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Habitat quality and surrounding landscape structures influence wild bee occurrence in perennial wildflower strips

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Abstract

Perennial wildflower strips (WFS) are known to have positive effects on wild bees in intensively used agricultural landscapes. Little knowledge exists, however, about the drivers of wild bee occurrence and if Red List species also profit from this agri-environmental scheme (AES). Therefore, we studied wild bees on transects along 20 four- to five-year-old WFS and in 10 cereal fields without AES (CONTROL sites) in differently structured landscapes across Saxony-Anhalt (Germany). In addition to local site parameters, we measured parameters of landscape structure in a 1 km radius of the WFS and CONTROL sites. The overall species richness of wild bees (125 species in total, 23 on average), including numerous specialist and Red List species, indicates a high attractiveness of perennial WFS sown with 30 native forbs. In CONTROL fields, 11 bee species (on average only one) were found.

The species richness and abundance of wild bees were positively affected by local site conditions of the WFS and CONTROL sites, such as the overall number of sown and spontaneous forbs, the amount of flower rewards of sown forbs available to pollinators (Pollinator Feeding Index), and negatively by the cover of grasses. Therefore, seed mixtures of future AES should comprise a high diversity of wildflower species relevant as pollen sources for wild bees. The share of Red List wild bee species was strongly influenced by the landscape context and increased e.g. with Shannon landscape diversity and the availability of non-forest woody habitats and water bodies in the 1 km surroundings. These results suggest that besides the establishment of high-diversity WFS, semi-natural habitat structures have to be promoted to preserve rare wild bees especially in structurally simple agricultural landscapes.

Keywords: Agri-environmental schemes; Wild bees; Wildflower strips; Landscape structures; Landscape heterogeneity

Introduction

Against the background of the continuing massive decline in biodiversity (Van Swaay et al., 2019; Lebuhn et al., 2013), determining factors that influence the success of agri-

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environmental schemes (AES) is of great importance. Flower strips are a valuable tool to promote biodiversity in agricultural landscapes (Haaland, Naisbit & Bersier, 2011; Vickery, Feber & Fuller, 2009) and can enhance pest control and pollination in adjacent crops (Albrecht et al., 2020; Blaauw & Isaacs, 2014). Subsidized within AES, perennial flower strips are sown on a part of the arable field once at the beginning of the funding period of five years. Afterwards, the areas have to be plowed and are again used for crop cultivation. In the Common Agricultural Policy (CAP) funding period 2014−2020, the federal state Saxony-Anhalt (Germany) focused on the creation of perennial wildflower strips (WFS) with certified seed mixtures containing 30 native forbs (Fenchel et al., 2015).

Up to now, most flower strips were sown with low-diversity mixtures of cultivated species or non-regional seed mixtures (but see Schmidt, Kirmer, Hellwig, Kiehl, & Tischew, 2021). Therefore, only a few studies have analyzed the establishment success and ecological effectiveness of perennial wildflower strips sown exclusively with seeds of regional origin under practical conditions by farmers (Schmidt, Fartmann, Kiehl, Kirmer & Tischew, 2022, Schmidt, Kiehl, Kirmer & Tischew, 2020).

Besides the local availability of flower resources (e.g. Wood, Holland, Goulson & Beggs, 2017), landscape ecological factors may play a role in the attractiveness of flower strips for insect species and should be taken into account in planning (Diekötter, Billeter & Crist, 2008; Tscharntke, Klein, Kruess, Steffan-Dewenter & Thies, 2005). To our knowledge, only one study has provided evidence for the influence of landscape heterogeneity on the flower strip effect in relation to the wild bee species group (Grass et al., 2016). Other studies were limited to bumblebees (Carvell et al., 2011; Korpela, Hyvönen, Lindgren & Kuussaari, 2013) or showed no effects of landscape ecological factors on wild bees (Ganser, Albrecht & Knop, 2021; Scheper et al., 2015). The latter study pointed to the need for accurately recording nesting and foraging sites of wild bees in the surrounding landscape.

Bommarco et al. (2010) stated that common generalist bee species are more likely to be found in structurally simple landscapes because they are less dependent on connectivity between semi-natural habitats than specialist species. Yet, it is unclear to what extent wild bee species composition (Red List species vs. common species), especially in WFS, is affected by surrounding landscape structures.

In this study, we investigated the attractiveness of WFS for wild bees in the CAP funding period 2014−2020 in Saxony-Anhalt in the fourth or fifth year after implementation, taking into account landscape structures within a radius of 1 km of the flower strip. We hypothesized that wild bee species richness, abundance and Red List species were affected by both WFS characteristics and surrounding landscape structures. The aim was to answer the following questions: (i) To what extent do WFS, sown with a prescribed mixture of 30 wildflower species, increase wild bee species richness and abundance, and also attract endangered or specialized bee species? (ii) Which WFS characteristics influence wild bee occurrence in WFS?; and (iii) Do surrounding landscape structures have an effect on wild bee species richness, abundance and Red List species? If so, which parameters play a decisive role?

