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Effects of perennial wildflower strips and landscape structure on birds in intensively farmed agricultural landscapes

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Abstract

Farmland bird populations are in a deep crisis across Europe. Agri-environment schemes (AES) were implemented by the European Union to stop and reverse the general decline of biodiversity in agricultural landscapes. In Germany, flower strips are one of the most common AES. Establishing high-quality perennial wildflower strips (WFS) with species-rich native forb mixtures from regional seed propagation is a recent approach, for which the effectiveness for birds has not yet been sufficiently studied. We surveyed breeding birds and vegetation on 40 arable fields with WFS (20 with single and 20 with aggregated WFS) and 20 arable fields lacking WFS as controls across Saxony-Anhalt (Germany). Additionally, vegetation composition, WFS quantity and landscape structure (e.g. distance to nearest woody element) were considered in our analyses. All WFS were established with species-rich native seed mixtures (30 forbs) in agricultural practice as AES. Arable fields with WFS had a higher species richness and territory density of birds than controls, confirming the effectiveness of this AES. A forb-rich vegetation was the main driver promoting birds. Flower strip quantity at the landscape level had positive effects only on bird densities, but also single WFS achieved benefits. A short distance from WFS to woody elements increased total bird species richness. However, the density of farmland birds, which are target species of these AES, were negatively affected by the proximity and proportion of woody elements in the vicinity. The effect of the proportion of non-intensively used open habitats and overall habitat richness was unexpectedly low in the otherwise intensively farmed landscape. Species-rich perennial WFS significantly promoted breeding birds. Successful establishment of WFS, resulting in high-quality habitats, a high flower strip quantity as well as implementation in open landscapes were shown to maximise the effectiveness for restoring declining and AES target farmland birds.

Keywords: agri-environment scheme; arable field; biodiversity conservation; farmland bird; flower strip; native plant species; seed mixture; species richness; vegetation composition; wildflower area

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Introduction

The sharp decline of bird species in agricultural landscapes throughout Europe has been well documented since the 1980s (Keller et al., 2020; PECBMS, 2020). The reasons are manifold and species-specific, but in many cases agricultural intensification has caused the loss of breeding and foraging habitats due to removal of semi-natural features, and the loss of food resources such as invertebrates and seeds (Benton, Vickery, & Wilson, 2003). With the integration of agri-environment schemes (AES) into the Common Agricultural Policy (CAP) in the 1990s, the European Union has tried to stop and reverse this ongoing decline of biodiversity by adopting more environment-friendly management practices (Batáry, Dicks, Kleijn, & Sutherland, 2015; Kleijn et al., 2006). Perennial flower strips are a major component of the European AES policy. In contrast to annual flower strips, they are sown once in the beginning of the funding period and most commonly have to stay in place for five years. Farmers get subsidies for implementation and maintenance of the flowering aspect, and to compensate for yield loss.

The benefits of AES for birds have been investigated in many European countries (Baker, Freeman, Grice, & Siriwardena, 2012; Redhead, Hinsley, Beckmann, Broughton, & Pywell, 2018; Tarjuelo et al., 2021; Zingg, Ritschard, Arlettaz, & Humbert, 2019) and have mostly shown positive effects (Díaz & Concepción, 2016). Nevertheless, studies focussing on the effectiveness of flower strips for birds are still rare (but see Meichtry-Stier, Jenny, Zellweger-Fischer, & Birrer, 2014) and often deal with other taxonomic groups such as pollinators. Detailed studies on related systems like field margins, fallows and grasslands do exist (Bright et al., 2015; Meichtry-Stier, Duplain, Lanz, Lugrin, & Birrer, 2018; Princé & Jiguet, 2013; Vickery, Bradbury, Henderson, Eaton, & Grice, 2004), but the results cannot be fully transferred to flower strips due to a different land use history, size and/or vegetation structure. With increasing competition for land between social, economic and ecological demands, however, subsidised high-quality AES like flower strips currently appear to be one of the most accepted and effective measures to maintain common farmland species in otherwise intensively used farmland. Therefore, they have to be optimised to increase their function for biodiversity support.

If AES aim to promote population increases, it is important to improve the understanding of how the measures affect farmland birds (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Redhead et al., 2018). The requirements of birds are often very specific. Vegetation composition is probably among the most important flower strip features determining habitat quality and is thus central to delivering benefits (Kleijn & Sutherland, 2003; Vickery et al., 2004). Species-poor mixtures containing mainly plant cultivars, as they are still commonly used in practice, often lead to dense and grass-dominated vegetation stands (Schmidt, Kirmer, Kiehl, & Tischew, 2020) that birds are reluctant to use as nesting sites or to access prey (Vickery, Feber, & Fuller, 2009). By using species-rich wildflower mixtures, originating from certified regional seed propagation and including only forb species, floristically diverse and flower-rich wildflower strips can be developed, if properly established (Schmidt et al., 2020). Such perennial wildflower strips sown with a high species richness and proportion of regionally typical native forb species are probably well suited to promote birds by providing a diverse range of food and nesting resources, but scientific evidence of their effects on birds are still lacking.

