Report on pressures and suitability of different indicators of pollinator declines in Natura 2000 habitats

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Fabian A. Boetzl[1], Carolin Biegerl[1], Andrea Holzschuh[1], Jochen Krauss[1], Jie Zhang[1], Ingolf Steffan-Dewenter[1]

[1]*Julius-Maximilians-Universität Würzburg, Germany*

Safeguard
Safeguarding European wild pollinators

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Summary

Reversing pollinator declines is crucial for securing the pollination of wild plants and arable crops and ultimately human wellbeing. However, policies for pollinator conservation require predictors and indicators for pollinator species richness and densities that are reliable across pollinator groups and regions and provide the evidence base for management of high-value Natura 2000 habitats and surrounding agricultural landscapes. As central element of Safeguard we established a standardised pollinator monitoring in 323 cultural landscapes centred around a focal protected, semi-natural grassland patch, spanning across 15 study locations in major biogeographical European regions. We aimed to assess (i) whether the relationship between habitat availability and species richness is modulated by the regional context, (ii) how it interacts with local habitat quality and landscape management intensity measured by the cover of cropland (iii) whether pollinator communities are impoverished in landscapes with little suitable habitat, and (iv) how consistent relationships are across the study regions. In order to obtain a broad picture and identify potent indicators across pollinator taxa with different life history, we sampled butterflies, bumblebees, solitary bees and hoverflies. We find that habitat availability alone is no suitable indicator for pollinator richness and density in protected semi-natural habitats across pollinator taxa, with responses varying across study regions and pollinator taxa. In contrast, local habitat quality, benefitted pollinators across taxa and study regions with flowering plant species richness being more universally beneficial than flower cover for species richness and densities across pollinator taxa. An increased cover of cropland had no consistent negative effect on pollinator species richness or densities. In fact, species richness of butterflies and solitary bees and butterfly densities peaked in mixed landscapes with representation of cropland and high habitat availability. In addition, we found no evidence for impoverished and homogenised pollinator communities in landscapes with little habitat availability, indicating that also landscapes with little remaining habitat and small habitat patches should not be neglected in pollinator conservation. Our results indicate that conservation policies for safeguarding pollinators in European cultural landscapes should not solely focus on increasing habitat amount but instead vitalise existing habitats by increasing their quality, even in landscapes with little remaining habitat.

List of abbreviations

EU	**European Union**
SE	**Standard error of the mean**
UK	**United Kingdom of Great Britain and Northern Ireland**

1. Introduction

Pollinator declines threaten wild plant pollination, agricultural production and human wellbeing (Ollerton et al. 2011, Potts et al. 2016, Dicks et al. 2021). Identifying drivers of pollinator decline at local and landscape scales, and suitable indicator taxa is vital for restoring pollinator communities and safeguarding the sustainability of agricultural landscapes and embedded high-value habitats such as Natura 2000 sites.

To date, many different drivers and indicators for pollinator declines have been suggested and identified across different regions and pollinator taxa (Westphal et al. 2008, Vanbergen 2014). Among others, habitat loss caused by land-use change, habitat and landscape management intensity and pesticide exposure have been suggested as the primary drivers of pollinator decline (Potts et al. 2010, Potts et al. 2016, Dicks et al. 2021). These conclusions, however, are primarily based on expert opinions yielded through questionnaires and similar methods or from a review of single case studies performed in a specific context and for a specific selection of pollinator taxa. While the plethora of different drivers reflects the context-dependence of interacting drivers of pollinator declines (Dicks et al. 2021), shaping a common policy for safeguarding pollinators requires a systematic identification and evaluation of indicators that allow a prioritization of over-arching effects. Such a unified assessment of indicators for high pollinator richness and density in a joint, standardised design across a variety of cultural landscapes and addressing key drivers of pollinator loss is, however, lacking.

Policies and initiatives to halt and reverse biodiversity declines are commonly area-based (Carroll and Noss 2022), i.e. they focus on protecting a certain habitat amount within a landscape that is deemed necessary to conserve biodiversity. While thresholds have been proposed for biodiversity (Garibaldi et al. 2021) or pollination service conservation (Eeraerts 2023, Mohamed et al. 2024), these thresholds originated from approximations or local case studies casting doubt on their generalisation ability and applicability across regions. Area-based pollinator conservation concepts build on species-area relationships that have been shown for some pollinator taxa such as butterflies (Krauss et al. 2003, Brückmann et al. 2010) or solitary bees (Steffan-Dewenter 2003, Krauss et al. 2009) in highly fragmented cultural landscapes, albeit not for all. For area-based conservation efforts to safeguard pollinators in the European Union (EU), it is essential to evaluate whether species-area relationships are indeed universal across pollinator taxa and to investigate to what extent species-area relationships are modulated by local habitat quality and surrounding landscape context. Despite their importance, the relative contributions of these potential indicators for pollinator species richness and densities at different spatial scales are surprisingly little studied across pollinator taxa. In a recent local case study, flower cover as a measure for habitat quality indeed turned out to be a more important predictor for pollinator populations than habitat amount (Fijen et al. 2025). Here, we assess for the first time the relative importance of local habitat quality, habitat amount, and landscape-level management intensity indicated by cropland cover across various European cultural landscapes and the four most common and important pollinator taxa, butterflies, bumblebees, solitary bees and hoverflies.

Assuming species-area relationships for pollinator taxa, small habitats and landscapes poor in habitat amount are expected to have comparably poor pollinator richness. Small habitat patches have been found to suffer from ‘ecosystem decay’, i.e. an erosion of individuals and thereby species with decreasing patch area, affecting specialist more than generalist species ultimately leading to the homogenisation of assemblages across habitat patches (Chase et al. 2020, Blowes et al. 2024). Patch sizes are, however, mostly not independent from the overall habitat availability in a landscape and landscapes with smaller habitat patches usually also have a lower total habitat amount. When the overall habitat amount is kept equal, landscapes with more fragmented habitats, in contrast, harbour a higher overall biodiversity, implying a special value of smaller habitats for conservation (Riva and Fahrig 2023). Whether small habitats are a valuable or futile target for pollinator conservation efforts thus is an important question. Assessing the beta diversity between habitats can yield an answer: If pollinator assemblages indeed homogenise across landscapes with decreasing patch / habitat area, we should see an increased turnover and a decreased nestedness between patches with increasing area.

To identify suitable indicators for pollinator decline in protected habitats and to evaluate the presence of pollinator assemblage homogenisation in small habitat patches across four main pollinator taxa, we established a common pollinator monitoring across 323 cultural landscapes in 15 European study regions. In each of the study regions, we sampled pollinator taxa in a focal grassland habitat and investigated the effects of focal habitat area and habitat quality (flower cover and pollinator useable plant species richness) as well as pollinator habitat amount and management intensity (via the cover of cropland) in the surrounding landscapes. We aimed to assess variations in the spatial scale of pollinator species-area relationships across our pan-European dataset. In a second step, we intended to assess additional effects of local habitat quality and surrounding land-use intensity on pollinator diversity in European cultural landscapes to unveil the relative contribution of these indicators to the species richness and density of each pollinator taxon. We expected positive effects of habitat quality on pollinator density and richness in protected grasslands and assumed pollinators to peak in landscapes dominated by cropland (concentration effect) and to reach a low in mixed landscapes with intermediate shares of cropland and non-crop habitats due to dilution. In addition, we assessed whether there was a difference in conservation value of smaller habitat patches and landscapes with lower habitat amount for pollinators by assessing the beta diversity turnover between habitats.

In a separate, more detailed analyses of two of the study regions in Germany we found that while habitat area was an important predictor for bee and butterfly species richness, with strongest effects on endangered species, the availability of local flower resources and nesting sites and landscape characteristics such as small field sizes, a high proportion of organic agriculture and a high connectivity with other grassland habitats enhanced pollinator species richness with responses varying among pollinator taxa (Biegerl et al. 2025). Pollinator assemblages did not benefit from wildflower fields established under agri-environment schemes. This study concluded that improving local habitat quality in combination with targeted landscape management were effective measures to promote pollinator richness in highly fragmented protected grassland habitats. The full text of this publication is attached to this deliverable.

2. Methods

2.1 Study design and site selection

Across 15 agriculturally dominated regions in 12 European countries, spanning from southern Spain to central Romania and from Southeast England to western Estonia, we selected 323 landscapes around a focal semi-natural pollinator habitat. These focal habitats differed across regions due to their location in different climatic and biogeographic zones, ranging from loess (Hungary) and calcareous grasslands (e.g. Germany, France, UK) to steppe fragments (Serbia) and forest grasslands (Spain). Based on the experience of local experts, the selected focal habitat types resembled the main pollinator refuge habitat in these landscapes, with habitats mostly protected under Natura 2000. Within each region, 17 to 30 landscapes (21.5 ± 1.4; average ± SE) were selected along gradients of habitat availability (same pollinator habitat as the focal habitat patch; henceforth ‘habitat amount’) and cropland cover, ranging from < 0.1 % to 93.9 % and 0 % to 89.6 %, respectively, in a radius of 2000 m surrounding the focal habitat patch across all regions (Figure 1 & Table S1). In one region in Serbia, only nine landscapes could be selected. As cropland, we defined all land under recurring soil management. The area of the focal habitats differed across regions, ranging overall between < 0.1 and 75.4 ha (13.9 ± 0.9 ha; average ± SE; for calculation, see below and Table S1).

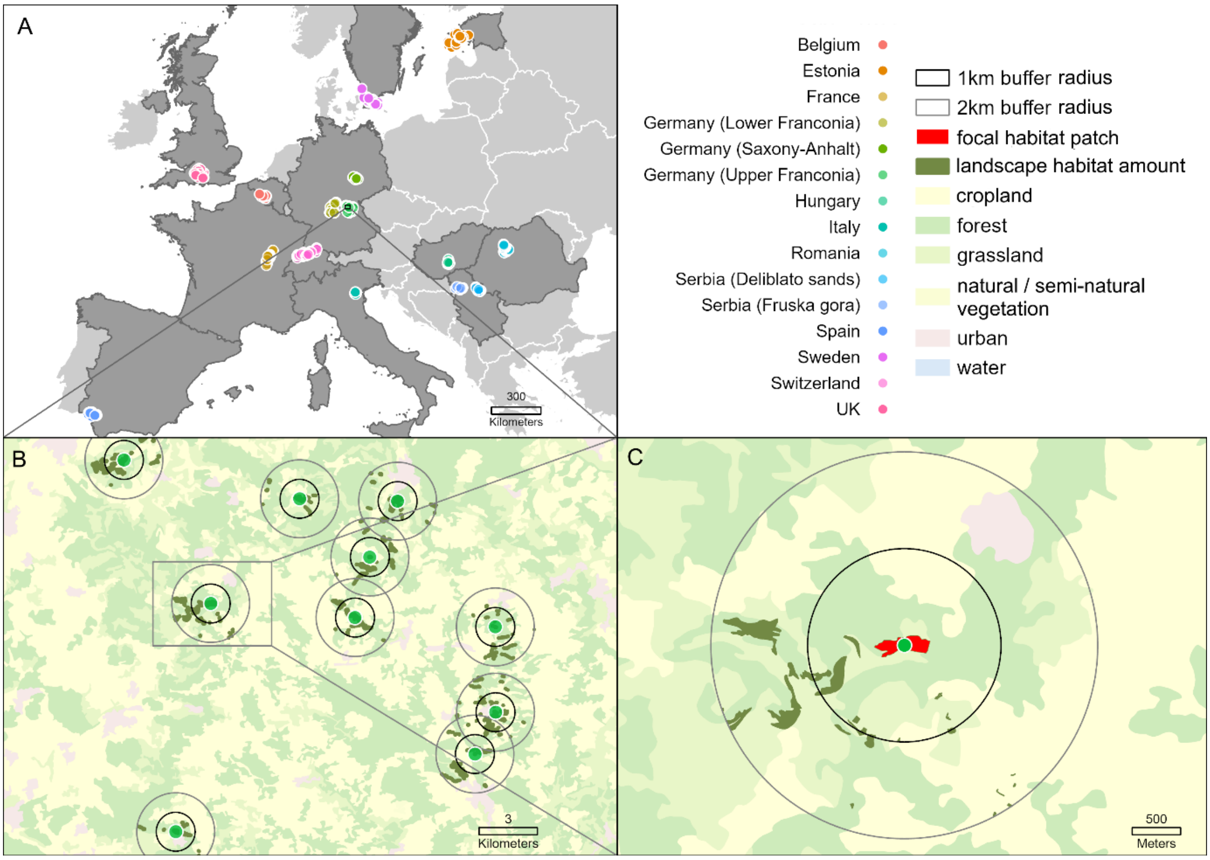

Fig. 1: Map of the 15 study regions spanning the major European agricultural landscapes (A) with participating countries highlighted in dark grey. Panels below show a subset of one of the study regions in Germany (Upper Franconia; B) with a detailed view of one of the landscapes (C) with the focal habitat patch indicated in red, habitat amount in the landscapes indicated in dark green, the 1000m and 2000m buffer radii and coarse land-use classes indicated in pastel colours. Habitat amount was mapped manually, land-use classes displayed in panels (B) and (C) are derived from the 2018 CORINE Land cover layer (Copernicus Land Monitoring Service 2020).

2.2 Geospatial analyses

For each landscape, we mapped the focal habitat patch as well as all habitat patches of the same habitat type and confirmed our mapping by ground truthing in the field. The area of the focal habitat patch was then calculated based on this mapping. In some regions, the focal habitat patches were interconnected with other habitat patches in a continuous network. We thus cut the area of the focal habitat patch at a distance of 1000 m around the centre point of the focal habitat patch, which resulted in a reduction of the focal patch area by on average 10.3 ± 1.3 percent in 25.4 percent of the landscapes. This was necessary to differentiate between 'local' habitat area and habitat amount in the landscape in diverse and strongly connected landscapes. We calculated habitat amount as the total area of the focal habitat type covered within a radius of 1000 m and 2000 m around the centre point of the focal habitat patch (and including the focal habitat patch). Cropland cover was extracted within a radius of 1000 m and 2000 m around the centre point of each focal habitat patch from the global ESA

WorldCover 2021 landcover map with 10 m resolution and a cropland detection accuracy of 82.3 ± 2.1 percent for Europe (Zanaga et al. 2022).

2.3 Pollinator sampling

In each focal habitat patch, we recorded indicators for habitat quality and resource availability as well as pollinator densities and richness across four important pollinator groups differing in their ecology and behaviour, butterflies (Lepidoptera), bumblebees and solitary bees (Hymenoptera, Apiformes) and hoverflies (Diptera, Syrphidae). Butterfly recordings included day active burnet moths (Zygenidae).

Pollinators were sampled in at least three sampling intervals, in some regions in up to six intervals (average ± SE: 3.8 ± 0.2) between 01 March and 29 September 2022. The number and timing of the sampling intervals were decided by local experts based on the geographical location and climate of the region, with regions further to the south sampled earlier then regions located to the north to account for macroclimatic phenology differences (Figure S1). Consulting local experts, the teams independently selected the timing and the number of sampling intervals that was expected necessary for a representative sampling of the local pollinator assemblages. Estimations of the sample completeness across taxa using the R package 'iNEXT.3D' (version 1.0.5, Chao et al. (2021)) confirmed an overall high sample completeness that was comparable across regions in all four taxa (94.8 ± 0.4 percent in butterflies, 83.4 ± 1.6 percent in bumblebees, 71.1 ± 1.1 percent in solitary bees and 80.4 ± 1.2 percent in hoverflies; average ± SE; Figure S2).

Within each interval, the order of sites sampled within each region was randomised and, on each site, we performed two independent variable transect walks without fixed direction. One transect walk was performed to record bees and hoverflies (500 m length; sampling 1 m to each side of the transect; total area covered: 1000 m^2) and the other transect walk to record butterflies (600 m length; sampling 2.5 m to each side of the transect; total area covered: 3000 m^2), with both transect walks taking 30 minutes (speed: 16.7 m / min in the bee transect, 20 m / min in the butterfly transect). Transects varied between intervals and transect walks covered different microhabitats as well as areas presumed beneficial to pollinators, e.g. patches of wildflowers or bare ground. In eight of the 15 regions, the bee transect was a full subset of the butterfly transect in each interval. Transect walks were performed between 9 am and 5 pm with good weather conditions (> 13°C in the sun, wind < 3 bft, no rain) and each site was sampled at least once in the morning, noon and afternoon across the different sampling intervals. Each transect was walked by the same observer and specimens were caught using a sweep net, identified in the field wherever possible and subsequently released. If no identification was possible in the field, specimens were collected for identification in the lab. For all analyses, pollinator species richness was accumulated across sampling intervals while pollinator density was calculated as pollinator individuals observed per sampling interval. For all analyses, the two migratory and ubiquitous butterfly species *Vanessa atalanta* and *Vanessa cardui* were removed. We used the accumulated species richness across all sampling intervals (henceforth 'species richness') and the average number of observed individuals per sampling interval (henceforth 'density') in all analyses.

2.4 Habitat quality assessment

As measures of pollinator related habitat quality, we recorded flower cover and pollinator useable plant species richness along the bee transects during each pollinator sampling interval. Flower cover was estimated based on the number of open flower units and their area in cm^2 and subsequently converted to a percentage of the transect area with flowers. Data for plant species richness and flower cover was not available for the regions in Hungary, Italy and Spain. These regions were hence excluded from all analyses that included flower cover and plant species richness (retaining 253 landscapes in these models). In all analyses, we used accumulated plant species richness and average flower cover across the sampling intervals.

2.5 Statistical analyses

All statistical analyses were performed in R 4.4.1 for Windows (R Development Core Team 2024). Prior to analyses, we checked whether sample completeness was related to focal patch area or habitat amount but found no strong correlations across pollinator taxa (Pearson: | r | < 0.17, average | r | = 0.08 ± 0.02).

