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Landscape simplification leads to loss of plant–pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators

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Abstract

Aim: Global change, especially landscape simplification, is a main driver of species loss that can alter ecological interaction networks, with potentially severe consequences to ecosystem functions. Therefore, understanding how landscape simplification affects the rate of loss of plant–pollinator interaction diversity (i.e., number of unique interactions) compared to species diversity alone, and the role of persisting abundant pollinators, is key to assess the consequences of landscape simplification on network stability and pollination services.

Location: France, Germany, and Switzerland.

Methods: We analysed 24 landscape-scale plant–pollinator networks from standardised transect walks along landscape simplification gradients in three countries. We compared the rates of species and interaction diversity loss along the landscape simplification gradient and then stepwise excluded the top 1%–20% most abundant pollinators from the data set to evaluate their effect on interaction diversity, network robustness to secondary loss of species, and flower visitation frequencies in simplified landscapes.

Results: Interaction diversity was not more vulnerable than species diversity to landscape simplification, with pollinator and interaction diversity showing similar rates of erosion with landscape simplification. We found that 20% of both species and interactions are lost with an increase of arable crop cover from 30% to 80% in a landscape. The decrease in interaction diversity was partially buffered by persistent abundant generalist pollinators in simplified landscapes, which were nested subsets of pollinator communities in complex landscapes, while plants showed a high turnover in interactions across landscapes. The top 5% most abundant pollinator species also contributed to network robustness against secondary species loss but could not prevent flowers from a loss of visits in simplified landscapes.

Main Conclusions: Although persistent abundant pollinators buffered the decrease in interaction diversity in simplified landscapes and stabilised network robustness, flower visitation frequency was reduced, emphasising potentially severe consequences of further ongoing land-use change for pollination services.

KEYWORDS
alpha-diversity, beta-diversity, habitat loss, interactions, land-use change, landscape complexity, plant–pollinator networks, specialists, wild bees

1 | INTRODUCTION

Landscape simplification, especially the expansion and intensification of agriculture and associated habitat degradation and fragmentation, is one of the main drivers of global biodiversity loss (Pereira et al., 2012), including the loss of wild pollinators (IPBES, 2016; Vanbergen & the Insect Pollinators Initiative, 2013) and plants (Biesmeijer et al., 2006). Pollinating insects and flowering plants are tightly linked to each other in mutualistic interaction networks: plants provide nectar and pollen resources for pollinators such as wild bees, while pollinators provide important pollination services to wild plants and crops (Ollerton et al., 2011), essential for ensuring food security (Potts et al., 2016). Hence, the loss of plant (Power et al., 2012) and pollinator diversity (e.g., Ganuza et al., 2022), driven by landscape simplification, are intertwined processes that ultimately shape changes in plant–pollinator interaction patterns (Martínez-Núñez et al., 2019). Understanding how a key anthropogenic global change process, such as landscape simplification, affects the structure of ecological networks will help identify shifts in interactions that likely have widespread consequences on ecosystem function and stability, and the maintenance of biodiversity (Tylianakis et al., 2008).

Landscape simplification may disassemble plant–pollinator networks through several, non-mutually exclusive, pathways: (i) altered species compositions of flowering plant or pollinator communities (i.e., presence/absence of species), (ii) changes in the relative abundances of species, and (iii) altered patterns of realised interactions among species (Tylianakis & Morris, 2017). The first two pathways may include changes in species richness, and thus overall network size, or predictable shifts in species composition, such as a higher probability of losing specialists (Weiner et al., 2014) and rare species (Winfree et al., 2014). The third pathway may include altered foraging behaviour and shifts in the diet breadth of pollinators (i.e., level of generalisation; Albrecht et al., 2010; Gómez-Martínez et al., 2022), possibly associated with altered abundance and spatial distribution of flowering plant species, beyond changes in species richness.

Landscape simplification may considerably affect the patterns of interactions among species within multi-trophic communities even if species richness remains relatively stable (Tylianakis et al., 2007). As many ecosystem functions depend on interactions between species, losing interactions likely has severe consequences on ecosystem functioning and stability (Tylianakis et al., 2008; Valiente-Banuet et al., 2015). For example, the reduced number and diversity of flower visits by pollinators is generally associated with impaired pollination, subsequently affecting the reproductive success of insect pollinated plants (Albrecht et al., 2012; Magrach et al., 2021). This can lead to smaller and more isolated plant patches (Reinula et al., 2021), and ultimately to local extinction of plant species, with further ramifications for the structure and dynamics of the entire food web that relies on such plant species (Biella et al., 2020). A decrease in interaction diversity (i.e., the number of unique interactions, e.g., Albrecht et al., 2007) could thus be a more sensitive early warning signal or indicator for the negative impacts of landscape simplification on ecosystem health before a decrease in species diversity is detected (Bascompte & Scheffer, 2023; Tylianakis et al., 2008). Support for this hypothesis comes from studies that have expanded the concept of species–area relationships (MacArthur & Wilson, 1967) from species to species interactions to investigate the relationship of diversity of species interactions with increasing habitat area. These studies find a steeper positive relationship for interaction richness than for species richness at the local scale: i.e., the richness of plant–pollinator interactions increased more strongly than total species richness with increasing area of isolated habitat fragments in the Pampean plains of Argentina (Sabatino et al., 2010), and the same was found for seed dispersal networks in the tropics (Emer et al., 2020). However, it is unclear whether at the landscape scale, landscape simplification erodes the diversity of plant–pollinator interactions faster than the diversity of plants or pollinators per se and, if so, which underlying mechanisms make interaction networks particularly sensitive (Valiente-Banuet et al., 2015).

A sharper decrease of interaction diversity compared to species diversity could occur when losing multiple interactions per species extinction (which is a likely scenario for the typically generalised plant–pollinator networks of temperate systems; Waser et al., 1996). This could be the case should landscape simplification and fragmentation reduce species abundances to a level where they are no longer able to maintain their original number of interactions (e.g., as a consequence of a reduced probability of interspecific encounters or if lost interactions cannot at least partly be compensated by new interactions, e.g., through adaptive foraging of generalist pollinators and rewiring; Gómez-Martínez et al., 2022; Lázaro & Gómez-Martínez, 2022). Alternatively, though less probable, the extirpation of core species playing central roles within and across modules (i.e., groups of species interacting more strongly with each other than with species of other modules) or within nested subsets of interactions (i.e., nestedness is the tendency of specialists interacting with a subset of the species that generalists interact with) could result in an immediate loss of a large number of interactions from the network (Aizen et al., 2012). However, generalist and abundant pollinators that interact with many different plant species are predicted to persist longest in simplified landscapes, while rare species and specialists with narrower requirements for specific partner species and habitats are disproportionately vulnerable to extinction (Burkle et al., 2013; Winfree et al., 2014). A loss of specialists or rare species with landscape simplification would lead to communities in simplified landscapes being nested subsets of species and interactions from more complex landscapes. This loss of interactions with rare species or abundant pollinators concentrating their visits on a few remaining plant species could reduce interaction diversity. On the contrary, the erosion of interaction diversity could be buffered if generalist species establish new interactions in simplified landscapes (Noreika et al., 2019). Thereby, they may also increase network robustness to secondary extinctions (Kaiser-Bunbury et al., 2010; Redhead et al., 2018) and secure the pollination of specialist plants through the nested structure of plant–pollinator networks (Bascompte & Jordano, 2007). In contrast to the first hypothesised pathways, the latter process would result in a similar, or even less pronounced, loss of interaction diversity compared to species diversity with landscape simplification, highlighting the possibly crucial role of abundant generalist pollinators. However, we currently lack a mechanistic understanding of these various hypothesised pathways regarding how land-use change, such as landscape simplification, is driving plant–pollinator interaction diversity via changes in community composition towards abundant pollinator species.

