Impact of landscape composition and configuration on pollinator movement and plant reproduction

Deliverable D2.5

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Preface

This deliverable (D2.5) assesses the impact of local habitat and landscape characteristics on pollinator communities, their interactions with insect-pollinated plants, and finally the respective pollination services and subsequent impacts on plant reproductive fitness. In particular, following Task 2.5, it uses data on pollinator communities, plant abundances, network characteristics, and plant population genetics, obtained from a selected set of sites from the Safeguard site network to showcase the mechanisms how anthropogenic land use impacts wild plant fitness moderated by affecting pollinator foraging behaviour within plant-pollinator networks.

Summary

Our mechanistic understanding of how changes in land management translate into impacts on the reproductive fitness of insect-pollinated plant species and thus on their long-term population viability and how this is actually moderated by their pollinators is still limited. Here, we analyse impacts of local habitat and landscape characteristics on pollinator community properties, pollinator foraging and movement behaviour and the consequences for three different aspects of plant reproductive fitness – seed set, outcrossing rate, and genetic diversity of plant offspring, using the insect-pollinated plant *Scabiosa ochroleuca* as an example species.

We found that impacts of habitat and landscape properties on (i) pollinator communities, measured as richness and abundance; (ii) foraging behaviour, based on plant-pollinator characteristics such as network connectance, and dietary niche overlap and specialisation of pollinators; and (iii) movement behaviour, indirectly inferred from land-use impacts on outcrossing rate and genetic offspring diversity, are subsequently impacting all measures of plant reproductive fitness.

In particular, the size of a bee-friendly habitat patch was the most influential factor with consistent positive effects on both plant reproductive fitness and pollinator specialisation. Small-scaled habitat mosaics, measured as edge density of all habitat types, were particularly positive for the quality of deposited pollen, likely by facilitating pollinator species with larger foraging ranges. The amount of arable fields in the landscape, on the other hand, had a consistent negative effect on all measures of plant reproductive fitness, mainly by reducing the level of dietary specialisation of pollinators, likely either by attracting generalist pollinators or by impeding viable populations of specialist pollinators.

In the frame of the recently adopted EU Nature Restoration Regulation, considerable efforts are needed to successfully restore pollinators and their habitats. To provide some guidance in this context, we recommend to increase the patch size and quality, e.g. in terms of flower density, of pollinator-friendly habitats as a first focus. As a second aim, these habitat patches should be embedded in structure-rich, small-scale habitat mosaics with suitable connecting linear elements and reduced amount of arable fields in the wider landscape.

1. Introduction

Anthropogenic land use considerably impacts plant and pollinator populations and communities, their respective interactions, and, in turn, the provision of critical pollination services with potentially severe effects on plant reproductive success and fitness. This is of particular concern since about 90% of flowering plants rely on animal pollinators for reproduction (Ollerton et al. 2011), making them reliant on stable mutualisms between plants and pollinators. Negative impacts of anthropogenic land use, at the landscape or local habitat scale, on pollinators or plant-pollinator network structures are well documented (Papanikolaou et al. 2017, Maurer et al. 2024). There is also evidence that land use changes can increase pollen limitation of insect-pollinated wild plants (Bennett et al. 2020, Aguilar et al. 2024) and that the structure of a plant-pollinator network also affects plant reproduction (Saunders and Rader 2019). However, a detailed mechanistic understanding of how local and landscape factors impact plant reproduction and fitness, and in particular how this is moderated by pollinator behaviour, is still limited.

Changes in landscape structure and local habitat quality can impact both pollinator movement and foraging behaviour. For instance, land use change can lead to a reduction in specialisation within plant-pollinator networks, either by losing dietary specialists or by narrowing dietary niches of local pollinator species under increased competition for floral resources (Biesmeijer et al. 2006, Weiner et al. 2014). It can also reduce pollinator diversity and thus the diversity of species-specific flight distances (Herrera 1987). Habitat quality and landscape structure can also affect the movement behaviour of pollinators, e.g. by lowering the residence time in lower-quality habitats (Haddad and Tewksbury 2005, Carvell et al. 2012).