In a first step, we assessed the presence of species-area relationships by fitting generalised mixed effects models (GLMMs; package 'glmmTMB', version 1.1.10 (Brooks et al. 2017)) for the species richness of the four pollinator taxa across all regions (323 landscapes) containing an interaction between 'habitat availability' (continuous, log-transformed) and 'study region' (factor, 15 levels) as fixed effect and a random intercept on 'study region'. These models allowed slopes of species-area relationships to differ across study regions. Separate models were fitted for the different predictors used for habitat availability: (i) focal patch area, (ii) habitat amount at the 1000 m scale and (iii) habitat amount at the 2000 m scale. In addition, we accounted for varying dispersion across the study regions by adding study region as a dispersion parameter to these models.

In a second step, we fitted separate models for the species richness and density of the four pollinator taxa for the regions where habitat quality data was available (253 landscapes). These models contained 'flower cover' (continuous), 'plant species richness' (continuous), 'habitat availability' (continuous, log-transformed; three different alternatives; see above), and 'cropland cover' (continuous) as well as an interaction between 'habitat availability' and 'cropland cover'. To account for variation in effects between study regions, these models contained random slopes for all continuous predictors and a random intercept on 'study region' allowing slopes for the predictors to vary across study regions. All models mentioned above were fitted using a Gamma distribution with log-link (butterflies) or a Gamma hurdle model with log-link (bumblebees, solitary bees and hoverflies).

To investigate biotic homogenisation of pollinator assemblages, we calculated the average abundance-weighted turnover and nestedness (Bray-Curtis) between any one of the focal habitat patches and all other focal habitat patches within each region (package 'betapart', version 1.6, Baselga and Orme (2012)). As beta diversity can only be calculated for pollinator taxa shared between sites, sites that had no observations for any of the four pollinator groups had to be excluded in these analyses (no sites in butterflies, 27 sites in bumblebees, six sites in solitary bees and nine sites in hoverflies). For each taxon, we fitted three GLMMs containing the average turnover or the average nestedness as response and the interaction between 'study region' (factor, 15 levels) and each measure for 'habitat availability' (continuous, log-transformed; three different alternatives; see above). These models were fitted using a Gamma distribution with log-link.

In all models, all continuous predictors were centred at their average and scaled to multiples of their standard deviation (z-scaling) prior to model fitting. Model fits were inspected visually and using various diagnostic tests with the package DHARMa (version 0.4.7 (Hartig 2022)). Model outputs were obtained using type III sums of squares Wald chi-square tests with the command 'Anova' (library 'car', version 3.0-12 (Fox and Weisberg 2019)).

3. Results

Across all regions, we observed 69622 butterflies (167 species), 8769 bumblebees (29 species), 13900 solitary bees (500 species) and 7385 hoverflies (169 species). The absolute number of pollinator observations and the pollinator individuals observed per visit in each landscape varied considerably both across regions and between taxa (Figure 2). Across regions, on average 56.8 ± 2.3 butterflies, 6.7 ± 0.7 bumblebees, 12.7 ± 0.5 solitary bees and 7.6 ± 0.4 hoverflies were observed in each visit (Figure 2). Butterflies dominated pollinator assemblages with on average 62.8 ± 1.0 percent of all observed individuals in all regions except Italy and Spain where solitary bees were the most observed taxon (Figure 2).

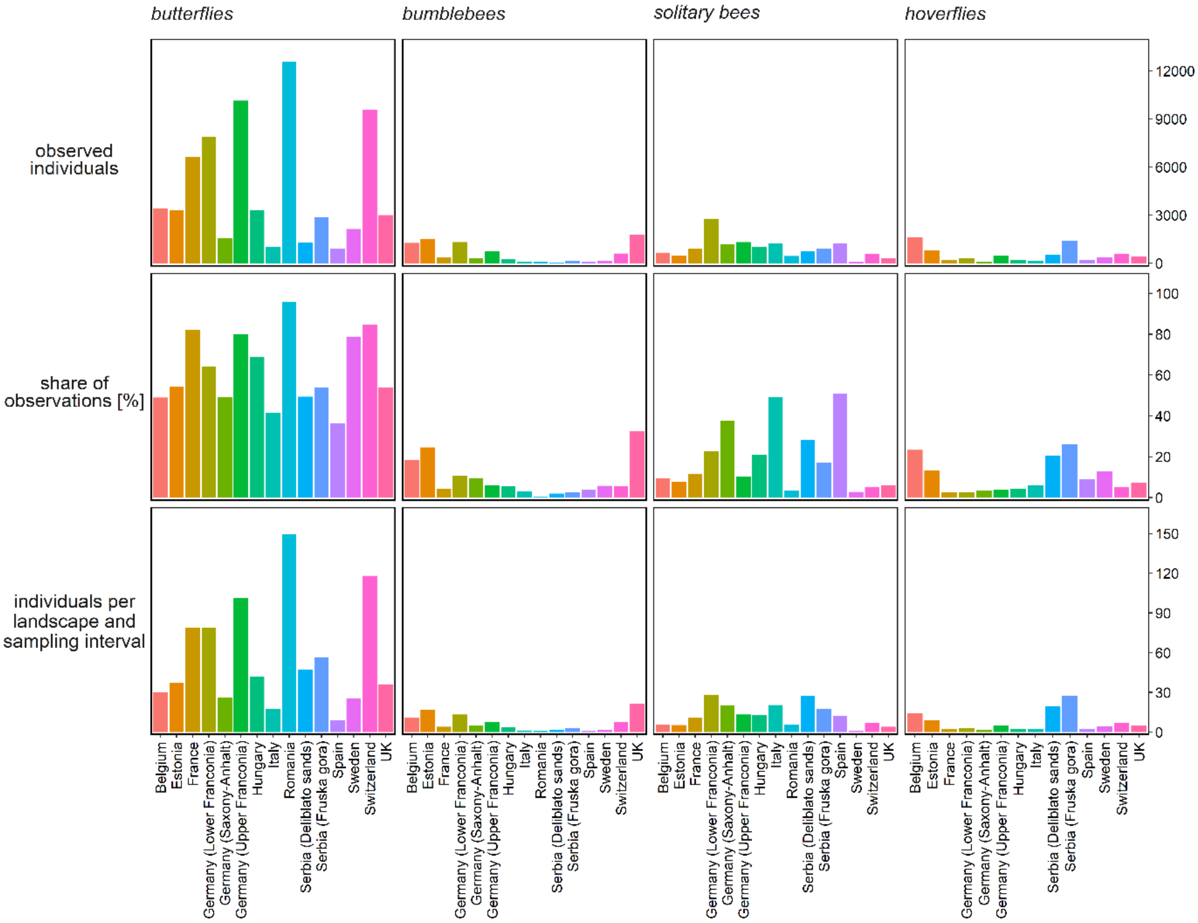

Fig. 2: Visualization of the observed individuals in the 15 regions and across the four pollinator taxa as well as the share of observations belonging to one pollinator taxon and the average number of individuals observed in a landscape per sampling interval.

3.1 Species-area relationships

We aimed to evaluate whether species-area relationships of pollinators are (i) present across European cultural landscapes and (ii) whether and how they are affected by habitat availability or management intensity in these regions. We, however, only detected positive species-area relationships for butterflies in Germany (Lower Franconia) and Sweden and for solitary bees in Sweden (Figure 3). Most of the detected significant relationships between species richness of the investigated pollinator taxa and focal patch area or habitat amount were, in fact, negative, as were all the significant predictions across countries (Figure 3). This absence of classical species-area relationships made a comparison of slopes across regions unfeasible.

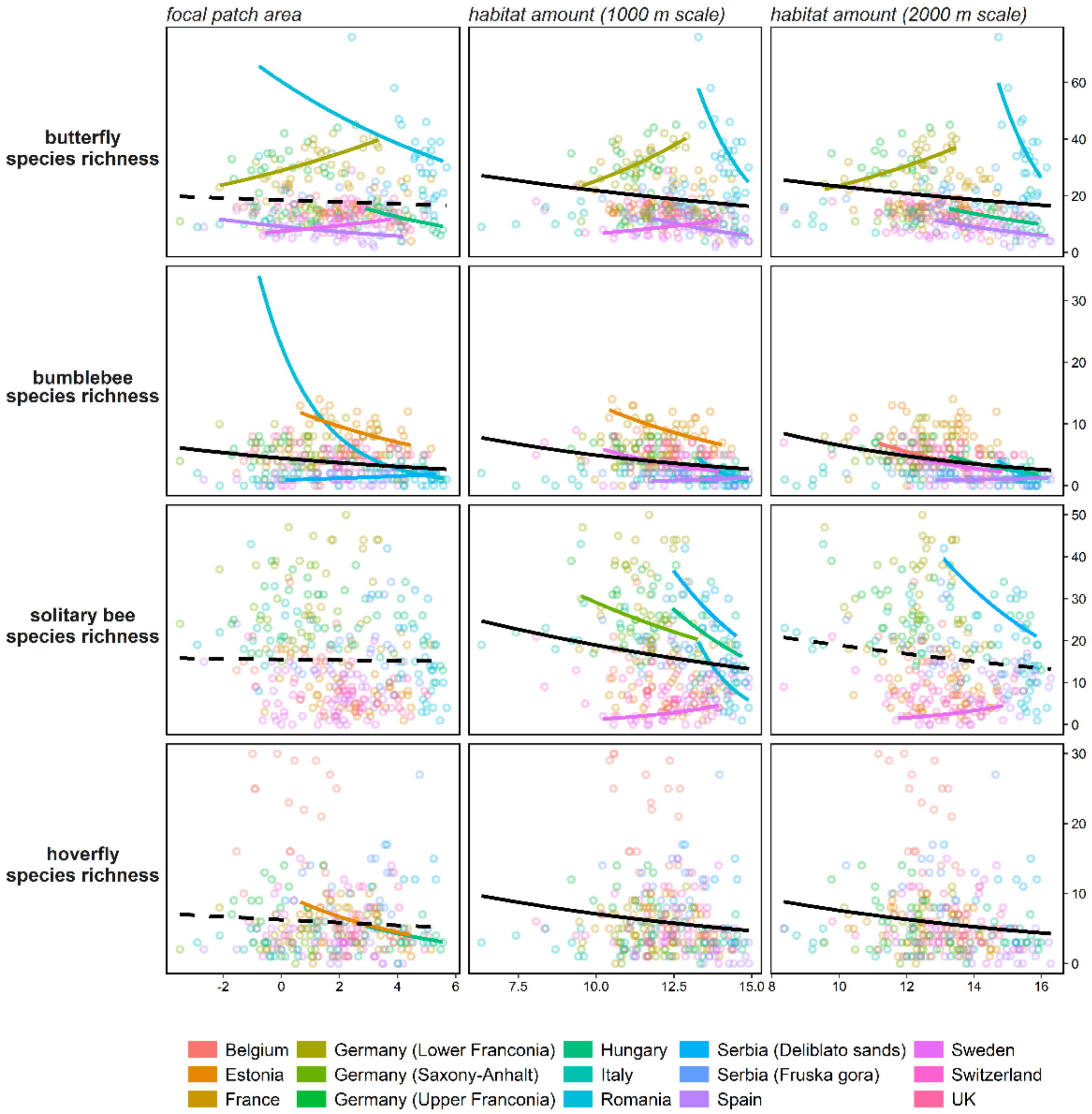

Fig. 3: The relationship between the observed species richness of butterflies, bumblebees, solitary bees and hoverflies and focal patch area and habitat amount at the 1000 m and 2000 m scales (log-transformed). Solid black lines indicate overall significant relationships, dashed black lines non-significant relationships. Solid, coloured lines indicate significant relationships in the respective regions. Lines are model predictions (estimated marginal means).

3.2 Effects of habitat quality

In the models including both local and landscape predictors, we found local plant species richness to be the most important predictor of pollinator species richness across groups and spatial scales. Plant species richness was positively related to the species richness of butterflies and solitary bees, increasing butterfly species richness by 0.9 percent and solitary bee species richness by 1.6 to 1.7 percent across models for each plant species added (Figure 4). Plant species richness was further marginally positively related to the species richness of bumblebees and hoverflies (Figure 4). Solitary bee species richness increased by 4.1 percent per 10 percent increase in flower cover and bumblebee species richness decreased by 2.5 and 0.8 percent with a 10 hectare increase of habitat amount at the 1000 m and 2000 m landscape scales while hoverfly species richness decreased by 1.8 and 0.7 percent, respectively (Figure 4). Cropland cover was marginally negatively related to the species richness of butterflies (Figure 4).

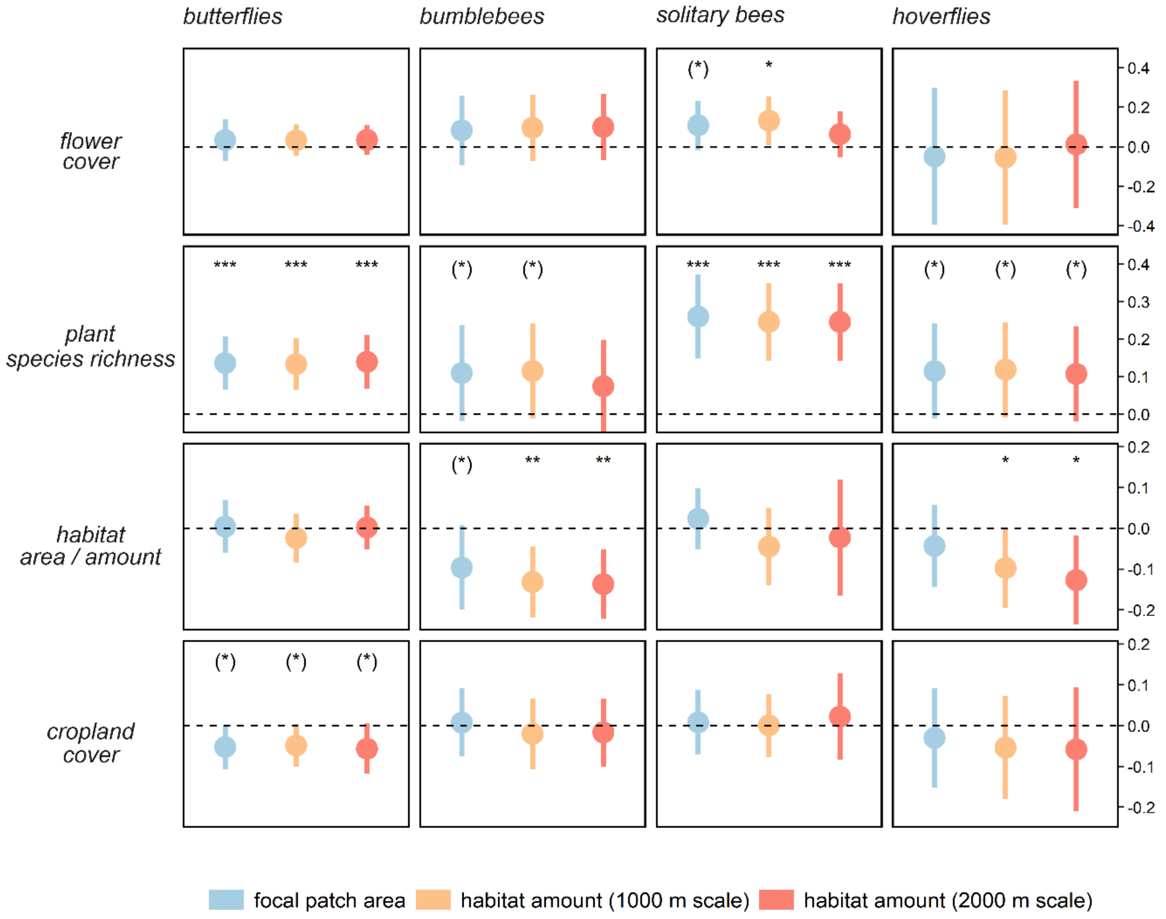

Fig. 4: Standardised model coefficients for the effects of flower cover, plant species richness, habitat area or amount and cropland cover on the observed species richness of pollinator taxa obtained from generalized mixed effects models. Separate models fitted for of butterflies, bumblebees, solitary bees and hoverflies and for different measures of habitat availability (focal patch area and habitat amount at the 1000 m and 2000 m scales). Coefficients with 95% confidence intervals, scaled to multiples of one standard deviation of the response. (*) indicates p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001.

Concerning pollinator densities, plant species richness emerged as the most important predictor across groups and spatial scales. Plant species richness was positively related to the densities of all pollinator taxa at least one of the spatial scales investigated (Figure 5). For each additional plant species, the butterfly density increased by 1.3 to 1.5 percent, bumblebee density increased by 1.3 percent, solitary bee density increased by 1.6 to 1.7 percent and hoverfly density increased by 1.2 percent across models (Figure 5). Per 10 percent increase in flower cover, bumblebee density increased by 22.9 to 30.7 percent and solitary bee density increased by 6.5 to 6.7 percent across models (Figure 5). Bumblebee density decreased by 5.3 and 1.6 percent with a 10 hectare increase of habitat amount at the 1000 m and 2000 m landscape scales (Figure 5). Cropland cover had no significant effects on the densities of any of the pollinator taxa at any of the spatial scales (Figure 5).