Here, we investigate how anthropogenic land-use can alter the structure and robustness of plant–pollinator networks by exploring a series of hypothesised pathways for these changes. We explored the relationships of α- and β-diversity of species and interactions with landscape simplification (i.e., increase in arable crop cover) and evaluated how abundant and generalist pollinators potentially persisting in simplified landscapes shaped the observed patterns. We analysed bee- and hoverfly-flower visitation data from standardised transect walks in 24 landscapes along landscape simplification gradients in France, Germany, and Switzerland to test the following hypotheses: (a) Interaction diversity declines at a faster rate than species diversity with landscape simplification. (b) Abundant generalist pollinators persisting in simplified landscapes buffer the decline in interaction diversity. (c) Pollinator communities and interactions in simplified landscapes are nested subsets of those in more complex landscapes. (d) Individual pollinator species become more generalised in simplified landscapes. (e) Network robustness significantly drops upon removal of the top fraction of the most abundant pollinators from the networks, especially in simplified landscapes. (f) Abundant pollinators ensure that flower visitation frequency does not decrease with landscape simplification.

2 | MATERIALS AND METHODS

2.1 | Study design

Landscapes dominated by agriculture or semi-natural habitats ($n=24$, 1 km radius, <20% of area covered by settlements) were selected along independent landscape simplification gradients within each of three western European countries (France, Germany, and Switzerland, $n=8$ in each; Table S1, Figure S1). Landscape edges were separated from each other by at least 3 km. The proportion of arable crops in a landscape was used as a relevant proxy for landscape simplification (e.g., Albrecht et al., 2020) with the advantage that it is often correlated with other proxies for landscape simplification such as edge density or habitat type diversity (Landis, 2017; Tscharntke et al., 2005), but not dependent on the categorisation of different land cover types. Within a 1 km radius from the centre of the landscapes, we determined habitat types using country-specific layers (France: Registre Parcellaire Graphique, https://geoservices.ign.fr/rpg, and Corine Land Cover, https://land.copernicus.eu; Switzerland: Landwirtschaftliche Bewirtschaftung, geodientste.ch) combined with manually digitising habitats from satellite imagery (all three countries, World Imagery, ESRI), in-field habitat mapping (Germany) and ground-truthing to assign EUNIS habitat types (level 2, Table S2) (Davies et al., 2004), using ArcGIS Pro versions 10.7 and 3.1.4 (ESRI). The proportional cover of arable crops was calculated using the R package *landscapemetrics* (Hesselbarth et al., 2019). Landscapes for the three countries were characterised by mosaics of varying proportions of semi-natural habitats such as permanent grasslands of different management intensity, hedgerows and forest patches, with the proportion of arable crops ranging from 29 to

97%. Arable crops included in all countries were mainly cereals and flowering crops such as oilseed rape, mustard, sunflower or field beans. Additionally, we categorised the landscapes as either “simple” (the four landscapes with highest arable crop cover per country) or “complex” (the four landscapes with lowest arable crop cover per country) (Table 1).

2.2 | Sampling of wild bees and hoverflies

Plant–pollinator interactions were sampled along transects in various flower-providing habitat types (e.g., grasslands, forest edges, hedgerows, flowering crops, and field edges) in the inner 500 m radius of the landscapes. The transect length per flowering habitat type was proportional to the area covered by a specific flowering habitat type within the inner 500 m radius of a landscape (Lami et al., 2021) (Table S3) and summed up to a total length of 1 km (2 m wide) per landscape. For example, if the flowering part of the landscape consisted of 40% meadows, 20% forest, 10% hedgerows and 30% flowering oilseed rape crops, we sampled 400 m in meadows, 200 m in forest, 100 m along hedgerows, and 300 m in oilseed rape crops. Non-flowering habitats such as conifer plantations or cereal fields that were unlikely to support considerable floral resources were excluded from the proportional assignment of transects. In all landscapes, a total of three sampling rounds, in April, May/June, and July, were conducted, adjusting the exact location and length of transect sections in each round according to the proportion and location of habitats supporting floral resources, with vegetation sampled up to 2 m high. In each landscape, we collected flower visiting pollinators with a net or small tube and recorded the plant species they visited, focusing on bees (wild bees and the mostly managed western honeybee, *Apis mellifera* L.; Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae) as the most important pollinators of wild plants and crops in Europe (Kleijn et al., 2015). Hereafter, we refer to plant–pollinator networks for the sake of simplicity, but acknowledge that not each flower visit by a potential pollinator necessarily results in a pollination event (Popic et al., 2013). Sampling was performed between 9 am and 6 pm on dry and warm days (min. 14°C) with low wind (mostly <5.4 m/s). The survey in Switzerland was carried out in 2020, in France and Germany in 2021. Transect walks were standardised for sampling effort so that each visit to a landscape always comprised a total of 120 min recording walks per 1 km transect (=3 min per 25 m section), pausing the clock for sample processing. Bees and hoverflies were identified to species level, or in a few cases to genus or morphospecies level; in France and Germany morphologically by experts (in France by WP, in Germany see Acknowledgements), in Switzerland by barcoding the cytochrome oxidase subunit I gene region (Hebert et al., 2003) by Microsynth Ecogenics GmbH (Balgach, Switzerland). Although barcoding is an objective and highly accurate method to identify species (Schmidt et al., 2015), there are a few cryptic species that cannot be unequivocally identified using barcodes (Gueuning et al., 2020; Schmidt et al., 2015). In our study, it is to our best knowledge only *Halictus simplex* and *H. eurygnathus* that might not be unequivocally identified, a limitation that should be considered adequately.

2.3 | Floral communities

Flower abundance and flowering plant diversity were surveyed in plots (2 m × 0.5 m) randomly placed along the transects (10 plots per 100 m transect; 1–3 plots per 100 m for very homogeneous vegetation such as flowering crops or species-poor grasslands dominated by one or few flowering plant species). Plots were arranged horizontally in herbaceous vegetation and vertically up to 2 m along woody vegetation of hedgerows and forest edges (Maurer et al., 2022). As a proxy for flower abundance per m^2 we multiplied the number of single flowers by flower area (calculated as circle area), as flower area and volume are generally strongly positively correlated with the amount of nectar and pollen resources of a flower (Ammann et al., 2024). We retrieved radii measures of single flowers (or inflorescences in the case of Asteraceae, *Knautia arvensis*., and *Plantago* spp.) for each species from a floral trait database including most plant species from the study regions (Frey D, Amman L, Albrecht M, Moretti M, *in prep.*) and the following trait databases: Info Flora (https://www.infoflora.ch/), PlantNET (https://plantnet.rbgsyd.nsw.gov.au/), and NatureGate (https://luontoportti.com/). We calculated flower richness as the total number of recorded vascular flowering plant species per each of the 24 landscapes.

TABLE 1 Range, mean, and standard deviation of percentage of arable crop cover in landscapes of the three countries (*n* = 8 per country).

Country	Range of arable crop cover [%]	Mean ± SD arable crop cover [%]	Category simple (arable crop cover [%])	Category complex (arable crop cover [%])
France	56–90	70.5 ± 10.5	69–90	56–63
Germany	29–97	67.0 ± 23.1	68–97	29–62
Switzerland	32–86	58.5 ± 17.1	62–86	32–50

Note: The last two columns show how the landscapes were assigned to either category “simple” or “complex” according to their percentage of arable crop cover (*n* = 4 landscapes per category per country).

2.4 | Plant–pollinator network metrics

Since we were interested in the effect of landscape simplification across sampling rounds, we pooled the three sampling rounds to build one quantitative plant–pollinator network for each landscape, with plant and pollinator species as nodes and interaction frequencies as links (Gómez-Martínez et al., 2022). We calculated raw interaction richness as the number of unique pairwise plant–pollinator interactions per network, the raw plant and pollinator richness as number of plant or pollinator species per network. Similarly, we calculated raw Shannon diversity of unique interactions, plant and pollinator species per network. To estimate richness and Shannon diversity for plants and pollinators, we used asymptotic estimates of Hill numbers of order $q=0$ and $q=1$ and the functions "ChaoRichness" and "ChaoShannon" from the R package *iNEXT* (Hsieh et al., 2016). We estimated richness and Shannon diversity of interactions in the same manner, by treating the unique pair of interacting plant and pollinator species as a species. The raw richness values for flowering plants, pollinators and their interactions per landscape are given in Table S4.