Such changes in pollinator movement and foraging behaviour can reduce conspecific pollen deposition on plant reproductive organs, thereby increasing pollen limitation. It may also reduce the ratio of outcross to self-pollen deposition. Particularly for plants that depend on or benefit from outcrossing, both can lead to reduced seed set and increased risk of inbreeding depression (Igic and Kohn 2006), and hence reduced plant reproductive success.

However, the number of seeds produced and the viability of offspring are not the only relevant factors affecting the population fitness of a plant. Long-term population viability depends on the effective population size (Reed and Frankham 2003), i.e. how well the genetic diversity within a population is represented and maintained in the offspring.

Here, we use selected sites from the Safeguard site network, to assess how landscape structure and local habitat conditions affect pollinator diversity and foraging behaviour within plant-pollinator networks, and how this translates to impacts on three plant reproductive fitness components – seed set, outcrossing rates, and relative offspring genetic diversity.

2. Methods

2.1. Study design

To assess the impacts of land use on pollinator communities and behaviour, and in turn on plant fitness, we used 16 semi-natural grassland sites of the Safeguard site network in Germany (9 sites) and Serbia (7 sites), many of them being part of the Natura 200 network.

To measure plant fitness, we focused *Scabiosa ochroleuca*, which is a perennial herbaceous plant belonging to the family of Dipsacaceae. It occurs in nutrient poor grasslands in the subcontinental areas of Europe and western Asia. Due to decreasing populations, it is ranked as endangered in Germany. *Scabiosa ochroleuca* is flowering between July and October and while it is classified to be self-compatible, it generally avoids self-pollination by protandry. In the field and following the standardised Safeguard protocol (Task 2.5), we collected 20 open-pollinated and 20 hand-pollinated seed families, i.e. ripe inflorescences, and 20 leave samples from individual plants along a 250 m transect per site. To assess the level of potential self-pollination we also collected 10 bagged flowers to exclude insect-pollination. Plant reproductive success was measured as the seed set, determined as the proportion of fertilised seeds of open-pollinated flowers relative to the total number.

Outcrossing rates and offspring genetic diversity were assessed through SNP genotyping of 1,302 maternal (leaves) and offspring samples (seed families) via ddRAD sequencing (Peterson et al. 2012) on an Illumina NovaSeq 6000 (PE150). Outcrossing rates were estimated at the site level using a Bayesian approach (Colicchio et al. 2020). Offspring genetic diversity was calculated as similarity between the allelic frequency composition within a seed family compared to the site-specific allelic frequency within the entire population, with values closer to 1 indicating a better genetic representation, hereafter referred to as ‘relative genetic diversity’.

To identify the proportions of the major visiting pollinator groups, we installed 10 insect camera traps per site along the same 250 m transect used for flower and leave sampling, focusing on three *S. ochroleuca* flowers per camera. Cameras were operated from 09:00 to 17:00 on a single day per site.

Pollinator communities and plant-pollinator interaction networks were surveyed in a standardised manner according to the Safeguard protocol (T2.3) along a 500 m transect for hover flies and wild bees and a 600 m transect for butterflies. Transects were walked in three rounds between May and August 2022 for a duration of 30 min walking time (excluding handling time).

Local habitat characteristics were obtained by the estimated flower density of *S. ochroleuca* and the size of the focal grassland patch. The wider landscape was characterised, based on digitised habitat maps, by edge density of all habitat types, proportion of arable fields, and Shannon diversity of all habitat types within a radius of 1 km.

To assess pollinator movement, we used a capture-mark-recapture approach in the German sites. We marked over 1500 individual wild bee specimens in the morning, but particularly low recapture rates of 8% on average in the afternoon of the same day prevented further analyses.

2.2. Statistical analyses

To measure pollinator diversity, we used abundance and richness (based on asymptotic richness estimates) of all pollinators and separately for solitary wild bees, bumble bees, hover flies, butterflies and honey bees (abundance only), pooled across the three visits per site. The following plant-pollinator network metrics were calculated based on the pooled data across the three visits per sites: nestedness (weighted NODF), connectance, specialisation of the entire network (H2'), niche overlap of pollinators, niche overlap of plants, mean specialisation of pollinators (d), and mean specialisation of plants (d').

For statistical analyses, we followed a two-step approach by identifying the set of ‘best’ regression models for each target variable first and then subjecting those models to structural equation models. This was done separately for all three measures of plant reproductive fitness (seed set, outcrossing, relative genetic diversity).