Materials and methods

Study design

WFS study sites were randomly selected from 272 perennial wildflower strips implemented by farmers in 2015 or 2016 under AES in the federal state of Saxony-Anhalt (Germany) (see Schmidt et al., 2021). Based on the biotope type mapping of Saxony-Anhalt from 2009, we calculated the proportion of semi-natural habitats relevant for wild bees (fallows, flower strips, parks, allotments, grassland, hedgerows and shrubs) in a 1 km radius around all WFS (regarding the selected radius see section Landscape context). For the wild bee surveys, we chose 20 WFS covering a gradient of landscape heterogeneity, from simple to complex agricultural landscapes (Appendix A). Flower strip area of the WFS ranged between 0.3 and 4.5 ha (mean area 1.8 ha ± 1.0 SD).

In addition, 10 cereal fields were selected as CONTROL sites, also covering a gradient of landscape heterogeneity (Appendix A). Per landscape unit (after Reichhoff, Kugler, Refior & Warthemann, 2001) where the WFS were situated (arable plains, southern lowlands, river valleys and lowlands, mid-mountain forelands) at least one CONTROL site was selected. All CONTROL and WFS sites were at least 1 km apart and distributed throughout Saxony-Anhalt (Fig. 1). The CONTROL sites were located at most 2 km away from a corresponding WFS.

All WFS were sown with a prescribed seed mixture that contained 30 native forbs from certified regional seed propagation (Appendix B; Fenchel et al., 2015). Exemplary photos of the four- to five-year-old WFS are provided in Appendix C.

Vegetation surveys and wild bee sampling

We recorded the occurrence of all vascular plants on a $5 \times 200\text{-m}^2$ transect placed 2 m parallel to the edge of the WFS or CONTROL field (Schmidt et al., 2021). In addition, we estimated the percentage cover of plant species and open soil on four $2 \times 2\text{-m}^2$ plots positioned in the middle of each 50-m section of the transect (Appendix D). Vegetation surveys were carried out in May and June 2019. Plant identification followed Jäger (2017).

To estimate pollen and nectar availability in each site, we used the Pollinator Feeding Index (PFI), developed by Schmidt et al. (2021), separately calculated for sown and

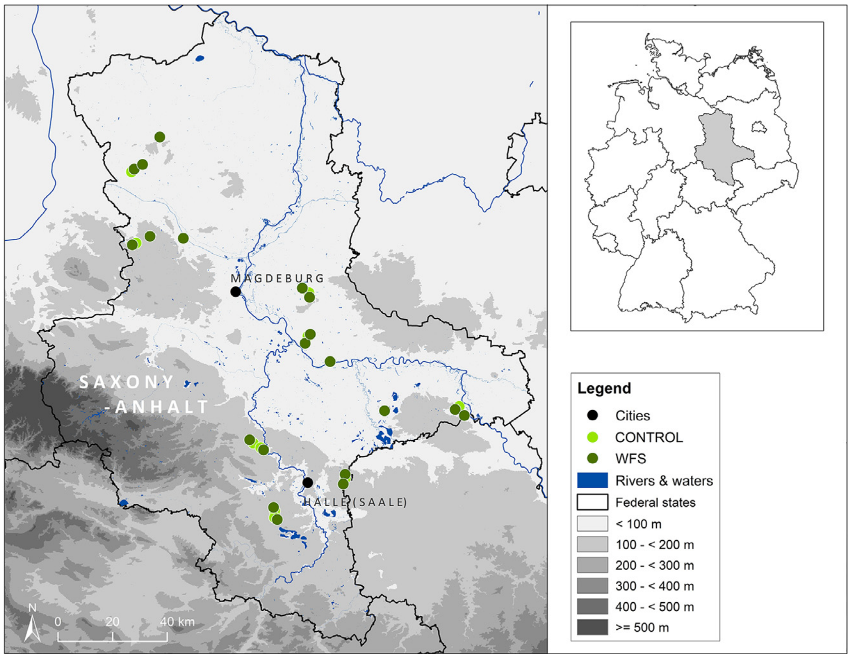

Fig. 1. Location of the 20 wildflower strips (WFS) and 10 CONTROL fields in Saxony-Anhalt, Germany (data basis: DLM 250, ArcGIS Online ILS_data).

spontaneously established forbs. The PFI includes pollen (P) and nectar production (N), flowering period (number of months after Jäger, 2017), and cover of the respective plant species (i):

$$PFI_{plot} = \sum_{i=1}^{n} (P_i + N_i) \times flowering\ period_i \times cover_i$$

Forb species were separately divided into classes of nectar and pollen productivity, ranging from 0 = without to 4 = very high (Pritsch, 2018). Finally, the PFI_{plot} values of the four 2 × 2-m^2 vegetation plots were averaged per site.