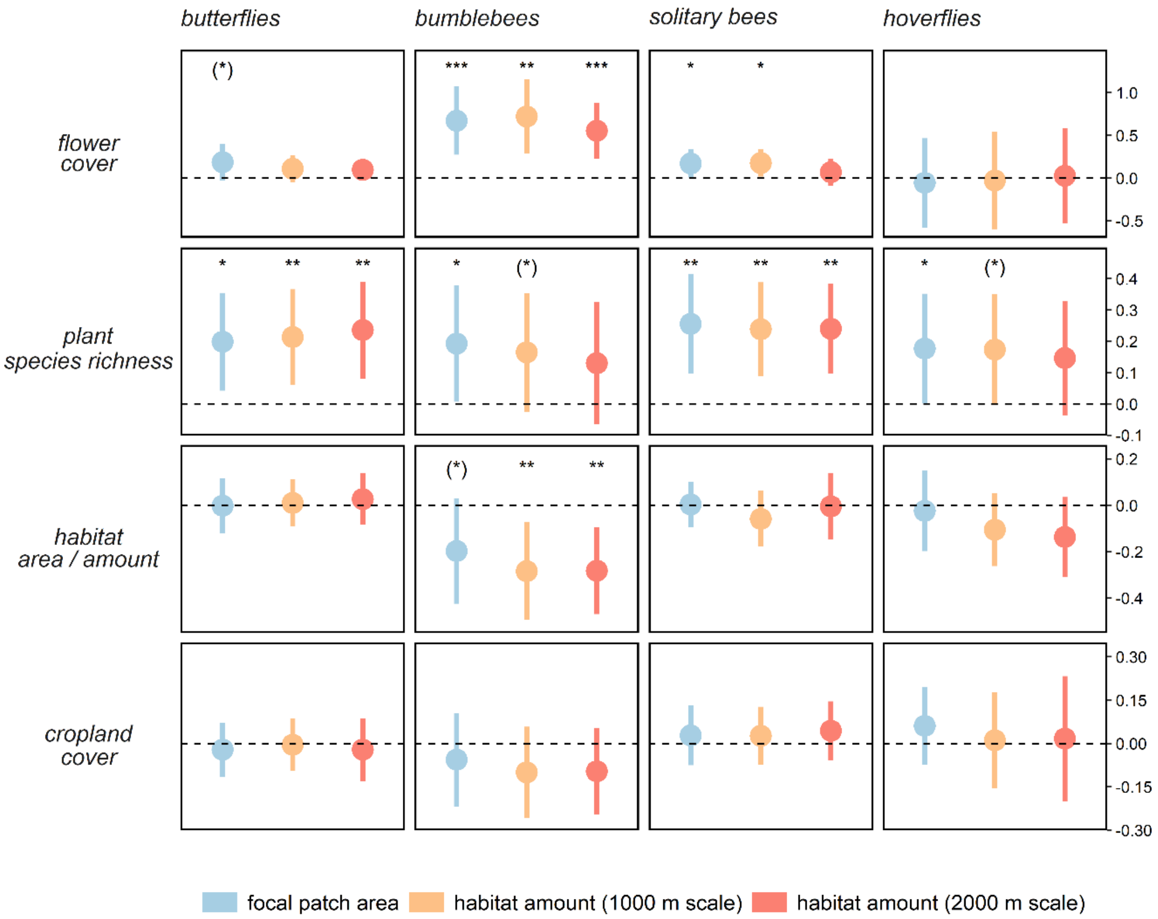

Fig. 5: Standardised model coefficients for the effects of flower cover, plant species richness, habitat area or amount and cropland cover on the observed density of pollinator taxa obtained from generalized mixed effects models. Separate models fitted for of butterflies, bumblebees, solitary bees and hoverflies and for different measures of habitat availability (focal patch area and habitat amount at the 1000 m and 2000 m scales). Coefficients with 95% confidence intervals, scaled to multiples of one standard deviation of the response. (*) indicates $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.3 Interactions between habitat and cropland cover

We detected significant interactive effects between habitat and cropland cover only in butterflies (species richness and density) and solitary bees (species richness). Species richness peaked in landscapes dominated by cropland with intermediate availability of remaining habitat and, in butterfly richness also in landscapes with both little cropland cover and little remaining habitat (Figure 6 A & B). Similarly, butterfly density was highest in landscapes dominated by cropland with intermediate remaining habitat availability (Figure 6 C).

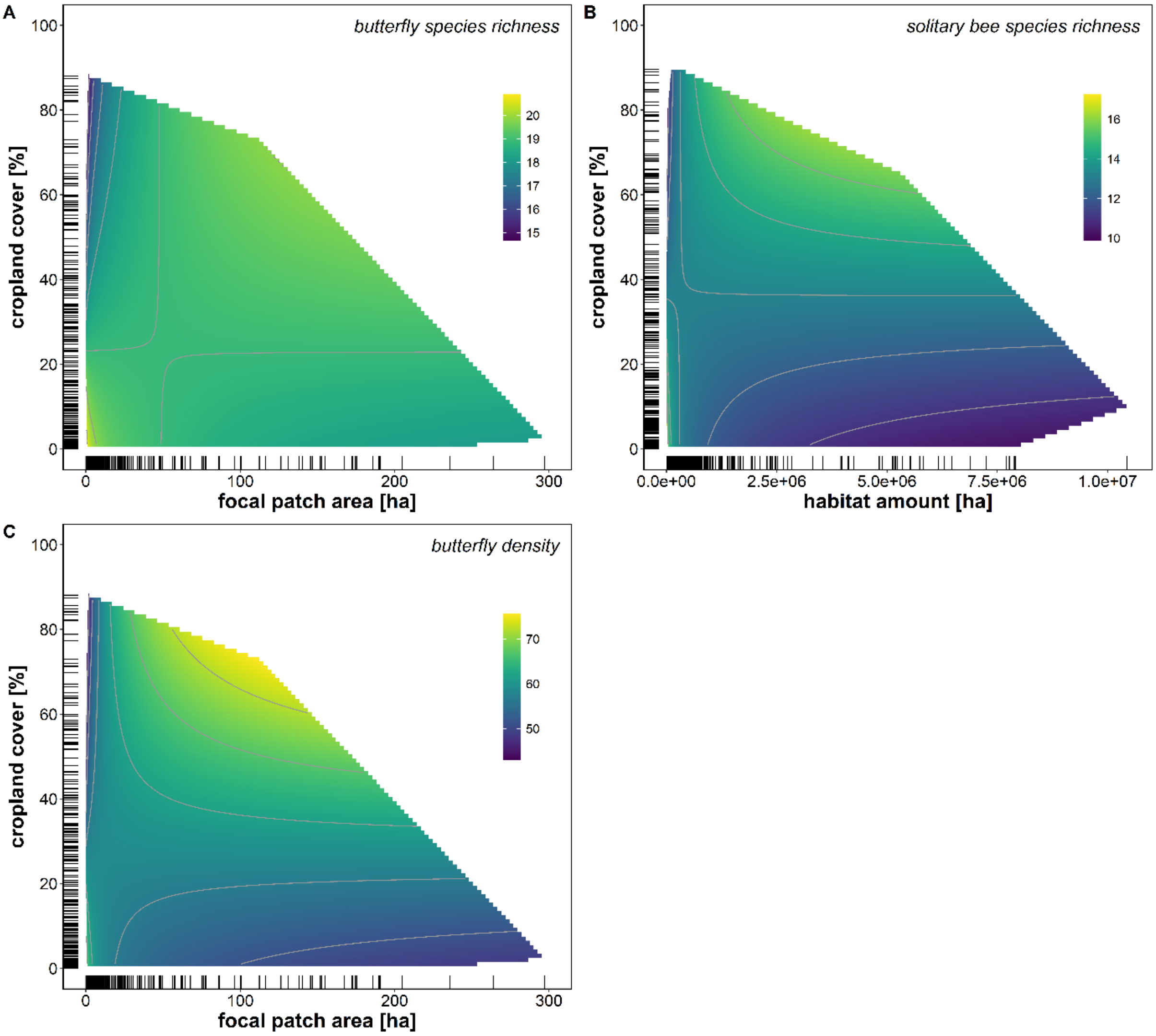

Fig. 6: Significant ($p < 0.05$) interactions between habitat area or amount and cropland cover for (A) butterfly species richness, (B) solitary bee species richness and (C) butterfly density. Coloured areas resemble model predictions (estimated marginal means) of the responses, the rugs along the axes indicate the location of data points used for the model fits.

3.4 Pollinator assemblage homogenisation in impoverished landscapes?

Across all landscapes and pollinator taxa, turnover was contributing more to beta diversity than nestedness, ranging from turnover being on average 44 percent higher than nestedness in bumblebees to turnover being on average 574 percent higher than nestedness in solitary bees. If the loss of habitat area or amount leads to a homogenisation of pollinator assemblages, we expected to find an increased turnover and a decreased nestedness between patches with increasing habitat area or amount, as assemblages in smaller patches should be more similar to those in each other patch. We did not detect clear evidence for homogenisation in any of the taxa, as turnover and nestedness remained largely constant with increasing focal patch area or habitat amount in all taxa. In contrast, we found a decreasing turnover with increasing habitat amount at the 2000 m scale in butterflies and an increasing nestedness with increasing habitat amount at the landscape scale in hoverflies (Figure 7). Only bumblebee turnover increased with increasing focal patch area (Figure 7).

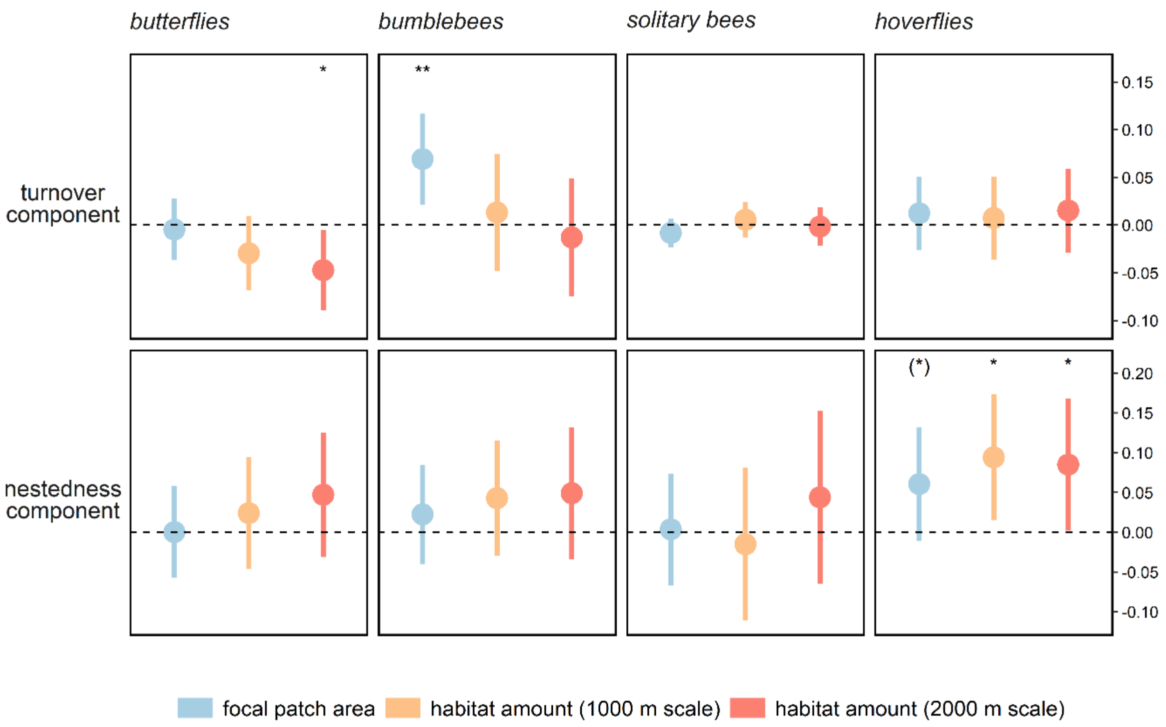

Fig. 7: Standardised model coefficients for the averaged turnover (top) and nestedness (bottom) components of the beta diversity (Bray-Curtis dissimilarity) of butterflies, bumblebees, solitary bees and hoverflies in relation to focal patch area and habitat amount at the 1000 m and 2000 m scales. Coefficients with 95% confidence intervals, scaled to multiples of one standard deviation of the response. (*) indicates $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

In contrast to previous assumptions, our analyses show that habitat area or amount cannot be used as a simple indicator for safeguarding pollinator diversity and populations in protected habitats across European cultural landscapes. We identified local habitat quality and especially pollinator useable plant species richness as better indicator for pollinator species richness and densities than focal habitat area, landscape habitat amount or landscape-level management intensity indicated by cropland cover. In hoverflies, however, species richness and density were affected less by the predictors tested than the remaining pollinator taxa revealing their limited useability as indicators for overall pollinator diversity. In addition, we found no clear indication that smaller habitat patches suffered from biotic homogenisation in any of the four pollinator taxa, indicating a high value of small patches even in landscapes with little remaining habitat for pollinator conservation.

4.1 Species-area relationships and their interaction with landscape management intensity

Species-area relationships originate in the theory of island biogeography where species richness on real islands increases, among others, with island area (MacArthur and Wilson 1967, Rosenzweig 1995, Turner and Tjørve 2005). In terrestrial ecosystems, species-area relationships are expected when habitats act as ‘islands’ embedded in a landscape matrix hostile to a taxon. Such relationships have been demonstrated repeatedly for terrestrial taxa in case studies (Drakare et al. 2006), among others also for several pollinator taxa, including butterflies (Krauss et al. 2003, Brückmann et al. 2010) and solitary bees (Steffan-Dewenter 2003, Krauss et al. 2009). In our assessment, however, species area-relationships were largely absent, and the classical relation was only found for butterflies and solitary bees in two of the fifteen study regions. In contrast, the overwhelming majority of relationships detected between species richness of the four pollinator taxa and focal patch area or landscape-scale habitat amount both across all study regions and within study regions were negative. This indicates that habitat availability, i.e. the habitat area or landscape-scale habitat amount, are per se not good indicators for the conservation of pollinator species richness in cultural landscapes.

While the absence of species-area relationships is remarkable, we see several plausible explanations. The detectability of species-area relationships for pollinators will likely be determined by region-dependent environmental drivers and vary with the concrete study context.

First, different pollinator taxa have different levels of habitat specialisation. These can vary both between pollinator taxa as well as within a pollinator taxon when assemblage composition changes with geographic context as traits are species-specific. For example, most butterflies are closely linked to their larval food plants which are usually more strictly bound to remaining semi-natural habitat fragments and solitary bees are closely linked to nesting habitats which can be a subset of all semi-natural habitat fragments or also include other habitat structures such as field margins or farm roads (Antoine and Forrest 2021, Tschanz et al. 2024). In contrast, many hoverfly species will be more bound to aphid resources as larval food or waterbodies and could thus be expected to be less strictly bound to semi-natural habitat cover (Meyer et al. 2009). Habitat specialization is, however, not sufficiently known across European pollinator species and may vary within the same species across geographic and climatic regions within Europe. Within a local context, the community weighted mean habitat specialisation degree of the species present in the assemblage will determine whether a species-area relationship is detected. This species composition, however, may also depend on the geographic and land-use context where communities are assessed. Not all species are distributed equally, and, in some communities, specialised species might be underrepresented due to the local potential species pool which could lead to obscured or absent species-area relationships in taxa where they would otherwise be expected.

Second, species-area relationships may be obscured when gradients of habitat area or amount do not have sufficient coverage, i.e. when the lowest habitat area or amount is already sufficient to accommodate the entire potential regional species pool, or in other words, when additional habitat area or amount cannot have any significant additional benefits. We believe that this can be ruled out for our study as we cover large gradients of habitat availability, starting at below 0.1 ha focal patch size and 0.02 percent habitat amount at the landscape-scale, which is low compared to other studies.

Third, species-area relationships could vary across study regions driven by the local land-use and management context. While the focal habitat used for assessing species-area relationships may resemble the only true habitat available for pollinators in intensively managed and structurally poor landscapes, it may only be a subset of suitable habitat or land-use types in extensively managed and complex landscapes, where field margins, road verges and similar habitats or even crop fields under biodiversity friendly management can complement the habitat for a share of the studied pollinator species (Tschanz et al. 2023, Tschanz et al. 2024). The assessment of ‘habitat’ may thus underestimate the true habitat available for pollinators in such structurally rich landscapes with extensive, biodiversity friendly management. As this is likely related to overall management intensity of the landscape, the effects of cropland cover may similarly be modulated by the management intensity of cropland in the respective regional context.

Lastly, species-area relationships may be obscured when the completeness of the pollinator sample is systematically linked to habitat area or amount, i.e. if the same, standardised sampling effort yielded a decreasing sample completeness / share of the real community with increasing habitat area or amount. In our data, we found no indication for such a systematic bias in sample completeness (Figure S3) and we thus believe that the absence of species-area relationships is not caused by differences in sample completeness.

Based on our results, habitat area or amount is not suitable as a general indicator for pollinator biodiversity in protected habitats and cultural landscapes in Europe.

4.2 The importance of habitat quality

Informing models with additional, potential indicators for pollinator species richness or density modulated previous effects found for habitat availability. Only negative effects of habitat amount on the landscape scale remained on the species richness and density of bumblebees and the species richness of hoverflies. In butterflies and solitary bees, habitat availability instead interacted with landscape-level cropland cover with species richness and density of butterflies and species richness of solitary bees peaking in complex landscapes with high covers of both cropland and habitat.

Habitat quality was overall a more reliable predictor for pollinator species richness and density across pollinator taxa. Increasing flower cover was positively related with solitary bee richness, solitary bee density and bumblebee density and increasing plant species richness was positively related with the species richness of butterflies and solitary bees and with the density of all four pollinator taxa. Our results are in line with a recent case study from Italy, in which habitat quality similarly arose as most important driver of pollinator species richness and density, outclassing habitat amount (Fijen et al. 2025). Increasing flower cover is directly linked to pollinator resource availability and a high flower cover can lead to local accumulations of mobile pollinators from the surrounding landscape (Holzschuh et al. 2016) and help nurture and thus sustain larger pollinator populations on the landscape scale (Kleijn et al. 2018). A higher plant species richness has been found to be positively related with butterfly species richness (Kitahara et al. 2008) and solitary bee species richness and density (Ebeling et al. 2008) and a recent meta-analysis confirmed positive effects across various pollinator taxa

(Kral-O’Brien et al. 2021). Pollinators can move throughout the landscape following floral resource availability, turning towards semi-natural habitats when floral resources elsewhere are sparse (Cole et al. 2017). As plant species differ in flowering phenology and floral traits, a high plant species richness ensures both resource availability for a wide range of pollinator species and a high level of continuity of flower resource availability across the season (Sponsler et al. 2023). The potential of increasing flower resource continuity to foster pollinator populations has been demonstrated previously (Hemberger et al. 2023).