We used generalised linear mixed-effects models with the respective error distribution for each finally relevant dependent variable (seed set, outcrossing rate, relative genetic diversity: beta distribution; pollinator abundance: Poisson distribution; connectance, niche overlap: log-normal distribution; pollinator richness, flower density, mean specialisation: Gaussian distribution). We designed the models in a hierarchical manner where (i) plant fitness measures were explained by network characteristics, pollinator community measures, flower density of *S. ochroleuca*, and landscape structure; (ii) network characteristics by pollinator community measures, flower density of *S. ochroleuca*, and landscape structure; (iii) pollinator community measures by flower density of *S. ochroleuca*, and landscape structure; and (iv) flower density of *S. ochroleuca* by landscape structure. We included country as a random factor and an observer term to control for overdispersion in Poisson models where necessary. To avoid impacts of collinearity, we excluded variables with a higher variance inflation factor of four. For model simplification, we applied a multimodel inference approach where all variables within the set of models with a difference in AICc values of lower than two compared to the best model were retained. These sets of models were then used in a structural equation modelling approach to disentangle direct, indirect and ‘net’ effects, i.e. combining direct and indirect effects.

3. Results

3.1. Flower visitation and reproductive fitness

Not a single seed from flowers of *S. ochroleuca* where pollinators were excluded (bagging) was fertile, indicating that the reproductive success of *S. ochroleuca* is entirely dependent on insect pollination. The data from insect cameras in German sites showed that the main flower visitors are wild bees (solitary wild bees and bumble bees taken together), followed by honey bees, ants, flies (including hover flies), and others (Figure 1a), and that visits of wild bees were most important to guarantee a high proportion of fertile seeds (Figure 1b). Data from sites in Germany and Serbia also showed that the number of visits by wild bees is not the only factor contributing to seed set, but there was also a positive impact of the level of outcrossing (Figure 2), highlighting the importance of both a sufficient number of visits by pollinators (primarily wild bees) and adequate pollinator movement and behaviour to allow for a high level of outcrossing.

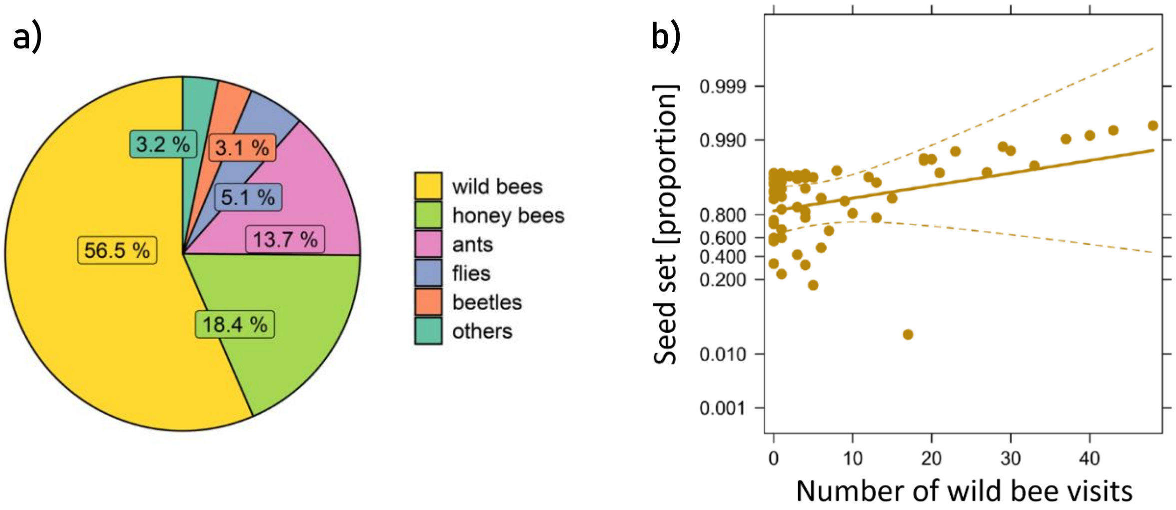

Figure 1: Proportional visits of flowers of *Scabiosa ochroleuca* by major insect groups (a) and impact of wild bee visits on seed set (b). Since the seed set was generally high, the y-axis in (b) is displayed at the logit-scale (link scale in the model) for better visualisation.

