



Landscape-level effects of local conservation interventions on the abundance and diversity of wild bees in agricultural landscapes of Germany

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Abstract

To counteract the decline of biodiversity in intensively used agricultural landscapes, a diversity of local conservation interventions, including on-field measures, such as extensification of cereal production, and off-field measures, such as flower strips, is taken. Pollinators, among which wild bees are of particular importance, are a focal group of biodiversity conservation. Although several studies have shown positive local effects of conservation interventions on wild bees, it remains unclear whether these lead to a real increase of wild bees at landscape level. Therefore, we surveyed wild bees in 18 agricultural landscape sections (1 × 1 km) distributed over nine agricultural regions across Germany. In one of the paired landscapes per region, local conservation interventions were implemented, while they were largely absent in the others. We recorded wild bees with a stratified transect sampling on 1000 × 4 m² per landscape where transect sections were distributed proportionally across the edges of all major land-cover types. Further, we conducted GIS-based landscape analyses to calculate the area of conservation interventions and additional landscape metrics, e.g., area of semi natural habitats and edge density. Then, we modelled the effects on landscape-level species richness and abundance of wild bees. Thereby, we also grouped bee species by taxonomy and frequency of occurrence. We found that the area of local conservation interventions was positively related to richness and abundance of solitary bees and rare bees. The abundance of bumble bees and frequent wild bees was positively influenced by crop richness or evenness. In contrast, semi-natural habitats and edge density had no significant effects in the studied landscapes. Our results show that local conservation interventions can promote wild bees at landscape level already few years after their implementation.

Keywords Agri-environment schemes · Pollinators · Land use · Landscape configuration · Crop diversity · Transect walks

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Introduction

Nearly 40% of Europe's land is exploited for agricultural purposes (EEA 2017). The European Environment Agency estimates that about 50% of all animal and plant species in Europe depend on agricultural land (EEA 2006). Therefore, agriculture has a special responsibility for the conservation of biodiversity. Of particular importance are habitats that can be attributed to extensive land-use types (Henle et al. 2008; Kleijn and van Langevelde 2006). In the last century, the transformation of extensively used habitats into intensively managed agricultural land has been omnipresent (Robinson and Sutherland 2002; Vanbergen et al. 2020). This resulted in an increasing homogenization of the landscapes in Europe, which in turn led to the progressive decline of farmland biodiversity (Kleijn et al. 2011; Seibold et al. 2019; Wesche et al. 2012). In particular, the diversity of wild bees (Hymenoptera, Apoidea) declined most severely in farmland compared to other land-use types in Central European agricultural landscapes (Potts et al. 2010, 2016).

Thus, land-use intensification and loss of natural and seminatural habitats are seen as causes for the decline of wild bee diversity and abundance across Europe (Goulson et al. 2008; Kovács-Hostyánszki et al. 2017; Potts et al. 2010; Xiao et al. 2016). Especially in intensively managed agricultural landscapes, available nesting sites, corresponding nesting material, sufficient food resources and their connectivity are often lacking throughout the activity period of the bees (Kleijn and van Langevelde 2006; Westrich 2019). This is alarming, also for agricultural food production, because wild bees belong to one of the most important pollinator groups. Moreover, they not only play an important role for wild plants, but are also the most important pollinators of cultivated plants (Garibaldi et al. 2013; Ollerton et al. 2011; Winfree 2010).

The conflict between maximizing yields and reducing costs of agricultural production and the need to conserve biodiversity urgently requires a solution (Butsic et al. 2020; Mouysset 2014). For this, agricultural transformative change, addressing biodiversity decline is urgently required (Mupepele et al. 2021). For diversity of wild bees, such change would have to include an increase of floral resource richness (Dicks et al. 2015). The promotion of floral resources in cultivated habitats is one of the most common interventions for the conservation of wild bees (Bretagnolle and Gaba 2015). It is known that the area of flower-providing habitats can positively affect pollinators (Diekötter et al. 2014), but also the diversity of habitats is important because different habitats often provide different floral resources, nest sites and nest materials for wild bee species (Steffan-Dewenter et al. 2002; Westrich 2019). Most of them nest in the ground which is why lack of soil disturbance and also the availability of bare ground are vital for providing nesting and overwintering habitat in agricultural landscapes (Gardein et al. 2022; Roulston and Goodell 2011; Westrich 2019).

Conservation interventions actively taken by farmers and other land users to support biodiversity are diverse and include on-field measures, such as extensification of production (e.g. wider rows between crop plants, less pesticide application, fallow periods) and diversification of cropping (e.g. mixed cropping, wider crop rotations), as well as off-field measures, such as flower strips, beetle banks, extensively managed field margins or planting of hedgerows (Klebl et al. 2024). Local conservation interventions, such as flower strips, temporary fallows or extensive grain production, may be particularly important in intensively managed landscapes, often lacking food resources and nesting habitats for wild bees (Dicks et al. 2013). Local conservation interventions in agricultural areas, targeting wild

bees and other pollinators, have shown positive effects depending on the type of measure, local management of fields and also on landscape structure, i.e., composition and configuration of the landscape (Alignier et al. 2020; Geppert et al. 2020; Hass et al. 2018; Kleijn and van Langevelde 2006; Martin et al. 2019). Thus, the same types of measures may vary in their effectiveness depending on local agricultural practices, combinations of interventions and surrounding landscape structure (Kleijn et al. 2018; Schubert et al. 2022; Czechofsky et al. 2025). Low effectiveness of interventions can arise from the development of undesired plant communities, including weeds (Kirmer et al. 2018), but also from missing complementary resources within the landscapes, such as nesting sites (Czechofsky et al. 2025).

Seminatural habitats can provide suitable nesting and foraging sites for pollinators throughout the year (Holzschuh et al. 2012; Kremen et al. 2002; Steffan-Dewenter et al. 2002) and increasing the amount of such habitats in a landscape may have positive effects on pollinators (Blaauw and Isaacs 2014; Ricketts et al. 2008). Also, mass-flowering crops can enhance the abundance of wild bees (Westphal et al. 2003; Beyer et al. 2020; but see Shaw et al. 2020). Especially solitary bee species can be promoted by mass-flowering crops when also seminatural habitats are present in the landscape (Holzschuh et al. 2013).

Regarding landscape structure, small fields and heterogeneous land use lead to a high proportion of field boundaries and edge habitats, which may supply important nesting and foraging resources (Holzschuh et al. 2009; Rands and Whitney 2011). Wild bees also use field boundaries and edge habitats for dispersing across landscapes (Hass et al. 2018). In addition, increasing crop diversity has been proposed as a strategy to support higher pollinator densities as different crop types may provide different food and nesting resources (Aguilera et al. 2020; Fahrig et al. 2010). However, there is no common understanding of the effects of crop diversity on bee species richness and abundance, and some studies even report negative effects (Hass et al. 2018; Martin et al. 2020) or no effects at all (Aguilera et al. 2020). Still, there is a lack of understanding, to what extent the effectiveness of local conservation interventions for pollinators may be mediated by the composition and configuration of the landscape they are embedded in (Pérez-Sánchez et al. 2023).

The aim of our study was to assess the effects of the amount and quality of local conservation interventions on the abundance and richness of wild bees at landscape level in intensively used agricultural landscapes, while controlling for the effects of landscape composition (crop diversity, area of seminatural habitat and mass-flowering crops) and landscape configuration (edge density). For this purpose, we used a landscape-level sampling approach based on stratified transects in landscape sections of $1 \times 1 \text{ km}^2$.