While positive effects of habitat quality and especially plant species richness on pollinators are all but surprising, they are to date insufficiently utilised for pollinator conservation. In addition to establishing new pollinator habitat under agri-environment schemes which always comes at a cost of area (Boetzl et al. 2021), conservation policies should prioritise vitalising existing habitat and ensuring the necessary and optimal habitat management to ensure a high and consistent flower cover, a species rich plant community and pollinator nesting sites (Hopfenmüller et al. 2020).

4.3 No evidence for pollinator assemblage homogenisation

Recent analyses have indicated that small habitat patches may host homogenised species assemblages implying landscapes with little remaining habitat may host impoverished pollinator communities (Chase et al. 2020, Blowes et al. 2024). If pollinator assemblages in landscapes with little remaining habitat are homogenised and impoverished, they should increasingly be a subset of those in landscapes with more remaining habitat. We tested whether the average turnover between the pollinator assemblages of each pollinator taxon indeed increased (and the average nestedness simultaneously decreased) with increasing habitat availability in the landscapes. Apart from bumblebees where the average turnover indeed increased with increasing focal patch area, we found no evidence for homogenised pollinator assemblages in landscapes with little remaining habitat. This indicates that also small habitats in simplified landscapes can harbour significant and unique biodiversity and contribute to regional species pools which is also in line with the general absence of species-area relationships across cultural landscapes in Europe (see above). Using an approach where absolute habitat availability is standardised, Riva and Fahrig (2023) demonstrated that smaller habitat patches, i.e. a higher degree of fragmentation can actually boost overall biodiversity. If this was the case for pollinators, we should have observed a decreasing average turnover between pollinator assemblages with increasing habitat availability, which we only observed for butterflies at the 2000 m spatial scale. Fragmentation is, however, usually accompanied by habitat loss and landscapes with smaller habitat patches usually also have a lower total habitat amount. Beneficial effects of a higher fragmentation would only be expected at constant habitat availability and would thus not be visible in our study design. Our results nevertheless indicate that pollinator assemblages in small habitat patches and landscapes with little remaining habitat do not necessarily suffer from biotic homogenisation which implies that also landscapes with little remaining habitat and small patches are good targets for pollinator conservation.

4.4 Implications for pollinator conservation in European cultural landscapes

Pollinator conservation policies are commonly focussing on protecting remaining semi-natural habitats or establishing new pollinator habitat. While we believe protecting pollinator habitat is important, we find little evidence that remaining pollinators suffer from a lack of habitat availability across European cultural landscapes although we assume that past pollinator decline was driven to a large extent by habitat loss and land use intensification. Instead, we show that improving habitat quality in terms of increased flower cover but especially also in terms of plant species richness holds great potential for fostering pollinator species richness and densities across pollinators taxa. As we, in addition, also do not find evidence for negative effects in cropland-dominated landscapes or for a homogenisation of pollinator communities in landscapes with little remaining habitat, small habitat fragments in cropland dominated landscapes should be included in policies for safeguarding pollinators. Pollinator conservation policies should thus focus on improving habitat quality and biodiversity friendly management in all available habitats, irrespective of size and landscape context.

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6. References

Antoine, C. M., and J. R. K. Forrest. 2021. Nesting habitat of ground-nesting bees: a review. Ecological Entomology **46**:143-159.

Baselga, A., and C. D. L. Orme. 2012. betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution **3**:808-812.

Biegerl, C., A. Holzschuh, B. Tanner, D. Sponsler, J. Krauss, J. Zhang, and I. Steffan-Dewenter. 2025. Landscape management can foster pollinator richness in fragmented high-value habitats. Proceedings of the Royal Society B: Biological Sciences **292**:20242686.

Blowes, S. A., B. McGill, V. Brambilla, C. F. Y. Chow, T. Engel, A. Fontrodona-Eslava, I. S. Martins, D. McGlinn, F. Moyes, A. Sagouis, H. Shimadzu, R. van Klink, W.-B. Xu, N. J. Gotelli, A. Magurran, M. Dornelas, and J. M. Chase. 2024. Synthesis reveals approximately balanced biotic differentiation and homogenization. Science Advances **10**:eadj9395.

Boetzl, F. A., J. Krauss, J. Heinze, H. Hoffmann, J. Juffa, S. König, E. Krimmer, M. Prante, E. A. Martin, A. Holzschuh, and I. Steffan-Dewenter. 2021. A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. Proceedings of the National Academy of Sciences **118**:e2016038118.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. Modeling zero-inflated count data with glmmTMB. bioRxiv:132753.

Brückmann, S. V., J. Krauss, and I. Steffan-Dewenter. 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology **47**:799-809.

Carroll, C., and R. F. Noss. 2022. How percentage-protected targets can support positive biodiversity outcomes. Conservation Biology **36**:e13869.

Chao, A., P. A. Henderson, C.-H. Chiu, F. Moyes, K.-H. Hu, M. Dornelas, and A. E. Magurran. 2021. Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. Methods in Ecology and Evolution **12**:1926-1940.

Chase, J. M., S. A. Blowes, T. M. Knight, K. Gerstner, and F. May. 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature **584**:238-243.

Cole, L. J., S. Brocklehurst, D. Robertson, W. Harrison, and D. I. McCracken. 2017. Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. Agriculture, Ecosystems & Environment **246**:157-167.

Copernicus Land Monitoring Service. 2020. CORINE Land Cover 2018 (raster 100 m), Europe, 6-yearly, May 2020. European Environment Agency.

Dicks, L. V., T. D. Breeze, H. T. Ngo, D. Senapathi, J. An, M. A. Aizen, P. Basu, D. Buchori, L. Galetto, L. A. Garibaldi, B. Gemmill-Herren, B. G. Howlett, V. L. Imperatriz-Fonseca, S. D. Johnson, A. Kovács-Hostyánszki, Y. J. Kwon, H. M. G. Lattorff, T. Lungharwo, C. L. Seymour, A. J. Vanbergen, and S. G. Potts. 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. Nature Ecology & Evolution **5**:1453-1461.

Drakare, S., J. J. Lennon, and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species–area relationships. Ecology Letters **9**:215-227.

Ebeling, A., A.-M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos **117**:1808-1815.

Eeraerts, M. 2023. A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. Biological Conservation **278**:109887.

Fijen, T. P. M., G. A. Bishop, C. Ganuza, J. Scheper, and D. Kleijn. 2025. Analyzing the relative importance of habitat quantity and quality for boosting pollinator populations in agricultural landscapes. Conservation Biology **39**:e14317.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. Third Edition edition. Sage, Thousand Oaks CA.

Garibaldi, L. A., F. J. Oddi, F. E. Miguez, I. Bartomeus, M. C. Orr, E. G. Jobbágy, C. Kremen, L. A. Schulte, A. C. Hughes, C. Bagnato, G. Abramson, P. Bridgewater, D. G. Carella, S. Díaz, L. V. Dicks, E. C. Ellis, M. Goldenberg, C. A. Huaylla, M. Kuperman, H. Locke, Z. Mehrabi, F. Santibañez, and C.-D. Zhu. 2021. Working landscapes need at least 20% native habitat. Conservation Letters **14**:e12773.

Hartig, F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hemberger, J., O. M. Bernauer, H. R. Gaines-Day, and C. Gratton. 2023. Landscape-scale floral resource discontinuity decreases bumble bee occurrence and alters community composition. Ecological Applications **33**:e2907.

Holzschuh, A., M. Dainese, J. P. González-Varo, S. Mudri-Stojnić, V. Riedinger, M. Rundlöf, J. Scheper, J. B. Wickens, V. J. Wickens, R. Bommarco, D. Kleijn, S. G. Potts, S. P. M. Roberts, H. G. Smith, M. Vilà, A. Vujić, and I. Steffan-Dewenter. 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecology Letters **19**:1228-1236.

Hopfenmüller, S., A. Holzschuh, and I. Steffan-Dewenter. 2020. Effects of grazing intensity, habitat area and connectivity on snail-shell nesting bees. Biological Conservation **242**:108406.

Kitahara, M., M. Yumoto, and T. Kobayashi. 2008. Relationship of butterfly diversity with nectar plant species richness in and around the Aokigahara primary woodland of Mount Fuji, central Japan. Biodiversity and Conservation **17**:2713-2734.

Kleijn, D., T. E. W. Linders, A. Stip, J. C. Biesmeijer, F. L. Wäckers, and T. Bukovinszky. 2018. Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. Methods in Ecology and Evolution **9**:1727-1738.

Kral-O’Brien, K. C., P. L. O’Brien, T. J. Hovick, and J. P. Harmon. 2021. Meta-analysis: Higher Plant Richness Supports Higher Pollinator Richness Across Many Land Use Types. Annals of the Entomological Society of America **114**:267-275.

Krauss, J., T. Alfert, and I. Steffan-Dewenter. 2009. Habitat area but not habitat age determines wild bee richness in limestone quarries. Journal of Applied Ecology **46**:194-202.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography **30**:889-900.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, New Jersey.

Meyer, B., F. Jauker, and I. Steffan-Dewenter. 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic and Applied Ecology **10**:178-186.

Mohamed, A., F. DeClerck, P. H. Verburg, D. Obura, J. F. Abrams, N. Zafra-Calvo, J. Rocha, N. Estrada-Carmona, A. Fremier, S. K. Jones, I. C. Meier, and B. Stewart-Koster. 2024. Securing Nature's Contributions to People requires at least 20%–25% (semi-)natural habitat in human-modified landscapes. One Earth **7**:59-71.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos **120**:321-326.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25**:345-353.

Potts, S. G., V. Imperatriz-Fonseca, H. T. Ngo, M. A. Aizen, J. C. Biesmeijer, T. D. Breeze, L. V. Dicks, L. A. Garibaldi, R. Hill, J. Settele, and A. J. Vanbergen. 2016. Safeguarding pollinators and their values to human well-being. Nature **540**:220-229.

R Development Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riva, F., and L. Fahrig. 2023. Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. Ecology Letters **26**:268-277.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Sponsler, D., A. Iverson, and I. Steffan-Dewenter. 2023. Pollinator competition and the structure of floral resources. Ecography **2023**:e06651.

Steffan-Dewenter, I. 2003. Importance of Habitat Area and Landscape Context for Species Richness of Bees and Wasps in Fragmented Orchard Meadows. Conservation Biology **17**:1036-1044.

Tschanz, P., S. Vogel, A. Walter, T. Keller, and M. Albrecht. 2023. Nesting of ground-nesting bees in arable fields is not associated with tillage system per se, but with distance to field edge, crop cover, soil and landscape context. Journal of Applied Ecology **60**:158-169.

Tschanz, P., A. Walter, T. Keller, and M. Albrecht. 2024. A review of soil tillage impacts on ground-nesting wild bees – mechanisms, implications, and future research perspectives. Agriculture, Ecosystems & Environment **375**:109224.

Turner, W. R., and E. Tjørve. 2005. Scale-dependence in species-area relationships. Ecography **28**:721-730.

Vanbergen, A. J. 2014. Landscape alteration and habitat modification: impacts on plant–pollinator systems. Current Opinion in Insect Science **5**:44-49.

Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morison, T. Petanidou, S. G. Potts, S. P. M. Roberts, H. Szentgyörgyi, T. Tscheulin, B. E. Vaissière, M. Woyciechowski, J. C. Biesmeijer, W. E. Kunin, J. Settele, and I. Steffan-Dewenter. 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecological Monographs **78**:653-671.

Zanaga, D., R. Van De Kerchove, D. Daems, W. De Keersmaecker, C. Brockmann, G. Kirches, J. Wevers, O. Cartus, M. Santoro, S. Fritz, M. Lesiv, M. Herold, N.-E. Tsendbazar, P. Xu, F. Ramoino, and O. Arino. 2022. ESA WorldCover 10 m 2021 v200 (Version v200) [Data set]. Zenodo.

7. Supplementary materials

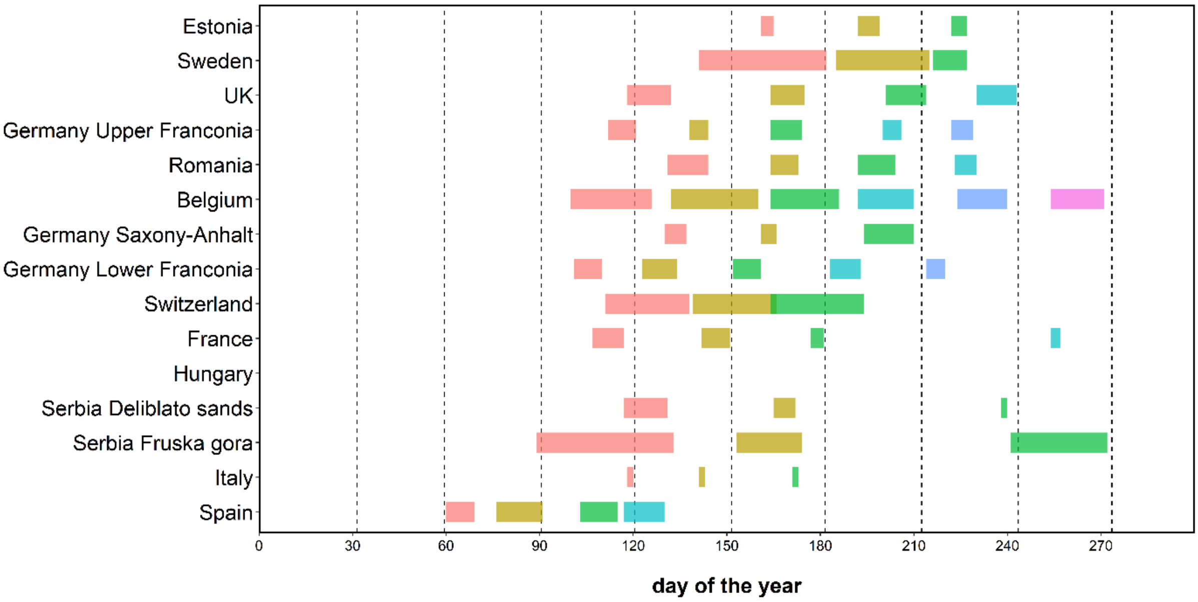

Fig. S1: Number of timings of the sampling intervals in the 15 study regions, approximately ordered top to bottom from north to south.

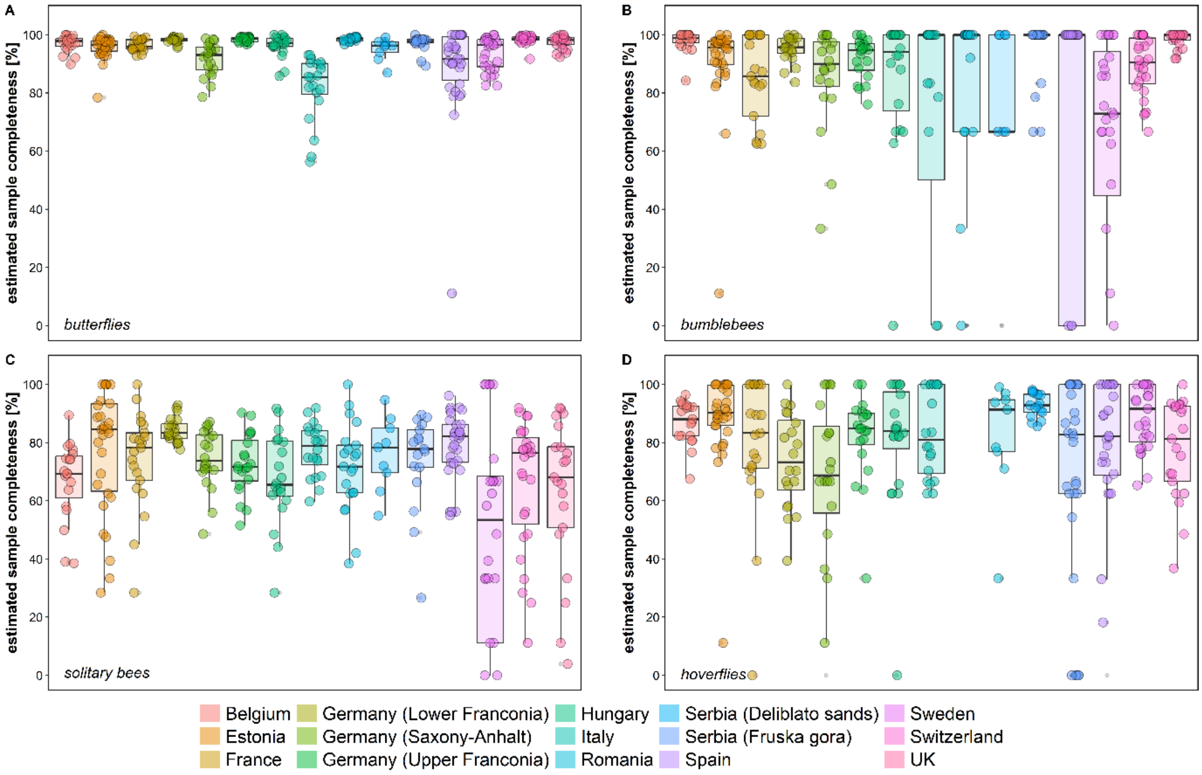

Fig. S2: Estimated sample completeness across the 15 study regions for (A) butterflies, (B) bumblebees, (C) solitary bees and (D) hoverflies. For calculation, see Methods.