Wild bee sampling was performed using a semi-quantitative transect method. Bee transects were located in the middle of the vegetation transects, with a length of 100 m and a width of 2 m (Appendix D). Over a period of 10 min, each transect was traversed and wild bees were caught with an aerial net by steady sweeping (‘transect catches’). After that, for another 10 min, wild bees were captured by targeted sweeping outside the bee transect (‘additional catches’) to better estimate total bee species richness of the study sites. Wild bees which could not be determined in the field were taken to the laboratory for identification. The sampling took place between 10 am and 5 pm in spring and between 9 am and 5 pm in summer under dry and warm weather conditions (minimum 13 °C) with low wind force (maximum 3 Bft). The surveys were carried out monthly from April to August 2019. Wild bee identification and nomenclature followed Scheuchl & Willner (2016) and the literature listed within.

The species richness of wild bees is based on data from transect catches and additional catches, whereas the abundance of wild bees includes only transect catches, since the additional catches covered only new species. The target variable ‘share of Red List wild bee species’ represents the Red List species of Germany (Westrich et al., 2011) and Saxony-Anhalt (Saure, 2020) (including categories ‘near threatened’ and ‘threat of unknown magnitude’) relative to total species richness per site.

To analyze influencing factors for wild bee occurrence on the level of wild bee traits, we aggregated wild bee species by nesting type and lecty after Westrich (1990) (Table 1). On the level of Red List status, we divided wild bee species into species of the German (Westrich et al., 2011) and Saxony-Anhalt’s Red Lists (Saure, 2020) (Table 1).

Landscape context

The classification of landscape structures was carried out using the biotope mapping key for Saxony-Anhalt (Peterson & Langner, 1992) complemented by habitat structures being relevant for wild bees (e.g. potential nesting sites, flower-rich biotopes; Appendix E). We mapped landscape structures within a radius of 1 km around the WFS and CONTROL sites in summer 2019 (1 km circle around the middle of each transect). The radius size corresponded to the maximum foraging ranges of most wild bee species (Zurbuchen & Müller, 2012). The collected data were digitalized using ESRI ArcMap 10.6.1. The following variables from landscape surveys in 2019 were considered in the analyses: Shannon landscape diversity index, percent cover of built-up area, water bodies, non-forest woody habitats, grasslands,

Table 1. Factors included in the analysis of WFS attractiveness for wild bees. Except 'pollen.cultivated', all factors regarding site characteristics and landscape context were surveyed in 2019. Letters in parentheses at the landscape context level refer to the code of the mapping key (Appendix E). Wild bee traits follow Westrich (1990). Red List status included the categories 'near threatened' and 'threat of unknown magnitude' and was divided into species of the German (Westrich et al., 2011) and Saxony-Anhalt's Red List (Saure, 2020).

Level	Independent factors	Definition
Site characteristics	Variant	WFS (wildflower strip) and CONTROL (cereal field)
	Number.forbs	Number of established sown and spontaneously established forb species
	PFI.sown.forbs	Pollinator Feeding Index of (established) sown forb species (the amount of flower rewards of sown forbs available to pollinators)
	PFI.spont.forbs	Pollinator Feeding Index of spontaneously established forb species (the amount of flower rewards of spontaneously established forbs available to pollinators)
	Cover.bare.soil	Cover of bare soil (%)
	Cover.grasses	Cover of grasses (%)
Landscape context (1 km radius)	Pollen.cultivated	Spatial index of pollen-providing cultivated plants (years 2014−2019) relevant for wild bees
	Shannon.index	Shannon landscape diversity index (SDHI)
	Built-up.area	Proportion of built-up area (B) (%)
	Water.bodies	Proportion of water bodies (including e.g. ponds, ditches, and watersides) (G) (%)
	Woody.habitats	Proportion of non-forest woody habitats (H) (%)
	Grasslands	Proportion of grasslands (K) (%)
	Forest	Proportion of forest (W) (%)
	Reeds	Proportion of reeds (GU.s) (%)
	Flower.strips	Proportion of flower strips and areas on arable land (AAa) (%)
	Flower.rich.all	Proportion of forb-rich biotope structures and flower-rich areas on arable land including flowering crops (%); details see Appendix F
Wild bee traits	Ground-nesting	Ground-nesting wild bee species (yes/no)
	Cleptoparasitic	Cleptoparasitic wild bee species (yes/no)
	Polylectic	Polylectic wild bee species (yes/no)
Red List	Red.List.Germany	Species on Red List of Germany (yes/no)
	Red.List.Saxony-Anhalt	Species on Red List of Saxony-Anhalt (yes/no)

forests, reeds, flower strips and flower-rich structures (Table 1). Flower strip area in the 1 km radius of the WFS ranged between 0.3 and 11.2 ha (mean area 4.3 ha ± 3.4 SD), and in the 1 km radius of the CONTROL sites between 0 and 1.7 ha (mean area 0.5 ha ± 0.6 SD).

To assess the possible effects of cultivated plants providing pollen, we used IACS (Integrated Administration and Control System) data for the period 2014 to 2019. For this purpose, the percent cover of each crop in a radius of 1 km around the WFS and CONTROL sites was multiplied by the respective class of pollen productivity, ranging from 0 = without to 4 = very high (Pritsch, 2018), and then averaged over all years. Cereals, including maize, were excluded, because they are rarely used by wild bees as food sources.