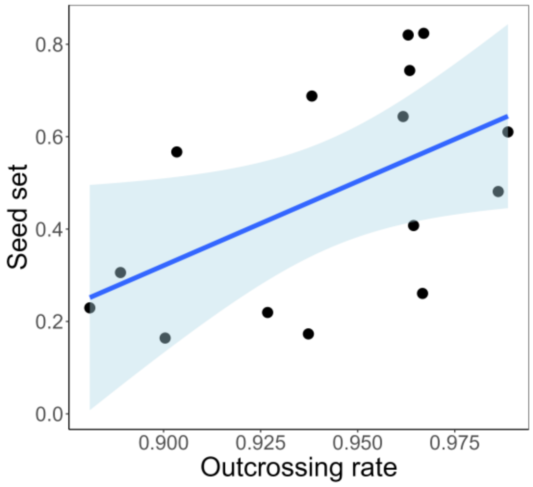

Figure 2: Relationship between outcrossing rate and seed set of *Scabiosa ochroleuca*.

3.2. Direct and indirect effects of landscape properties on plant fitness

We found strong net-effects (i.e. combining direct and indirect effects moderated by flower density, pollinator community measures and plant-pollinator network properties from structural equation models) of local patch and landscape properties on all three measures of reproductive fitness of *S. ochroleuca* (Figure 3).

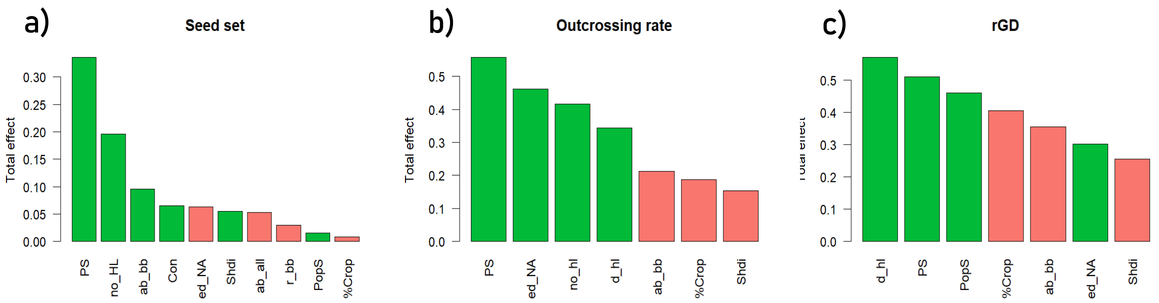

Figure 3: Net-effects of habitat and landscape properties, flower densities, pollinator community measures, and plant-pollinator network characteristics on the reproductive fitness of *Scabiosa ochroleuca*. rGD (relative genetic diversity) measures the allelic frequency composition within a seed family compared to the site-specific allelic frequency of the entire population. PS, size of the focal habitat patch; no_HL, niche overlap of the higher level (i.e. pollinators) in the network; ab_bb, abundance of bumble bees; con, network connectance; ed_NA, edge density of all habitat types; Shdi, Shannon diversity of all habitat types; ab_all, abundance of all pollinators; r_bb, species richness of bumble bees; PopS, population size of *S. ochroleuca* (measured as flower density); %Crop, percentage of cropland in the landscape; d_HL, mean specialisation of higher level (i.e. pollinators) in the network. Green bars indicate positive effects, red bars indicate negative effects.

Patch size turned out to be the most important factor increasing all three aspects of reproductive fitness, i.e. seed set, outcrossing rate and relative genetic diversity (Figure 3). These effects were mostly directly affecting plant fitness, or were moderated by the population size of *S. ochroleuca* and plant-pollinator network metrics (Figure 4).

Edge density of all habitat types had a positive effect and was most important for outcrossing rates and to some extent for the relative genetic diversity of *S. ochroleuca* offspring. In contrast, it was less important for seed set where the effect was negative (Figure 3). The effects of edge density were mainly indirect, with negative impacts on bumble bee abundance which either directly translated into negative impacts on seed set, or were converted into positive effects on outcrossing and the relative genetic diversity of *S. ochroleuca* offspring via increasing the average dietary specialisation in the entire pollinator communities (Figure 4).