Since the effectiveness of conservation actions seems to be a function of measure-induced ecological contrast and landscape context (landscape-moderate conservation effectiveness hypothesis, Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011), benefits should not only be assessed based on local field conditions. Hence, the impact of wildflower strips on birds may only be fully understood if effects caused by landscape composition and configuration of their vicinity are also taken into account. Since birds have comparatively large home ranges, it is worth knowing if there are stronger positive effects with increasing overall flower strip proportion in the landscape (Zingg et al., 2019). In addition, bird species richness, species composition and abundance considerably respond to presence, proportion and configuration of semi-natural habitats like woody elements or non-intensively used open habitats e.g. grassland at larger scales (Fartmann et al., 2018; Meichtry-Stier et al., 2018; Tschumi et al., 2020). From this, it can be derived in which landscape context species richness and density of birds, and especially of AES target farmland birds, may be higher and thus, wildflower strips would probably develop their highest effectiveness and should preferably be placed.

As the crisis of farmland bird populations is ongoing and financial resources are limited, evaluation of the still insufficiently investigated ecological effectiveness of species-rich perennial wildflower strips (WFS) in practice is mandatory. The present study compared arable fields with perennial WFS and control fields to evaluate the effects of vegetation composition, WFS quantity and landscape structure in the 1000-m vicinity on species richness and territory density of all and AES target farmland birds. All flower strips were implemented as AES by farmers and were spread across the federal state of Saxony-Anhalt (Germany).

We addressed the following questions:

(1) Do arable fields with wildflower strips (WFS) have higher species richness and territory density of birds in agricultural landscapes than arable fields lacking WFS? Do effects differ between all birds and AES target farmland birds?

(2) Are bird species richness and territory density positively correlated with high-quality forb-rich vegetation, WFS quantity or depend on landscape structure (proportion of forest and non-intensively used open habitats at the landscape level, distance to the nearest woody element, habitat richness)? Do effects differ between all birds and AES target farmland birds?

Materials and methods

Study area

The study was conducted in the agriculturally used lowland areas of the federal state of Saxony-Anhalt, central Germany (ca. 18,000 km^2). The climate is rather dry (annual mean temperature 9.3°C; annual precipitation 579 mm; long-term mean 1981-2010 (German Meterological Service, 2020)). About two-thirds of the state's area is agricultural land, the majority of which is intensively used as arable land, mainly cereal, rape and maize cultivation, with high fertilization and herbicide application rates. The average field size is high (c. 30 ha) in all sub-regions of Saxony-Anhalt, leading to an overall low number of semi-natural habitats such as field margins and hedgerows. A quarter of Saxony-Anhalt is forest. Study sites were located in the landscape units Southern lowlands, arable plains, river valleys and lowlands, and mid-mountain forelands (Fig. 1).

Study design and WFS specification

Study sites with WFS were selected from 272 perennial wildflower strips (WFS) implemented by farmers in agricultural practice on arable fields according to the Saxony-Anhalt AES directive for a funding period of five years (Fig. 1). Additionally, we chose 20 cereal crop fields lacking WFS as controls. Since we investigated either single or aggregated WFS each with 20 replicates, study site selection was stratified-randomized. No other WFS was located in the 1000-m vicinity of the single WFS (mean distance ± SD: 2,629.3 ± 3,171.4 m). Aggregated WFS comprised several WFS, which were spatially and functionally related due to their short distance to each other (mean distance ± SD: 48.0 ± 80.1 m). Only one WFS was surveyed within each aggregated WFS. The uneven spatial distribution of the study plots in Saxony-Anhalt corresponds to a regionally varying participation of farmers in the AES. Controls were also stratified-randomly selected from cereal crop fields located in a distance of 1,185.9 ± 260.4 m (mean ± SD) to the nearest WFS plot to ensure they were similar to WFS plots regarding abiotic site conditions, landscape structure and species pool. WFS (single and aggregated) and controls were always selected in a 2:1 ratio per landscape unit (Fig. 1).

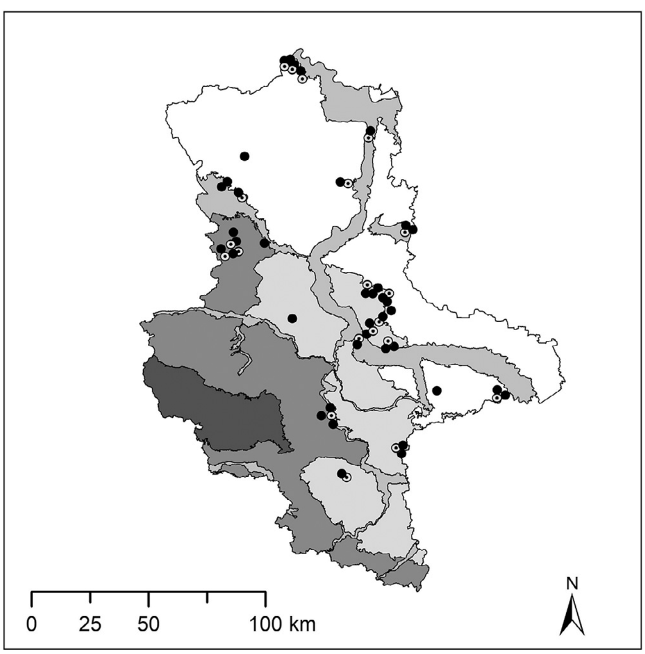

Fig 1. Location of the study plots in Saxony-Anhalt (central Germany): wildflower strip plots (black dots) and controls (two-coloured dots). Filled in greyscale: landscape units simplified based on Reichhoff, Kugler, Refior, and Warthemann (2001). Southern lowlands (white), arable plains (lightest grey), river valleys and lowlands (light grey), mid-mountain forelands (grey), mid-mountains (dark grey).