Species of wild bees differ greatly in foraging distances and life-history traits and, hence, do not respond equally to habitat types, food resources, and landscape structure (Westrich 2019). The differences are most pronounced between bumblebees and solitary bees, but also within those two groups bee species differ in traits, such as body size or food preferences (Beyer et al. 2021). Based on this, we expected that different groups of wild bees would respond differently to local conservation interventions and landscape parameters (Carrié et al. 2017; Coutinho et al. 2021; Fründ et al. 2010; Osborne et al. 1999). Therefore, the sampled wild bee species were classified into six groups based on taxonomy and on commonness of occurrence.

In general, we hypothesized that both abundance and richness of wild bees increase with higher amount and quality of local conservation interventions. We expected that particularly common wild bee species would benefit from local conservation interventions, while rare

species would benefit less. Further we hypothesized that crop diversity (richness and evenness), semi-natural habitats, mass-flowering crops and edge density would have additional positive effects on wild bee abundance and richness in agricultural landscapes.

Materials and methods

Study design

Study regions

The study was conducted in 2017 and 2018 in nine intensively managed agricultural regions within eight federal states of Germany (Fig. 1, Table S1, Table S2). The regions were chosen because they represent different agricultural farming systems of above average land-use intensity and, moreover, differed in landscape composition and configuration (Budde-von Beust 2020). The focus was on landscapes and farms where a limited number of local conservation interventions had been implemented in the past. Our selection of study regions, therefore, mirrors the realistic situation in many agricultural landscapes across Europe with very little effective measures implemented and little improvement of habitat conditions for farmland fauna and flora (European Court of Auditors 2020; Pe'er et al. 2020). The selection of study landscapes within the regions was guided by farmers who were willing to implement farm-adapted conservation interventions on their land. In each of the nine regions, one farm was collaborating with the project by implementing standard agri-environmental measures from the respective agri-environmental programs as well as some 'farm adapted' interventions which were developed by the project and tailored to the economic and environmental characteristics of the respective farms (Budde-von Beust 2020). The farmers participating in the project were and had to be open for innovation and environmental improvement of their farming practices but did not differ from their colleagues in their perspectives about economic restrictions and their reticence in implementing conservation interventions due to the risks of control and sanctioning (Joormann and Schmidt 2017).

Local conservation interventions

Up to the start of their involvement in the project, few agri-environment measures had been established by the collaborating farmers on their farmland. By joining the project, farmers agreed to establish both standard agri-environmental measures according to the federal states' agri-environmental schemes (AES) and, on top of those, specific farm-adapted measures (not eligible in AES) which were designed or adapted to the needs of the particular farms (Beyer et al. 2023; Stupak and Sanders 2021). In the following, we refer to all implemented measures as 'local conservation interventions'.

Implementation of local conservation interventions or bundles of such interventions varied between regions because the types and number of interventions depended on the local settings of the individual farms, such as farm type and choice of crops, but also on exposition and landscape features. The interventions aimed at increasing farmland biodiversity in general and were not specifically designed to benefit bees or other pollinating insects. Nevertheless, most of them provided additional floral resources, some of them also

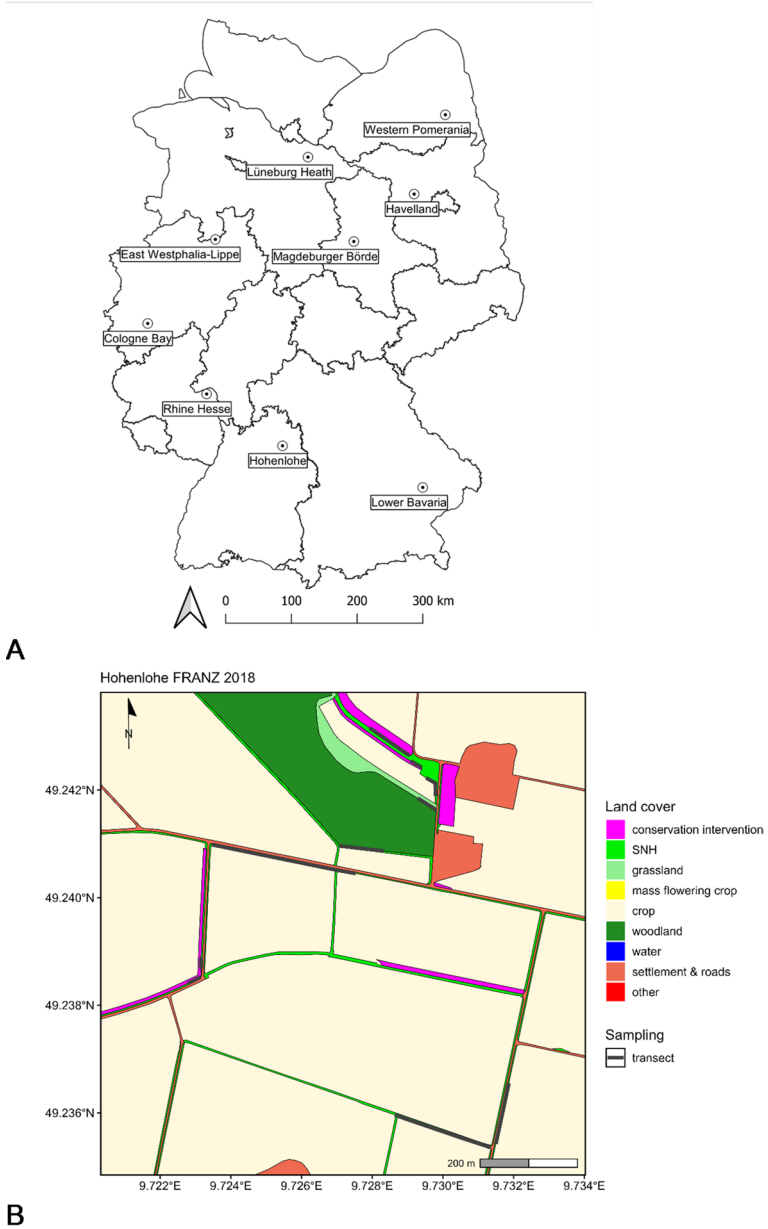


Fig. 1 A) Map of Germany with all study regions, B) land-cover map of the ‘treatment’ study area in the region Hohenlohe with overlay of locations of transect sections for sampling wild bees

nesting sites (Table 1). The following conservation interventions were implemented during the study period: structural flower strips, perennial flowering strips, extensive grain crops, extensive grain with undersowing of flowers, flowering headland, fallow land, extensification of grassland, topsoil removal, maize-bean intercropping, clover and alfalfa cultivation (for a detailed description of measures see Table 1).

Treatment and control landscapes

To test the effects of local conservation interventions on wild bees at the landscape level, we used a paired experimental design by rigorously matching pairs of ‘treatment’ and ‘control’ landscapes with respect to their composition and soil characteristics, each covering an area of 1 km² (see below). The ‘treatment’ landscapes included fields of the farms cooperating with our project, whereas the ‘control’ landscape represented the ‘normal’ land use of the respective regions. Both ‘treatment’ and ‘control’ landscapes could include agri-environmental and climate measures, contractual nature conservation measures and greening measures of the common agricultural policy (CAP) of the EU, which were implemented by farmers independently of our project. However, in the ‘treatment’ landscapes, the amount of local conservation interventions was substantially increased compared to ‘control’ landscapes due to implementation of additional project-specific measures (Table S3). The interventions varied among the treatment landscapes in terms of number, spatial extent and quality, depending on the structural and economic specificities of the respective participating farms. Most or all of the land within the landscapes was managed conventionally although we cannot exclude that some fields may have been managed organically.