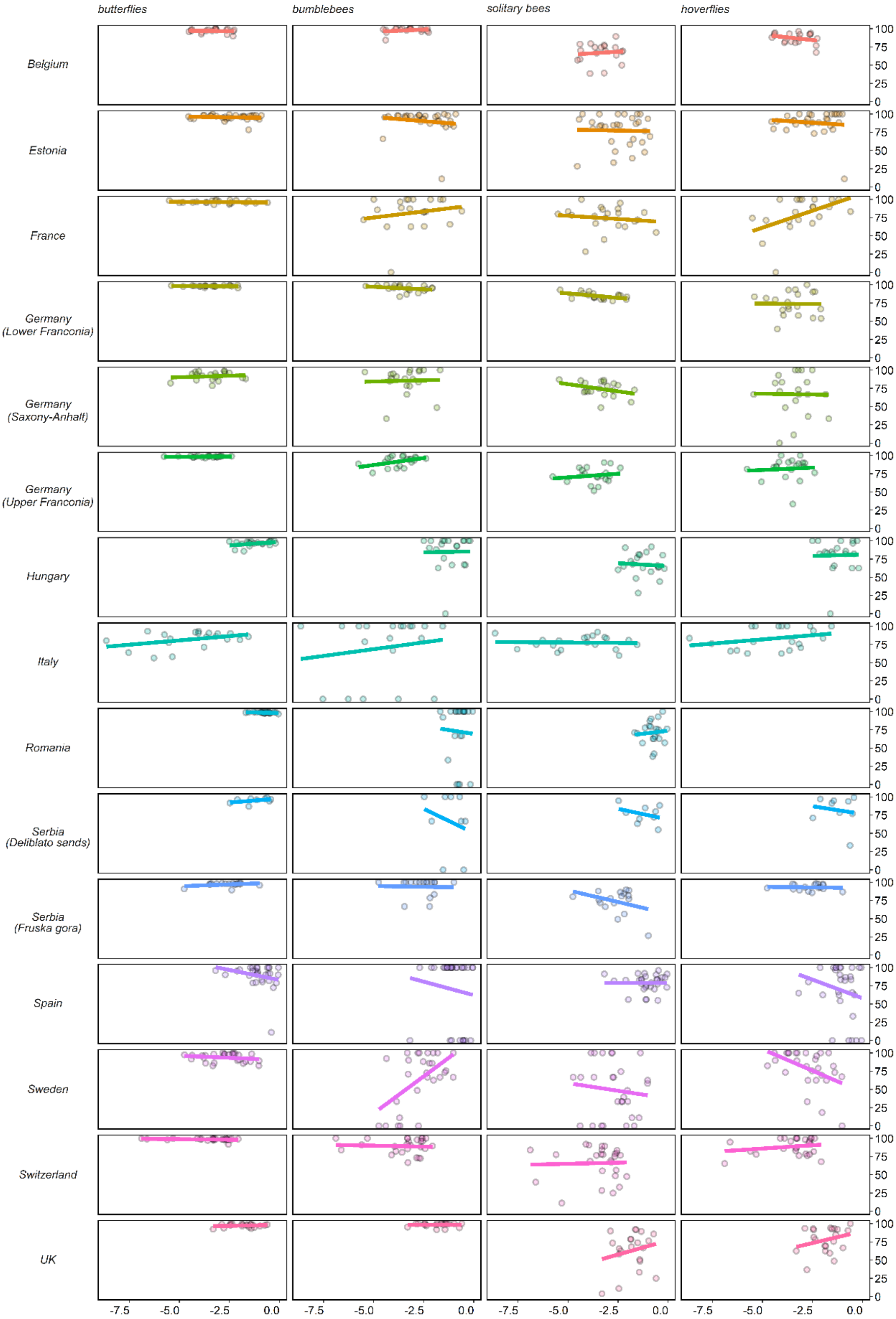

Fig. S3: Relationships between estimated sample completeness across the 15 study regions for butterflies, bumblebees, solitary bees and hoverflies and focal patch area (log-transformed; simple correlations). No systematic pattern between sample completeness and focal patch area is visible.

Table S1: Areas of the focal habitat patch and area covered by habitat and cropland in the landscapes for all regions. Presented are averages ± standard error with the range of the data [minimum; maximum]. The local field teams mapped focal patch size and habitat amount, cropland cover was extracted from the remote-sensed ESA Global Land Cover map with 10 m resolution (see methods). All values rounded to two decimals.

region	**focal patch area [ha]**	**habitat amount [%] (1000 m scale)**	**habitat amount [%] (2000 m scale)**	**cropland cover [%] (1000 m scale)**	**cropland cover [%] (2000 m scale)**
Belgium	2.30 ± 0.43 [0.21; 5.99]	4.56 ± 0.73 [1.09; 10.40]	2.49 ± 0.32 [0.56; 5.52]	18.13 ± 4.30 [0; 65.10]	22.60 ± 4.56 [2.09; 64.49]
Estonia	15.03 ± 1.84 [1.92; 34.01]	13.52 ± 2.09 [1.07; 40.49]	6.44 ± 0.97 [0.27; 19.06]	1.77 ± 0.46 [0; 11.34]	2.40 ± 0.65 [0.03; 15.01]
France	12.58 ± 3.86 [0.56; 56.05]	9.62 ± 2.82 [0.41; 54.95]	5.08 ± 1.04 [0.23; 15.48]	17.52 ± 3.52 [0.06; 57.13]	22.14 ± 3.50 [1.49; 62.60]
Germany / Lower Franconia	6.61 ± 1.64 [0.12; 22.04]	4.52 ± 0.84 [0.45; 12.66]	2.71 ± 0.37 [0.11; 5.60]	27.88 ± 4.33 [3.02; 84.19]	34.13 ± 3.13 [16.37; 78.75]
Germany / Saxony-Anhalt	4.37 ± 1.39 [0.03; 25.08]	4.98 ± 1.05 [0.43; 18.59]	2.49 ± 0.52 [0.28; 8.43]	49.36 ± 5.31 [3.42; 88.08]	57.30 ± 4.79 [6.71; 88.16]
Germany / Upper Franconia	2.74 ± 0.72 [0.18; 11.39]	3.17 ± 0.48 [0.31; 9.18]	1.38 ± 0.25 [0.14; 4.67]	21.53 ± 2.33 [2.73; 37.98]	25.99 ± 2.28 [9.12; 43.62]
Hungary	34.95 ± 4.18 [12.96; 71.57]	36.46 ± 5.24 [8.21; 82.58]	32.79 ± 4.63 [4.63; 70.23]	56.23 ± 4.95 [16.39; 86.02]	56.66 ± 4.37 [20.90; 86.98]
Italy	2.00 ± 0.73 [0.06; 13.82]	3.74 ± 1.22 [0.02; 21.24]	2.35 ± 0.63 [0.03; 9.49]	13.78 ± 2.90 [0.06; 39.79]	19.49 ± 3.27 [0.98; 44.96]
Romania	41.57 ± 4.36 [0.46; 75.40]	50.49 ± 4.19 [18.70; 94.61]	46.53 ± 3.18 [19.71; 83.08]	20.39 ± 4.41 [0.43; 72.99]	20.95 ± 3.88 [0.98; 64.77]
Serbia / Deliblato sands	33.06 ± 6.88 [1.14; 63.75]	36.28 ± 7.12 [8.41; 65.29]	31.45 ± 6.23 [3.91; 61.85]	20.64 ± 7.40 [0; 67.11]	22.32 ± 7.51 [0; 68.54]
Serbia / Fruska gora	15.65 ± 2.82 [1.53; 39.29]	9.86 ± 1.99 [0.86; 37.10]	4.39 ± 1.01 [0.21; 18.13]	38.72 ± 7.98 [0; 84.14]	45.47 ± 7.80 [0.12; 89.56]
Spain	10.99 ± 1.96 [0.07; 36.64]	42.91 ± 4.45 [4.12; 94.92]	32.87 ± 4.13 [3.01; 93.94]	10.72 ± 1.79 [0; 29.72]	15.47 ± 1.77 [0; 34.94]
Sweden	7.70 ± 1.50 [0.53; 35.61]	10.40 ± 1.83 [0.87; 36.00]	7.22 ± 1.04 [0.94; 22.61]	49.37 ± 5.08 [2.22; 87.37]	51.45 ± 4.84 [5.52; 84.77]
Switzerland	7.69 ± 1.07 [0.32; 17.90]	4.76 ± 0.61 [0.10; 12.70]	1.92 ± 0.26 [0.03; 5.59]	6.24 ± 1.53 [0; 30.40]	7.05 ± 1.08 [0.07; 20.43]
UK	24.48 ± 3.55 [4.25; 56.01]	20.35 ± 2.97 [3.66; 54.56]	12.10 ± 2.41 [1.55; 41.34]	36.06 ± 4.49 [0; 62.16]	40.07 ± 4.18 [0.04; 65.03]

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Author for correspondence:
Carolin Biegerl
e-mail: carolin.biegerl@uni-wuerzburg.de

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Landscape management can foster pollinator richness in fragmented high-value habitats

Carolin Biegerl, Andrea Holzschuh, Benjamin Tanner, Douglas Sponsler, Jochen Krauss, Jie Zhang and Ingolf Steffan-Dewenter

Department of Animal Ecology and Tropical Biology, Biocenter, University Würzburg, Am Hubland, Würzburg 97074, Germany

CB, 0009-0004-9131-3287; AH, 0000-0002-5235-4746; BT, 0009-0002-5267-5731; DS, 0000-0002-4892-9332; JK, 0000-0003-2304-9117; JZ, 0000-0003-2599-5983; IS-D, 0000-0003-1359-3944

Pollinator diversity is declining due to habitat loss, low habitat quality, limited habitat connectivity and intensification of agriculture in remaining high-value habitats within human-dominated landscapes, such as calcareous grasslands. Options to increase the local area of protected habitats are often limited. Therefore, we asked how local habitat quality as well as agri-environmental schemes (AES) and configuration of the surrounding landscape can contribute to the preservation of pollinator diversity. We sampled bees, butterflies and hoverflies in 40 calcareous grasslands in Germany, and assessed the effects of calcareous grassland area, quality and connectivity, agricultural configuration, and AES on species richness and abundance. While calcareous grassland area was an important predictor for bee and butterfly species richness, with strongest effects sizes for endangered species, local flower resources and nesting sites and landscape characteristics such as small field size, high proportion of organic fields and connectivity with other grasslands significantly enhanced pollinator richness with responses differing among the three studied taxa. In contrast to expectations, AES flowering fields did not benefit pollinator communities in grasslands. We conclude that improving local habitat quality in combination with targeted landscape management are effective measures to promote pollinator richness in highly fragmented protected grassland.

1. Introduction

Habitat loss and land-use change have been the main drivers of the rapid decline of insects in recent decades [1–3]. The loss of wild pollinating insects in particular poses a serious threat to humanity and nature, as 35% of crops [4] and about 88% of all angiosperms worldwide benefit from pollination by insects or other animals [5]. In Central Europe, semi-natural habitats like calcareous grasslands are major remaining refuges for wild pollinators in human-dominated agricultural landscapes. Crop fields alone are unlikely to fulfil the actual needs of pollinators, whereas calcareous grasslands are valuable habitats because of their ability to provide a variety of floral resources and nesting sites [6,7]. The low disturbance intensity of these grasslands allows many pollinators, including many endangered species, to survive and provide pollination services to adjacent crop fields [8,9]. Calcareous grasslands were once an integral part of the landscape and were created by extensive grazing. However, due to the unprofitability of extensive farming and the continued agricultural intensification, calcareous grasslands have become increasingly fragmented and isolated [10].

Through the lens of island biogeographic [11] and ecosystem decay theory [12], the decreasing area of calcareous grasslands should be accompanied by a loss of within-patch biodiversity and habitat quality, including floral and nesting resources. The positive effect of habitat area [13,14] and flower resources on pollinators has been shown frequently [15,16]. However, nesting resources are also important for wild bees, but this driver has rarely been studied, and even more rarely in combination with calcareous grassland areas and floral resources in the context of grasslands [17,18]. Above the scale of a single patch, the proportion of calcareous grasslands in the landscape is expected to affect pollinator diversity by determining habitat connectivity [17,19]. The positive effects of a higher cover and connectivity of calcareous grasslands could be due to more abundant, diverse and temporally continuous floral resources. Additionally, the higher probability of dispersal events in a well-connected metacommunity decreases the risk of populations becoming extinct in fragmented habitats [20].

To reach other calcareous grassland fragments, pollinators often have to cross the surrounding agricultural matrix. However, it is unclear how hostile this matrix is to pollinators found in protected grasslands [21,22]. In addition, it is difficult in practice to foster pollinators by increasing calcareous grassland and improving habitat connectivity, as land is a valuable commodity, and much land is already under cultivation. Therefore, a comparison between the classically considered variables of calcareous grassland area and connectivity and the changes that can be achieved through land management is desirable and has not been widely studied. Pollinators often use flower resources in agricultural fields and adjacent perennial habitats [23,24], but it has rarely been studied how the composition and configuration of the agricultural matrix contribute to pollinator diversity in grassland patches. Smaller crop fields in the surrounding landscape, for instance, can lead to higher structural and vegetative diversity, as more crop edges lead to the presence of uncultivated field margins and hedgerows [25]. The lower management intensity of field edges leads to reduced use of fertilizers and insecticides, which can support higher levels of flower density and pollinator colonization in field edges compared with centres [26]. This together could result in more area that provides food and nesting resources [27,28]. Another approach to enhancing agricultural land for biodiversity is through agri-environmental schemes (AES), such as organic farming and flowering fields. Both AES are expected to benefit pollinators on calcareous grasslands because the absence of pesticides in organically managed fields and the establishment of flowering fields lead to a higher floral cover [29,30] and improve connectivity at the landscape scale [31,32]. However, there are only a few studies focusing on landscape-scale effects of organic farming [30,33] and knowledge about the effect of AES on pollinators in high-value habitats is lacking.

This study assesses the effects of calcareous grassland area and quality, habitat connectivity, agricultural landscape configuration and AES, on wild bee, butterfly and hoverfly species richness and abundance in calcareous grasslands. Consistent with the island biogeographic and ecosystem decay theory, we expect that (i) pollinator species richness and abundance will increase with calcareous grassland area and connectivity, as well as with patch-scale habitat quality. With respect to the agricultural matrix, (ii) smaller field sizes in the surrounding landscape should lead to higher pollinator species richness and abundance on calcareous grasslands through more small-structured crop edges. In addition, the presence of AES such as organic farming and flowering fields should increase pollinator species richness and abundance by augmenting food resources on the landscape scale.

2. Methods

(a) Study region and sampling sites

The study was conducted in 2022 across two study regions in northern Bavaria, Germany: Lower Franconia and Upper Franconia (figure 1). The two regions differ in their annual mean temperature of 2022 (11.06°C in Lower and 10.29°C in Upper Franconia), annual precipitation 2022 (565.6 mm in Lower and 698.8 mm in Upper Franconia) and altitude (284 m above sea level in Lower and 465 m above sea level in Upper Franconia) [34–36]. The geology of Lower Franconia is characterized by shell limestone, whereas Jurassic limestone is dominant in Upper Franconia [37]. In both regions, calcareous grasslands were formerly widespread on slopes of the valleys [38], and are nowadays embedded in an agricultural matrix characterized by annual crop fields and, especially in Lower Franconia, vineyards.

Forty calcareous grasslands (20 grasslands per study region) were selected as study sites to test the effects of local and landscape variables on wild pollinator species richness and abundance, and flower resources. To cover a broad gradient of local and landscape variables, study sites were selected with different habitat areas (ranging from 0.07 to 31.54 ha), and different habitat connectivity, measured as the proportion of calcareous grasslands in a buffer with a 2 km radius around the study sites (ranging from 0% to 4.7%) excluding the study site area. Distance between study sites was always at least 2 km to ensure independent landscapes and species communities.

(b) Wild pollinators

Bees (Hymenoptera: Apiformes), hoverflies (Diptera: Syrphidae), butterflies (Lepidoptera: Hesperioidea and Papilionoidea) and burnet moths (Lepidoptera: Zygaenidae) were sampled on the study sites five times from April to August 2022. In the following, butterflies always include burnet moths. We analysed bumblebees separately from other wild bees, as bumblebees differ from other bees in their ecology and sociality, and we omitted honeybees altogether. In the following, the term solitary bees refers to all bees except bumblebees and honey bees and includes solitary bees as well as primitively eusocial halictid bees. The order of study sites visited was randomized for each sampling round. In order to sample bees, hoverflies and butterflies, variable transect walks with no fixed direction were carried out (figure 1). Transects were not a straight line but were directed

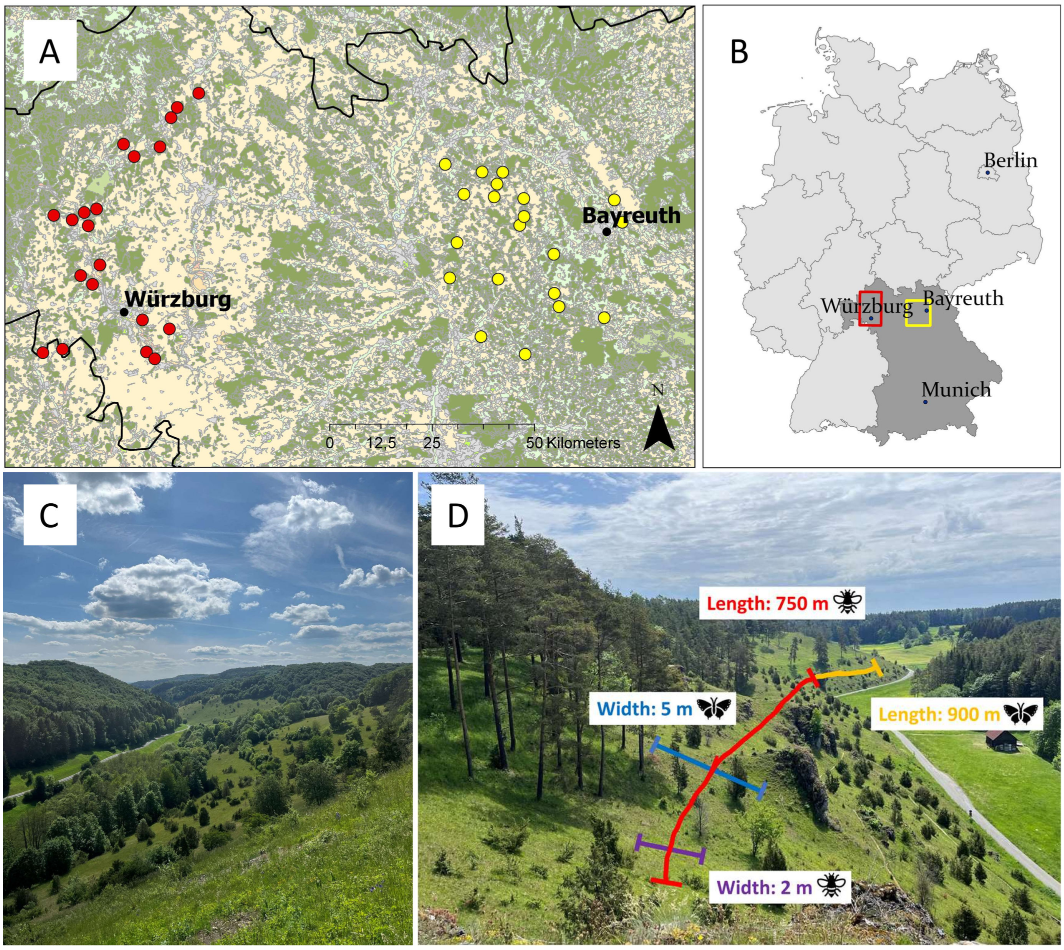

Figure 1. (A,B) Locations of the 40 study sites (calcareous grasslands) in two study regions: Lower (red) and Upper Franconia (yellow). Map source: Corine Landcover 2018 © GeoBasis-DE / BKG (2023). (C) Calcareous grassland in Upper Franconia. (D) Visualization of variable transect walks for bees, hoverflies and butterflies on calcareous grassland in Upper Franconia.