To assess species-level changes in diet specialisation, we calculated specialisation (d′, Blüthgen et al., 2006) of pollinators and plants in each landscape (excluding species with abundance <5 individuals per landscape to avoid overestimating their specialisation, Gómez-Martínez et al., 2022). When interpreting the results, it is imperative to be aware that these least abundant species are not included. Specialisation d′ denotes how specialised a species is while taking into account the presence and abundance of the other species (as detected within the interaction sampling in our study rather than based on a separate sampling of species abundances; d′ ranges from 0 = no specialisation to 1 = perfect specialist; Blüthgen et al., 2006).

We investigated dissimilarity (β-diversity) of interactions among landscapes with distinct levels of simplification (simple or complex) as described above (Table 1). For the simple-complex pairs, we paired landscapes that were most distinct in their arable crop cover, while for the simple-simple and complex–complex pairs, we paired landscapes that were most similar in arable crop cover, without using a single landscape twice for a comparison within a comparison category (simple–complex, simple–simple, and complex–complex), and accounting for spatial distance among the paired landscapes in the statistical models. We calculated the weighted Jaccard dissimilarity index (spatial estimate accounting for variation in the strength of interactions among species) of interactions among pairs of landscapes within each country (due to different communities across countries and to avoid otherwise potentially resulting artefacts), using the function "betalinkr" in R package *bipartite* (Dormann et al., 2008; Fründ, 2021). We partitioned the total interaction dissimilarity into the species turnover component, which is driven by changes in species composition, and the rewiring component, which reflects the changing interactions among species occurring in both networks using the additive partitioning method originally proposed by Novotny (2009) (partitioning = "commondenom"; partition.st = TRUE, binary = FALSE, index = "jaccard", Fründ, 2021). High values of β-diversity or their partitions mean a high dissimilarity of plant–pollinator communities. The species turnover was further partitioned to discriminate between turnover due to the absence of pollinators, the absence of plants or due to the absence of both (i.e., partition.st = TRUE, Novotny, 2009). The partitions were normalised between 0 and 1. All network analyses were performed using the R package *bipartite* (Dormann et al., 2008).

2.5 | Statistical analysis

Species rarefaction curves were used to assess sampling completeness of species and interactions for each landscape per country, which was within the range of previously published studies (Gómez-Martínez et al., 2022; Grass et al., 2018; see Appendix S1 and Table S1 for details). Proportion of arable crop cover within the 1 km radius buffer of each landscape, a proxy for landscape simplification, was *z*-transformed per country because the countries covered different sections of the whole simplification gradient (Table 1), this ensured comparability of gradients across countries in all analyses. Country was included as a fixed categorical predictor in all models rather than as a random term since inclusion of grouping factors with fewer than five levels as random effects are not advised due to potentially underestimated variance and increased risk of type 1 errors (Harrison, 2015; results of models including country as a random effect were qualitatively identical). The interaction term of arable crop cover and country did not significantly improve the fit of any of the tested models and was therefore not included in the final models.

2.5.1 | Species and interaction diversities along the landscape simplification gradient

To test hypothesis (a) that interaction richness or Shannon diversity decline more strongly than species richness or Shannon diversity with landscape simplification, we built two linear mixed effects models with landscape ID as random effect. Estimated richness or estimated Shannon diversity of interactions, plants and pollinators (afterwards referred to as the three types of richness/diversity) were included as response variable, while percentage of arable crop cover and its interaction with type of richness (or Shannon diversity; factor with three levels: plant, pollinator, interaction) were included as explanatory variables. To allow for the comparison of slopes between the different types of richness (or Shannon diversity), we *z*-transformed the values per type. To investigate the buffering role of abundant pollinator species, i.e., how many of the abundant pollinators are currently responsible for the observed high interaction richness (hypothesis b) we first fitted separate linear models for observed (*z*-transformed) richness and Shannon diversity of flowering plants, pollinators, and interactions as response variables, with percentage of arable crop cover as explanatory variables. We then removed the top 1%–20% most abundant pollinator species (including *A. mellifera*) in each country in 1%-steps from the networks of each landscape and then re-calculated the observed richness and Shannon diversity of pollinators and interactions. Using the same model structure as above, we re-estimated the slopes for their relationships with the percentage of arable crop cover. Bootstrapping was used to obtain 95% confidence intervals for the estimates.

To evaluate whether β-diversity (weighted Jaccard dissimilarity) of interactions differed between landscapes of distinct simplification levels, we fitted a separate linear model for each β-diversity component (turnover due to absence of plants, pollinators or both, and rewiring) with the type of landscape comparison (three levels: simple–complex, simple–simple, and complex–complex) as the explanatory variable and the spatial distance between landscape pairs as an additional covariate to account for differences due to spatial distance (no spatial autocorrelations were detected in the models).

2.5.2 | Nestedness of communities and specialisation of plants and pollinators along the landscape simplification gradient

To test hypothesis (c) of whether pollinator or flowering plant communities or interactions were nested along the landscape simplification gradient, we created an ordered landscape × pollinator species matrix (for each country separately) (Grab et al., 2019). The matrices were ordered by decreasing species abundance (columns) and landscape simplification (increasing percentage arable crop cover; rows). Then, we calculated nestedness of the ordered matrices as weighted NODF (Almeida-Neto & Ulrich, 2011) and compared the observed values to the mean value of 1000 null models generated by the "quasiswap_count" algorithm implemented in the function "oecosimu" of the R package *vegan* (Oksanen et al., 2016). Besides keeping constant row and column sums, the "quasiswap_count" algorithm also keeps connectance (realised proportion of species-landscape combinations) constant, avoiding unrealistic deviations of null model networks from observed connectance. To similarly assess nestedness of flowering plant species and interactions along the gradient, we performed the same analysis with an ordered landscape × flowering plant species (from plant survey) and landscape × plant–pollinator interaction matrix for each country.

To test whether plants and pollinators change their degree of specialisation with landscape simplification (hypothesis d), we fitted linear mixed effects models with specialisation d′ of each plant or pollinator species as response variables, arable crop cover as the explanatory variable and landscape ID and species ID as random factors. Since the analyses testing hypothesis (b) showed that the top 5% of the most abundant species (including *A. mellifera*) were most influential in maintaining interaction richness (Figure 1e), we repeated the analysis with a subset of these 5% most abundant pollinator species per country.

2.5.3 | The role of abundant pollinators for robustness of networks and flower visitation

To evaluate the role of the few abundant pollinator species for network robustness (hypothesis e), we assessed the robustness of each network with and without the 5% most abundant pollinators. As a measure of stability of the networks, we calculated robustness as area below the secondary extinction curve (for pollinators and plants; Memmott et al., 2004) with the "robustness" function implemented in the R package *bipartite* (Dormann et al., 2008). We assumed that the less abundant species have a higher probability of extirpation from a network during the disassembly process compared to more abundant species (Winfree et al., 2014). We compared the obtained robustness values (where we excluded the 5% most abundant pollinators from the networks) to a null-scenario, where we randomly pre-excluded 5% of the pollinator species. This was repeated 1000 times to calculate *z*-scores of robustness per network as $z = (r_{\text{abun}} - \text{mean}(r_{\text{random}}))/\text{sd}(r_{\text{random}})$, where r_{abun} is the robustness of the networks for which the 5% most abundant pollinators have been removed a priori and r_{random} is the robustness of networks where 5% of pollinator species have been randomly removed a priori. *z*-Scores are assumed to follow a normal distribution, and thus *z*-score values >2 or <-2 are considered to indicate a significant difference compared to the null-scenario (Dormann et al., 2014). Since the highly abundant *A. mellifera* is almost exclusively a managed species in our study regions and therefore less prone to go extinct due to habitat loss, we repeated the same analysis keeping this species in the networks (but pre-excluding the remaining 5% abundant pollinators). To assess the relationship of landscape simplification with robustness of networks from which the most abundant pollinators (with and without *A. mellifera*) were a priori removed compared to networks with random a priori removal of pollinators, linear models with *z*-scores of robustness as response variables and percentage of arable crop cover as the explanatory variable were fitted.

