inouye 2013). Such an increase in modularity is a consequence of disturbance also observed in other plant-pollinator networks (Spiesman and Inouye 2013, although see, Albrecht et al. 2014) and it can affect species persistence. It is worth noting, however, that we have not included rewiring within our simulations (Kaiser-Bunbury et al. 2010) - i.e. when certain pollinators are lost their function may be taken over by others - which could have attenuated some of the observed effects. However, this is probably not a limiting factor in our analyses because the species that are lost to the crop are generalist species, whose roles might not be easily filled by the remaining pollinators. Moreover, it is important to highlight that our study is restricted to diverse arable landscapes that still retain semi-natural habitat cover (2-32%), such as forests or other grasslands which can provide nesting sites, refuges, and feeding grounds that could potentially dilute the effects of OSR on plant-pollinator networks. Finally, OSR may have long term positive effects for some species ((e.g. those where attraction probability was negative due to larger abundances within areas surrounded by high OSR covers, see also (Jauker et al. 2012)) increasing their populations at the landscape level and minimizing the impacts of a temporal attraction. Most of these results based on raw network metric values hold when comparing them to null models that control for network size and link density. However, we also note that some of these results, albeit real and measurable, are driven by the loss of species as reflected by the contrasting results of the null-corrected plant-pollinator networks. This finding could be explained by the fact that the magnitude of pollinator loss suffered by semi-natural grasslands adjacent to OSR fields is dwarfed by the changes in both pollinator and plant communities due to phenology. However, we find the landscapes in different countries vary in their resistance to the expansion of OSR, particularly if their pollinator community is composed of central place foragers (those that depend on nests, e.g. bumblebees in the UK) as opposed to those dominated by free-moving species whose life cycle depends less on floral resources (e.g. hoverflies in Sweden). The resistance of networks to flowering pulses shows that the mismatching phenology between OSR (which flowers in early spring) and wild plants makes the abundance of OSR flowers complement rather than shift pollinator diets, boosting pollinator communities with the extra resources. Overall, our study represents a step towards understanding the effect of entomophilous crops on mutualistic plant-pollinator networks. Nevertheless, we do not know which effect flowering crops have on pollinator function (Ballantyne et al. 2015) or pollinator-dependent wild flower species reproduction. Future studies should evaluate the effect of OSR and other mass-flowering crops on seed set in wild plants with different flowering phenologies (e.g. flowering synchronously with the crop vs. those flowering before or after the crop, cf. (Kovács-Hostyánszki et al. 2013)).

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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
Period: Flower cover	-0.03, 0.06	-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

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

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	-

Figure Legends

Figure 1. a) Location of study sites across the three countries sampled. b) Schematic representation of the study design showing the number of sites sampled at each landscape type-period combination. c) Expectation in pollinator abundances during and after OSR flowering in the crop and semi-natural grasslands. During flowering OSR is expected to attract common and generalist species which will see their abundances decrease within semi-natural grasslands surrounded by high OSR proportions. These pollinators are then expected to return to the grasslands after the crop has ceased flowering, while no apparent changes are expected within grasslands surrounded by low OSR proportions. The change in pollinator abundance in grasslands surrounded by high OSR proportions during crop blooming is reflected in lost links in the semi-natural grassland plant-pollinator network.

Figure 2. Boxplots showing the effect of period (during and after oilseed rape flowering, OSR) on link density and interaction evenness in nearby semi-natural grasslands for the three countries. Boxes around median extend from first to third quartiles. Inset in top panels shows examples of real networks for each country and period. Brown filled circles represent pollinator species, and grey filled circles plant species.

Figure 3. Partial residual plot showing the interactive effect between the scaled proportion of oilseed rape and period on modularity in Germany and complementary specialization and nestedness in Sweden.

Figure 4. Results of simulations showing the effect of extracting individuals belonging to shared pollinator species from control sites (landscapes with low or no oilseed rape

cover (OSR) during oilseed rape flowering) on different network metrics for Germany a)-e), Sweden f)-j) and the UK k)-o). Black dashed line indicates the mean proportion of shared pollinator species that are lost in landscapes of high OSR for each country based on Equation 2 (8.1%, 26.6% and 35.3% for Germany, Sweden and the UK respectively). Different coloured lines indicate segmented regression fits for different sites pooled across both study years. Networks in some cases were too small to compute some of the metrics and are not shown in the figure. In cases where we were unable to find breakpoints using segmented regression, we present linear regressions instead.