All WFS were established in 2015 or 2016. At the time of data collection in 2017, they were therefore in the second/third year. Seed mixtures prescribed for AES within the CAP funding period 2014−2020 in Saxony-Anhalt, contained 30 native forbs from certified regional seed propagation (Appendix A: Table 1, Fenchel et al., 2015). The produced seeds originated from parent seeds collected in the wild with proof of provenance (Mainz & Wieden, 2019). The mean width of the examined WFS was 20.1 ± 9.1 m (mean ± SD) and all had a minimum length of 200 m.

Bird surveys

Birds were surveyed through territory mapping (Südbeck et al., 2005) on a 4-ha plot per site. The quadratic

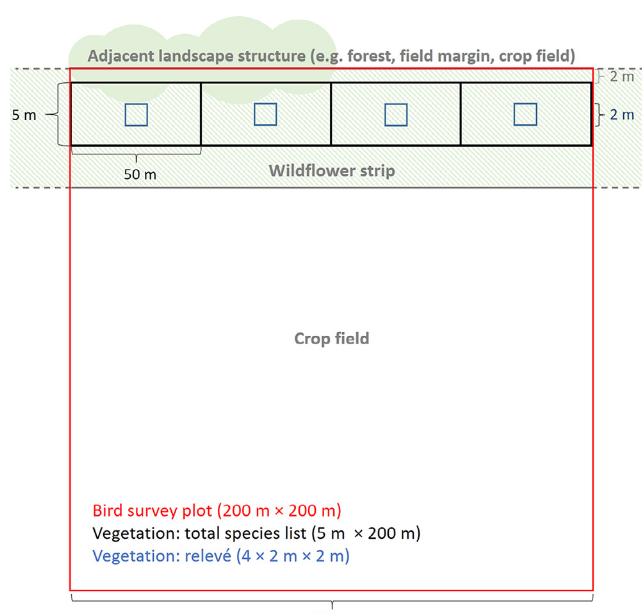

Fig. 2. Bird and vegetation survey plots. The total number of plant species was recorded along a 5 m x 200 m transect. Relevé plots were centered within the four 5 m x 50 m plant transect-sections.

200 × 200-m plots included the WFS and parts of the associated cereal crop field (Fig. 2). Depending on WFS width, WFS made up 10 ± 4.6% (Mean ± SD) of the plots with WFS. For 30-minute periods, all birds seen or heard were recorded with their behaviour and location marked on an aerial map, paying special attention to simultaneous observations (especially for skylarks). Plots were visited six times each at intervals of ca. two weeks between April and July 2017 between sunrise and 10:00 am at the peak of bird singing activity. Bird species that should be monitored at dusk or night might be underrepresented in this study. For building territories, data on bird locations and activities were digitalised in ArcGIS 10.4.1 (Esri Inc., 2016). Any two records on separate dates during the main breeding season of each species were counted as a territory (Südbeck et al., 2005). Single observations were counted as a territory only if clear signs of breeding (such as an active nest) were found.

Vegetation surveys

The presence of all vascular plant species was recorded along a 5 × 200-m transect, nested in the bird survey plots on each of the selected WFS and controls, at the field edge and within 2 m to the adjacent landscape structure (Fig. 2). Percentage cover was noted for each species in four permanent 2 × 2-m sub-plots within the 5 × 200-m transect. For each WFS and control, means of the four sub-plots were used for further statistical analyses to avoid pseudoreplication. Vegetation was recorded between mid-May and end of June.

Landscape surveys

Habitat types were mapped within a 1,000-m radius around each WFS plot or control (see Appendix A: Fig. 1) using the standard habitat mapping key of Saxony-Anhalt (Peterson & Langner, 1992), adjusted with respect to farmland-bird relevant structures (see Appendix A: Table 2). The radius size corresponds to the maximum home range of passerine farmland bird species during the breeding season in arable-dominated agricultural landscapes (see Bauer, Bezzel, & Fiedler, 2005). The mapped data were digitalised, habitat proportions calculated and the distance to the nearest woody element was measured using ArcGIS 10.4.1 (Esri Inc., 2016).

Statistical analyses

We classified farmland birds as all bird species selected Europe-wide for the assessment of agricultural landscapes (PECBMS, 2020), including characteristic ground-nesting birds of open and semi-open landscapes (pheasant and quail). Cavity breeding species (starling) were not included as farmland bird species. Bird species were considered as threatened if they were included in the Red List of Saxony-Anhalt (Schönbrodt & Schulze, 2020). Mann-Whitney U-tests were used to analyse statistical differences between the WFS plots and controls for the species richness and density of all, farmland and threatened birds.