To test hypothesis (f) of whether the flower visitation frequency of abundant pollinator species does not decrease with landscape simplification, we calculated the mean of flower visitation frequency per landscape (sum of flower visits per plant species divided by the estimated number of flowers per plant species in a landscape, then averaging these values per landscape); a proxy for the contribution of animal pollinators to the pollination of plants (Vázquez et al., 2005). The mean visitation frequency of all pollinators, including only the 5% most abundant pollinators, and of all other (less abundant) pollinators per landscape were analysed in separate linear models with arable crop cover as the explanatory variable.

The software R version 4.2.1 (R Core Team, 2022) was used for all statistical analyses. Models were fitted with the package *lme4* (Bates et al., 2015). Estimates and standard errors, or confidence intervals, for the factor variables in plots were obtained with the function "emmeans" (R package *emmeans*, Lenth, 2022), model predictions and confidence intervals for plotting continuous variables were obtained with the function "ggpredict" (R package *ggeffects*, Lüdecke, 2018), except where stated differently. Model assumptions were checked by inspection of residual plots using the R package *DHARMa* (Hartig, 2022).

3 | RESULTS

We recorded 62 species of hoverflies, 190 species of bees and 380 flowering plant species (from flower surveys), forming 1430 unique interactions. In each landscape, we observed an average of 40 ± 0.5 pollinator species and 54 ± 0.8 plant species, forming an average of 83 ± 1.4 unique interactions (mean ± SE). Networks of each landscape are displayed in Appendix S2, Figures S3–S5.

3.1 | Species and interaction diversities along the landscape simplification gradient

Estimated richness and Shannon diversity of plants, pollinators and their interactions decreased with similar slopes with landscape simplification (non-significant interaction percentage arable crop cover × type (plant, pollinator, and interaction); Table 2, Figure 1a,b; results were qualitatively identical when not *z*-transforming richness and Shannon diversity, Table S5). An increase of arable crop cover from 30% to 80% thus reflects a loss of 78 interactions, 41 pollinator species and 19 flowering plant species, which is a loss of 20.3%, 19.1% and 19.5% of the maximum number of unique interactions, pollinator species and plant species, respectively, detected in

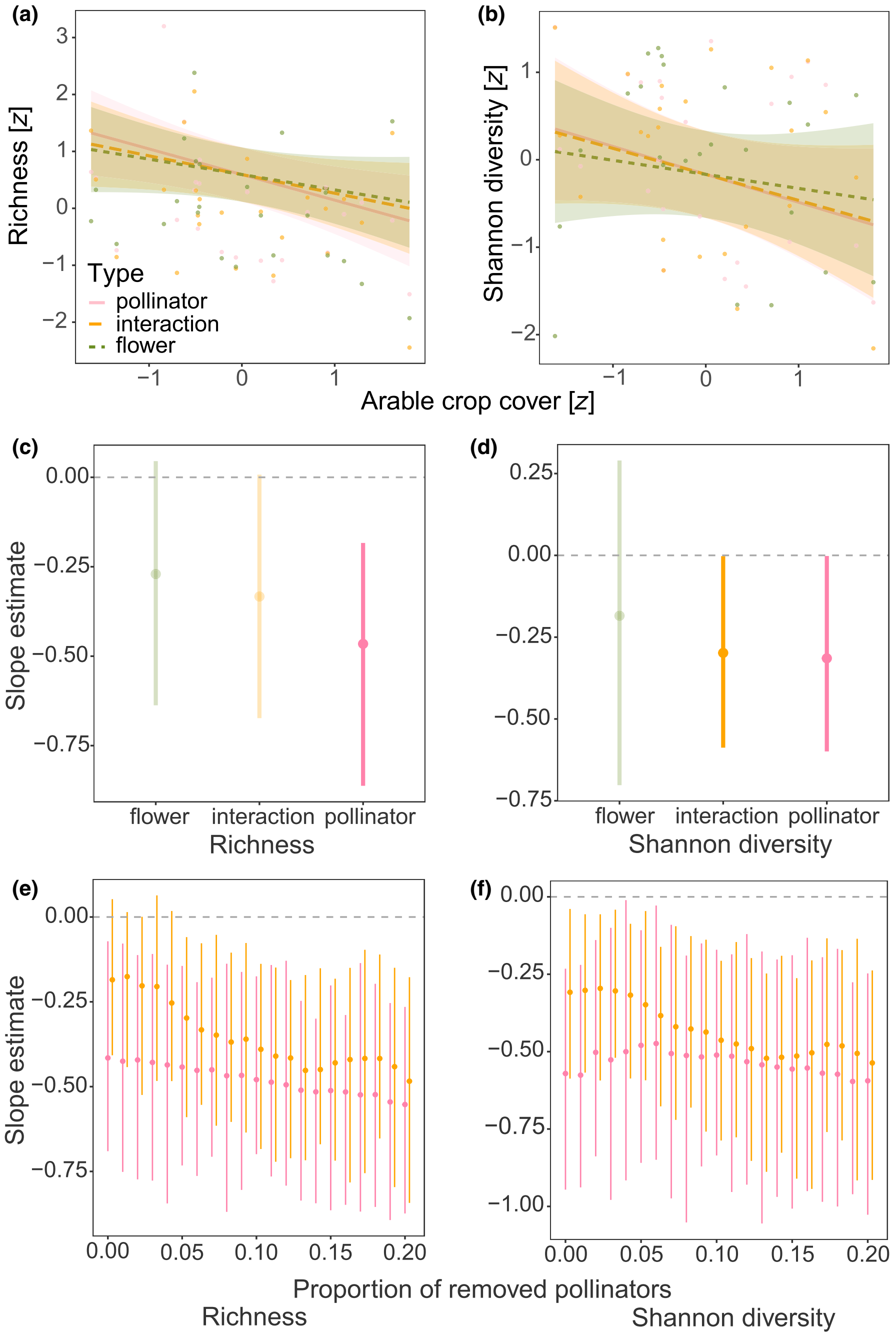


FIGURE 1 Relationships of (estimated) pollinator, plant, and interaction richness (first column a, c, e) and (estimated) Shannon diversity (second column b, d, f) as response variables with percentage of arable crop cover (*z*-transformed) as explanatory variable and country (France, Germany, or Switzerland) as a fixed categorical predictor are shown. (a, b) display model predictions and (c, d) display slope estimates and 95% confidence intervals of the separate models predicting estimated richness (a, c) or estimated Shannon diversity (b, d) of interactions, pollinators or plants along the landscape simplification gradient. (e, f) display the slope estimates of arable crop cover related to observed pollinator or interaction richness (e) or observed pollinator or interaction Shannon diversity (f) when removing 1%–20% of most abundant pollinators (per country). Pink = pollinators, orange = interactions, green = plants.

TABLE 2 Results of linear mixed effects models analysing the effect of arable crop cover and the interaction of arable crop cover with type of richness and Shannon diversity (i.e., plant, pollinator, and interaction) on estimated richness and Shannon diversity of plants, pollinators and interactions (*z*-transformed).

Model	Fixed effects	df	*F*-value	*p*-Value	R^2m	R^2c
Richness	Arable crop cover:type	44	0.39	.682	.37	.56
	Arable crop cover	**20**	**7.22**	**.014**		
	Type of richness	46	0.00	1.000		
	Country	**20**	**9.15**	**.002**		
Shannon diversity	Arable crop cover:type	44	0.205	.816	.21	.28
	Arable crop cover	20	4.30	.051		
	Type of Shannon diversity	46	0.00	1.000		
	Country	**20**	**8.27**	**.011**		

Note: Degrees of freedom (df), *F*-values, *p*-values of *F*-tests, marginal (R^2m) and conditional *r* squared (R^2c). Country (3 factor levels: Switzerland, France, and Germany) was included as a covariate in all models. Landscape ID was included as a random factor. Bold font highlights significant effects ($p < .05$).

TABLE 3 Results of linear models analysing the effect of landscape type comparison (simple–complex, simple–simple, or complex–complex), distance between site-pairs (m) and the covariate country (3 factor levels: Switzerland, France, and Germany) on the different components of β-diversity (rewiring, plant turnover, pollinator turnover, and interaction turnover).