We found a consistent negative impact of the amount of arable fields in the landscape on all three aspects of plant fitness (Figure 3). This was most pronounced for the relative genetic diversity of *S. ochroleuca* offspring, but was of only little relevance for seed set. Those impacts were mainly driven by indirect effects increasing the average dietary specialisation in the entire pollinator communities, which in turn decreased the relative genetic diversity and outcrossing rates (Figure 4b and c).

The diversity of habitats in the landscape negatively influenced the relative genetic diversity of *S. ochroleuca* offspring and outcrossing rates, while it had a minor but positive effect on seed set (Figure 3). There was no direct effect of habitat diversity on the fitness of *S.*

ochroleuca, but it strongly increased the abundance of bumble bees, which decreased the average level of specialisation of pollinators, leading to a decrease in outcrossing rates and relative genetic offspring diversity (Figure 4b and c). However, habitat diversity also increased the overall abundance of pollinators which in turn increased seed set (Figure 4a).

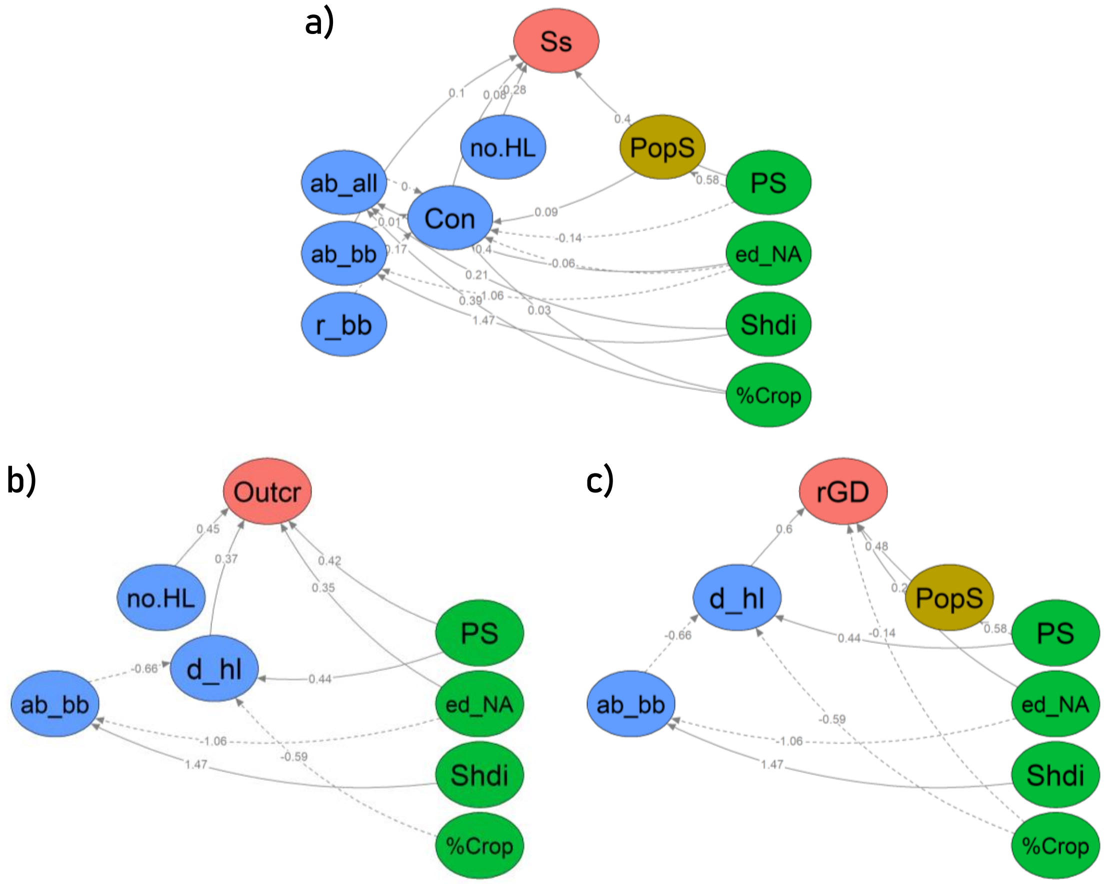

Figure 4: Path diagram showing direct and indirect effects of patch, landscape, pollinator community, and plant-pollinator network characteristics on the reproductive fitness of *Scabiosa ochroleuca*. (a) Impacts on seed set (Ss). (b) Impacts on outcrossing rate (Outcr). (c) Impacts on relative genetic diversity (rGD). Landscape-level factors are indicated in green: PS, size of the focal habitat patch; ed_NA, edge density of all habitat types; Shdi, Shannon diversity of all habitat types; %Crop, percentage of cropland in the landscape. Patch-level factors are indicated in brown: PopS, population size of *S. ochroleuca* (measured as flower density). Pollinator community and plant-pollinator network characteristics are depicted in blue: ab_bb, abundance of bumble bees; ab_all, abundance of all pollinators; ab_bb, abundance of bumble bees; r_bb, species richness of bumble bees; no_HL, niche overlap of the higher level (i.e. pollinators) in the network; d_HL, mean specialisation of higher level (i.e. pollinators) in the network. Solid arrows indicate positive effects, dashed arrows indicate negative effects. Numbers are standardised coefficients estimates.

3.3. Effects of habitat, pollinator community and plant-pollinator network properties on plant fitness

Plant-pollinator network properties played the most important role among the biotic moderators of the effects of landscape characteristics on plant fitness (Figure 3) with positive effects on network connectance, niche overlap and average dietary specialisation of pollinators (Figure 4).

Pollinator community characteristics did, in most of the cases, not directly affect plant reproductive fitness, but they had indirect impacts via changing the structure of plant-pollinator networks (Figure 4). All relevant pollinator community measures (bumble bee richness and abundance, and the abundance of all pollinators) had negative impacts on network connectance or the average dietary specialisation of pollinators. Across all pollinator community measures, bumble bee abundance was most influential. It also showed a direct positive effect on seed set. This led to an overall increase in seed set with bumble bee abundance, while, moderated via the negative effects on network properties, high bumble bee abundance also decreased outcrossing rate and the relative genetic offspring diversity (Figure 3).

The population size of *S. ochroleuca*, measured as flower density and used as a proxy for habitat quality, was only relevant for the relative genetic offspring diversity with a strong positive direct effect (Figures 3 and 4c).