in parts of the study site representative and attractive for wild pollinators (i.e. flower patches and bare ground slopes). Transect location could change from round to round and between bee/hoverfly and butterfly sampling. The transect length for bees and hoverflies was 750 m and the transect width was 2 m resulting in a 1500 m² transect area regardless of the study site area. The transect length for butterflies was 900 m and the transect width was 5 m resulting in a 4500 m² transect area to account for higher mobility of butterflies. Transect time was 45 min. Sampling was conducted from 9:00 to 17:00 during suitable weather conditions (temperatures above 13°C in the sun, low wind (<3 bft) and no rain). Each study site was sampled at least once in the morning, noon and afternoon and changed from round to round. One single person carried out collections and taxonomic identification in the field for bees and hoverflies and another person for butterflies. Wild pollinators were caught with a net if not identified on the wing. Wild pollinators which could not be identified to species level in the field were collected and identified in the laboratory; otherwise, the pollinator was released after identification. Bumblebee queens were not collected and were identified to species level in the field. Bee and butterfly species were classified as endangered or not endangered according to the Red List of Bavaria [39]. Too few endangered hoverfly and bumblebee species were sampled to warrant a separate analysis of these taxa. Pollinator species richness and abundance were pooled across rounds. Due to the equal sampling size in time and area on all study sites, pollinator species richness is equivalent to species density per transect and pollinator abundance is equivalent to population density per transect, rather than the total species number or total abundance of the calcareous grassland fragment. Following frequently used terminology including recent studies [12,40,41], we use the terms species richness and abundance throughout the manuscript.

(c) Local and landscape variables

To estimate the influence of local variables, we used calcareous grassland area and habitat quality, consisting of the variables flower richness, flower cover and nesting sites on the transects. The calcareous grassland area is the area of the sampled calcareous grassland fragment and was calculated in Esri ArcGIS Pro using satellite and aerial imagery from the layer 'World Imagery' [42]. As a measure of flower richness, each flowering plant species was recorded during the transect walk for each sampling round and bee/hoverfly and butterfly transect separately. Flower cover on the transect was estimated for all flowering vascular plants in cm² and then converted to per cent cover. Nesting sites is the estimated percentage of the cover of potential nesting sites for solitary bees on the transect. Potential nesting sites for ground-nesting solitary bees are slopes with open ground and loamy sandy spots [43,44], whereas above-ground-nesting bees rely on dead wood and hollow stems [45]. Suitable open soil spots and the surface of dead wood were estimated in m² and then converted to percentage cover. Flower resources (but not nesting resources) were correlated with calcareous grassland area. Flower richness, flower cover and nesting sites were averaged for each plot across rounds.

Landscape variables were calculated within a 2 km radius around the study site centre, to estimate the influence of landscape composition and configuration. The landscape analysis was conducted within the 2 km radius because it represents a reasonable pollinator foraging and dispersal range [19,46–48]. To analyse the influence of habitat connectivity on wild pollinator species richness and abundance, the total amount of calcareous grasslands in the surrounding landscape excluding the study site area itself was calculated. To test the influence of the surrounding landscape configuration on wild pollinators in calcareous grasslands, percentage cover of annual crop fields (excluding leys) and mean field size of annual crop fields in hectares were calculated, as a measure of intensity and diversity of the agricultural matrix. As small fields have a higher proportion of edges than large fields and lower management intensity in field edges compared with field centres, smaller fields are expected to lead to more food and nesting resources for pollinators at the landscape scale. In order to understand if and how agri-environmental schemes promote wild pollinators in protected grasslands, the two best-known and most well-established AES were quantified: the percentage cover of organic farming and flowering fields in relation to the total annual crop cover. Organic farming uses fewer pesticides, provides more non-crop vegetation and a more diverse crop rotation than conventional farming [49]. Flowering fields are likewise financially subsidized measures to increase the food resources and shelter for wild plants and animals in arable farming. Both measures are expected to promote wild pollinators even in calcareous grasslands because they lead to a higher flower cover at the landscape scale [29,30]. The calculation of landscape variables was done in ArcGIS Pro 2.2.0 [50]. Aerial photos [42] and data from the biotope mapping Bavaria (Bayerisches Landesamt für Umwelt 2021, https://www.lfu.bayern.de/index.htm) and the integrated management and control system for Bavarian agriculture (InVeKos, Bayerische Landesanstalt für Landwirtschaft 2022) showing detailed information about land-use classes, field crops and agri-environmental schemes (AES) from 2022 were used.

(d) Statistical analysis

We used structural causal modelling to design statistical models to estimate the causal effects of local and landscape variables on pollinator species richness and abundance. Briefly, we constructed a directed acyclic graph (DAG) expressing plausible causal relations among our variables (figure 2), then identified via the back door criterion sets of covariates needed to obtain an unbiased estimate of the causal effect of each explanatory variable [51]. To ensure the appropriateness of the DAG, we tested the DAG-data consistency. We show that our DAG contains no open biasing paths, and all implied independencies are consistent with the observational dataset. We also tested the variables in our DAG for residual spatial autocorrelation using the DHARMa Morans I test for distance-based autocorrelation and multicollinearity using the Variance Inflation Factor (VIF). Despite the advantages of DAGs, possible limitations of the approach are that DAGs build on assumptions based on domain knowledge, literature and the experience of researchers to explain the studied system. The DAG can therefore help to understand complex ecological processes, but there is no guarantee that all assumptions are correct [51]. More details about DAG construction, validation and possible limitations can be found in the supplementary material (electronic supplementary material, methods S1).

The effects of local and landscape variables on pollinator species richness and abundance and flower resources were estimated using generalized linear models (GLM). Response variables were pollinator species richness and abundance, with separate models fitted for each pollinator group and, in the case of bees and butterflies, for endangered species. Local explanatory variables were flower richness and flower cover for bees/hoverflies and butterflies, respectively, nesting sites for solitary bees and calcareous grassland area. Grassland area was log10-transformed to increase linearity. Explanatory landscape variables were habitat connectivity, mean field size, cover of organic farming, cover of flowering fields and annual crop cover. At the regional level, we included mean annual temperature (1970–2010) as well as the region identity (Upper versus Lower Franconia). Models were fitted using a Poisson distribution for pollinator species richness and a negative binomial distribution (to correct over-dispersion) for pollinator abundance. Obtaining unbiased causal estimates for each variable of interest required fitting separate models for local- and landscape-level inferences, since the effects of landscape are partially mediated by local conditions. We also included models in which flower cover and richness were response variables explained by the other explanatory variables. The generalized linear model to analyse the effect of calcareous grassland area and landscape variables was: $x \sim$ calcareous grassland area + habitat connectivity + mean field size + organic farming + flowering fields + annual crop cover + mean annual temperature + region. The generalized linear model to analyse the effect of habitat quality was: $x \sim$ calcareous grassland area + habitat connectivity + mean field size + organic farming + flowering fields + annual crop cover + flower richness + flower cover + nesting sites + mean annual temperature + region. The variables included in the models were tested for residual spatial autocorrelation and multicollinearity and no correlations ($p > 0.05$) were identified.

The statistical analyses were performed using the software R v 4.3.1 and RStudio v 2023.06.1 [52]. The package *tidyverse* [53] was used for data handling. GLMs with negative binomial distribution were performed using the package *MASS* [54]. The packages *dagitty* [55], *DHARMA* [56], *car* [57], *ncf* [58] and *performance* [59] were used for model validation. The packages *marginaleffects* [60] and *modelsummary* [61] were used to derive marginal effects of the GLMs. All graphs were generated using R packages *ggplot2* [62] and *ggeffects* [63]. A complete description and reproducible workflow for model fitting, validation and visualization is provided in the electronic supplementary material S1.

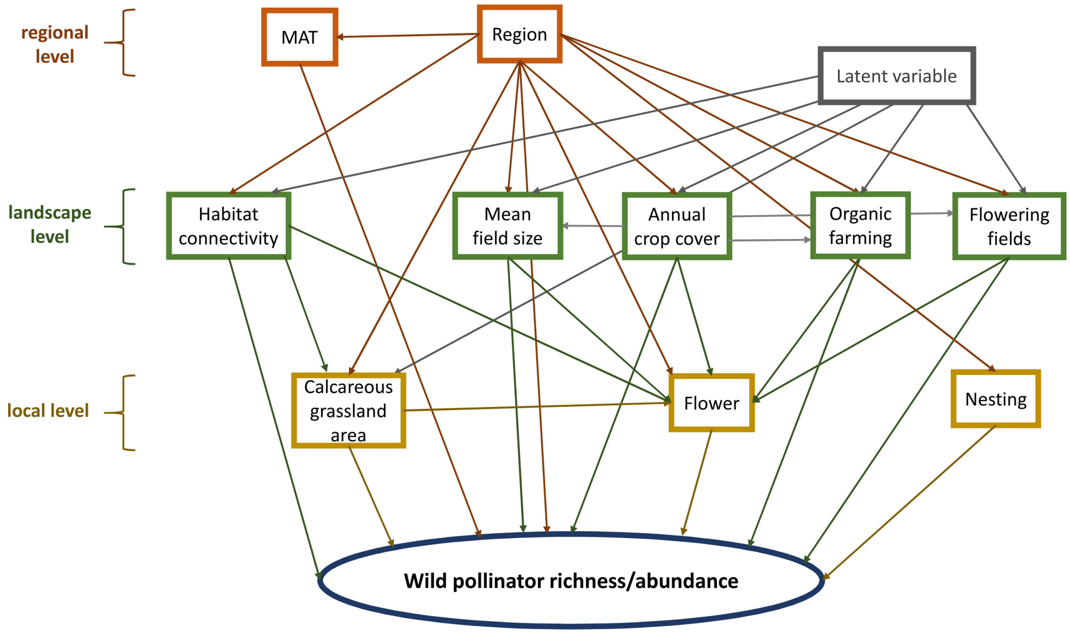

Figure 2. DAG showing the causal structure (arrows) among local, landscape and regional variables (rectangles) hypothesized to be driving wild pollinator species richness and abundance (oval). MAT = mean annual temperature.

3. Results

In total, we recorded 231 wild bee species and 10 859 wild bee individuals (of which 21 were bumblebee species and 2830 bumblebee individuals), 90 butterfly species (24 917 butterfly individuals), 62 hoverfly species (1524 hover fly individuals) and 274 flowering plant species on the 40 calcareous grasslands (see electronic supplementary material, figure S3 for species richness and abundance data among sites). We detected 44% of all wild bees known from Bavaria, 48% of butterflies and 16% of hoverflies. Furthermore, 23% of the sampled wild bee species, 33% of butterfly species and 3% of hoverfly species were endangered according to the Red List of Bavaria.

(a) Local effects

Calcareous grassland area had the strongest effect on solitary bees, butterflies and flower resources. A tenfold increase in calcareous grassland area resulted in an increase in species richness of solitary bees, endangered solitary bees, butterflies and endangered butterflies by 12.6%, 28%, 17.9% and 52.5%, respectively. Furthermore, flower richness and cover of the studied calcareous grasslands increased with increasing area (figures 3 and 4). However, calcareous grassland area had no significant effect on hoverflies and bumblebees (electronic supplementary material, table S1).

Habitat quality affected solitary bees, butterflies and hoverflies. An increasing proportional amount of potential nesting sites had a positive effect on solitary bee species richness and abundance. With additional 5% of the transect area covered with potential nesting sites, 18% more solitary bee species are expected. Endangered solitary bees were not significantly affected by the proportional amount of potential nesting sites (electronic supplementary material, table S1). Hoverfly species richness and abundance increased with increasing flower richness. Flower cover had a significant positive effect on butterfly abundance (figures 3 and 4).

(b) Landscape effects

Habitat connectivity (i.e. the total amount of calcareous grassland in the surrounding landscape buffer excluding the study site area itself) affected endangered butterfly species and flower resources on calcareous grasslands positively. If habitat connectivity was increased because calcareous grasslands covered an additional 1% of the landscape buffer, endangered butterfly species increased by 15% and flower richness by 4% (figures 3 and 5).

The configuration of the agricultural landscape, as a measure of quality of the agricultural matrix, affected solitary bee abundance: if mean field size of the annual crop fields in the matrix increased by one hectare, solitary bee abundance decreased by 30%. Pollinator species richness and abundance on calcareous grasslands of other pollinator groups were not significantly affected by mean field size. Organic farming (i.e. cover of this AES as a proportion of annual crop fields) had a positive effect on the abundance of bumblebees and endangered butterflies. If an additional 10% of annual crop fields in the landscape buffer were managed organically, bumblebee abundance increased by 10% and endangered butterfly abundance increased by 20%. It should be noted that abundances in this study represent the density of individuals per 1500 and 4500 m² for bees/hoverflies and butterflies, respectively, from which the population size for the total grassland fragment can be derived. Flowering fields (i.e. cover of this AES in proportion to annual crop fields) enhanced flower richness on calcareous grassland. If an additional 1% of annual crop fields in the landscape buffer was converted to flowering fields, 2% more flowering plant species were found

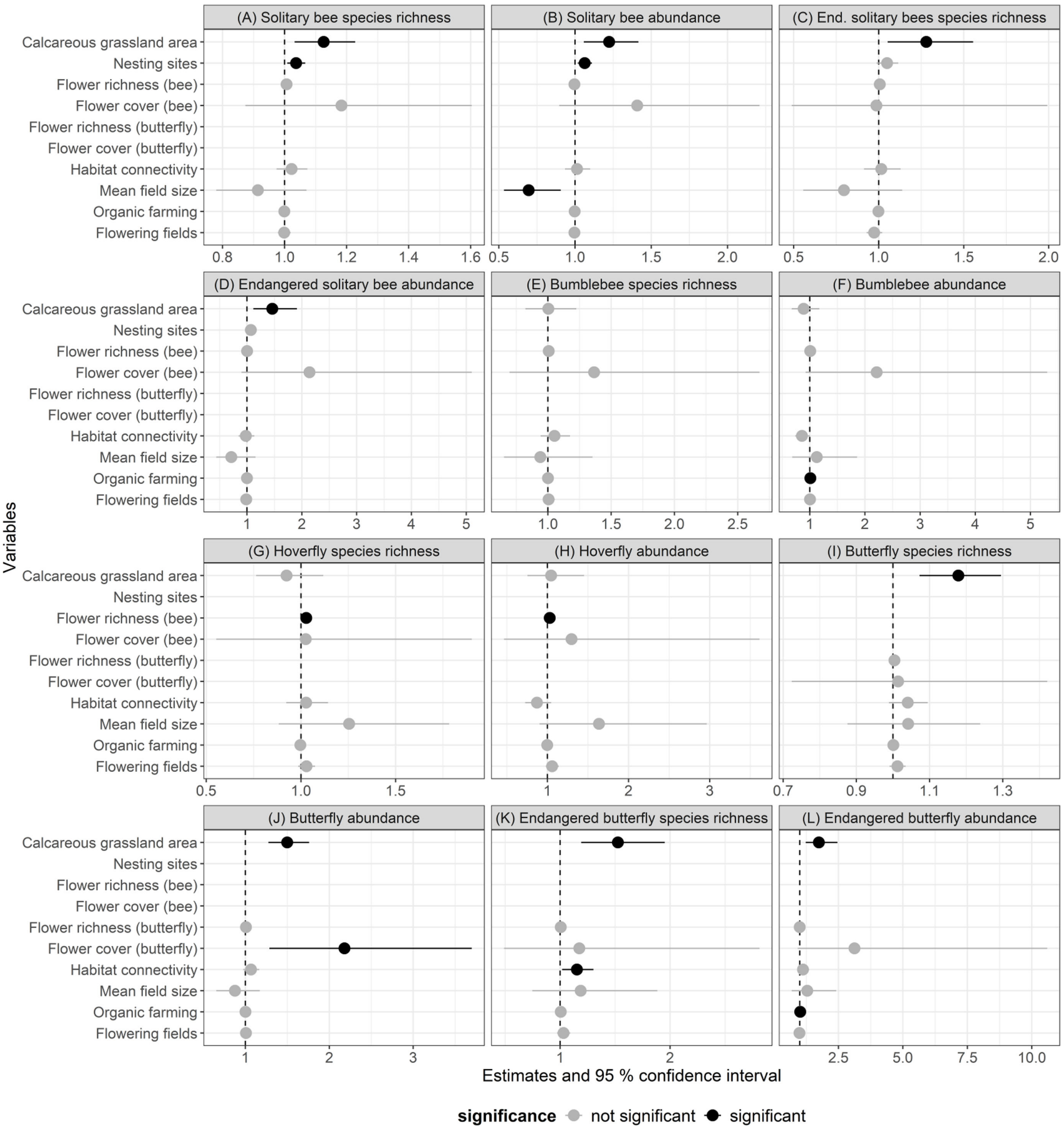

Figure 3. Coefficient estimates and 95% confidence intervals of GLMs analysing the effect of local variables (calcareous grassland area (log10-transformed), flower richness, flower cover (log10-transformed), nesting sites) and landscape variables (habit connectivity, mean field size, organic farming and flowering fields) on pollinator species richness and abundance. Black coefficient estimates and confidence intervals indicate significant results ($p < 0.05$). Parameter estimates have been back-transformed from log-link scale to the response scale, which is why the estimates change around 1 and not 0.

on calcareous grassland (figures 3 and 5). Organic farming and flowering fields did not significantly affect pollinator species richness and abundance of other pollinator groups (electronic supplementary material, table S1).