Model	Fixed effects	df	*F* value	*p* Value	R^2m
Rewiring	Landscape comparison	2	0.04	.963	.58
	Distance	1	1.75	.203	
	Country	2	14.62	<.001	
Turnover plants	Landscape comparison	2	0.36	.703	.53
	Distance	1	6.82	.018	
	Country	2	13.01	<.001	
Turnover pollinators	Landscape comparison	2	0.12	.888	.35
	Distance	1	4.70	.044	
	Country	2	3.73	.044	
Turnover interactions	Landscape comparison	2	0.23	.798	.56
	Distance	1	0.64	.433	
	Country	2	13.49	<.001	

Note: Degrees of freedom (df), *F*-values, *p*-values of *F*-tests, marginal *r* squared (R^2m).

a complex landscape with 30% arable crop cover (calculated based on the slopes of the modelled linear relationships). When examining the individual slope estimates of interaction, pollinator or plant richness/Shannon diversity, only pollinator richness (estimate and 95% confidence intervals: −0.47, −0.86 to −0.18), Shannon diversity of pollinators (−0.32, −0.60 to −0.002) and Shannon diversity of interactions (−0.30, −0.59 to −0.002) showed a decrease with simplification (Figure 1c,d).

Shannon diversity of interactions always decreased with simplification, irrespective of sequential removal of the 20% most abundant pollinators (Figure 1f). In contrast, interaction richness only started to significantly decrease with landscape simplification when 5% or more of the most abundant pollinator species were removed (i.e., 5%–20% removed; Figure 1e). The mean number of interactions of a pollinator species was strongly positively correlated with its mean abundance across all landscapes (Spearman rank correlation: rho = .81, $p < .001$).

Interaction β-diversity (dissimilarity) among networks was high (mean ± SE: 0.92 ± 0.01): 70% of total β-diversity were due to changes in species composition (species turnover) (0.67 ± 0.04), while only 30% were due to rewiring (0.26 ± 0.03). Species turnover was primarily driven by plant turnover, which contributed on average 65% (0.44 ± 0.03) to total turnover, while a change in both plant and pollinator turnover contributed on average 20% (0.14 ± 0.02), and

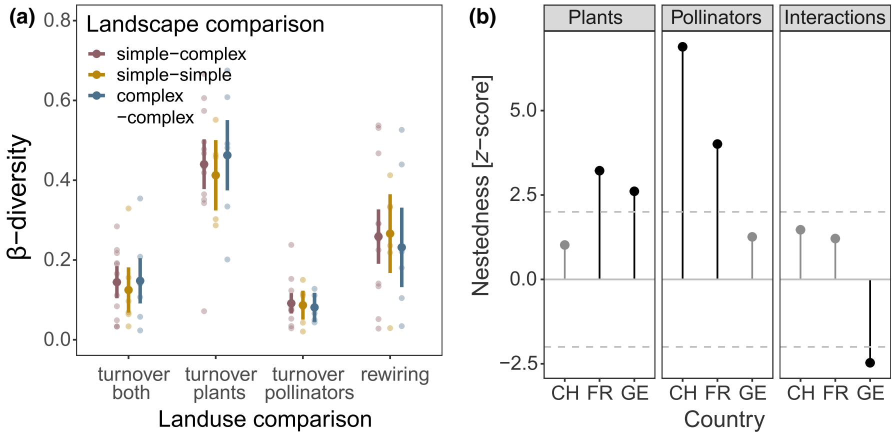
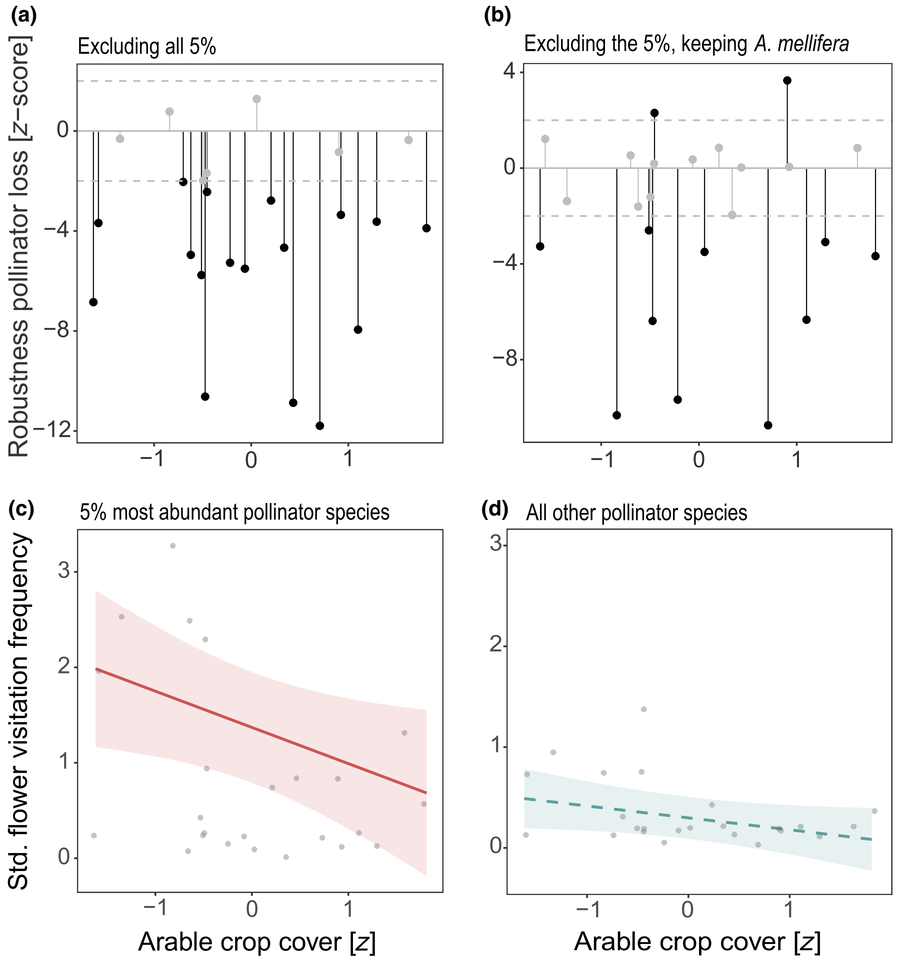


FIGURE 2 (a) Estimated marginal means and 95% confidence intervals of the linear models comparing the different components of β-diversity (interaction turnover due to absence of both, only plants, or only pollinators, and rewiring) among the different landscape types (landscape comparisons: red = simple–complex, orange = simple–simple, and blue = complex–complex). There were no differences between the different β-diversity components among landscape types. (b) Standardised effect sizes (*z*-scores) of community nestedness (plants from plant survey, pollinators or interactions) along the landscape simplification gradient. *z*-Scores on the *y*-axis of >2 or <−2 (dashed lines) are considered as significantly bigger or smaller values than expected based on null models (black lollipops). CH = Switzerland, FR = France, GE = Germany.

FIGURE 3 (a, b) Standardised effect sizes (*z*-scores) of robustness of each network upon pollinator loss when excluding the 5% most abundant pollinator species (a) or excluding the 5% but keeping the managed *A. mellifera* (b) compared to excluding randomly 5% of pollinator species. Landscapes are ordered along increasing arable crop cover (per country). *z*-Scores on the *y*-axis of >2 or <−2 (dashed lines) are considered as significantly bigger or smaller values than expected (black lollipops). There was no effect of arable crop cover on robustness (Table S8). (c, d) Flower visitation frequency (mean number of flower visits standardised by flower abundance) by the 5% most abundant pollinators (c) and by the other pollinators (d) (model predictions and 95% confidence intervals). Visitation frequency of abundant pollinators decreased with increasing arable crop cover ($p = .051$, Table S9), while there was only a decreasing trend for the visits by the other pollinators ($p = .087$, Table S9).



pollinator turnover contributed only 14% (0.09 ± 0.01). β-Diversity components did not differ when comparing different landscape types (simple–complex, simple–simple, or complex–complex) (Table 3, Figure 2a).