Data analyses

We estimated a maximum number of species by calculating a species accumulation curve for wild bees found in the 20 WFS sites, applying the Michaelis-Menten function (Appendix G: Fig. G.1; Dengler, 2009). Significant differences in total richness and abundance of wild bee species between WFS and CONTROL sites were analyzed with Mann-Whitney U test.

To statistically analyze the attractiveness of WFS for wild bees, we selected 21 factors at the following levels: site characteristics (of WFS and CONTROL sites), landscape context (1 km radius), wild bee traits and Red List status (Table 1). We used statistical models to analyze the relationships between these factors and three target variables: (1) the total species richness of wild bees, (2) the total abundance of wild bees, and (3) the share of Red List wild bee species. None of these variables was spatially autocorrelated based on empirical variogram analysis.

The effects of influencing factors on wild bees were analyzed by aggregating wild bee data in two ways: (1) per species, including only the WFS sites (n = 2520, as result of 20 WFS sites multiplied by 126 sampled species in total), and (2) per site, including the WFS and CONTROL sites (n = 30). The one-to-one relationships between influencing factors and target variables (species richness of wild bees, abundance of wild bees, and share of Red List wild bee species) were quantified by Pearson correlation analysis. Multivariate influences on wild bees were analyzed in five model variants (Table 2). To achieve a sufficient sample size at site level (Models C, D and E), we included all 30 study sites in

Table 2. Model variants for the analysis of multivariate influences on wild bees (GLM = generalized linear model, GLMM = generalized linear mixed model).

Model	Data aggregation	Sample size	Target variable	Influencing factors	Model approach
A	per species	$n = 2520$	Species presence (binary data)	Site characteristics + Landscape context + Wild bee traits + Red List	GLMM (Logistic Mixed Regression)
B	per species	$n = 2520$	Abundance per species	Site characteristics + Landscape context + Wild bee traits + Red List	GLMM (Negative Binomial Mixed Regression)
C	per site	$n = 30$	Wild bee species richness	Site characteristics + Landscape context	GLM (Negative Binomial Regression)
D	per site	$n = 30$	Wild bee abundance	Site characteristics + Landscape context	GLM (Negative Binomial Regression)
E	per site	$n = 30$	Share of Red List species	Site characteristics + Landscape context	GLM (Linear Regression)

generalized linear models (GLMs). None of the influencing factors (Table 1) were intercorrelated with $|r| > 0.7$ (Appendix H).

All models were built using the best subset selection based on Bayesian Information Criterion (BIC) from all model candidates with one to four predictors. Species richness and abundance of wild bees were modeled as negative binomial distributed random variables. We chose BIC as the criterion for model selection to prefer simple over complex models in view of the small number of study sites in relation to the number of influencing factors (Brewer, Butler, Cooksley & Freckleton, 2016). BIC model weights were calculated according to Buckland, Burnham and Augustin (1997). All statistical analyses were implemented in R, version 4.0.2 (R Core Team, 2020). For modeling, we applied the R packages "lme4″ (Bates, Mächler, Bolker & Walker, 2015) and "MASS" (Venables & Ripley, 2002). All model results are provided in detail in Appendix I.

Results

Wild bee occurrence in WFS and CONTROL sites

From April to August 2019, a total of 1253 individuals, representing 126 wild bee species, were caught, 125 species (1232 individuals) in WFS and 11 species (21 individuals) in CONTROL sites (species list in Appendix J). The species accumulation curve predicted a maximum of 177 wild bee species if more WFS were sampled (Appendix G: Fig. G.1). The species richness of wild bees detected in WFS represents about 30% of the species inventory for Saxony-Anhalt (Fig. 2A) and 21% of the German inventory. Of all bee species recorded in the WFS, 16% are on the Red List of Saxony-Anhalt and 34% on the Red List of Germany (on average 29 ± 11% Red List species per WFS; ± SD). In the WFS, 15% of the recorded wild bee species were oligolectic species (on average 2.7 ± 1.7 species per WFS; ± SD), 22% were cleptoparasitic, while the rest represented polylectic species (Fig. 2B). The non-parasitic species were predominantly ground-nesting (51% of all collected species), while the remaining fraction were above-ground nesting (24%) or both (3%). On average, 23 wild bee species and 44 individuals were recorded per WFS and one species and two individuals per CONTROL site. The differences between WFS and CONTROL sites were highly significant (Fig. 2C and D; WFS vs. CONTROL sites: $p \leq 0.001$; Mann-Whitney U test).

WFS exhibited on average 58 (± 10 SD) forb species, of which 24 (± 4 SD) were sown. The five most abundant forb species in WFS were the sown forbs *Achillea millefolium* (11 ± 14%), *Galium album* (5 ± 12%), *Centaurea jacea* (3 ± 4%), *Origanum vulgare* (3 ± 7%) and *Leucanthemum vulgare* (3 ± 6%) (mean forb cover ± SD).