We chose a distance of at least 3 km and up to 9 km between the respective ‘treatment’ and ‘control’ landscapes to secure independence of sampling, considering the relatively large foraging distances of some wild bees, especially of bumblebees (Westphal et al. 2006). ‘Control’ landscapes were selected so that landscape composition and soil characteristics were similar to the ‘treatment’ landscapes (Beyer et al. 2020). For this purpose, we analyzed the composition of all ‘treatment’ landscapes and their wider surroundings (9 km²) based on official land-cover maps (ATKIS - Official Topographic Cartographic Information System © GeoBasis-DE/BKG 2018; information of this digital map is based on the content of the 1:25,000 topographic map, but has a higher positional accuracy (the aim is ± 3 m) for point and linear objects). Landscape composition was described as proportions of arable land, grassland, forest and urban infrastructure. Then, we conducted a semi-automated selection of the ‘control’ landscapes within ring buffers around the treatment landscapes with an inner radius of 3 km and a width of 6 km. Within these buffers, a similarity measure based on Euclidean distance was calculated for all possible candidate landscapes using the data described above. Three landscapes that were most similar to the ‘treatment’ landscape were selected as ‘control’ candidates. In consultation with locally knowledgeable farm advisors, sourcing their local knowledge on comparability of farming types, crop rotations and their consent to bee sampling on their land, one ‘control’ landscape per region was ultimately selected.

Table 1 Definition of all local conservation interventions included in the study. ‘F.R.A.N.Z. Measures’ are novel measures that were implemented in the study landscapes in the framework of the F.R.A.N.Z. Project (<https://www.franz-projekt.de/>). ‘Non-F.R.A.N.Z. Measures’ are agri-environmental measures that were implemented by farmers in the study landscapes independent of the Project. F: intervention is providing food resources (nectar and pollen) for wild bees; N: intervention is providing nesting habitat for wild bees

F.R.A.N.Z. measures	Code	Definition
Structural flower strip F/N	1a	Perennial measure (target duration 5 years), fall or spring sowing (before May 31), no use of pesticides or fertilizers on the entire strip. Driving on the area of the measure is not allowed. The strip is divided crosswise into two parts, which are alternately tilled with flower mixture, turned over and reseeded.
Perennial flower strip F/N	1b	Perennial measure (target duration 5 years), fall or spring sowing (before May 31), no use of pesticides or fertilizers on the whole strip. If the strip is cultivated with a biogas seed mixture, organic fertilization is allowed.
Extensive grain F	2a	No mineral fertilizers, liming or pesticides allowed, double row spacing and 50% of normal seed rate, different options for harvesting: (i) normal harvest and plowing, (ii) normal harvest and stubble fallow over winter, (iii) no harvest (grain standing over winter)
Extensive grain with undersowing of flowers F	2b	Undersowing of at least four flowering species, double row spacing and 50% of normal seed rate, no mineral fertilization or application of plant protection products after sowing, grain is harvested normally, use of the undersown material is allowed.
Flowering headland F	3a	Cultivation with a small-grain legume mixture of at least four species, no fertilizer or pesticides, access to the area remains guaranteed, mulching or mowing and use of the grown legumes is permitted, plowing is possible after August 31
Fallow land F	3b	Fallow strips with annual tillage, optional greening by seeding in autumn in the first year, no pesticides, no fertilization, mowing and removal of plant material in autumn
Extensive grassland F/N	6b	Perennial measure (target duration: 10 years), no fertilization or pesticides, 1–2 cuts/year with removal of mown material, no cultivation (no mowing, rolling or dragging) for eight weeks between May 10 and July 5
Topsoil removal F/N	6c	Topsoil, incl. vegetation, is scraped off to a depth of approx. 10–15(–20) cm and removed from the area, width approx. 5–10 m, removal: September/October or March/April, depending on the location, area can be sown with hay transfer or meadow-flower mixture or left to self-vegetate, maintenance requirements like old-grass strips
Maize-bean intercropping F	7	Area of mixed cultivation, use of pesticides only before cultivating beans, no mineral fertilizers (fertilizers up to 80 kg N/ha possible), sowing can be done simultaneously (one row of corn and one row of bean at a distance of 37.5 cm) or successively, seed strength: 50% climbing beans and 50% corn (6.5–7.5 grains/m ² of bean and corn seeds), preferred varieties: Annelino Verde, Annelino Giallo for beans, and a stable corn variety (e.g. KWS Figaro)
Non-F.R.A.N.Z. measures	Code	Definition
Flower strip F/(N*)	1	Flower strip as local conservation intervention implemented in the frame of agri-environmental schemes (AES) or contractual nature conservation. Exact requirements for implementation not known
Extensive grain F	2	Extensive grain as local conservation intervention implemented in the frame of AES or contractual nature conservation. Exact requirements for implementation not known
Fallow land F/(N*)	3	Fallow land as local conservation intervention implemented in the frame of AES or contractual nature conservation. Exact requirements for implementation not known

Table 1 (continued)

F.R.A.N.Z. measures	Code	Definition
Clover F	8	Cultivation of different varieties of clover on fields in the form of strips or wider areas, for example red clover or incarnate clover. Exact requirements for implementation not known
Alfalfa F	9	Cultivation of alfalfa on fields in the form of strips or wider areas. Exact requirements for implementation not known

* only valid for perennial interventions

Table 2 Statistics (medians, quartiles) of landscape metrics in ‘treatment’ and ‘control’ landscapes in the years 2017 and 2018. Differences between treatment and control landscapes were tested with Wilcoxon rank sum tests

Landscape metric	Treatment, <i>N</i> = 17	Control, <i>N</i> = 17	<i>P</i> -value
Area of cons. interv. (ha)	3.01 (1.60, 6.35)	0.00 (0.00, 0.00)	<0.001
Quality index of cons. interv.	2.07 (0.19, 4.91)	0.00 (0.00, 0.00)	<0.001
Crop richness	5.00 (4.00, 5.50)	5.00 (4.00, 5.00)	0.6
Crop evenness	0.79 (0.70, 0.83)	0.69 (0.49, 0.74)	0.001
Mass-flowering crops (ha)	4 (0, 18)	6 (0, 20)	0.8
Seminal natural habitats (ha)	4.13 (2.53, 8.55)	4.26 (3.43, 6.07)	0.6
Edge density (km/km ²)	15 (11, 19)	15 (11, 19)	0.5

Landscape analysis

We produced land-cover maps of all 1 × 1 km landscapes (both treatment and control) based on digital topographic maps (ATKIS) distinguishing arable land, grassland, forest, settlement, roads and further infrastructure. In addition, local conservation interventions and linear landscape elements, such as hedgerows and field margins, were manually digitized into the land-cover maps based on digital orthophotos and on-site mapping. The crop types of all arable fields were also mapped on site during the cropping season (Table S4). The spatial resolution of our land-cover maps was approx. 5 × 5 m for areal objects and min. 2 m width for linear landscape elements. The land-cover data were processed with ArcMap 10.7.1 (ESRI, USA).

To characterize the eighteen landscapes in terms of quantity and quality of implemented conservation interventions and landscape structure, we calculated seven landscape metrics to serve as predictor variables in statistical data analyses: (1) area of conservation interventions, (2) quality index of conservation interventions, (3) area of mass-flowering crops, (4) crop richness, (5) crop evenness (6) area of semi natural habitats and (7) edge density (see Table 2 for summary of descriptive statistics).