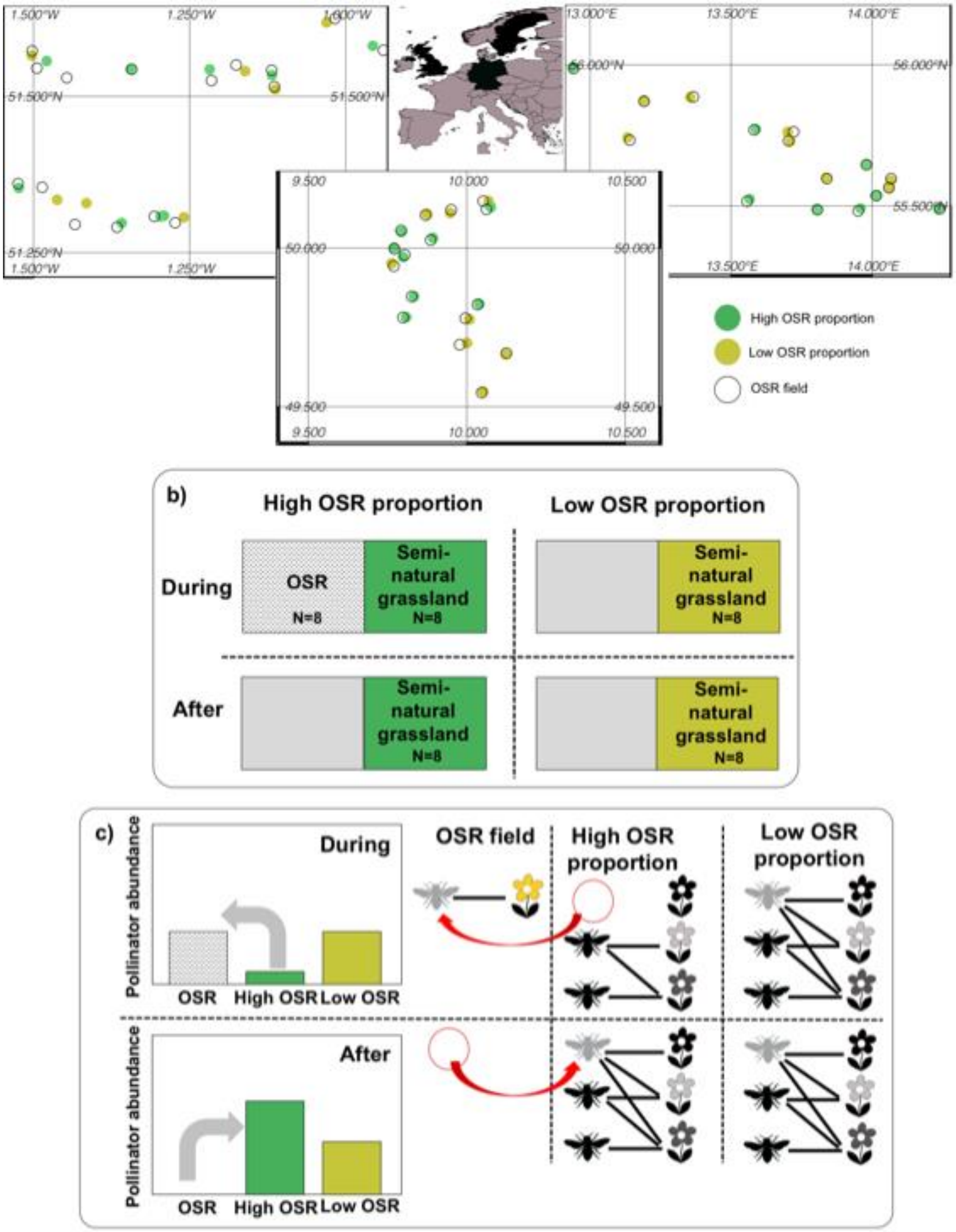
1.500°W
1.250°W
1.000°W
51.500°N
51.250°N
13.000°E
13.500°E
14.000°E
56.000°N
55.500°N
9.500
10.000
10.500
50.000
49.500
High OSR proportion
Low OSR proportion
OSR field
b)
High OSR proportion
Low OSR proportion
During
After
OSR
N=8
Semi-natural grassland
N=8
c)
Pollinator abundance
During
After
OSR
High OSR
Low OSR
OSR field
High OSR proportion
Low OSR proportion

Figure 1.