Site and landscape effects on wild bee occurrence

In general, species richness and abundance of wild bees were moderately to strongly correlated with local site characteristics of WFS/CONTROL sites (number of forbs and the Pollinator Feeding Index of sown forbs) and only to a lesser extent with landscape factors (Table 3). In contrast, the share of Red List species was only slightly affected by site characteristics, but several landscape factors showed a strong positive influence (Shannon landscape diversity, water bodies, woody habitats, grasslands, and reeds; Table 3). The one-to-one correlation analyses confirmed the modeling results in Table 4 (also when considering only WFS sites, Appendix G: Table G.1).

The species richness of wild bees in Model A (n = 20 WFS sites) was only explained by local site characteristics (Table 4). This model showed a significantly higher probability that one of the recorded wild bee species occurred at a WFS site with increasing number of forb species and decreasing cover of grasses. Further, a Red List status decreased the probability of wild bee occurrence at the WFS sites. In Model C, which included all WFS and CONTROL sites (n = 30), species richness of wild bees was affected by the site characteristics number of forbs (positively) and cover of grasses (negatively) in the best model, and additionally by landscape factors in the second and third best models (positive effects of woody habitats and built-up area).

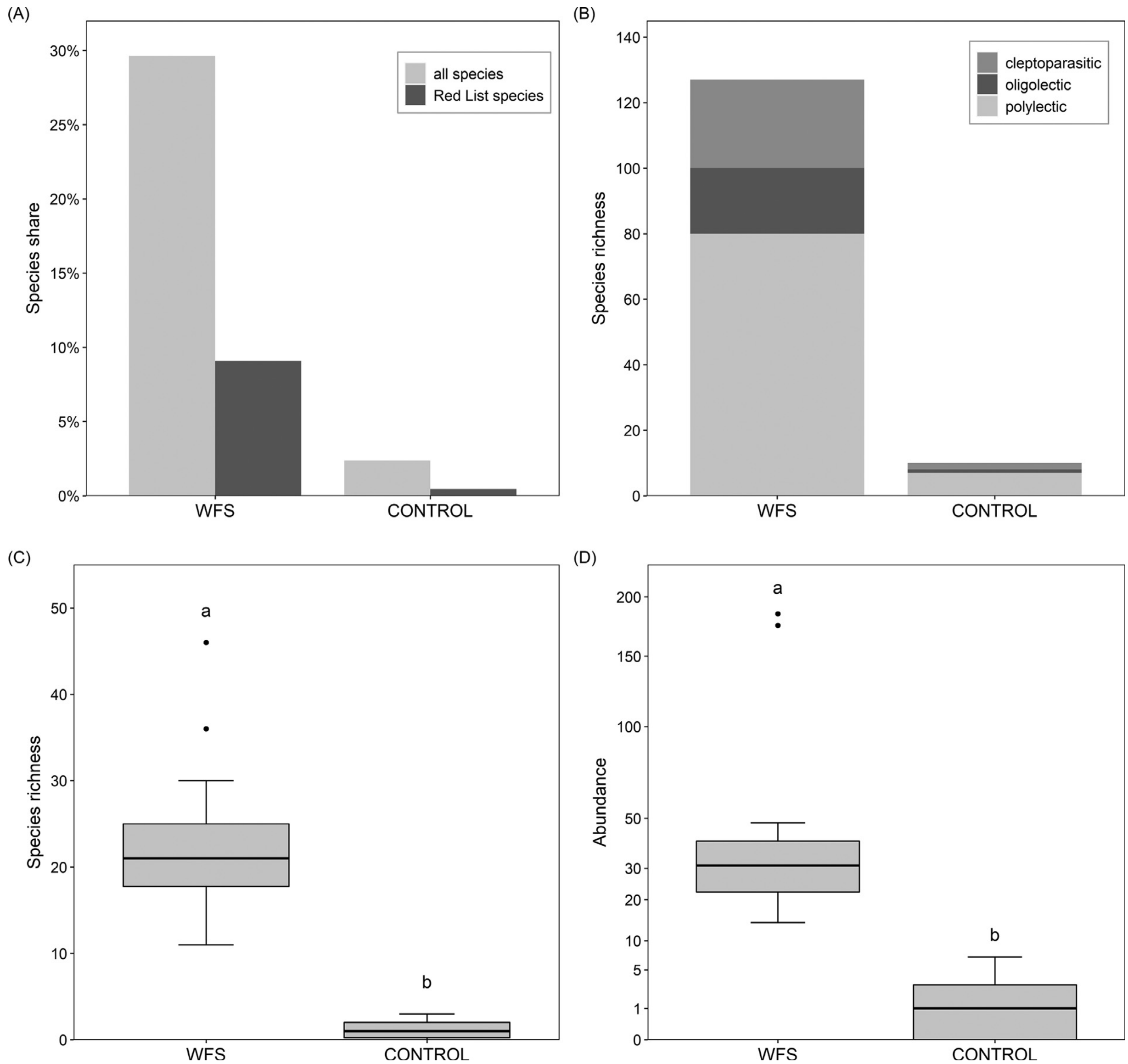

Fig. 2. Occurrence of wild bees in wildflower strips (WFS) and CONTROL sites. Letters a and b denote significant differences ($p \leq 0.05$). (A) Species share of all wild bee species for Saxony-Anhalt, and those listed on the Red Lists of Germany or Saxony-Anhalt; (B) Species richness of wild bees concerning their lecty (Westrich, 1990); (C) Species richness of wild bees per site; (D) Abundance of wild bees per site.