We calculated a quality index of the interventions to account for the differences between the types and bundles of measures implemented in the respective landscapes (Jönsson et al. 2015). To calculate this quality index, each intervention was evaluated by five attributes which represented relevant quality indicators of wild bee habitats: (1) flower diversity (number of species), (2) flowering period (period from first to last flowering day), (3) food

quantity (cover percentage of flowering plants), (4) provisioning of nest and overwintering habitats (based on lack of soil disturbance, ‘yes’ or ‘no’) and (5) the duration of measures (‘annual’ or ‘biennial’). Information on the different attributes was collected during the project and obtained from Flora Web (<https://www.floraweb.de/>). For each measure, we assigned specific weighting factors to the five attributes reflecting the putative strengths of positive effects on wild bees (Table S5). To calculate the quality index, the areas of the different types of measures were multiplied by the mean of their five weighting factors and, then, summed up per landscape using the formula:

$$quality\ index = \log\left(\sum (area_{measure\ type} * mean (weighting\ factors_{n=5}))\right) + 1$$

For crop richness, we calculated the total number of different crop-type categories per landscape (Table S5). Crop evenness was measured as Pielou index. The Pielou index is defined as $J' = H' / \ln(S)$ where H' is the Shannon-Wiener diversity index and S is the crop richness (Pielou 1966). If all crop types are represented in equal numbers in the sample, then $J' = 1$. If one crop type dominates, J' is close to zero. For calculating the variable ‘mass-flowering crops’, we summed up the area (in ha) of all occurring crops with flowers that can be used as food resource by bees, including *Brassica napus* (oilseed rape), *Trifolium spp.* (clover), *Vicia faba* (faba bean), and *Pisum sativum* (peas). The area of semi natural habitats (SNH) was summed up (in ha) across the habitat types hedges, field margins, orchards, woody elements, ditches, waters and ponds, and streamsides. Edge density was calculated as the sum of the lengths (km) of boundaries between all distinguished land-cover types (Table S4) per 1 km².

The landscape analysis confirmed a significant difference in area of local conservation interventions between treatment and control landscapes (Wilcoxon rank sum test, $p < 0.001$). Apart from that, the paired landscapes differed only in crop evenness ($p = 0.001$), but not in other landscape metrics (Table 2).

Sampling of wild bees

To record the abundance and richness of wild bees at landscape level, we conducted transect walks along edges of multiple land-cover types within the landscapes. Transects had a width of 4 m and a total length of 1000 m, which was subdivided into sections that were distributed among the major land-use types (forest, field, grassland, orchard), local conservation interventions and linear landscape elements proportionally to the lengths of their respective edges within the 1 km² landscapes. For this purpose, we classified all edges by the two adjacent land-cover types (e.g. arable field-forest or arable field-arable field or grassland-flower strip). Then, we calculated the proportions of the total edge length for each occurring edge class and multiplied these proportions with the total transect length of 1000 m in order to determine the class-specific lengths of the transect sections per landscape which ranged between 3 m (min.) and 484 m (max.) with a mean of 129 m. However, we excluded all edge classes that comprised aquatic habitats, settlements and traffic infrastructure from these calculations because we focused on farmed landscape components. Transect sections were distributed across the real landscapes as follows: during fieldwork, all mapped edge types and their corresponding edge areas were examined and the most appropriate ones were selected based on ranking of flower availability (i.e. visual assessment of cover of potential

foraging plants for wild bees), spatial distribution of other transects and accessibility. The 4-m wide transect sections were equally divided up between the two bordering habitat types. Depending on the width of the respective edges between the habitat types, the border of the more flower-rich habitat type defined the location of the transect section. Hence, 2 m of the respective transect sections covered the most flower-rich habitat type (e.g., flowering crop, conservation intervention), and 2 m covered the habitat type directly adjacent to the flower-rich habitat (e.g., field margin, dirt track, ditch, other crop or grassland). The locations of transect sections remained the same throughout the study.

The sampling took place during suitable weather conditions for pollinators (minimum of 17 °C, low wind, no rain and dry vegetation) from May to August 2017 and 2018 (Supplementary Material, Table S6). Bees (*Apiformes*) were recorded during three sampling periods over the sampling season ('early', 'mid' and 'late' season). All regions were sampled by the same person to avoid observer bias. Transects were walked along their center line. All observed bees (flying, resting, foraging) were caught with an insect net. For every 10 m of the transects, bees were observed for 1 min. While bees were captured and stored, time was stopped to standardize both sampling area and observation time (Westphal et al. 2008). Landscape pairs (treatment and control) were sampled on two consecutive days if weather conditions were suitable. Transect sections were sampled in a random order. All bees were collected for subsequent identification in the laboratory. All insects were processed, needed, and all bumblebee species (*Bombus spp.*) were identified. Solitary bees were identified by an external expert (Dr. Daniela Warzecha, Senckenberg Research Institute and Natural History Museum).

Classification of bee groups

As response variables for statistical analyses, we calculated species richness and abundance summed up across all transect sections per landscape of six bee groups: (I) all wild bees, (II) bumblebees and (III) solitary bees and, further, (IV) frequent, (V) common or (VI) rare bees. All recorded species that Westrich (2019) classified as 'very frequent' were assigned to the group 'frequent bees', while the group of 'common bees' comprised all species with Westrich's status 'frequent' and 'moderately frequent' and the group 'rare species' included species with the status 'rare' or 'very rare' (Table 3). Honey bees were not included, as their abundance is related to the presence of bee keepers in the landscapes, for which we had no information, and honey bees also cover longer flight distances (up to 10 km) and thus the independence of treatment and control landscapes would not be ensured. We analyzed different bee groups separately because they have specific traits and, thus, may respond differently to changes in land use (Forrest et al. 2015).

Statistical analysis

We analyzed whether species richness or abundance of bees were affected by characteristics of the landscapes (the seven landscape metrics described above) with Generalized Linear Mixed Models (GLMM), modelling each bee group separately. For this purpose, we used the *glmmTMB* package in R version 4.0.3. As the number of predictor variables was high in proportion to the sample size, we chose to conduct best-subset modelling and subsequent

Table 3 Abundance (A) and species richness (S) of wild bee groups per study region and landscape type, ‘treatment’ (T) or ‘control’ (C) landscape

Region	Landscape	Total		Bumblebee		Solitary		Frequent		Common		Rare	
		A	S	A	S	A	S	A	S	A	S	A	S
Havelland	T	117	33	48	11	69	22	35	5	73	22	6	4
	C	80	29	20	5	60	24	25	5	48	20	6	3
Hohenlohe	T	97	25	53	10	44	15	33	6	53	15	9	2
	C	53	19	34	9	19	10	26	6	20	11	7	2
Cologne Bay	T	167	16	139	5	28	11	65	3	96	12	0	0
	C	47	18	19	7	28	11	17	4	29	13	0	0
Lüneburg Heath	T	90	19	60	5	30	14	38	3	43	12	7	2
	C	66	14	48	5	18	9	50	4	15	9	1	1
Magdeburger Börde	T	101	26	39	5	62	21	24	5	74	19	1	1
	C	65	22	26	6	39	16	11	1	42	16	6	3
Lower Bavaria	T	158	24	69	8	89	16	44	5	110	17	4	2
	C	76	11	47	3	29	8	22	1	54	10	0	0
East Westphalia-Lippe	T	95	17	81	6	14	11	33	4	61	12	1	1
	C	64	16	42	5	22	11	37	3	27	13	0	0
Rhine Hesse	T	176	35	18	7	158	28	9	3	158	25	9	7
	C	124	35	18	8	106	27	11	6	103	22	10	7
Western Pomerania	T	122	31	70	11	52	20	26	4	73	21	23	6
	C	33	12	26	8	7	4	8	3	25	9	0	0

model averaging (multi-model inference) for estimating the effect sizes and testing significance using the MuMIn package (Barton and Barton 2020).