Vegetation, WFS quantity and landscape structure variables were generated for plot level (bird survey plots of 4 ha) and/or landscape level (landscape survey plot in the 1,000-m radius). Since we expected that both, species richness and cover of forbs would affect birds, we decided to assess vegetation composition by a forb index (forb species richness × proportion of forb cover). By using the proportion of forbs of the total plant cover and not cumulative cover of forbs, plots with sparse vegetation, which is beneficial for many farmland bird species (Benton et al., 2003; Fartmann et al., 2018; Meichtry-Stier et al., 2018), were not necessarily rated lower. Since the proportion of WFS at the landscape level varied greatly within single and aggregated WFS, we included the proportion of area under WFS management within a 1,000-m radius as a metric variable in our analysis (% WFS). Habitat types that were considered as non-intensively used open habitats (%), intensively used open land (%) or forest (%) at landscape level are listed in Appendix A: Tables 3-5. Habitat richness refers to the number of different biotope types that were recorded (see Appendix A: Table 2). The distance to the nearest woody element included the distance to all features that can be perceived as a vertical barrier (mainly forests, tree rows, copses, but also single trees, hedges and taller shrubs).

Generalized linear mixed-effect models (GLMM) were fitted to analyse potential effects of WFS and landscape structure on species richness and territory density of all and farmland bird species, respectively (package lme4; Bates, Maechler, Bolker, & Walker, 2015). To prevent collinearity between factors, we quantified vegetation composition, WFS quantity and landscape structure only based on seven variables (Table 1), which were selected by avoiding strong intercorrelations ($|r| \geq 0.7$, Pearson's correlation analysis, see Appendix A: Table 4). For example, the proportion of intensively used open land (mean ± SD: 63.7 ± 22.5) was excluded from multivariate analysis due to strong correlation with proportion of forest ($r = -0.86$).

Except for species richness of farmland birds (Poisson error distribution), all models were conducted with negative binomial error distribution to account for overdispersion. Possible dependence in the data due to spatially close locations was controlled by incorporating landscape units (see Fig. 1) as a random factor in the models. The initial models included all explanatory variables listed in Table 1 as fixed factors and showed variance inflation factors < 2. Since explanatory variables had different scales and ranges, they were standardised and mean-centered prior to model fitting. All models were simplified as much as possible by using stepwise backwards selection procedures with likelihood ratio tests (Crawley, 2013).

Table 1. Description of explanatory variables used in initial models for analysing potential effects of WFS and landscape structure on bird species richness and territory density. Variables were generated at the plot (4 ha) or landscape level (1,000-m radius). Additional values are provided for mean WFS width and proportion of WFS calculated from WFS sites only (n=40).

Level	Explanatory variables	Description	Mean ± SD (n=60)
Plot	Forb index	Number of forb species × proportion of forbs on cumulative total plant cover	19.2 ± 15.5
	Mean WFS width	Mean WFS width (corresponding to proportion of WFS per bird survey plot)	13.4 ± 12.1 m 20.1 ± 9.1 m (n = 40)
Landscape	% WFS	Proportion of WFS	0.8 ± 0.9% 1.1 ± 1.0% (n = 40)
	% Open habitats	Proportion of non-intensively used or abandoned open habitats, e.g. grassland, other AES such as fallows, tall herbaceous vegetation (see Appendix A: Table 3A)	11.8 ± 9.4%
	% Forest	Proportion of forests (see Appendix A: Table 3B)	15.1 ± 17.1%
	Habitat richness	Number of different habitats (see Appendix A: Table 2)	34.2 ± 8.3
	Dist. woody	Distance to the nearest woody element (e.g. forest, copses)	19.1 ± 39.0 m

Statistical analyses were performed using R version 3.5.3 (R Core Team, 2020).

Results

Vegetation and landscape structure

On WFS, species richness and proportion of forbs was significantly higher than on controls, resulting in a mean forb index (mean ± SD: WFS 28.7 ± 9.3, control 0.2 ± 0.4) more than hundred times higher on WFS (Mann-Whitney U-test, $P < 0.001$; see Appendix A: Fig. 2). We found 37.0 ± 6.7 (mean ± SD) forb species on WFS and 4.5 ± 3.1 (mean ± SD) on controls. Forbs accounted for 76.3 ± 17.6% (mean ± SD) of the cumulative cover of all plant species on WFS and 3.0 ± 8.2% on controls (mean ± SD).

Landscape composition did not differ significantly between plots with WFS and controls concerning the proportion of intensively used open land (mean ± SD: WFS 60.5 ± 23.4%, control 70.1, ± 19.5%), non-intensively used open habitats (mean ± SD: WFS 12.5 ± 10.4%, control 9.8 ± 6.8%), and forest (mean ± SD: WFS 16.8 ± 18.1%, control 11.9 ± 14.9%) (Mann-Whitney U-test, $P > 0.05$.; Appendix A: Fig. 3). With more than 60%, intensively used open land covered most of the area on WFS and control sites.