For the abundance of wild bees in Model B (n = 20 WFS sites), only local site characteristics and some functional traits of wild bees played a role (positive effect of number of forbs and ground-nesting species and negative effect of cleptoparasitic life form, Table 4). When analyzing the abundance of wild bees per site (Model D, n = 30 sites, Table 4), we found relevant site characteristics and landscape factors: the abundance was positively influenced by the number of forbs and the Pollinator Feeding Index of sown forbs and negatively by the cover of grasses, water bodies, and Shannon landscape diversity in the 1 km radius.

The share of Red List bee species was positively related to several landscape factors, such as the proportion of woody habitats, grasslands, water bodies and reeds, whereas built-up areas had a negative effect (Table 4, Model E).

Discussion

Attractiveness of wildflower strips for wild bees

The AES ‘perennial WFS’ strongly supported a much higher variety of wild bee species and individuals than reported by most European flower strip studies (e.g. Grass et al., 2016; Holland, Smith, Storkey, Lutman & Aebischer, 2015; Jönsson et al., 2015; Ouvrard, Transon & Jacquemart, 2018). Although generalists prevailed, Red List species, oligolectic and cleptoparasitic bees reached a considerable share of total wild bee species richness. Other studies mainly reported common wild bee species in flower strips (Haaland et al., 2011; Warzecha et al., 2018, but see Pywell et al., 2012). The wildflower mixes in our study are

Table 3. Relationships between target variables (species richness and abundance, and share of Red List species of wild bees) and influencing factors (see Table 1) based on data from WFS+CONTROL sites ($n = 30$), as evaluated by the Pearson correlation coefficient r. Significant correlations are in bold and labeled by asterisks: *** $p \leq 0.01$, ** $p \leq 0.05$, * $p \leq 0.1$. WFS = wildflower strip.

Influencing factor	WFS+CONTROL sites ($n = 30$)		
	Species richness	Abundance	Red List species share
Site characteristics			
Number.forbs	**0.903*** **	**0.582*** **	0.165
PFI.sown.forbs	**0.708*** **	**0.559*** **	0.180
PFI.spont.forbs	**0.496*** **	0.250	0.214
Cover.bare.soil	−0.088	0.133	−0.234
Cover.grasses	0.238	0.005	−0.055
Landscape context (1 km radius)			
Pollen.cultivated	0.158	−0.049	−0.265
Shannon.index	0.125	−0.040	**0.315***
Built-up.area	−0.116	−0.158	−0.173
Water.bodies	0.204	−0.121	**0.406** **
Woody.habitats	0.045	0.104	**0.318***
Grasslands	−0.125	−0.139	**0.535*** **
Forest	0.248	−0.064	0.063
Reeds	0.054	−0.064	**0.551*** **
Flower.strips	**0.485*** **	0.201	0.010
Flower.rich.all	−0.019	−0.117	0.035

Table 4. Best three model candidates for Models A-E from the best subset selection based on the Bayesian Information Criterion (BIC). Model responses include the probability p that a wild bee species is present at a study site (Model A, based on $n = 20$ WFS sites), the species richness of wild bees (w_{rich}) per study site (Model C, based on $n = 30$ sites), the wild bee abundance (w_{abund}) per species (Model B, based on $n = 20$ WFS sites) and per study site (Model D, based on $n = 30$ sites), and the share of Red List wild bee species (w_{red}) per study site (Model E, based on $n = 30$ sites). Models A and B include random intercepts r(Site) and r(Species). BIC weights are based on all models with ΔBIC < 2. See Table 1 for definition of influencing factors and Appendix I for more details on model results.