4. Discussion

(a) Local effects

Calcareous grassland area was the strongest predictor of pollinator species richness and thus is in accordance with the species–area relationship predicted by island biogeographic theory [11]. Large calcareous grasslands promote solitary bees and butterflies [64,65] and endangered species even more since these species are often specialized on one habitat [64,66]. At the local scale, larger fragments reduce the risk of extinction and can provide a larger number of food and nesting resources, enabling the coexistence of more pollinator species and larger, more viable populations [12,65,67]. This also becomes clear through the positive relationship between calcareous grassland area and flower resources in this study. In addition to calcareous grassland area, we found that the percentage cover of potential nesting sites was important for solitary bees [17,18]. This is particularly relevant as most bee species in Central Europe are ground nesting [45], and most of the studied calcareous grasslands are located on slopes and have rocky and sandy soil which are suitable nesting substrates [44]. According to our data, already a 5% increase of area providing potential nesting sites increased solitary bee richness by approximately 20%. To achieve the same richness increase based on the species–area relationship a theoretical 30-fold increase of calcareous grassland area would be required, underpinning the value of management options targeted on nesting sites for pollinator conservation. Although calcareous grassland area is the strongest predictor of pollinator species richness and abundance, it is challenging, if not impossible, to expand the size of existing calcareous grasslands. This study indicates that it is not always necessary to increase

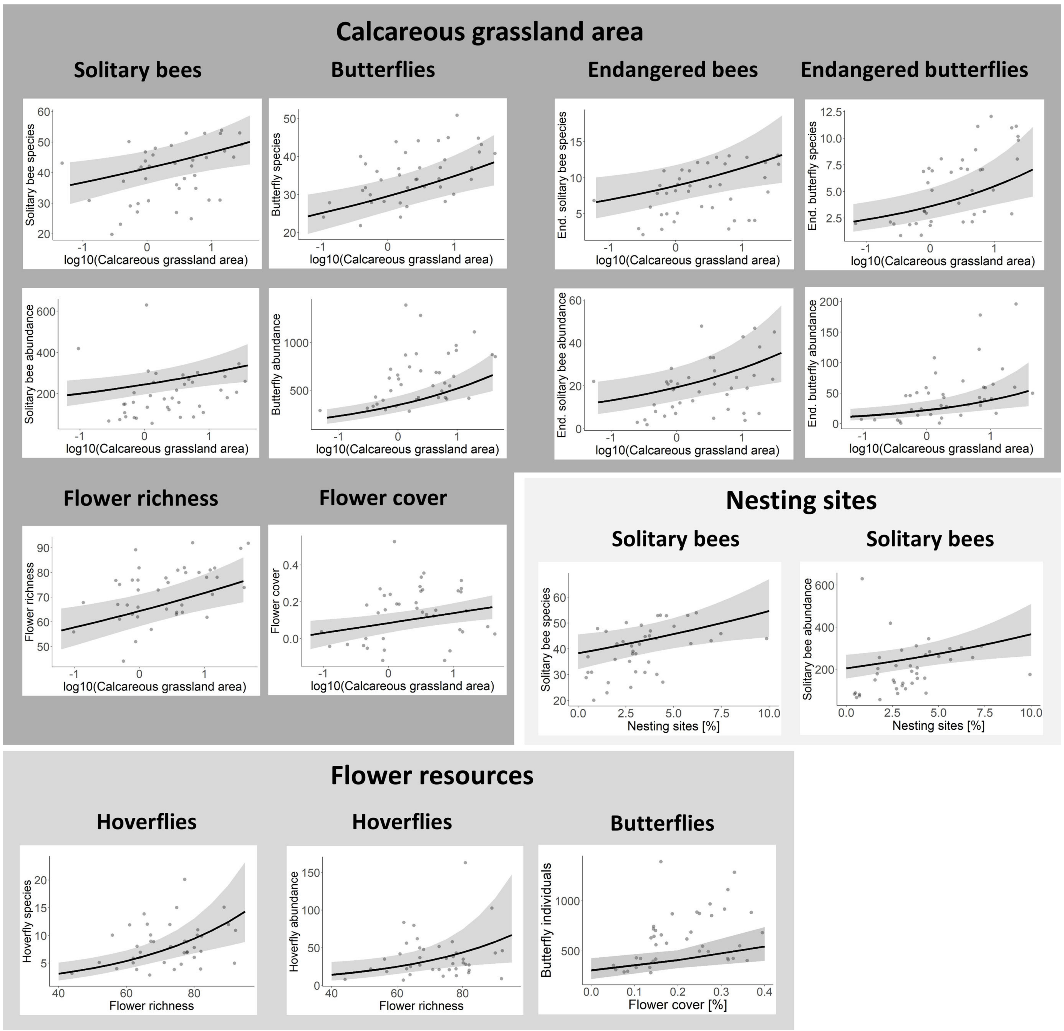

Figure 4. Relationship between (endangered) solitary bee, bumblebee, (endangered) butterfly, hoverfly species richness and abundance and local variables: calcareous grassland area (log10-transformed), flower richness, flower cover and nesting sites. Only significant results of GLMs are shown ($p < 0.05$). A discrepancy between the regression line and the location of the original observed data points (grey points) is possible because the regression line represents the predicted values that have been adjusted by the covariates in the model, with all covariates set to their mean values. Figure with all sub-plots is shown in the supplementary material (electronic supplementary material, Figure S4).

the calcareous grassland area; rather, improving the quality can be an effective measure. For instance, nesting structures such as open ground and slope edges can be maintained by keeping the area in an open state through mowing, grazing and preventing scrub encroachment.

The positive relationship between flower resources and pollinators on calcareous grasslands also indicates that enhancing the quality of the habitat is a logical course of action when the expansion of calcareous grasslands seems not feasible. Pollinators require nectar and pollen to feed both themselves and their larvae [68,69] and some species are highly restricted in their flower selection [45]. Hence, it is crucial to maintain a high cover of flowers and a diverse range of flowering plant species. This was reflected in the positive relationship between flower cover and butterfly abundance. Recent studies have shown that the availability of flower resources has an impact on the species richness of butterfly [70], solitary bee and bumblebee species [43,71]. However, in our study, solitary bee and butterfly species richness were better explained by calcareous grassland area. In turn, hoverflies benefited from calcareous grasslands through diverse flowering plant species, even when area was held constant. Hoverflies have different requirements than bees and butterflies (i.e. they need a cooler microclimate and their larvae have diverse requirements for their developmental habitat [72]), suggesting that hoverflies do not rely on calcareous grasslands themselves but on flower resources and landscape heterogeneity [47,73]. In general, increasing the size of the habitat is still preferable for pollinator protection. In practice, however, this often encounters difficulties. It is then advisable to pay particular attention to habitat quality, as management changes can significantly impact pollinators. However, smaller calcareous grassland areas are often accompanied by lower habitat quality and loss of ecological processes that lead to a more rapid decay of the ecosystem [12]. Therefore, where it is not feasible to maintain either calcareous grassland area or quality, the focus of conservation approaches should be beyond local habitats at landscape scales.

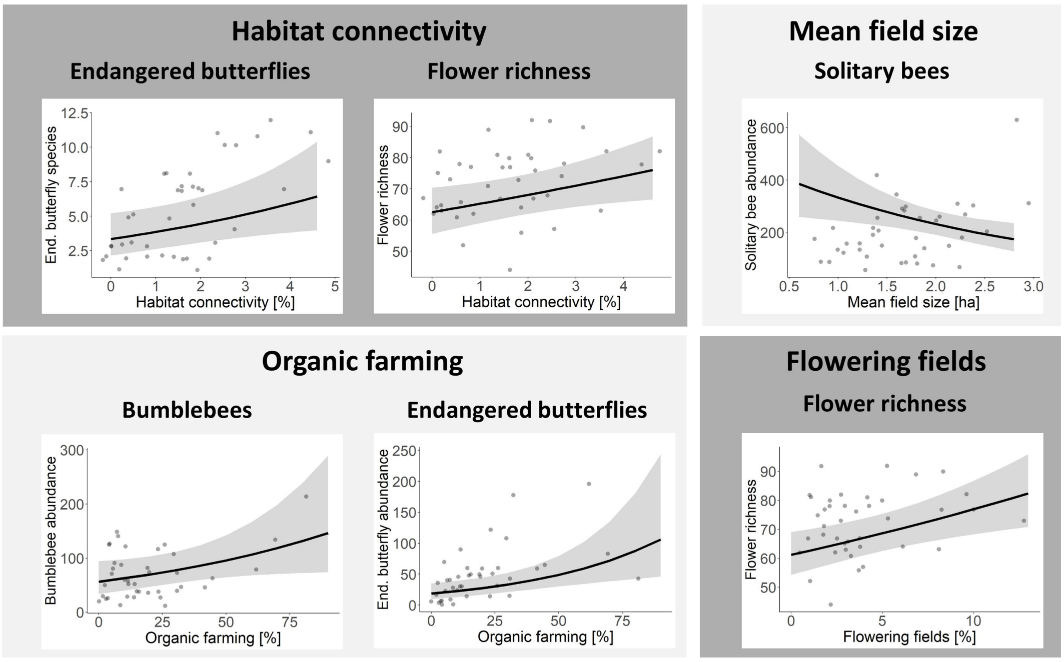

Figure 5. Relationship between (endangered) solitary bee, bumblebee, (endangered) butterfly, hoverfly species richness and abundance and landscape variables: habitat connectivity, mean field size, organic farming and flowering fields. Only significant results of GLMs are shown ($p < 0.05$). A discrepancy between the regression line and the location of the original observed data points (grey points) is possible because the regression line represents the predicted values that have been adjusted by the covariates in the model, with all covariates set to their mean values. Figure with all sub-plots is shown in the supplementary material (electronic supplementary material, figure S4).

(b) Landscape effects

Habitat connectivity—measured as the amount of calcareous grasslands at the landscape scale—positively influenced endangered butterfly species. This positive pattern has also been found in other semi-natural grasslands [19,74] and can be explained by increased dispersal of butterflies. Higher colonization rates reduce the risk of extinction in fragmented habitats [75]. The connectivity effects indicate the importance of immigration for the survival of endangered species. A positive effect of habitat connectivity on flower richness suggests that habitat connectivity enhances seed dispersal and genetic diversity of plants [76]. This, in turn, can promote pollinators in their local habitats by diversifying their food resources.

Habitat connectivity may also be important for bees, as the presence of multiple habitat fragments is necessary for their survival as suggested by the metapopulation theory [77]. However, in our study region, connectivity was not a limiting factor for solitary bees. Landscape variables regarding agricultural management were more important. Landscapes with smaller crop fields were beneficial for solitary bee abundance, and our data suggest that a reduction of field sizes is an effective measure to promote solitary bees where calcareous grassland area cannot be enlarged. To increase the abundance of solitary bees by 20%, a reduction of the average field size by 0.5 ha is already sufficient, while the calcareous grassland area would have to be six times larger than before to achieve the same effect. It should be noted that the density of bee individuals per transect (1500 m^2) is being discussed here, rather than the total abundance of the calcareous grassland fragment. An increase in calcareous grassland area not only leads to an increase in densities per transect, but also to an increase in population sizes due to the effect of the increase in area alone. The effect achieved by increasing calcareous grassland area is therefore many times greater and should therefore be favoured in nature conservation measures. However, smaller fields result in longer and more edge structures between adjacent annual crop fields [27]. Structures such as field margins, hedgerows and small open paths provide additional food and nesting resources by having a higher flower cover and experiencing fewer disturbances. Additionally, field edges receive less management intensity than field centres and are therefore better habitats for pollinators. The additional colonization of plants in the field edges has the effect of an increased food supply. Pollinators also colonize the less intensively managed field edges [26,78]. Field boundaries and edges therefore enhance the presence of food and nesting sites and connectivity since pollinators can more easily move across crop fields [79,80]. This study emphasizes that dividing large crop fields into smaller ones may be an effective approach to benefit solitary bees not only inside the agricultural matrix but even in high-value habitats. This relatively easy-to-implement measure could be accompanied by an establishment of new hedgerows and unmanaged field margins to further increase structural heterogeneity at the landscape scale. Moreover, the study indicates that adaptations in landscape management can have a more pronounced impact than changes in conventional landscape variables, such as calcareous grassland area and connectivity, which are frequently challenging to implement in practice. However, mean field size did not affect bumblebees, hoverflies or butterflies, despite the likelihood of a more structurally diverse agriculture and increasing food and shelter resources resulting from it [81–83].

For bumblebees and endangered butterflies on calcareous grasslands, organic farming in the surrounding landscape was found to be a determining factor, likely due to the positive aspects of organic compared with conventional farming. Pollinators are less exposed to insecticides in calcareous grassland adjacent to organic fields [49,84], and reduced herbicide use leads to a higher flower cover of non-crop vegetation in organically managed fields [29]. Bumblebees and endangered butterflies likely benefited from higher floral and larvae plant resources [23,85]. In general, few studies have tested the effect of organic farming on pollinator species richness and abundance at the landscape scale [30]. It is therefore all the more remarkable that this study showed positive effects of organic farming on bumblebees and butterflies in protected high-value habitats. This study also shows that increasing the cover of organic farming can be an effective measure in pollinator conservation where the expansion of calcareous grassland area is not feasible. Our data suggest that there is a 20% increase in endangered butterfly abundance if an additional 10% of the surrounding crop cover is converted to organic farming. To achieve the same result, the calcareous grassland area would have to be 2.25-times larger. As previously stated, these are densities per transect and not total abundances of the grassland fragment. An increase in calcareous grassland area is also associated with an increase in population sizes and, therefore, should be favoured as a measure. For bumblebee abundances, organic farming was the only influencing variable and resulted in a 10% increase in abundances per additional 10% of annual crop cover managed organically. Solitary bee abundance was not affected by the cover of organic farming but by mean field size of annual crops in the surrounding landscape, suggesting that for solitary bees in calcareous grasslands, the structure of the agricultural landscape is more important than management type. However, Holzschuh *et al*. [30] showed that a high organic land cover in the landscape had a positive impact on wild bee species richness and density in fallow strips due to increased flower resources. While other studies show that AES are not effective for conserving endangered species in crop fields themselves [84,86], our study suggests that organic farming can support endangered butterflies as well as bumblebees on landscape scales and in high-value pollinator habitats.

We found no direct effect of flowering fields in the surrounding landscape on pollinator richness or abundance on calcareous grasslands. Recent studies provide evidence for the effectiveness of flowering fields along crop field edges for pollinator species richness and abundance in field edges [31,87]. It becomes clear that flowering fields attract many pollinators and are advantageous compared with other habitats, such as flowerless crop fields. The low gradient of flowering fields in the landscape in our study could explain missing correlations. However, we found a positive effect of flowering fields on flower richness in calcareous grasslands, presumably through seed dispersal, underpinning the importance of using autochthonous origins for seed mixtures. In addition, the seed mixtures eligible for federal funding can contain over 40 plant species, including those found on calcareous grasslands. Therefore, pollinators profit at least indirectly from sown flowering fields in the agricultural landscape. Hoverflies were not influenced by any landscape variable. Since hoverflies are not specialised on calcareous grasslands, heterogeneous landscapes, in general may be more beneficial [73].

5. Conclusion

Our study reveals the potential of combined management options focused on improving local habitat quality and the creation of beneficial AES in the surrounding landscape as an alternative to the classically considered variables of calcareous grassland area and connectivity to ensure the long-term survival of diverse and partially endangered pollinator groups. Future conservation approaches should focus on the preservation of calcareous grassland fragments with attention to area and quality to counteract pollinator species decline through habitat loss and ecosystem decay. In practice, however, it is often not possible to increase the calcareous grassland area or connectivity in order to improve pollinator richness. This study shows that adapted landscape management and an improvement of habitat quality, especially of nesting sites, can be an effective and more feasible method for pollinator conservation. The configuration of agriculture and AES in the surrounding landscape favours pollinators not only within the agricultural matrix but even in embedded high-value habitats. Small fields and organically managed crops support the conservation of different wild pollinator groups, including endangered species, in protected high-value habitats like calcareous grasslands by providing additional flower and nesting resources at the landscape scale. Nonetheless, more efforts to expand the area and connectivity of high-value habitats will be necessary to mitigate extinction debts in fragmented habitats [67] and ensure the long-term preservation of pollinator richness in human-modified landscapes.

Ethics. Permission to enter nature conservation areas and to collect wild pollinators was granted by the nature conservation authorities of Lower Franconia (permit number RUF-55.1.2-8646.7-4-42-8 issued by the government of Lower Franconia) and Upper Franconia (permit number 55.1-8622 issued by the government of Upper Franconia).

Data accessibility. All datasets and the R code supporting this article have been made publicly available at the Dryad Digital Repository [88].