3.2 | Nestedness of communities and specialisation of plants and pollinators along the landscape simplification gradient

Pollinator and plant communities (from the plant survey), but not interactions, of simplified landscapes were nested subsets of those from more complex landscapes (pollinators: in France and Switzerland and plants: in France and Germany; Figure 2b, Table S6). Plant and pollinator specialisation d′ (all pollinator species or only the 5% most abundant pollinators) was not affected by landscape simplification (Table S7).

3.3 | The role of abundant pollinators for robustness of networks and flower visitation

Networks were less robust when a priori excluding the 5% most abundant species (including *A. mellifera*) in each country compared to randomly excluding 5% of pollinator species (mean ± 1 SE *z*-score of robustness pollinators: −4.13 ± 0.72, Figure 3a; robustness plants: −2.85 ± 0.54, Figure S2A). When not including *A. mellifera* in the most abundant 5% a priori removed pollinator species, robustness of networks upon pollinator loss varied among landscapes (Figure 3b), while upon plant loss, all 5% most abundant pollinators (with or without *A. mellifera*) were important for robust networks (−2.63 ± 0.39) (Figure S2B). The *z*-scores of robustness were not affected by landscape simplification in any scenario (Table S8). The mean flower visitation frequency decreased with landscape simplification (Table S9, Figure 3c,d). With an addition of 50% arable crop cover, the mean flower visitation frequency by the 5% most abundant pollinators decreased on average by 1 visit per flower (−33.3%), while the visits of all other pollinators decreased on average by 0.3 visits per flower (−24.3%) compared to the maximum observed average visitation frequency of 2.5.

4 | DISCUSSION

Interaction diversity, proposed as an indicator of ecosystem health and functioning (Tylianakis et al., 2008), has been hypothesised to be more sensitive to anthropogenic environmental change than to species diversity (Valiente-Banuet et al., 2015). We found no difference between the rates of decline in plant–pollinator interaction diversity and pollinator diversity with landscape simplification. This was likely due to the buffering role of the 5% most abundant generalist pollinators with many interactions persisting in simplified landscapes (Redhead et al., 2018; Winfree et al., 2014). Accordingly, the pollinator communities of simplified landscapes tended to be nested subsets of those from the more complex landscapes, in contrast to a high plant species turnover among landscapes. These 5% most abundant pollinators also made the networks robust against the predicted secondary species loss from the networks, even in simplified landscapes. However, flower visitation frequency was lower in simplified agricultural landscapes and therefore pollination functions might be threatened despite the persistence of abundant generalists.

Plant–pollinator interaction richness has been found to decline faster than pollinator richness with decreasing area of local habitat fragments (Burkle & Knight, 2012; Sabatino et al., 2010). In contrast, our study of landscape-level simplification found that the decrease in interaction diversity with landscape simplification was not significantly steeper than that of pollinator or plant diversity. This indicates that interaction diversity may not be a more sensitive early warning signal than pollinator diversity of impacts of landscape simplification on interacting plant–pollinator communities. The lack of a strong decrease in plant species diversity with landscape simplification suggests that, despite the loss of potential pollinator habitat, there was not a marked concurrent loss of local quality of habitat remnants, at least in terms of floral diversity (Maurer et al., 2022), and that local management intensity was comparable among landscapes. Thus, the erosion of pollinator and interaction diversity was likely mainly driven by landscape-scale loss of pollinator habitat, although we cannot rule out other possible confounding factors such as management intensity. This highlights the importance of landscape scale processes for pollinator conservation and ecosystem functioning beyond local habitat management (Senapathi et al., 2017). Only interaction Shannon diversity, but not interaction richness, decreased significantly with landscape simplification. Interactions may become less evenly distributed among all plant and pollinator species in the network as certain interactions may increasingly dominate with landscape simplification, as previously reported for host–parasitoid networks along land-use intensification gradients (Tylianakis et al., 2007) and for plant–solitary bee networks with intensive farming (Martínez-Núñez et al., 2019). Such shifts in interaction evenness could be driven by highly abundant generalist pollinators persisting in simplified landscapes (Kleijn et al., 2015; Redhead et al., 2018), while rare and specialised species are lost (Aizen et al., 2012; Burkle & Knight, 2012). In testing this hypothesis, we detected a significant decrease in interaction richness after excluding 5% of the country-wide most abundant pollinators from the network, which were mostly polylectic below-ground nesters, e.g., sweat bees (Halictidae) and bumblebees (*Bombus* spp.) (Table S10), thus species with many interactions. As a consequence, pollinator and plant communities (from the separate plant survey, not necessarily visited by pollinators) – but not plant–pollinator interactions – of simplified landscapes were generally nested subsets of those in more complex landscapes. In contrast, plant species turnover (those visited by pollinators) contributed much more to total changes in interaction composition (β-diversity) than pollinator species turnover, which has also been found along gradients in elevation (Sponsler et al., 2022) and urbanisation (White et al., 2022). This indicates that, despite a relatively similar available plant community (from the separate plant survey) in all landscapes (as indicated by our nestedness result), pollinators appear to visit very different sets of plants in different landscapes (i.e., pollinators change the composition of diet, but largely at similar levels of specialisation d′ in terms of use of available floral resources). In contrast to previous work reporting changes in the degree of plant–pollinator interaction turnover along agricultural-urban gradients (White et al., 2022), we did not find any effect of the landscape type. A possible reason for this discrepancy could be that we analysed β-diversity among simple categories of landscapes (i.e., simple vs. complex) while White et al. (2022) analysed β-diversity along a continuous landscape gradient.

Specialisation (d′) of all pollinators, or of the 5% most abundant pollinators, alone did not change with simplification, except in Germany, where our exploratory analyses showed a decline in specialisation of the whole pollinator community, which is consistent with previous findings of decreasing specialisation with decreasing flower richness or floral resource availability (Gómez-Martínez et al., 2022; Kelly & Elle, 2021; Lázaro & Gómez-Martínez, 2022). This may have contributed to maintaining a certain level of interaction diversity in simplified landscapes. Hence, landscape simplification filtered out rare or specialised species or species unable to adapt their foraging, supporting predictions that rarity (Winfree et al., 2014) and specialisation (Aizen et al., 2012; Burkle et al., 2013) of species are key drivers of plant–pollinator disassembly with increasing anthropogenic disturbance.

The 5% most abundant pollinators not only buffered networks against a more severe loss of interaction richness they were also important for network robustness against predicted secondary loss of species from the networks, irrespective of landscape type. The presence of the managed *A. mellifera* – which was among the 5% most abundant species in all three countries (Table S10) – was also associated with an increased robustness of networks upon pollinator loss. On the contrary, all 5% most abundant species (not only the managed *A. mellifera* but also abundant wild pollinators) were required for robust networks upon simulated plant loss. These results support our hypothesis that abundant generalist pollinator species (the top 5%) and the resulting nested and asymmetric interaction structure (e.g., a plant species depends strongly on a pollinator, the pollinator does often not strongly depend on this plant) (Bascompte et al., 2006; Vázquez et al., 2007) promote network stability (Kaiser-Bunbury et al., 2010; Redhead et al., 2018). The results also indicate that the presence of *A. mellifera* in the landscape alone is not sufficient for enhancing network robustness upon forage plant species loss in simplified landscapes, and thus simply introducing colonies of managed honeybees alone does not mitigate negative consequences of landscape simplification on the functioning and stability of plant–pollinator networks. In fact, high reliance on a single managed species is a risky strategy given the major threats to the health of managed honey bee colonies such as various diseases and pesticide hazards (IPBES, 2016). Even though our measure of robustness, i.e., predicted secondary species loss, did not include detailed information on differential mutual dependence of visited plant species and pollinators or potential rewiring (Kaiser-Bunbury et al., 2010; Vanbergen et al., 2017), it assumes a non-random order of species loss that takes into account the abundance of species, which is in agreement with our findings. This approach to testing species loss has even been found to perform better than those attempting to account for pollinator dependence or rewiring (Biella et al., 2020), and thus should provide a rough approximation for the stability of networks (Martínez-Núñez et al., 2019). Despite our relatively robust networks, and in contrast to our hypothesis, the pollinators (the abundant and to a lesser extent the less abundant pollinators) in simplified landscapes were unable to fully maintain similar flower visitation frequencies. As a result, pollination functions, for which flower visitation frequency is generally a good proxy (Vázquez et al., 2005), are likely reduced in simplified landscapes compared to more complex landscapes. Moreover, it is conceivable that these negative effects of landscape simplification on pollination functions are reinforced by less effective pollen transfer and heterospecific pollen deposition on stigmas by persisting generalist pollinators compared to specialised or rare pollinators (Burns et al., 2022; Genung et al., 2023; King et al., 2013). Further, the presence of rare or specialised pollinators may increase niche complementarity at the community level, thereby enhancing plant reproductive success (Magrach et al., 2021).