Model formula	BIC	BIC weight
Model A		
$\log(p / (1 - p)) = 0.031 * \text{Number.forbs} - 3.733 + \text{r(Site)} + \text{r(Species)}$	2095.27	0.45
$\log(p / (1 - p)) = 0.030 * \text{Number.forbs} - 0.008 * \text{Cover.grasses} - 3.405 + \text{r(Site)} + \text{r(Species)}$	2095.93	0.32
$\log(p / (1 - p)) = 0.031 * \text{Number.forbs} - 0.748 * \text{Red.List.Saxony-Anhalt} - 3.617 + \text{r(Site)} + \text{r(Species)}$	2096.65	0.23
Model B		
$\log(w_{abund}) = 0.034 * \text{Number.forbs} - 4.397 + \text{r(Site)} + \text{r(Species)}$	2391.08	0.66
$\log(w_{abund}) = 0.034 * \text{Number.forbs} + 0.670 * \text{Ground-nesting} - 4.760 + \text{r(Site)} + \text{r(Species)}$	2392.42	0.34
$\log(w_{abund}) = 0.034 * \text{Number.forbs} - 0.784 * \text{Cleptoparasitic} - 4.234 + \text{r(Site)} + \text{r(Species)}$	2393.30	−
Model C		
$\log(w_{rich}) = 0.020 * \text{Number.forbs} - 0.006 * \text{Cover.grasses} + 1.924 * \text{VariantWFS} + 0.181$	162.36	0.54
$\log(w_{rich}) = 0.018 * \text{Number.forbs} - 0.007 * \text{Cover.grasses} + 0.030 * \text{Woody.habitats} + 2.075 * \text{VariantWFS} + 0.046$	163.85	0.26
$\log(w_{rich}) = 0.020 * \text{Number.forbs} - 0.006 * \text{Cover.grasses} + 0.014 * \text{Built-up.area} + 1.959 * \text{VariantWFS} + 0.090$	164.31	0.20
Model D		
$\log(w_{abund}) = 0.038 * \text{Number.forbs} - 0.011 * \text{Cover.grasses} - 0.124 * \text{Water.bodies} + 1.424 * \text{VariantWFS} + 0.547$	226.99	0.15
$\log(w_{abund}) = 0.039 * \text{Number.forbs} - 0.015 * \text{Cover.grasses} - 0.553 * \text{Shannon.index} + 1.434 * \text{VariantWFS} + 1.524$	227.08	0.14
$\log(w_{abund}) = 0.039 * \text{Number.forbs} + 0.001 * \text{PFI.sown.forbs} - 0.115 * \text{Water.bodies} + 0.658 * \text{VariantWFS} + 0.537$	227.61	0.11
Model E		
$w_{red} = 2.495 * \text{Woody.habitats} + 0.973 * \text{Grasslands} + 11.706 * \text{VariantWFS} - 4.069$	266.83	0.10
$w_{red} = - 1.443 * \text{Built-up.area} + 3.082 * \text{Water.bodies} + 3.498 * \text{Woody.habitats} + 0.678 * \text{Grasslands} + 5.951 * \text{VariantWFS} + 1.904$	266.91	0.10
$w_{red} = 3.051 * \text{Water.bodies} + 61.492 * \text{Reeds} + 3.904 * \text{VariantWFS} + 14.111$	266.99	0.09

adapted to the needs of native insect communities and include 30 native wild forbs from several key plant families for wild bees such as Asteraceae, Fabaceae, Lamiaceae and Campanulaceae, which address also rare bee species (see also Scheper et al., 2014). Especially oligolectic bee species are dependent on certain plant families or genera for pollen supply. The oligolectic bee species recorded in our WFS are specialized on Asteraceae, Fabaceae and *Reseda* that are included in the seed mixtures, as well as Brassicaceae and *Salix* that occurred spontaneously in or next to the WFS sites. For example, *Pseudoanthidium nanum* relies on Asteraceae (Cynareae) pollen (Westrich, 2019), which was represented by the sown forbs *Centaurea jacea* and *C. stoebe* in the WFS. Another Red List bee, *Hoplitis tridentata*, is specialized on Fabaceae (Westrich, 2019) and may have benefitted from *Lotus corniculatus*. In contrast to our species-rich mixture of native forbs, many low-diversity mixtures contained mostly annual and cultivated forbs and grasses (Holland et al., 2015; Jönsson et al., 2015) that fail to support a diverse bee community.

Regarding the total richness of wild bee species in flower strips, comparisons to other European studies are difficult. Methodological differences, e.g. fewer sampling sites (Grass et al., 2016; Scheper et al., 2015), fewer sampling dates per season (Grass et al., 2016; Jönsson et al., 2015) or younger flower strips (Grass et al., 2016; Scheper et al., 2015) complicate comparability. Regarding the number of sampling sites, our species accumulation curve (Appendix G: Fig. G.1) illustrated that in total 24% fewer bee species are expected to be found if only ten instead of 20 WFS were studied. Moreover, many studies concentrated only on bumblebees or used experimental plots (Haaland et al., 2011; Warzecha et al., 2018) instead of flower strips established by farmers under practical conditions.

Factors influencing wild bee occurrence in perennial wildflower strips

Wild bee species richness and abundance were mostly affected by local habitat characteristics, namely the overall number of sown and spontaneous forbs, the Pollinator Feeding Index of sown forbs (positive effects) and the cover of grasses (negative effect). Several authors (e.g. Haaland et al., 2011; Scheper et al., 2015; Wood et al., 2017) also stated that a high diversity of wildflowers supports a high diversity of wild bees, as different plant species attract different wild bee species. Ebeling, Klein, Schumacher, Weisser and Tscharntke (2008) reported a positive relationship between the number of flowering plant species and the number of pollinator species.