Bird assemblage and comparison of arable fields with or without wildflower strips

In total, 47 bird species were detected on the 60 study plots, which nested on the plots or used the plots as part of their territory, while nesting outside the plots (Table 2, complemented by Appendix A: Table 5). Altogether, 15 of these species were farmland bird species and 14 were considered threatened, including nine farmland bird species.

Mean species richness and territory densities of all, farmland and threatened bird species were more than twice as high on WFS plots and differed significantly from the controls (Fig. 3). Among the 15 detected farmland bird species, six had significantly higher densities on WFS plots than on controls (Table 2). Ten farmland bird species (e.g. corn bunting and whinchat) were only found on WFS plots. Among the 14 detected threatened species, the farmland species corn bunting, red-backed shrike and skylark occurred in significantly higher densities (Mann-Whitney U-test, $P < 0.001$), while the non-farmland species tree pipit occurred in a marginally higher density on WFS plots (Table 2). In contrast, no species preferred controls. Only skylark and yellow wagtail had more than two territories on the controls in total (n = 20).

Effects of wildflower strip and landscape structure

Generalized linear mixed-effect models predicted that the forb index (assessed by forb species richness × proportion of forb cover) had the largest positive effect on both, species richness and territory density of all and farmland birds (Tables 3-4, Fig. 4). Mean WFS width had a marginally positive effect on density and species richness of all bird species (Tables 3-4).

Both total and farmland bird densities correlated positively with the proportion of WFS at the landscape level (Table 4). Total bird species richness decreased with increasing distance between the WFS and the nearest woody element (Table 3), whereas the proximity of woody elements had a negative effect on the density of farmland birds (Table 4). In addition, the proportion of forest also correlated negatively with the species richness and density of farmland birds and tended to show a negative effect on density of all birds (Tables 3-4). Habitat richness tended to increase

Table 2. Number of territories of bird species on wildflower strip (WFS) plots and controls. All farmland bird species (FB; PECBMS, 2020) and threatened species (RL, Red List of Saxony Anhalt; Schönbrodt & Schulze, 2020) are shown; additional species only if they occupied at least two territories. Bold type indicates species with at least five territories. Differences between WFS plot and control were tested using Mann-Whitney U-test (n.s. = not significant, (.) P < 0.1, * P < 0.05, ** P < 0.01, *** P < 0.001).

Common name	Scientific name	FB	RL	WFS (n = 40)		Control (n = 20)		Total	*P*
				Number	Mean	Number	Mean		
Blackbird	*Turdus merula*	.	.	2	0.05	1	0.05	3	n.s.
Blackcap	*Sylvia atricapilla*	.	.	5	0.13	1	0.05	6	n.s.
Blue Tit	*Cyanistes caeruleus*	.	.	3	0.08	1	0.05	4	n.s.
Chaffinch	*Fringilla coelebs*	.	.	8	0.20	1	0.05	9	n.s.
Chiffchaff	*Phylloscopus collybita*	.	.	3	0.08	.	.	3	n.s.
Corn Bunting	*Emberiza calandra*	x	x	17	0.43	.	.	17	**
Garden Warbler	*Sylvia borin*	.	.	2	0.05	.	.	2	n.s.
Goldfinch	*Carduelis carduelis*	.	.	9	0.23	.	.	9	*
Great Tit	*Parus major*	.	.	5	0.13	1	0.05	6	n.s.
Greenfinch	*Chloris chloris*	.	.	2	0.05	.	.	2	n.s.
House Sparrow	*Passer domesticus*	.	x	2	0.05	.	.	2	n.s.
Icterine Warbler	*Hippolais icterina*	.	x	1	0.03	.	.	1	n.s.
Lapwing	*Vanellus vanellus*	x	x	1	0.03	.	.	1	n.s.
Lesser Whitethroat	*Sylvia curruca*	.	.	2	0.05	.	.	2	n.s.
Linnet	*Linaria cannabina*	x	x	1	0.03	.	.	1	n.s.
Nightingale	*Luscinia megarhynchos*	.	.	2	0.05	.	.	2	n.s.
Ortolan Bunting	*Emberiza hortulana*	x	x	3	0.08	1	0.05	4	n.s.
Pheasant	*Phasianus colchicus*	x	.	3	0.08	.	.	3	n.s.
Quail	*Coturnix coturnix*	x	.	7	0.18	.	.	7	*
Red-backed Shrike	*Lanius collurio*	x	x	10	0.25	.	.	10	*
Skylark	*Alauda arvensis*	x	x	166	4.15	49	2.45	215	*
Starling	*Sturnus vulgaris*	.	x	4	0.10	1	0.05	5	n.s.
Stonechat	*Saxicola rubicola*	x	.	5	0.13	1	0.05	6	n.s.
Tree Pipit	*Anthus trivialis*	.	x	14	0.35	2	0.10	16	(.)
Tree Sparrow	*Passer montanus*	x	x	3	0.08	.	.	3	n.s.
Turtle-dove	*Streptopelia turtur*	x	x	1	0.03	.	.	1	n.s.
Whinchat	*Saxicola rubetra*	x	x	5	0.13	.	.	5	n.s.
White Wagtail	*Motacilla alba*	.	.	5	0.13	.	.	5	n.s.
Whitethroat	*Sylvia communis*	x	.	24	0.60	.	.	24	***
Woodlark	*Lullula arborea*	.	x	6	0.15	.	.	6	n.s.
Yellow Wagtail	*Motacilla flava*	x	.	37	0.93	10	0.50	47	n.s.
Yellowhammer	*Emberiza citrinella*	x	.	12	0.30	1	0.05	13	*

species richness of farmland birds (Table 3), but had no effect on density (Table 4). The proportion of non-intensively used open habitats had no effect on the species richness and density of all and farmland birds in the models.