Achieving sufficient sampling completeness of pollinator species and interactions is a major challenge in most plant–pollinator network studies. As expected, our results show that sampling completeness of interactions increased with landscape simplification, indicating that our results are conservative and that the relationships between either interaction, pollinator species diversity, or flower visitation frequency with landscape simplification could become even steeper with more complete sampling in complex landscapes. Nevertheless, we cannot rule out possible sampling effects on β-diversity or specialisation d′. For instance, specialisation may be overestimated in networks with low sampling completeness, although d′ was shown to be relatively robust to sampling effects (Fründ et al., 2016).

In conclusion, our study provides several important insights that contribute to a better understanding of how landscape simplification alters the structure and robustness of plant–pollinator networks relevant for pollination functions, and the underlying community processes driving these impacts. Contrary to predictions, our findings indicate that interaction diversity is not a more sensitive early warning signal for landscape simplification impacts on plant–pollinator communities than species diversity because of persisting abundant generalist pollinators that buffer against a more rapid loss of interaction diversity upon landscape simplification. Therefore, if the focus is solely on assessing the status of plant–pollinator communities in simplified landscapes, monitoring species diversity appears to be sufficient, as it is easier and more cost-effective than monitoring interactions. However, evaluating interactions can provide valuable additional insights into the functioning and health of these communities and the underlying processes shaping them, as highlighted by our study. The relatively few, yet very abundant generalist pollinators in the networks that prevent a rapid impairment of interaction diversity upon landscape simplification likely provide a critical insurance function for network stability, but limited insurance for pollination services. This emphasises the likely severe consequences for ecosystem stability and functioning, particularly in simplified agricultural landscapes, should wild generalist pollinators and the partial compensation capacity of managed pollinators also be lost once anthropogenic pressures exceed a critical threshold. We currently do not know when such a tipping point could be reached; those well-connected species contributing most to community persistence might, despite their current abundance, be more vulnerable than we currently believe (Saavedra et al., 2011). To avoid such risks, our findings strongly encourage the consistent implementation and reinforcement of conservation policy efforts such as the COP 15 goals of the Convention on Biological Diversity (CBD Secretariat, 2020) or the Nature Restoration Law of the European Union (The European Commission, 2023) to maintain and restore the green infrastructure in agroecosystems and to promote biodiversity-friendly management of agricultural land. Such actions are indispensable to preserve diverse plant–pollinator interaction networks and their essential role in securing vital pollination functions and services, and resilient agroecosystems.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data is archived in Dryad Digital Repository https://doi.org/10.5061/dryad.1zcrjdg0b (Maurer et al., 2024).

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REFERENCES

Aizen, M. A., Sabatino, M., & Tylianakis, J. M. (2012). Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science*, *335*, 1486–1489.

Albrecht, M., Duelli, P., Schmid, B., & Mueller, C. B. (2007). Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *The Journal of Animal Ecology*, *76*, 1015–1025.

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., Entling, M. H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., … Sutter, L. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters*, *23*, 1488–1498.

Albrecht, M., Riesen, M., & Schmid, B. (2010). Plant–pollinator network assembly along the chronosequence of a glacier foreland. *Oikos*, *119*, 1610–1624.

Albrecht, M., Schmid, B., Hautier, Y., & Muller, C. B. (2012). Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4845–4852.

Almeida-Neto, M., & Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling and Software*, *26*, 173–178.

Ammann, L., Bosem-Baillod, A., Herzog, F., Frey, D., Entling, M. H., & Albrecht, M. (2024). Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agriculture, Ecosystems and Environment*, *359*, 108754.

Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 567–593.

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*, 431–433.

Bascompte, J., & Scheffer, M. (2023). The resilience of plant–pollinator networks. *Annual Review of Entomology*, *68*, 363–380.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Biella, P., Akter, A., Ollerton, J., Nielsen, A., & Klecka, J. (2020). An empirical attack tolerance test alters the structure and species richness of plant–pollinator networks. *Functional Ecology*, *34*, 2246–2258.

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

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 9.

Burkle, L. A., & Knight, T. M. (2012). Shifts in pollinator composition and behavior cause slow interaction accumulation with area in plant–pollinator networks. *Ecology*, *93*, 2329–2335.

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science*, *339*, 1611–1615.

Burns, C., Villalobos, S., & Vamosi, J. C. (2022). When less is more: Visitation by generalist pollinators can have neutral or negative effects on plant reproduction. *Frontiers in Ecology and Evolution*, *10*, 1012809.

CBD Secretariat. (2020). Updated synthesis of the proposals of parties and observers on the structure of the post-2020 global biodiversity framework and its targets. https://www.cbd.int/conferences/post2020/submissions/2019-075

Davies, C. E., Moss, D., & Hill, M. O. (2004). EUNIS habitat classification revised 2004. Report to: European Environment Agency-European topic centre on nature protection and biodiversity: 127–143.

Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite Package: Analysing ecological networks. R News, 8/2, 8–11.

Dormann, C. F., Strauss, R., & Peres-Neto, P. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, *5*, 90–98.

Emer, C., Jordano, P., Pizo, M. A., Ribeiro, M. C., da Silva, F. R., & Galetti, M. (2020). Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. *Biotropica*, *52*, 81–89.

Fründ, J. (2021). Dissimilarity of species interaction networks: How to partition rewiring and species turnover components. *Ecosphere*, *12*, e03653.

Fründ, J., McCann, K. S., & Williams, N. M. (2016). Sampling bias is a challenge for quantifying specialization and network structure: Lessons from a quantitative niche model. *Oikos*, *125*, 502–513.

Ganuza, C., Goslee, S. C., Uhler, J., Tobisch, C., Rojas-Botero, S., Peters, M. K., Zhang, J., Benjamin, C. S., Englmeier, J., Ewald, J., Fricke, U., Haensel, M., Kollmann, J., Riebl, R., Uphus, L., Müller, J., & Steffan-Dewenter, I. (2022). Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. *Science Advances*, *8*, eabm9359.

Genung, M. A., Reilly, J., Williams, N. M., Buderi, A., Gardner, J., & Winfree, R. (2023). Rare and declining bee species are key to consistent pollination of wildflowers and crops across large spatial scales. *Ecology*, *104*, e3899.

Gómez-Martínez, C., González-Estévez, M. A., Cursach, J., & Lázaro, A. (2022). Pollinator richness, pollination networks, and diet adjustment along local and landscape gradients of resource diversity. *Ecological Applications*, *32*, e2634.

Grab, H., Branstetter, M. G., Amon, N., Urban-Mead, K. R., Park, M. G., Gibbs, J., Blitzer, E. J., Poveda, K., Loeb, G., & Danforth, B. N. (2019). Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science*, *363*, 282–284.

Grass, I., Jauker, B., Steffan-Dewenter, I., Tscharntke, T., & Jauker, F. (2018). Past and potential future effects of habitat fragmentation on structure and stability of plant–pollinator and host–parasitoid networks. *Nature Ecology & Evolution*, *2*, 1408–1417.

Gueuning, M., Frey, J. E., & Praz, C. (2020). Ultraconserved yet informative for species delimitation: Ultraconserved elements resolve long-standing systematic enigma in Central European bees. *Molecular Ecology*, *29*, 4203–4220.

Harrison, X. A. (2015). A comparison of observation-level random effect and beta-binomial models for modelling overdispersion in binomial data in ecology & evolution. *PeerJ*, *3*, e1114.