Although wild bee relevant habitats in the 1 km radius of all study sites were mapped in detail, only water bodies and Shannon landscape diversity negatively influenced the abundance of wild bees in Model D. This negative effect can be explained by the ecological contrast phenomenon (Scheper et al., 2013). A high Shannon landscape diversity index means a more diverse landscape with more forb-rich structures and nesting sites, offered for example along the banks of water bodies. It is possible that wild bee individuals were more concentrated in WFS that lacked these structures in their vicinity, and thus had high ecological contrast to their surroundings.

Regarding wild bee species richness, there was only little evidence for the influence of landscape structures in the 1 km surroundings (positive effect of woody habitats and built-up areas only in the second and third best models of Model C), but see Hellwig, Schubert, Kirmer, Tischew and Dieker (2022) for other spatial scales. Several studies showed positive effects of semi-natural habitats (Jauker, Diekötter, Schwarzbach & Wolters, 2009; Kratschmer et al., 2018; Steffan-Dewenter, Münzenberg, Bürger, Thies & Tscharntke, 2002) or negative effects of arable land cover (Grass et al., 2016) on wild bee occurrence. In our study, the higher importance of local factors as compared to the landscape context could be caused by the strong influence of WFS site characteristics that may have masked landscape effects, as also noted by Jönsson et al. (2015).

Another explanation could be that the four- to five-year-old WFS, due to their age, served not only as foraging habitat, but also as nesting habitat for wild bees. Even though flower resources are particularly important for structuring wild bee communities (Torné-Noguera et al., 2014), nesting requisites must also be considered (Schmid-Egger & Witt, 2014). Observations of nest entries in the WFS during the field season (Appendix C) and the positive effect of bare soil cover of WFS on bee richness and abundance (Appendix G: Table G.1) support this idea.

Studies which observed distinct effects of the surrounding landscape so far surveyed younger flower strips or patches (Grass et al., 2016; Steffan-Dewenter et al., 2002). In older WFS, an accumulation effect is probable. For example, Buhk et al. (2018) found that oligolectic bee species increased significantly from the third year onwards. The expected accumulation of bee species in WFS over time is one reason to demand perennial instead of one-year AES. But due to the multifunctionality of four- to five-year-old WFS as foraging and nesting sites, their abrupt destruction after the funding period could lead to a collapse of the wild bee populations. Therefore, an even longer funding period, e.g. up to ten years, would be the most beneficial to support locally established bee communities as would continuously newly created WFS in the surroundings.

Factors influencing Red List wild bee occurrence

Our study gives evidence for the first time that the occurrence of Red List bee species in WFS is strongly determined by landscape factors such as Shannon landscape diversity and the proportions of grasslands, woody habitats, reeds and water bodies in the 1 km radius. Those landscape structures can provide specific nesting sites and therefore appear as limiting factors in intensively managed agricultural landscapes especially for endangered wild bees. In contrast, local site characteristics were less important for these species.

An important contribution to the high share of Red List bee species in WFS is the amount of semi-natural habitats in the surroundings. On average, about 19% (± 12 SD) semi-natural habitats were found in the 1 km radius of WFS (see Appendix A). Wood et al. (2017) confirmed that a landscape composed of about 20% semi-natural habitats supported a relatively high bee diversity. In more simple landscapes, on the contrary, our WFS supported only some Red List species, but a high number of common wild bee species, which nevertheless are important for pollination services (Kleijn et al., 2015).

Model limitations

The analyses in this study were based on a limited number of 20 WFS, but corresponded to previous studies in WFS effectiveness for wild bees (e.g. Grass et al., 2016; Jönsson et al., 2015). Moreover, the data were based on a high collection standard with five inspections per site. Given the limited sample size and the diversity of independent factors (Table 1), multivariate models are subject to uncertainties and are only valid to describe the multivariate influences in the site and the landscape context of this study. It remains a future challenge to enhance the understanding of interactions, causalities and mechanisms of the here described factors in their effects on wild bees in WFS based on larger data sets.

Conclusion and implications for future AES

Our results illustrate the high value of the AES 'perennial WFS', as they can serve as habitats for numerous wild bee species, including Red List species. In contrast, only few wild bee species with low abundance were found in the cereal fields without WFS. Besides a high number of forb species in WFS, their attractiveness for wild bees also depends on the landscape context, which is particularly relevant for Red List species. We have shown that endangered wild bee species benefit from WFS primarily in complex landscapes, where WFS can offer valuable foraging resources due to the high quality of the seed mixture, containing a high diversity of native forb species relevant as pollen sources for wild bees. Nevertheless, we also recommend the establishment of WFS in simply structured landscapes, where they support common bee species and contribute to connecting habitat structures (Grass et al., 2019). The establishment of perennial forb-rich WFS, at least five years of age, is of great benefit for wild bee conservation in both structurally simple and complex landscapes to support common as well as Red List wild bee species. Furthermore, our findings suggest that, in addition to perennial WFS, permanent structures such as forb-rich grasslands, field margins, orchards and hedges need to be established, improved and sustained, especially in simply structured agricultural areas.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.12.007.

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