4. Discussion

4.1. Direct and indirect impacts of land use on plant fitness

Our study provides insights into mechanisms of how changes in land use can impact pollinators, their interactions with plants and finally plant reproductive fitness. We found that habitat and landscape properties indeed affect pollinator communities and behaviour which, in turn, drives plant fitness.

We found obvious relationships, such as beneficial effects of high habitat diversity on bumble bee abundances, leading to an increased seed set, likely via increased visitation rates of such a highly efficient pollinator group. However, our results also revealed more complex patterns. For instance, we found that the effects of high bumble bee abundances are not positive for all aspects of plant fitness. On the contrary, high bumble bee abundance actually decreased the level of average dietary specialisation in the pollinator community, which then decreased the outcrossing rate and relative genetic diversity of plant offspring. This is concerning since we showed that the outcrossing rate is directly related to seed set, and moreover it can have considerable impacts on the viability of the next generation (Bailay and McCauley 2006). In addition, the relative genetic diversity of plant offspring is also affected by the same mechanism. The relative genetic diversity of plant offspring is a measure of panmixia, i.e. the level of random mating. Reducing the level of panmixia will ultimately decrease the effective population size and thus overall genetic diversity with potentially considerable consequences on population viability and resilience against environmental changes. This shows, that for the assessment of potentially beneficial effects of land management interventions to sustain insect-pollinated plant species, it is not sufficient to consider the respective impacts on seed set only, but additional information on the quality of the seed set in terms of outcrossing and level of panmixia is needed to assess long-term population consequences.

In addition to direct, pollinator abundance-driven effects, we also found strong impacts of the structure of the plant-pollinator networks, and in particular of the connectance within the network and the level of niche overlap and dietary specialisation of pollinators in the community. Overall dietary specialisation of pollinators was the most influential factor and increased pollen quality in terms of relative genetic offspring diversity and, together with niche overlap in pollinators, outcrossing rate. A higher level of specialisation might enforce the pollinator to forage across a larger area of the population within a habitat patch, or even to visit other patches in the landscape, rather than focussing on a smaller area and thus a subset of the population by alternatively utilising multiple different flowering plant species. As a consequence, such a behaviour would increase random mating across a larger part of the population and thus also overall genetic diversity of the plant offspring. Dietary specialisation increased with patch size but decreased with the proportion of arable land in the landscape. This indicates the beneficial effects of large patches of pollinator-friendly habitat to host a larger number of dietary specialists with positive effects on the quality of deposited pollen. On the other hand, large amounts of arable fields in the landscape have negative effects, potentially by attracting generalist pollinators or reducing population viability of specialists, both with negative effects on deposited pollen quality.