Discussion

Comparison of arable fields with or without wildflower strips

This study evaluated the effect of species-rich AES perennial wildflower strips (WFS) on the species richness and territory density of birds across the federal state of Saxony-Anhalt (Germany). To our knowledge, it is the first study in Europe focussing on WFS and considering vegetation composition (assessed by forb index: forb species richness × proportion of forb cover), WFS quantity as well as landscape structure. Our results showed that perennial species-rich WFS sown with native seed mixtures from regional seed propagation benefited local bird populations in intensively used agricultural landscapes, and thus temporarily compensated for the loss of extensively used arable land and grassland-like semi-natural habitats like field margins. Species richness as well as the territory density of all, farmland and threatened birds were more than twice as high on WFS plots than on controls, which is in line with previous reports of positive effects of other high quality AES (e.g. hedgerows) on birds (Meichtry-Stier et al., 2014; Princé & Jiguet, 2013; Zingg et al., 2019).

Many farmland bird species that are threatened occurred exclusively or more frequently on WFS plots (e.g. the strongly declining whinchat), which confirms the value of

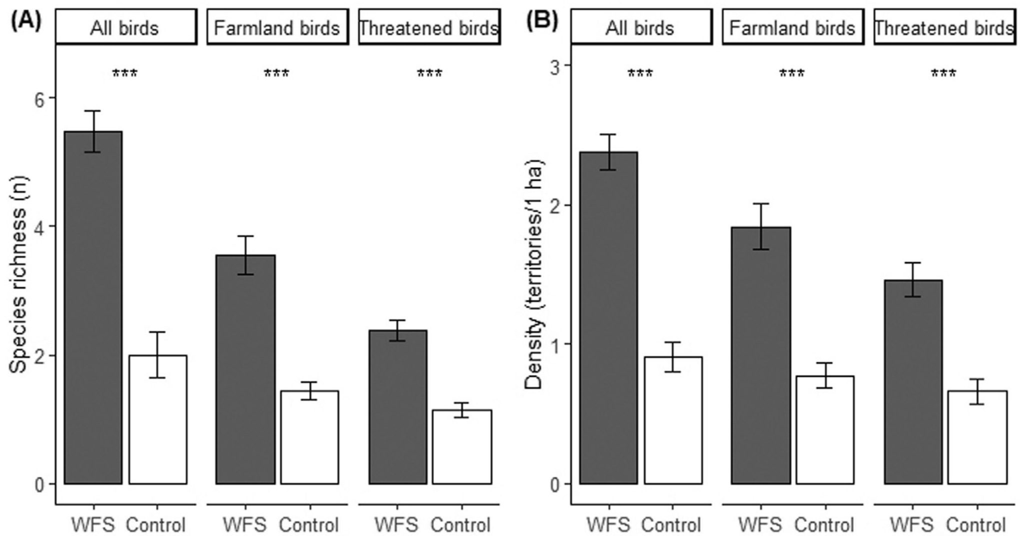

Fig. 3. Mean species (A) richness and territory density (B) (± SE) of all birds, farmland bird and threatened bird species on wildflower strip (WFS) and control plots. Differences between plot types were tested using Mann-Whitney U-tests (*** $P < 0.001$).

Table 3. Results of generalized linear mixed-effect models for species richness of all and farmland birds, using stepwise backwards selection procedures. For abbreviations of explanatory variables, see Table 1.

Species richness	All birds			Farmland birds		
	Est.	SE	*P*	Est.	SE	*P*
Intercept	1.391	0.067	<0.001	0.967	0.082	<0.001
Forb index	0.287	0.081	<0.001	0.250	0.092	0.007
Mean WFS width	0.133	0.079	0.094	.	.	.
% WFS	.	.	.	0.084	0.083	0.308
% Open habitats	.	.	.	.	.	.
% Forest	.	.	.	-0.223	0.092	0.015
Habitat richness	.	.	.	0.158	0.084	0.061
Dist. woody	-0.141	0.068	0.037	.	.	.

Table 4. Results of generalized linear mixed-effect models for territory density of all and farmland birds, using stepwise backwards selection procedures. For abbreviations of explanatory variables, see Table 1.