First, we constructed global models for each response variable (abundance or richness of the respective six bee groups) that contained all seven predictors to be tested and additional covariates of weather conditions during the sampling, i.e., sunshine duration, wind speed, and temperature, as well as a random intercept for the nine study regions. To derive weather data for the sampling per landscape and sampling season, we calculated the means of daily mean temperature, sunshine duration per hour and mean wind speed over the actual days of sampling using data from the nearest weather stations of the German Meteorological Service (Deutscher Wetterdienst, DWD). Additionally, we included the predictor variables ‘sampling season’ and ‘landscape type’ (treatment or control) in the global models, if they improved model fit as assessed by Akaike’s Information Criterion (AIC). Following this approach, a specific global model was found for each response variable (Supplementary Material, Table S7). The global models were set up with Poisson distribution or, in case of significant overdispersion as evaluated with the ‘overdisp_fun’ function by Bolker (<http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html>), with negative binomial distribution (Supplementary Material, Table S7). In all cases, logarithm was used as link function. To check for linearity, we used the cumres-function from the package ‘gof’ (Lin et al. 2002). Further, we calculated Variance Inflation Factors (VIF) to assess multicollinearity of the predictor variables with ‘vif’ function from the package ‘car’ (Fox and Weisberg 2019).

In the second step, we conducted best-subset modelling using the dredge function (package MuMIn) to generate a model selection table. The candidate models included at maximum two fixed effects and, additionally, the random intercept of ‘region’. Further, we set the constraint that models could only contain one of the predictors conservation interventions index or area of conservation interventions because of collinearity of these variables. Following this approach, models with all eligible two-way combinations of predictors were fitted to the data.

Finally, parameter estimation and significance testing were conducted by averaging all models for which the difference of the corrected Akaike’s information criterion (AICc) (Burnham and Anderson 2002) compared to the best model was smaller than 4 ($\Delta AICc < 4$) (Barton and Barton 2020). For this purpose, we used the function ‘model.avg’ from package MuMIn on the fitted models (option ‘fit=TRUE’).

Results

In total, 1731 individuals of 117 wild bee species were recorded (Supplementary Material, Table S8). Of those, 857 (49%) were bumblebee individuals from 18 (15%) species and 874 (51%) individuals were solitary bees from 99 (85%) species. Most of the species were usual crop-visiting species (Kleijn et al. 2015) classified as frequent (514 (29.7%) individuals, 12 (10.3%) species) or common (1104 (63.8%) individuals, 81 (69.2%) species). Bees classified as ‘rare’ occurred in small numbers (90 (5.2%) individuals, 20 (17.1%) species; see Table 3 for regional differences). Four species could not be assigned to any group due to insufficient data (Westrich 2019). According to the Red Data List of Germany (Westrich et al. 2011), 85 wild bee species recorded in this study were listed as not endangered, 14 species as near-threatened, 10 species as endangered and four species as critically endangered.

For two species their endangerment is unknown and for two more species there was insufficient knowledge to assess the status.

In the ‘treatment’ landscapes, abundance and richness of all bees and of common bees as well as richness of bumblebees were significantly higher compared to ‘control’ landscapes (Table 4). Still, both quantity and quality of local conservation interventions varied considerably between and among treatment and control landscapes (Table S3). Hence, we further considered the potential effects of area and of quality index of conservation interventions in our models. Solitary bee abundance and richness were positively affected by area of conservation interventions and, the former, also by quality index of conservation interventions (Fig. 2; Table 4). Likewise, abundance and richness of rare bees were significantly positively affected by area of conservation interventions and quality index of conservation interventions (Fig. 2; Table 4). Richness of common bees was also positively affected by area of conservation interventions (Fig. 2; Table 4).

The other landscape metrics also showed some importance in the models, with crop evenness, in particular, positively affecting abundances of bumblebees and frequent bees and richness of common bees (Figs. 2 and 3; Table 4). Crop-type richness had a significant positive effect on total bee abundance (Fig. 2; Table 4). Surprisingly, area of mass-flowering crops only showed a significantly negative effect on the abundance of frequent bees, but no positive effects (Fig. 3; Table 4). Further, we could not detect any effects of edge density or area of semi-natural habitats on any of the bee groups.

Discussion

Landscape-level effects of local conservation interventions

Several studies demonstrated that environmental measures, including many agri-environment schemes (AES), can benefit species richness and abundance of wild bees at both field and farm scale (Doublet et al. 2022; Hellwig et al. 2022; Klatt et al. 2020; Klaus et al. 2021; Scheper et al. 2015). Meta-analyses showed that the local effects of agri-environmental measures on pollinators in Europe increase with the quality of the measures regarding food (nectar, pollen) supply and with the ecological contrast in floral resources between the measures and control sites in studies of local abundance and richness (Scheper et al. 2013; Pérez-Sánchez et al. 2023). The finding that ecological contrast is a key driver of the local effect size of measures on pollinators may be explained by an attraction process in combination with the small scale of implementation (Scheper et al. 2013; Veddeler et al. 2006). Hence, the question remains whether local conservation interventions have only local effects through attracting pollinators from the surroundings and, thus, only spatially redistribute individuals from otherwise unaffected populations or whether they also result in increased pollinator abundance and richness at the landscape level and long-term population effects (Kleijn et al. 2018). Thus far, there is still scarce evidence for such landscape-level effects of local conservation interventions on wild bees (Beyer et al. 2021; Jönsson et al. 2015).

The results of our study suggest that local conservation interventions have positive landscape-level effects on wild bees already shortly after their implementation. Besides enhancing floral resources, the conservation interventions may benefit pollinators by providing

Table 4 Summaries of averaged models of effects of local conservation interventions and other landscape metrics on different target variables of wild bee abundance and richness. Only significant predictors are shown, excluding covariates of weather and sampling season. For complete summaries see supplementary Material, Table S9 and for best-subset selection tables see Table S10

Target	Predictor	Estimate	Std. Error	Adjusted SE	Z value	P
Total bee abundance						
	Intercept	3.1215	0.1138	0.1166	26.7722	<0.001
	Landscape type	0.5846	0.1357	0.1389	4.2101	<0.001
	Crop richness	0.1448	0.0638	0.0654	2.2148	0.027
Total bee richness						
	Intercept	2.1927	0.1142	0.1169	18.7555	<0.001
	Landscape type	0.3432	0.0882	0.0904	3.7988	<0.001
Bumblebee abundance						
	Intercept	2.6118	0.2056	0.2083	12.5401	<0.001
	Crop evenness	0.3218	0.1235	0.1264	2.5462	0.011
Bumblebee richness						
	Intercept	1.2277	0.1421	0.1447	8.4872	<0.001
	Landscape type	0.3120	0.1469	0.1505	2.0733	0.038
Solitary-bees abundance						
	Intercept	2.5444	0.2175	0.2231	11.4070	<0.001
	Area of conservation interventions	0.2605	0.0828	0.0849	3.0669	0.002
	Conservation interventions index index	0.2522	0.0896	0.0918	2.7467	0.006
Solitary-bees richness						
	Intercept	1.7444	0.1331	0.1365	12.7802	<0.001
	Area of conservation interventions	0.1820	0.0720	0.0738	2.4667	0.014
Rare-bees abundance						
	Conservation interventions index index	0.5509	0.1321	0.1354	4.0680	<0.001
	Mean temperature	-0.4004	0.1140	0.1168	3.4283	<0.001
	Area of conservation interventions	0.4407	0.1042	0.1068	4.1258	<0.001
Rare-bees richness						
	Area of conservation interventions	0.3872	0.1558	0.1596	2.4263	0.015
Common-bees abundance						
	Intercept	2.5692	0.1725	0.1769	14.5251	<0.001
	Landscape type	0.6527	0.1582	0.1621	4.0256	<0.001
Common-bees richness						
	Intercept	1.7697	0.1251	0.1274	13.8930	<0.001
	Landscape type	0.3183	0.1128	0.1154	2.7575	0.006
	Crop evenness	0.1405	0.0642	0.0658	2.1362	0.033
	Area of conservation interventions	0.1175	0.0570	0.0585	2.0109	0.044
Frequent-bees abundance						
	Intercept	2.1721	0.1134	0.1163	18.6814	<0.001
	Crop evenness	0.2512	0.1043	0.1069	2.3486	0.019
	Mass-flowering crops	-0.3538	0.1378	0.1412	2.5048	0.012
Frequent-bees richness						
	Intercept	0.8051	0.1118	0.1141	7.0539	<0.001