An increased niche overlap of pollinators also increases the chances of a plant species to be visited by different pollinator species. Since foraging ranges and patterns differ among pollinators (Herrera 1987), this will also increase the chances to be visited by pollinators that utilise a larger area for foraging and, with that, the chances for pollen deposition from plant specimens being further apart. Niche overlap of pollinators was not affected by any of our assessed habitat and landscape measures, but additional analyses of nectar depletion in German Safeguard sites (Sponsler et al. 2024) indicate that patterns in niche overlap might have been more driven by variation in the levels of drought and food scarcity.

The influence of plant-pollinator network connectance was comparably small and only affected seed set. However its impact highlights the potential of well-connected networks, i.e. a large number of realised interactions relative to all potential interactions, to support a high seed set of plants. However, network connectance was negatively impacted by patch size, but these effects were counterbalanced by positive effects on flower density and thus on seed set. Edge density had also a negative effect on network connectance, but this was also reflected by a net negative effect on seed set.

While the discussed indirect effects of land use on plant fitness via network characteristics can be interpreted as impacts on pollinator foraging behaviour, in particular with respect to dietary specialisation, the observed direct impacts of land use on plant fitness might be seen in the light of pollinator movement behaviour. A relationship to movement behaviour is also indicated by the fact that such direct effects were predominantly observed for outcrossing rate and relative genetic offspring diversity. Edge density, for instance, increased both of these aspects of plant fitness. Edge density, measured as the length of patch edges per area, is often interpreted as a measure of fragmentation. However, patch edges can often be accompanied by more or less narrow lines of flower (and nesting) resources and thus might act as corridors connecting suitable habitat patches. In both cases, bee communities might be filtered accordingly to overcome potential restrictions by highly fragmented habitats via increased abilities to forage over larger distances utilising corridors to move from one suitable patch to the other.

4.2. Relevance for policy and land management

Within the frame of the recently adopted EU Nature Restoration Regulation, considerable restoration efforts are needed for the benefits of overall biodiversity and pollinators in particular. On the basis of our results, we can provide clear management recommendations. The size of pollinator-friendly habitats, as in our case most of them in Natura 2000 areas, turned out to be the most important factor to increase all aspects of plant fitness. In addition, increasing the size of such patches does not only benefit plant population viability but also ensures a higher level of pollinator dietary specialisation, species of which are usually among the most threatened. Increasing the size of such patches will consequently benefit both pollinators and plants.

While the negative effects of edge density on seed set were small, they were by far outweighed by positive effects on the quality of deposited seeds. This can be seen in combination with the proportion of arable fields in the landscape which was negative for all plant fitness aspects. Thus, changing the landscape towards smaller fields embedded in a highly structured mosaic with many connecting linear elements will impact the movement behaviour of the pollinators and correspondingly increase long-term plant population viability by sustaining a high level of panmixia and resulting genetic diversity at the population level.

The predominantly negative effects of high habitat diversity in the landscape seem counterintuitive. But these effects were basically driven by increased abundances of bumble bees, which is in principle desirable. But the consequent decrease in overall dietary specialisation of the pollinator communities, and potentially also the foraging patterns of this highly efficient pollinator group itself, led to a reduction in the quality of deposited pollen. However, we do not recommend to reduce habitat diversity, but rather try to compensate the negative effects, which actually might not apply to all plant species in an area, by investing in other promising actions such as mentioned before or in improving local habitat quality.

A beneficial impact of local habitat quality was shown by the positive direct effects of plant population size, measured as flower densities, on the quality of deposited pollen in terms of relative genetic offspring diversity. In our study, we only focused on one plant species, but we believe that most of our results can be generalised for many flowering plant species benefiting from or depending on outcrossing. Thus increasing flower densities for a diversity of plant species at larger patches of bee-friendly habitat will ensure long-term population viability, and as other studies showed also that of wild pollinators.

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