Territory density	All birds			Farmland birds		
	Est.	SE	*P*	Est.	SE	*P*
Intercept	1.943	0.052	<0.001	1.684	0.095	<0.001
Forb index	0.261	0.067	<0.001	0.253	0.080	0.002
Mean WFS width	0.106	0.058	0.070	.	.	.
% WFS	0.117	0.052	0.025	0.204	0.073	0.005
% Open habitats	.	.	.	.	.	.
% Forest	-0.097	0.053	0.067	-0.221	0.079	0.005
Habitat richness	.	.	.	.	.	.
Dist. woody	.	.	.	0.133	0.062	0.032

WFS for AES target farmland birds as also acknowledged by Meichtry-Stier et al. (2014). In our study, effect size was species-specific. Skylark, whitethroat, corn bunting and yellow wagtail were the species that benefited most from WFS as they appeared in considerably higher densities and numbers on WFS plots. Besides typical species of the open landscape, threatened ecotone or woodland species such as the tree pipit and woodlark also benefited from WFS when woody structures were close to the WFS.

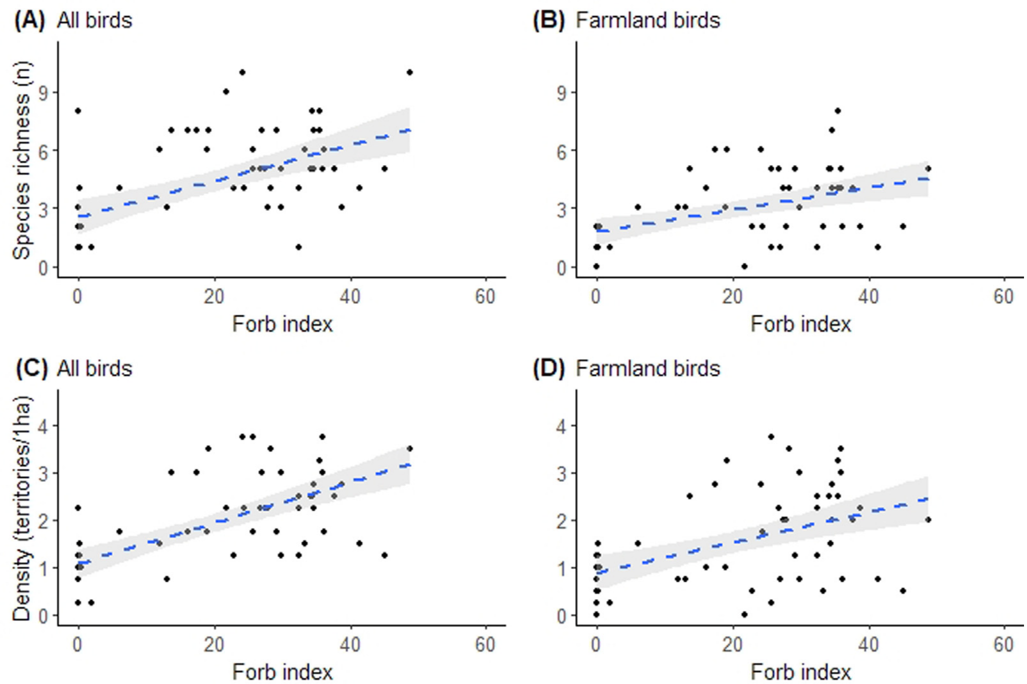

Fig. 4. Effect of forb index (forb species richness × proportion of forb cover) on species richness and territory density of all birds (A, C) and farmland birds (B, D) (n = 60). Shaded area represents 95% confidence intervals.

Effects of wildflower strips and landscape structure

In our study, vegetation composition assessed by the forb index, and thus species richness and the proportion of forb cover had the greatest effect on bird species richness and also on territory density, which is in agreement with Meichtry-Stier et al. (2014). Both forb species richness and proportion were much higher on WFS plots than on controls. Although our AES seed mixtures are already of a very high standard containing 30 forb species, there were individual WFS with lower quality (i.e. higher grass cover), resulting in lower benefits for birds (Fig. 4, see Appendix A: Fig. 2), thus confirming our assumption that the creation of forb-rich vegetation is crucial to achieve the highest possible ecological effectiveness (Birrer et al., 2007; Kleijn & Sutherland, 2003). The strong effect of the forb index is probably due to the fact that a high cover and species richness of forbs shape a more diverse horizontal and vertical vegetation structure than species-poor or grass-dominated stands and thus provide a broad range of nesting and foraging habitats for a larger number of bird species and breeding pairs. Many WFS had also open patches with very low vegetation (field observation) and, thus, in contrast to Meichtry-Stier et al. (2014), also promoted the declining farmland bird skylark. Furthermore, stands rich in forb species provide more diverse food for birds over a longer period of the year, as different native plants will flower and seed at different times and are more likely to support a broader range of species and more biomass of invertebrates by increasing their local populations (Vickery, Carter, & Fuller, 2002). Additionally, by promoting heterogeneous wildflower structures, both foraging and visitation frequency of predators can be reduced (Hummel, Meyer, Hackländer, & Weber, 2017) and hence the probability of brood survival should increase significantly. As a result, to maximise the positive effects of WFS, it is necessary to establish species-rich native seed mixtures as successfully as possible, as this is the key to high quality flower strip vegetation (Piqueray, Gilliaux, Bodson, & Mahy, 2021; Schmidt et al., 2020).