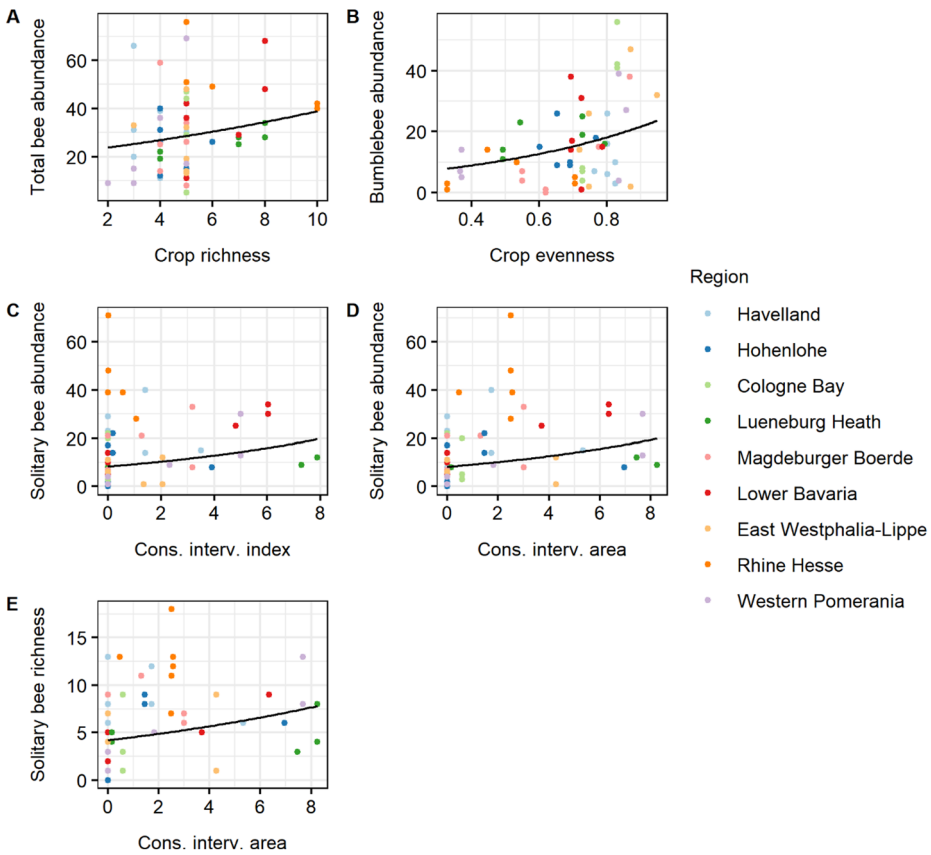


Fig. 2 Total bee abundance (A), bumblebee abundance (B), solitary bee abundance (C-D), and solitary bee richness (E) relative to the significant predictors of each, as indicated by multimodel inference. Regression lines were built from coefficients of averaged models (intercept and slope of x-variable). If ‘landscape type’ (treatment vs. reference landscape) was significant in the averaged model, half of the amount of its estimate was added to the intercept in order to display an average regression curve

nesting sites or reduced exposure to pesticides (Scheper et al. 2013). Some local conservation interventions, such as perennial flower strips, can remain undisturbed for a longer period of time. Ground-nesting species can, therefore, find suitable nesting sites on flower strips and also on fallows and other perennial measures that are not disturbed by tillage (Pfiffner et al. 2018). Lack of soil disturbance and, as a result, potential nest and overwintering habitat is crucial for the survival of primarily ground-nesting bee species (Westrich 2019).

Previous studies showed that local conservation interventions seem to be particularly valuable for common species of broad floral diets because the measures often include plant species that are visited by generalist pollinators, such as bumblebees and honeybees (Bänisch et al. 2020; Wood et al. 2015). In line with this, we found positive effects of the landscapes with increased area of local conservation interventions (‘treatment’ landscapes) on the species groups of bumblebees and common wild bees. However, in contrast to previous

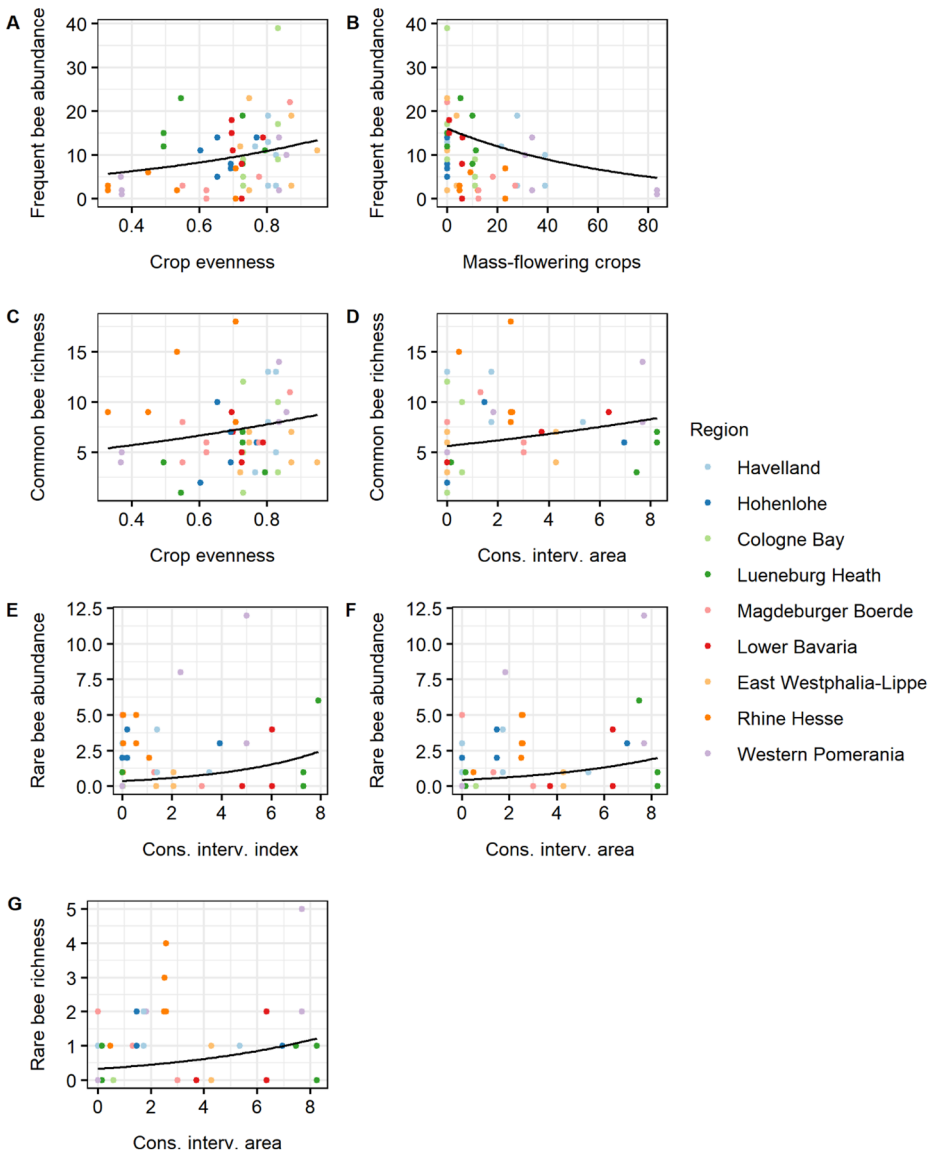


Fig. 3 Frequent bee abundance (A–B), common bee richness (C–D), rare bee abundance (E–F) and rare bee richness (G) relative to the significant predictors of each, as indicated by multimodel inference. For details see Fig. 2

research, we found stronger effects of increasing area of local conservation interventions on solitary bees and rare bees, whereas we found no effects on the most frequent bee species.