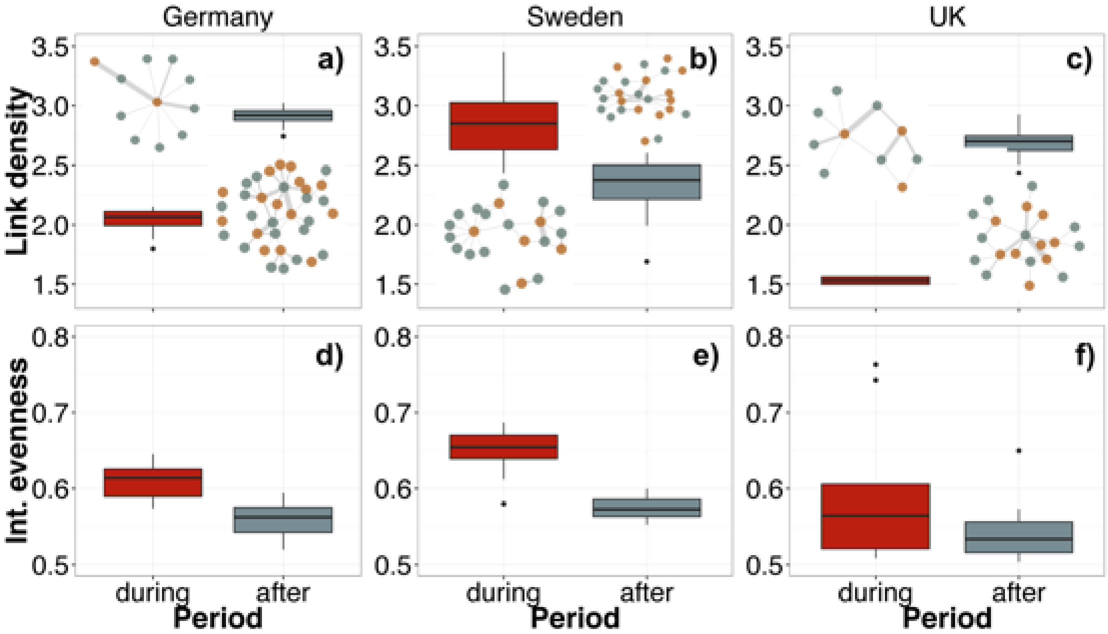
Germany
Sweden
UK
Link density
Int. evenness
3.5
3.0
2.5
2.0
1.5
0.8
0.7
0.6
0.5
a)
b)
c)
d)
e)
f)
during
after
Period

Figure 2.

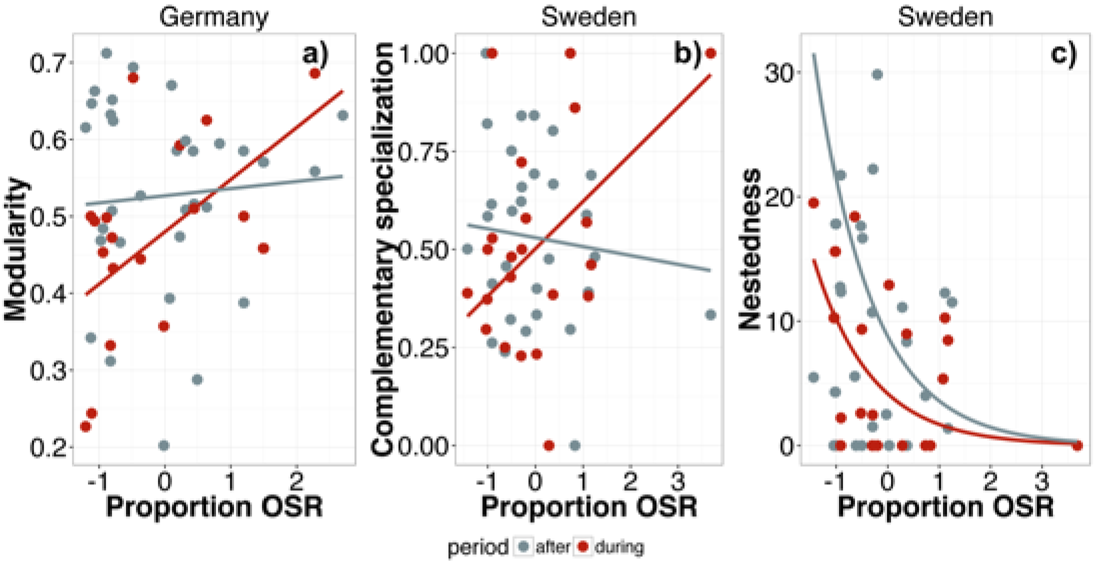
Germany
a)
Modularity
0.7
0.6
0.5
0.4
0.3
0.2
-1
0
1
2
Proportion OSR
Sweden
b)
Complementary specialization
1.00
0.75
0.50
0.25
0.00
-1
0
1
2
3
Proportion OSR
Sweden
c)
Nestedness
30
20
10
0
-1
0
1
2
3
Proportion OSR
period ● after ● during