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (Multi-level/mixed) regression models. R package version 0.4.6. https://cran.r-project.org/package=DHARMa

Hebert, P. D. N., Cywinska, A., Ball, S. L., & deWaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London – Series B: Biological Sciences*, *270*, 313–321.

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography*, *42*, 1648–1657. (ver. 1.5.5).

Hsieh, T. C., Ma, K. H., Chao, A., & McInerny, G. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*, 1451–1456.

Info Flora. (2023). Das nationale Daten- und Informationszentrum der Schweizer Flora. https://www.infoflora.ch/de/

IPBES. (2016). *The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production*. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B., & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecology Letters*, *13*, 442–452.

Kelly, T. T., & Elle, E. (2021). Investigating bee dietary preferences along a gradient of floral resources: How does resource use align with resource availability? *Insect Science*, *28*, 555–565.

King, C., Ballantyne, G., & Willmer, P. G. (2013). Why flower visitation is a poor proxy for pollination: Measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, *4*, 811–818.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., Klein, A. M., Kremen, C., M'Gonigle, L. K., Rader, R., Ricketts, T. H., Williams, N. M., Lee Adamson, N., Ascher, J. S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J. C., Blitzer, E. J., … Potts, S. G. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, *6*, 7414.

Lami, F., Bartomeus, I., Nardi, D., Beduschi, T., Boscutti, F., Pantini, P., Santoiemma, G., Scherber, C., Tscharntke, T., & Marini, L. (2021). Species-habitat networks elucidate landscape effects on habitat specialisation of natural enemies and pollinators. *Ecology Letters*, *24*, 288–297.

Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, *18*, 1–12.

Lázaro, A., & Gómez-Martínez, C. (2022). Habitat loss increases seasonal interaction rewiring in plant–pollinator networks. *Functional Ecology*, *36*, 2673–2684.

Lenth, R. V. (2022). emmeans: Estimated marginal means, aka least-squares means. R package version 1.8.1-1. https://cran.r-project.org/package=emmeans

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*, 772.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of Island biogeography*. Princeton University Press.

Magrach, A., Molina, F. P., & Bartomeus, I. (2021). Niche complementarity among pollinators increases community-level plant reproductive success. *Peer Community Journal*, *1*, e1.

Martínez-Núñez, C., Manzaneda, A. J., Lendínez, S., Pérez, A. J., Ruiz-Valenzuela, L., & Rey, P. J. (2019). Interacting effects of landscape and management on plant–solitary bee networks in olive orchards. *Functional Ecology*, *33*, 2316–2326.

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., & Albrecht, M. (2022). Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *Journal of Applied Ecology*, *59*, 2604–2615.

Maurer, C., Martínez-Núñez, C., Dominik, C., Heuschele, J., Liu, Y., Neumann, P., Paxton, R. J., Pellissier, L., Proesmans, W., Schweiger, O., Szentgyörgyi, H., & Albrecht, M. (2024). Landscape simplification leads to loss of plant-pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators (Version 6) [Data set]. *Dryad*. https://doi.org/10.5061/DRYAD.1ZCRJDG0B

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London – Series B: Biological Sciences*, *271*, 2605–2611.

NatureGate. (2023). NatureGate: Species identification made easy! https://luontoportti.com/en

Noreika, N., Bartomeus, I., Winsa, M., Bommarco, R., & Öckinger, E. (2019). Pollinator foraging flexibility mediates rapid plant-pollinator network restoration in semi-natural grasslands. *Scientific Reports*, *9*, 15473.

Novotny, V. (2009). Beta diversity of plant–insect food webs in tropical forests: A conceptual framework. *Insect Conservation and Diversity*, *2*, 5–9.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2016). vegan: Community ecology package. R package version 2.6-2. https://CRAN.R-project.org/package=vegan

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*, 321–326.

Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annual Review of Environment and Resources*, *37*(1), 25–50. https://doi.org/10.1146/annurev-environ-042911-093511

PlantNET. (2023). *The NSW plant information network system*. Royal Botanic Gardens and Domain Trust. https://plantnet.rbgsyd.nsw.gov.au

Popic, T. J., Wardle, G. M., & Davila, Y. C. (2013). Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, *38*, 76–86.

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

Power, E. F., Kelly, D. L., & Stout, J. C. (2012). Organic farming and landscape structure: Effects on insect-pollinated plant diversity in intensively managed grasslands. *PLoS One*, *7*, e38073.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Redhead, J. W., Woodcock, B. A., Pocock, M. J. O., Pywell, R. F., Vanbergen, A. J., & Oliver, T. H. (2018). Potential landscape-scale pollinator networks across Great Britain: Structure, stability and influence of agricultural land cover. *Ecology Letters*, *21*, 1821–1832.

Reinula, I., Träger, S., Hernández-Agramonte, I. M., Helm, A., & Aavik, T. (2021). Landscape genetic analysis suggests stronger effects of past than current landscape structure on genetic patterns of Primula veris. *Diversity and Distributions*, *27*, 1648–1662.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, *478*, 233–235.

Sabatino, M., Maceira, N., & Aizen, M. A. (2010). Direct effects of habitat area on interaction diversity in pollination webs. *Ecological Applications*, *20*, 1491–1497.

Schmidt, S., Schmid-Egger, C., Moriniere, J., Haszprunar, G., & Hebert, P. D. (2015). DNA barcoding largely supports 250 years of classical taxonomy: Identifications for central European bees (Hymenoptera, Apoidea partim). *Molecular Ecology Resources*, *15*, 985–1000.

Senapathi, D., Goddard, M. A., Kunin, W. E., & Baldock, K. C. R. (2017). Landscape impacts on pollinator communities in temperate systems: Evidence and knowledge gaps. *Functional Ecology*, *31*, 26–37.

Sponsler, D. B., Requier, F., Kallnik, K., Classen, A., Maihoff, F., Sieger, J., & Steffan-Dewenter, I. (2022). Contrasting patterns of richness, abundance, and turnover in mountain bumble bees and their floral hosts. *Ecology*, *103*, e3712.

The European Commission. (2023). Nature restoration law. https://environment.ec.europa.eu/topics/nature-and-biodiversity/nature-restoration-law_en#objectives

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology Letters*, *8*, 857–874.

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*, 1351–1363.

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 25–48.

Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, *445*, 202–205.

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*, 299–307.

Vanbergen, A. J., & Insect Pollinators Initiative. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*, 251–259.

Vanbergen, A. J., Woodcock, B. A., Heard, M. S., & Chapman, D. S. (2017). Network size, structure and mutualism dependence affect the propensity for plant–pollinator extinction cascades. *Functional Ecology*, *31*, 1285–1293.

Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, *116*, 1120–1127.

Vázquez, D. P., Morris, W. F., & Jordano, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, *8*, 1088–1094.

Waser, N. M., Chittka, L., Price, M. V., Williams, N. M., & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology*, *77*, 1043–1060.

Weiner, C. N., Werner, M., Linsenmair, K. E., & Blüthgen, N. (2014). Land-use impacts on plant–pollinator networks: Interaction strength and specialization predict pollinator declines. *Ecology*, *95*, 466–474.

White, C. D., Collier, M. J., & Stout, J. C. (2022). Anthropogenic induced beta diversity in plant–pollinator networks: Dissimilarity, turnover, and predictive power. *Frontiers in Ecology and Evolution*, *10*, 806615.

Winfree, R., Williams, N. M., Dushoff, J., & Kremen, C. (2014). Species abundance, not diet breadth, drives the persistence of the most linked pollinators as plant-pollinator networks disassemble. *The American Naturalist*, *183*, 600–611.

BIOSKETCH

The main research interest of the first author is investigating how landscape-scale processes such as landscape simplification are affecting species communities, especially how it changes the diversity and structure of the interactions between plants and pollinators.

Author Contributions: CM, CMN, LP and MA conceived the ideas for the analysis; AV, OS, HS, RP, PN and MA designed the project and sampling methodology; CM, WP, JH, YL, CD and AV collected the data; CM analysed the data; CM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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