Although the local conservation interventions within our study landscapes of 1×1 km cover only 2 ha on average (range 0 ha to 7.7 ha), they have a significant effect on the richness of common bees and on the richness and abundance of solitary bees and rare bees. According to the model of solitary bees, each hectare of local conservation intervention

increases the abundance by the factor 1.10, and 7 ha of local conservation interventions per square kilometer yield a doubling of the abundance compared to agricultural landscapes without any measures. For rare bees, the effect size of the area of local conservation interventions is even larger with a factor of 1.18 per hectare and a doubling of the abundance at 4 hectares. For comparison, the model of all wild bees together predicts 1.8 times higher abundances in the treatment landscapes that had a median area of local conservation interventions of 3 ha compared to control landscapes with virtually no measures.

Enhanced solitary bee abundance at the landscape level in response to sown wildflower fields was also reported by Kleijn et al. (2018), where introducing wildflower fields significantly enhanced abundances of solitary bees in an area of 10–26 ha. Kleijn et al. (2018) concluded that positive large-scale effects on solitary bee abundance can be explained by the fact that the sown wildflower fields in their study mostly replaced crop monocultures.

As expected, we generally found only very few individuals and species of the rare group. Rare species often have very specific requirements with respect to both food and nesting sites. Thus, a possible explanation for the significant relationship between abundance and richness of rare bees and the area of local conservation interventions could be that the measures include flower types or microhabitats for specialized species that are largely missing in the agricultural landscapes of our study areas. When those rare species do occur, they probably react particularly sensitively to the implementation of measures, as these often represent the only food source in addition to semi-natural habitats, which are often of poor quality with respect to flower diversity and abundance in our study areas. However, most of the rare species that we found are polylectic, while only five species, represented by 22 individuals, actually depend on specific plant families. They feed on Brassicaceae and Asteraceae, which are present in the most frequently implemented measure type, i.e., perennial flower strips. Additionally, the local conservation interventions included plant families for several oligolectic bee species, e.g., Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Fabaceae and Resedaceae. Altogether, it appears that some rare bee species can benefit from local conservation interventions in agricultural landscapes with low flower diversity in semi-natural habitats, but it is unlikely that the measures are sufficient to sustain all rare bee species.

Surprisingly, our study did not show an effect of area of measures on bumblebee abundance and richness. Bumblebees have a larger flight radius and are, accordingly, less dependent on resources in the close neighborhood compared to solitary bees (Osborne et al. 2008a, b). One reason why bumblebees and frequent bees (the majority of this group consists of bumblebees) generally benefit from measures, but do not achieve significantly higher abundance or richness in our study is possibly their ability to access more distant food sources so that they are less dependent on additional food or nesting resources provided by local conservation interventions. Also, social bees often prefer mass-flowering resources while many solitary bees exploit more sparsely distributed flowers (Bänsch et al. 2021).

With the quality index, inspired by (Jönsson et al. 2015), we aimed to better represent the habitat qualities for wild bees of different types of measures in terms of floral resources (quantity, diversity, flowering period) and nesting sites. Not all measures improved floral abundance in the landscapes, because they were not specifically designed to benefit bees, but to increase biodiversity in general. Therefore, we expected a stronger relationship between the quality index of conservation interventions and the abundance and species richness of wild bee groups compared to the area of local conservation interventions. In fact, the

quality index showed similar results as the area of measures, but did not perform better in the models. A possible explanation might be that we had to assess the quality of measures based on the sown seed mixtures, as precise records of the actually established and flowering plant species on the plots of the measures were not available. However, the realized plant composition may deviate substantially from the sown seed mixture (Warzecha et al. 2021). Further, the quality of floral resources, e.g., specific flower types or plant families and genera, may be more important than quantity of flowers and overall species richness of flowering plants. Thus, for future studies, the quality index of conservation interventions should be improved so as to include the number of different flower types and plant diversity at the family/genera level and it should be calculated based on field records of the established plants on each measure. Alternatively, the quality of the measures may not have been more important than their quantity in our studied landscapes because they are of comparatively low structural complexity. Fijen et al. (2025a) found that increasing habitat quantity was by far the most effective approach for boosting pollinator populations in simple landscapes, whereas in more complex agricultural landscapes, characterized by cover of seminatural habitat above 15%, improving habitat quality increased pollinator populations more effectively than increasing habitat quantity.

Implications for implementation of local conservation interventions

Wood et al. (2016) found that bee species occurring in agricultural fields varied widely in their pollen choices and that species with the widest foraging range were the most abundant. They advised increasing plant diversity as part of local conservation interventions to provide a wider range of pollen resources to promote diverse bee communities on agricultural land (Wood et al. 2016). Essential for the provision of floral resources for bees is not only plant diversity but also the cover of particular plant species (Potts et al. 2010). Sutter et al. (2017) suggested that key plant species, e.g., *Origanum vulgare* and *Achillea millefolium*, which are visited by all groups, should receive special attention as part of local conservation interventions and to promote also rare species. According to Warzecha et al. (2018), the quality of seed mixtures is not dependent on the number of plant species, but can be increased by selecting a few key plant species during the flowering period.

Our models of solitary and rare bees suggest that increasing area of local conservation interventions has continuous positive log-linear effects on wild bees that do not seem to level off within the studied range of 0–7.7 ha. Hence, there does not seem to be a minimum required area of local conservation interventions, but already a single hectare has some effect. However, it is not possible to identify an optimal area that would be most cost-effective based on our data. If the goal was to increase the abundance of rare and solitary bees by 30%, our models suggest that 1.6/2.7 ha of local conservation interventions were required. However, the quality of measures and the surrounding landscape will also play a role and, therefore, these values cannot be easily transferred to other settings.

Crop richness and crop evenness

A higher number of different crops in the landscapes (crop richness) had a substantial positive effect on the overall abundance of wild bees. Further, crop evenness had a positive effect on the abundance of bumblebees and of frequent bees as well as on the richness

of common bees (Fig. 2). Crop richness and evenness can be essential as each crop type is associated with a typical accompanying vegetation. If there is an equal distribution of the different crop types, it is more likely that the crops that are providing resources for wild bees, such as legumes, are also better distributed and, thus, more accessible to species with shorter foraging ranges. Additionally, increased crop richness and evenness may imply greater resource continuity across seasons for pollinators in the landscape (Fahrig et al. 2011). Moreover, crop rotation and management affect the flower-plant communities in field margins, which are important for bumblebees (Marja et al. 2018). Sirami et al. (2019) found that greater crop heterogeneity can be an effective way to increase biodiversity in agricultural landscapes without having to take land out of agricultural production. Such positive effects of crop diversification on pollinating insects were corroborated by Fijen et al. (2025b). In contrast, other studies have found no effects or even negative effects of crop diversity. Hass et al. (2018) detected a decreased abundance of bees and argued that high crop diversity (Shannon index) may be due to an increase in crops with particularly intensive management, highlighting the importance of crop identity. Further, Kleijn et al. (2018) argued that observed pollinator densities at a given sampling location and time are influenced by variation in the availability of co-flowering resources from other crops and semi-natural habitats across the landscape and, thus, the effects of crop diversity on pollinators may also vary.