Supplementary material is available online [89].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.B.: formal analysis, investigation, methodology, writing—original draft, writing—review and editing; A.H.: conceptualization, methodology, writing—review and editing; B.T.: investigation, writing—review and editing; D.S.: formal analysis, writing—review and editing; J.K.: conceptualization, methodology, writing—review and editing; J.Z.: data curation, writing—review and editing; I.S.-D.: conceptualization, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Uhler J *et al*. 2021 Relationship of insect biomass and richness with land use along a climate gradient. *Nat. Commun*. **12**, 5946. (doi:10.1038/s41467-021-26181-3)
2. Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. 2021 Insect decline in the Anthropocene: death by a thousand cuts. *Proc. Natl Acad. Sci. USA* **118**, e2023989118. (doi:10.1073/pnas.2023989118)
3. Seibold S *et al*. 2019 Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674. (doi:10.1038/s41586-019-1684-3)
4. Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci*. **274**, 303–313. (doi:10.1098/rspb.2006.3721)
5. Ollerton J, Winfree R, Tarrant S. 2011 How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326. (doi:10.1111/j.1600-0706.2010.18644.x)
6. Hendricks F *et al*. 2007 How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol*. **44**, 340–351. (doi:10.1111/j.1365-2664.2006.01270.x)
7. Öckinger E, Smith HG. 2007 Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J. Appl. Ecol*. **44**, 50–59. (doi:10.1111/j.1365-2664.2006.01250.x)
8. Boetzl FA *et al*. 2021 A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *Proc. Natl Acad. Sci. USA* **118**, e2016038118. (doi:10.1073/pnas.2016038118)
9. van Swaay CAM. 2002 The importance of calcareous grasslands for butterflies in Europe. *Biol. Conserv*. **104**, 315–318. (doi:10.1016/s0006-3207(01)00196-3)
10. Poschlod P, WallisDeVries MF. 2002 The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. *Biol. Conserv*. **104**, 361–376. (doi:10.1016/s0006-3207(01)00201-4)
11. MacArthur RH, Wilson EO. 1963 An equilibrium theory of insular zoogeography. *Evolution* **17**, 373–387. (doi:10.1111/j.1558-5646.1963.tb03295.x)
12. Chase JM, Blowes SA, Knight TM, Gerstner K, May F. 2020 Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* **584**, 238–243. (doi:10.1038/s41586-020-2531-2)
13. Krauss J, Alfert T, Steffan-Dewenter I. 2009 Habitat area but not habitat age determines wild bee richness in limestone quarries. *J. Appl. Ecol*. **46**, 194–202. (doi:10.1111/j.1365-2664.2008.01582.x)
14. Steffan-Dewenter I. 2003 Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conserv. Biol*. **17**, 1036–1044. (doi:10.1046/j.1523-1739.2003.01575.x)
15. Fantinato E, Sonkoly J, Török P, Buffa G. 2021 Patterns of pollination interactions at the community level are related to the type and quantity of floral resources. *Funct. Ecol*. **35**, 2461–2471. (doi:10.1111/1365-2435.13915)
16. Roulston TH, Goodell K. 2011 The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol*. **56**, 293–312. (doi:10.1146/annurev-ento-120709-144802)
17. Hopfenmüller S, Steffan-Dewenter I, Holzschuh A. 2014 Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS One* **9**, e104439. (doi:10.1371/journal.pone.0104439)
18. Potts SG, Vulliamy B, Roberts S, O'Toole C, Dafni A, Ne'eman G, Willmer P. 2005 Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol*. **30**, 78–85. (doi:10.1111/j.0307-6946.2005.00662.x)
19. Brückmann SV, Krauss J, Steffan-Dewenter I. 2010 Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *J. Appl. Ecol*. **47**, 799–809. (doi:10.1111/j.1365-2664.2010.01828.x)
20. Bergman KO, Dániel-Ferreira J, Milberg P, Öckinger E, Westerberg L. 2018 Butterflies in Swedish grasslands benefit from forest and respond to landscape composition at different spatial scales. *Landsc. Ecol* **33**, 2189–2204. (doi:10.1007/s10980-018-0732-y)
21. Vandermeer J, Carvajal R. 2001 Metapopulation dynamics and the quality of the matrix. *Am. Nat*. **158**, 211–220. (doi:10.1086/321318)
22. Cook WM, Lane KT, Foster BL, Holt RD. 2002 Island theory, matrix effects and species richness patterns in habitat fragments. *Ecol. Lett*. **5**, 619–623. (doi:10.1046/j.1461-0248.2002.00366.x)
23. Carrié R, Ekroos J, Smith HG. 2018 Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *Biol. Conserv*. **227**, 48–55. (doi:10.1016/j.biocon.2018.08.022)
24. Holzschuh A, Dormann CF, Tscharntke T, Steffan-Dewenter I. 2013 Mass-flowering crops enhance wild bee abundance. *Oecologia* **172**, 477–484. (doi:10.1007/s00442-012-2515-5)
25. Holzschuh A, Steffan-dewenter I, Kleijn D, Tscharntke T. 2007 Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *J. Appl. Ecol*. **44**, 41–49. (doi:10.1111/j.1365-2664.2006.01259.x)
26. Clough Y, Holzschuh A, Gabriel D, Purtauf T, Kleijn D, Kruess A, Steffan-dewenter I, Tscharntke T. 2007 Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *J. Appl. Ecol*. **44**, 804–812. (doi:10.1111/j.1365-2664.2007.01294.x)
27. Tscharntke T, Grass I, Wanger TC, Westphal C, Batáry P. 2021 Beyond organic farming: harnessing biodiversity-friendly landscapes. *Trends Ecol. Evol*. **36**, 919–930. (doi:10.1016/j.tree.2021.06.010)
28. Clough Y, Kirchweger S, Kantelhardt J. 2020 Field sizes and the future of farmland biodiversity in European landscapes. *Conserv. Lett*. **13**, e12752. (doi:10.1111/conl.12752)
29. Geppert C, Hass A, Földesi R, Donkó B, Akter A, Tscharntke T, Batáry P. 2020 Agri-environment schemes enhance pollinator richness and abundance but bumblebee reproduction depends on field size. *J. Appl. Ecol*. **57**, 1818–1828. (doi:10.1111/1365-2664.13682)
30. Holzschuh A, Steffan-Dewenter I, Tscharntke T. 2008 Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* **117**, 354–361. (doi:10.1111/j.2007.0030-1299.16303.x)
31. Lowe EB, Groves R, Gratton C. 2021 Impacts of field-edge flower plantings on pollinator conservation and ecosystem service delivery – A *meta*-analysis. *Agric. Ecosyst. Environ*. **310**, 107290. (doi:10.1016/j.agee.2020.107290)
32. Holzschuh A, Steffan-Dewenter I, Tscharntke T. 2010 How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *J. Anim. Ecol*. **79**, 491–500. (doi:10.1111/j.1365-2656.2009.01642.x)
33. Rundlöf M, Bengtsson J, Smith HG. 2008 Local and landscape effects of organic farming on butterfly species richness and abundance. *J. Appl. Ecol*. **45**, 813–820. (doi:10.1111/j.1365-2664.2007.01448.x)
34. DWD Climate Data Center (CDC). 2023 *Jahresmittel der Stationsmessungen der Lufttemperatur in 2 m Höhe in °C für Deutschland*. See https://cdc.dwd.de/portal/202209231028/mapview (accessed 24 October 2023).
35. DWD Climate Data Center (CDC). 2023 *Jahressumme der Stationsmessungen der Niederschlagshöhe in mm für Deutschland*. See https://cdc.dwd.de/portal/202209231028/mapview (accessed 24 October 2023).

36. Google LLC. 2023 Google Earth v 10.71.0.2. See https://earth.google.com/web/@34.27381363,-173.76670724,-40931.16409662a,22292683.93853188d,35y,0h,0t,0r/data=CgRCAggBQgIIAEoNCP_______________wEQAA.
37. Doppler G, Fiebig M, Freudenberger W, Glaser S, Meyer R, Pürner T, Rohrmüller J, Schwerd K. 2004 *GeoBavaria 600 millionen jahre bayern*. Munich, Germany: Bayerisches Geologisches Landesamt.
38. Boehmer HJ. 1994 Die Halbtrockenrasen der Fränkischen Alb. *Mitteilungen Der Fränkischen Geographischen Gesellschaft* **41**, 323–344.
39. Voith J, Doczkal D, Dubitzky A, Hopfenmüller S, Mandery K, Scheuchl E, Schuberth J, Weber K. 2021 *Rote Liste und Gesamtartenliste Bayern–Bienen–Hymenoptera, Anthophila*. Augsburg, Germany: Bayerisches Landesamt für Umwelt.
40. Connor EF, Courtney AC, Yoder JM. 2000 Individuals–area relationships: the relationship between animal population density and area. *Ecology* **81**, 734–748. (doi:10.1890/0012-9658(2000)081[0734:iartrb]2.0.co;2)
41. Watling JI *et al*. 2020 Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecol. Lett*. **23**, 674–681. (doi:10.1111/ele.13471)
42. Esri, M. 2022 *World imagery*. Earthstar Geographics & GIS User Community. See https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9.
43. Gardein H, Fabian Y, Westphal C, Tscharntke T, Hass A. 2022 Ground-nesting bees prefer bare ground *areas* on calcareous grasslands. *Glob. Ecol. Conserv*. **39**, e02289. (doi:10.1016/j.gecco.2022.e02289)
44. Sardiñas HS, Kremen C. 2014 Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic Appl. Ecol*. **15**, 161–168. (doi:10.1016/j.baae.2014.02.004)
45. Westrich P. 1996 *Habitat requirements of central european bees and the problems of partial habitats*. London, UK: The Linnean Society of London and The International Bee Research Association.
46. Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S. 2010 Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol. Conserv*. **143**, 669–676. (doi:10.1016/j.biocon.2009.12.003)
47. Meyer B, Jauker F, Steffan-Dewenter I. 2009 Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol*. **10**, 178–186. (doi:10.1016/j.baae.2008.01.001)
48. Osborne JL, Martin AP, Carreck NL, Swain JL, Knight ME, Goulson D, Hale RJ, Sanderson RA. 2008 Bumblebee flight distances in relation to the forage landscape. *J. Anim. Ecol*. **77**, 406–415. (doi:10.1111/j.1365-2656.2007.01333.x)
49. Federal Ministry of Food and Agriculture (BMEL). 2022 Organic farming in Germany. See https://www.bmel.de/SharedDocs/Downloads/EN/Publications/Organic-Farming-in-Germany.pdf?__blob=publicationFile&v=4.
50. Esri Inc. 2018 ArcGIS Pro 2.2.0. See https://www.esri.com/de-de/arcgis/products/arcgis-pro/overview.
51. Arif S, MacNeil MA. 2023 Applying the structural causal model framework for observational causal inference in ecology. *Ecol. Monogr*. **93**. (doi:10.1002/ecm.1554)
52. R Development Core Team. 2023 R v 4.3.1 and RStudio v 2023.06.1. See https://cran.r-project.org/bin/windows/base/old/4.3.1/ and https://dailies.rstudio.com/version/2023.06.1+524/.
53. Wickham H. 2016 tidyverse: easily install and load the 'Tidyverse'. See https://cran.r-project.org/web/packages/tidyverse/index.html.
54. Venables WN, Ripley BD. 2002 *Modern applied statistics with s*, 4th edition. New York, NY: Springer.
55. Textor J, Zander B, Ankan A. 2023 Graphical analysis of structural causal models. Version 0.3-4. See https://cran.r-project.org/web/packages/dagitty/dagitty.pdf.
56. Hartig F, Lohse L. 2022 DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. *Version 0.4.6*. See https://cran.r-project.org/web/packages/DHARMa/index.html.
57. Fox J, Weisberg S, Price B. 2019 car: companion to applied regression. Version 3.1-3. See https://cran.r-project.org/web/packages/car/index.html.
58. Bjornstad ON. 2008 ncf: dsatial covariance functions. ()
59. Lüdecke D *et al*. 2024 Package 'performance': assessment of regression models performance. *Version 0.11.0*. See https://cran.r-project.org/web/packages/performance/performance.pdf.
60. Arel-Bundock V, Augusto Diniz M, Greifer N, Bacher E. 2024 Package 'marginaleffects': means, and hypothesis tests. *Version 0.20.1*. See https://cran.r-project.org/web/packages/marginaleffects/marginaleffects.pdf.
61. Arel-Bundock V, Gassen J, Eastwood N, Huntington-Klein N, Schwarz M, Elbers B, McDermott G, Wallrich L. 2019 Package 'modelsummary': summary tables and plots for statistical models and data: beautiful, customizable, and publication-ready. *Version 2.1.0*. See https://cran.r-project.org/web/packages/modelsummary/modelsummary.pdf (accessed 12 March 2024).
62. Wickham H. 2007 ggplot2: create elegant data visualisations using the grammar of graphics. *Version 3.5.1*. See https://cran.r project.org/web/packages/ggplot2/index.html.
63. Lüdecke D, Aust F, Crawley S, Ben-Shachar MS, Anderson SC. 2017 ggeffects: create tidy data frames of marginal effects for 'ggplot' from model outputs. *Version 1.6.0*. See https://cran.r-project.org/web/packages/ggeffects/ggeffects.pdf.
64. Botham MS, Fernandez-Ploquin EC, Brereton T, Harrower CA, Roy DB, Heard MS. 2015 *Lepidoptera* communities across an agricultural gradient: how important are habitat area and habitat diversity in supporting high diversity? *J. Insect Conserv*. **19**, 403–420. (doi:10.1007/s10841-015-9760-y)
65. Jauker B, Krauss J, Jauker F, Steffan-Dewenter I. 2013 Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landsc. Ecol.* **28**, 107–120. (doi:10.1007/s10980-012-9820-6)
66. Krauss J, Steffan-Dewenter I, Tscharntke T. 2003 Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia* **137**, 591–602. (doi:10.1007/s00442-003-1353-x)
67. Kuussaari M *et al*. 2009 Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571. (doi:10.1016/j.tree.2009.04.011)
68. Curtis RJ, Brereton TM, Dennis RLH, Carbone C, Isaac NJB. 2015 Butterfly abundance is determined by food availability and is mediated by species traits. *J. Appl. Ecol*. **52**, 1676–1684. (doi:10.1111/1365-2664.12523)
69. Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S. 2006 Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee–flower relationships. *Biol. Conserv*. **130**, 604–615. (doi:10.1016/j.biocon.2006.01.023)
70. Luppi M, Dondina O, Orioli V, Bani L. 2018 Local and landscape drivers of butterfly richness and abundance in a human-dominated area. *Agric. Ecosyst. Environ*. **254**, 138–148. (doi:10.1016/j.agee.2017.11.020)
71. Neumüller U, Burger H, Krausch S, Blüthgen N, Ayasse M. 2020 Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities. *Landsc. Ecol.* **35**, 2209–2224. (doi:10.1007/s10980-020-01096-4)
72. Hoiß B. 2020 Schwebfliegen – vergessene Helfer mit faszinierender Ökologie. *ANLiegen Nat* **42**, 81–90. https://www.anl.bayern.de/publikationen/anliegen/doc/an42106hoiss_2020_schwebfliegen.pdf

73. Schirmel J, Albrecht M, Bauer P, Sutter L, Pfister SC, Entling MH. 2018 Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. *J. Appl. Ecol*. **55**, 1747–1758. (doi:10.1111/1365-2664.13095)

74. Öckinger E, Smith HG. 2006 Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia* **149**, 526–534. (doi:10.1007/s00442-006-0464-6)

75. Fernández-Chacón A, Stefanescu C, Genovart M, Nichols JD, Hines JE, Páramo F, Turco M, Oro D. 2014 Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features. *J. Anim. Ecol*. **83**, 276–285. (doi:10.1111/1365-2656.12118)

76. Clough Y *et al*. 2014 Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecol. Lett*. **17**, 1168–1177. (doi:10.1111/ele.12325)

77. Hanski I, Ovaskainen O. 2003 Metapopulation theory for fragmented landscapes. *Theor. Popul. Biol*. **64**, 119–127. (doi:10.1016/s0040-5809(03)00022-4)

78. Krimmer E, Martin EA, Krauss J, Holzschuh A, Steffan-Dewenter I. 2019 Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agric. Ecosyst. Environ*. **284**, 106590. (doi:10.1016/j.agee.2019.106590)

79. Hass AL *et al*. 2018 Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc. Biol. Sci*. **285**. (doi:10.1098/rspb.2017.2242)

80. Morandin LA, Kremen C. 2013 Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl*. **23**, 829–839. (doi:10.1890/12-1051.1)

81. Muljar R, Viik E, Marja R, Svilponis E, Jogar K, Karise R, Mänd M. 2010 The effect of field size on the number of bumble bees. *Agron. Res*. **2**, 357–360.

82. Pywell RF, Warman EA, Sparks TH, Greatorex-Davies JN, Walker KJ, Meek WR, Carvell C, Petit S, Firbank LG. 2004 Assessing habitat quality for butterflies on intensively managed arable farmland. *Biol. Conserv*. **118**, 313–325. (doi:10.1016/j.biocon.2003.09.011)

83. Sutherland J, Sullivan M, Poppy G. 2001 Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agri For. Entomol*. **3**, 57–64. (doi:10.1046/j.1461-9563.2001.00090.x)

84. Kleijn D *et al*. 2006 Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett*. **9**, 243–254. (doi:10.1111/j.1461-0248.2005.00869.x)

85. Goded S, Ekroos J, Azcárate JG, Guitián JA, Smith HG. 2019 Effects of organic farming on plant and butterfly functional diversity in mosaic landscapes. *Agric. Ecosyst. Environ*. **284**, 106600. (doi:10.1016/j.agee.2019.106600)

86. Scheper J, Holzschuh A, Kuussaari M, Potts SG, Rundlöf M, Smith HG, Kleijn D. 2013 Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. *Ecol. Lett*. **16**, 912–920. (doi:10.1111/ele.12128)

87. Ganser D, Albrecht M, Knop E. 2021 Wildflower strips enhance wild bee reproductive success. *J. Appl. Ecol*. **58**, 486–495. (doi:10.1111/1365-2664.13778)

88. Biegerl C, Holzschuh A, Tanner B, Sponsler D, Krauss J, Zhang J, Steffan-Dewenter I. 2025 Landscape management can foster pollinator richness in fragmented high-value habitats. Dryad Digital Repository. (doi:10.5061/dryad.dncjsxm90)

89. Biegerl C, Holzschuh A, Tanner B, Sponsler D, Krauss J, Zhang J. 2025 Supplementary material from: Landscape management can foster pollinator richness in fragmented high-value habitats. Figshare. (doi:10.6084/m9.figshare.c.7634285)