Figure 3.

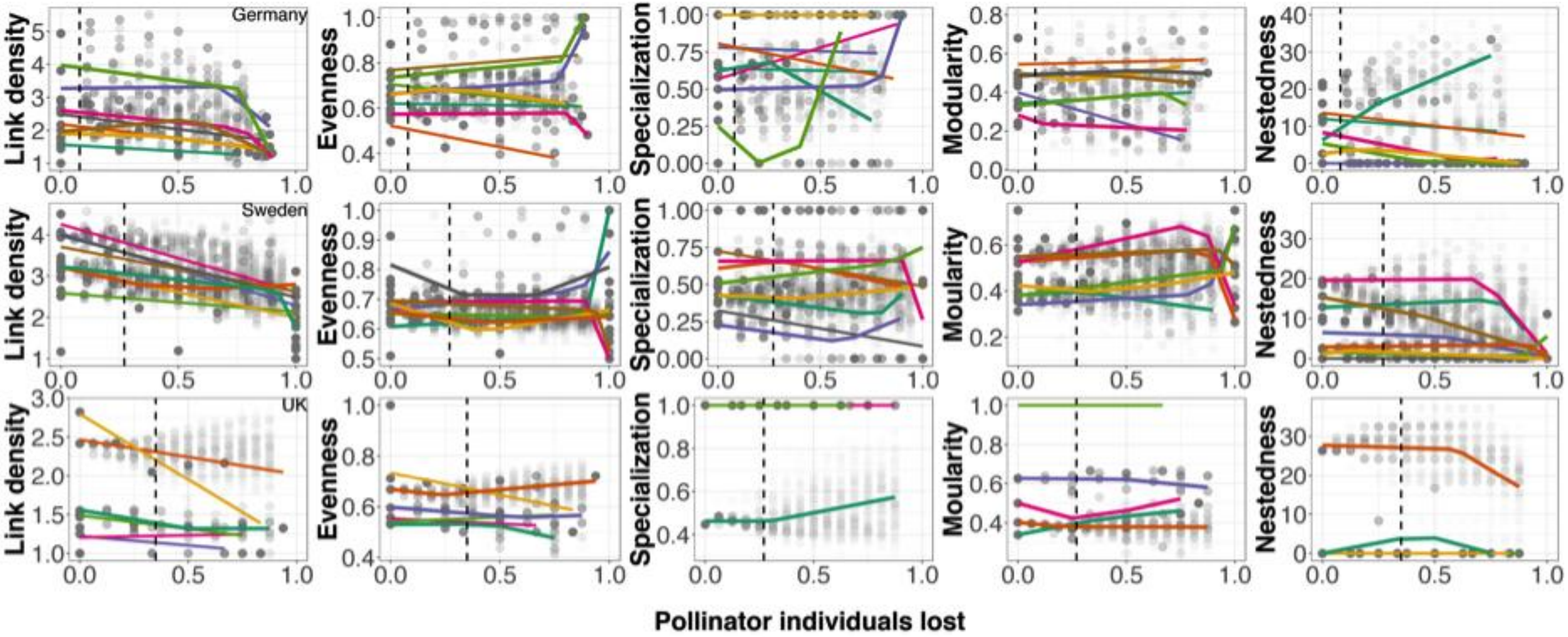
Germany
Sweden
UK
Link density
Evenness
Specialization
Modularity
Moularity
Nestedness
0.0
0.5
1.0
Pollinator individuals lost

Figure 4.

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