Mass-flowering crops

For most bee groups, our results indicate that abundance and species richness in the landscape are not affected by availability of mass-flowering crops (Table 4). We even found that the abundance of frequent bees is negatively affected by increasing area of mass-flowering crops. This is in contrast to previous studies showing that mass-flowering crops can increase wild bee abundance at the landscape level by providing more resources, i.e., pollen and nectar, over the time span of their respective flowering period (Diekötter et al. 2014; Holzschuh et al. 2013; Rundlöf et al. 2014; Westphal et al. 2003). Especially, oilseed rape is one of the most important mass-flowering crops and can promote pollinators, e.g., the growth of bumblebee colonies (Westphal et al. 2009). Furthermore, oilseed rape can also be important for population growth of solitary bees, which can reproduce in the early seasons when oilseed rape is flowering (Diekötter et al. 2014; Jauker et al. 2012). However, the floral resources of oilseed rape are only available for a relatively short period of time. Therefore, pollinators also need other complementary food sources throughout the season (Marja et al. 2018; Riedinger et al. 2015; Westphal et al. 2009; Williams et al. 2012).

As all surveys were carried by the same observer, there were time lags between the surveys in different regions. The earliest sampling took place in early May, while the latest sampling period of the early season was in late June (Supplementary Material, Table S6). Although we considered the phenological differences within Germany in the order of sampling, certain early wild-bee species with short activity periods that potentially benefit from oilseed rape and other early mass-flowering crops may have been missed during the transect walks in study areas where sampling started comparatively late. However, there was a strong negative correlation between the date of earliest sampling (day of year) and area of mass-flowering crops, which would rather bias our data towards a positive effect.

Therefore, the lack of positive effect of mass-flowering crops does not appear to be due to the sampling scheme.

Agricultural management should also focus on growing flower-morphologically diverse mass-flowering crops, which increases functional plant diversity and, as a consequence, improves pollinator diversity (Beyer et al. 2020, 2021; Sutter et al. 2017). In addition to oilseed rape, very small areas of field bean, pea, clover and alfalfa were cultivated in individual regions during the surveys. Especially Fabaceae, like clover, field bean and pea, that produce high protein pollen, are important for social species, like bumblebees (Beyer et al. 2021; Goulson et al. 2005). Consistent with our results, Holzschuh et al. (2016) found a similar dilution effect, i.e., a negative relationship between the cover of mass-flowering crops and pollinator densities in fields across Europe. Beyer et al. (2021) also found that a high proportion of oilseed rape in the surrounding landscape had a slightly negative effect on the proportion of social bees. They argue that single mass-flowering crops cannot maintain a functionally diverse wild bee community in agricultural landscapes because the additional availability of nesting sites and the continuity of floral resources after the end of mass-flowering is of enormous importance (Potts et al. 2005; Riedinger et al. 2015; Rundlöf et al. 2014). Alternatively, our selection of transect sections only covered the edges of some of the mass-flowering crops and the effects on the more frequent bees may have been underestimated due to the aforementioned dilution effect.

Seminatural habitats

We did not find effects of the area of semi-natural habitats on abundance or richness of any of the bee groups. This is in contrast to previous studies, which generally showed that a higher proportion of semi-natural habitats increases species richness and abundance of wild bees (Meyer et al. 2009; Ricketts et al. 2008; Steffan-Dewenter et al. 2002). For example, bee species richness in wildflower strips on cropland increased with the proportion of semi-natural habitats in the landscape (Krimmer et al. 2019; Scheper et al. 2015). Beyond species richness, also flower-visitation rates and overall pollination service decrease with distance from (semi-)natural habitats (Garibaldi et al. 2011; Kennedy et al. 2013; Ricketts et al. 2008). In general, semi-natural habitats provide nesting and overwintering sites (Goulson 2003; Kells et al. 2001) as well as nectar and pollen via flowering plants (Hicks et al. 2016; Kraemer and Favi 2005) which often are insufficient in managed agricultural landscapes.

Hass et al. (2018) suggested that limited variation of the area of semi-natural habitats among study areas in intensively used agricultural landscapes may explain the lack of statistically significant relationship with pollinator abundance and richness. In our study, the area of semi-natural habitats ranged between 1.1 and 12.2% of the study areas (cf. also Table 2) and there was not the slightest tendency towards a positive relationship. This suggests that the lack of positive effect is rather not a statistical issue.

The environmental conditions and local management of semi-natural habitats are important determinants of their habitat quality (Byrne and DelBarco-Trillo 2019). In our study, the semi-natural habitats included many field margins, ditches and similar linear landscape elements, which often are not very diverse and may be affected by agrochemicals (pesticides, fertilizer) from adjoining crops in intensive agricultural landscapes (Holland et al. 2016). However, there were very few hedgerows, which are important foraging and nesting sites for pollinators (Osborne et al. 2008a, b), and also very few extensive grasslands and groves.

Altogether, it appears that low habitat quality of the semi-natural habitats in our study due to intensive agricultural land use is a likely explanation for not finding a positive effect on pollinators.

Edge density

For none of the wild bee groups, we detected effects of edge density. This contradicts our expectations and the literature showing beneficial effect of higher edge densities on pollinator abundance (Fahrig 2017; Gayer et al. 2021; Martin et al. 2019). We expected that especially solitary bees would benefit from higher edge density as they rely on small-structured habitats and short distances to nesting and foraging sites due to their limited flight capacities compared to bumblebees (Westrich 2019; Zurbuchen et al. 2010). However, solitary cavity-nesting bee species do not seem to respond to dispersion and connectivity of habitats in the landscape (Holzschuh et al. 2009; Steckel et al. 2014).

It appears unlikely that the lack of effect of edge density was due to the sampling design, i.e., recording wild bees along transects on the edges of the major land-use and land-cover types. If our sampling had favoured bee species that preferentially occur in edge habitats, the relationship between edge density and species richness and abundance should have become even stronger. We assume that the specific landscape settings in our study areas are the cause for finding no effects of edge density.

In our study, we did not distinguish between the types and qualities of edges. Often linear elements, such as field margins, are of poor quality, with few available food and nesting sites. Thus, the missing effect of edge density might be explained by low habitat quality of the edges. Another reason may be that landscapes did not differ sufficiently in terms of field sizes and edge densities. Hass et al. (2018) demonstrated effects of edge density on pollinators using more than 200 agricultural landscapes and a much longer gradient of 68–625 m/ha) compared to our study with 37–289 m/ha.

Conclusions

We found that local conservation interventions in intensively managed agricultural landscapes can have positive effects on bee abundance and richness at landscape level already shortly after their implementation. Besides common bee species and bumblebees, particularly solitary bees and rare bees can benefit from increased area and quality of local conservation interventions. Already few hectares of local conservation interventions per square kilometer can have substantial effect on the abundance of wild bees in intensively managed and structurally simple agricultural landscapes (30% increase of abundance of rare and solitary bees at 1.6 and 2.7 ha of local conservation interventions, respectively). Beyond local conservation interventions, crop richness and evenness have positive influence on abundance and richness of wild bees, while semi-natural habitats (here: mostly field margins) and edge density appear to be less important in the studied landscape settings. Mass-flowering crops do not seem to be a vital alternative to local conservation interventions for promoting wild bees at landscape level. Hence, local conservation interventions which increase the availability of floral resources and may serve as habitat for ground-nesting species, together

with crop diversification could be part of the solution for pollinator conservation in intensive agricultural landscapes.

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Author contributions JD developed the conception and design of the study. JD and JK selected the study landscapes. JK performed the field research. JT supported statistical and landscape analyses. JK analyzed the data and wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

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Data availability Data are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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