In our study, WFS quantity was assessed by the proportion of wildflower strips at both the plot and landscape level. The WFS proportion at the plot level corresponded to mean WFS width that only tended to have a positive effect on total bird density and total bird species richness, but not on farmland birds. Probably, the WFS width differed too little between the WFS in our study (mean ± SD: 20.1 ± 9.1 m) to cause significant differences in territory size on WFS plots and thus higher territory density of ground-nesting farmland bird species (Meichtry-Stier et al., 2018). However, since predators such as foxes concentrate their activity at the very edge of linear structures like WFS (only 6 m inside their activity is reduced) a higher width should increase the chances of survival and breeding success (Hummel et al., 2017). Contrary to Zingg et al. (2019), where farmland birds were not affected, and only the total bird species richness but not density correlated positively with the proportion of AES, in our study bird species richness did not considerably increase with the WFS proportion at the landscape level, but the bird density of all and farmland birds did. This is probably caused by the high habitat quality of the WFS. This means that single WFS probably already supported a diverse range of AES target farmland bird species, but that a higher proportion of the area under WFS management increased their effectiveness by attracting more individuals. Efforts should therefore be made to reach a high proportion of WFS at the landscape level, for example by increasing farmers' acceptance of participation in the program and professional planning, e.g. by incorporating advisory tools (Díaz & Concepción, 2016).

Woody elements generally benefit bird diversity in cereal-dominated landscapes (Tschumi et al., 2020; Wuczyński, Kujawa, Dajdok, & Grzesiak, 2011). In our study, total bird species richness also increased with the proximity to woody elements. This is not surprising, since ecotones are mostly very species-rich due to their heterogeneity and structural diversity. An increasing distance of woody elements had no effect on the species richness of farmland birds, but a positive effect on their territory density. As most of the adjacent woody elements were tall and dense forests or groves, this pattern was most likely determined by the habitat requirements of the most abundant skylark, which is well known to avoid proximity to tall vertical structures (Meichtry-Stier et al., 2014). In our study, plots with a high proportion of forest at the landscape level showed generally low farmland bird diversity and territory density, which means that also other farmland species were negatively affected. However, in practice, farmers often place WFS on heavily shaded, north-exposed forest edges because the yield would be low there anyway. As AES target farmland birds are species of open landscapes, WFS should preferably be implemented in open landscapes and not adjacent to dense and/or tall woody vegetation (Meichtry-Stier et al., 2018). Furthermore, predators' visits would be lower with increasing distance to woody elements, as predator activity is higher in the immediate vicinity of their shelter (Červinka, Šálek, Pavluvčík, & Kreisinger, 2011; Hummel et al., 2017). Nevertheless, the importance of hedges or single woody elements in agricultural landscapes dominated by arable farming should generally not be questioned (Alignier, Uroy, & Aviron, 2020) as they provide e.g. resting and nesting sites for hedge/tree breeding birds and threatened farmland species like the linnet (Fartmann et al., 2018).

Many farmland birds are typical inhabitants of species-rich grasslands. Thus, we expected positive effects with a higher proportion of non-intensively used open habitats (mainly grassland, see Appendix A: Table 3) at the landscape level on their species richness and territory density due to a higher regional species pool. Contrary to our hypothesis and other studies (Princé & Jiguet, 2013) but in line with Tschumi et al. (2020), the proportion of non-intensively used open habitats had no effect in our final models. A probable hypothesis for the low influence is that the effects of nature conservation initiatives depend on the landscape context (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011). In very complex landscapes, WFS provide less ecological contrast, and in large-scale intensively used landscapes, they cannot be colonized due to the lack of target species source populations. Our study sites were imbedded in landscapes with a moderate share of non-intensively used open habitats (see Appendix A: Fig. 3), but the occurring grasslands or even fallows showed a dense, species-poor and grass-dominated vegetation structure and poor forb richness, and thus were not particularly well suited for nesting (Fartmann et al., 2018; Schwarz, Trautner, & Fartmann, 2018). We therefore assume that the remaining semi-natural open habitats in the current agricultural landscapes of Saxony-Anhalt have a lower functional heterogeneity for accomplishing the different life cycle phases of farmland birds (Fahrig et al., 2011; Meichtry-Stier et al., 2014; Zingg et al., 2019) than floristically-diverse WFS. Possible interactions between the proportion of WFS and adjacent non-intensively used open habitats could unfortunately not be included in our statistical analyses due to the limited number of samples.

By contrast, habitat richness (number of different habitats) at the landscape level tended to show a positive effect but only on the species richness of farmland birds. A higher diversity of habitats generally offers a wider range of resources (Vickery & Arlettaz, 2012), but did not seem to be associated with a higher local proportion of well-suited habitats for the detected breeding (mainly farmland) bird species in our study, or it was of secondary importance compared to other environmental parameters (e.g. vegetation composition).

Conclusions and implications for practice

Our results indicate that temporal structures like perennial WFS have the potential to enhance the diversity and territory density of all and AES target farmland bird species. A forb-rich and diverse vegetation, ensured by successful establishment of species-rich native high-quality WFS seed mixtures, decisively influenced the effectiveness of this AES. WFS should therefore be obligatorily implemented with high quality mixtures in other countries as well. Since declining farmland bird species depend on farmland as their major breeding habitat, agriculture has a special responsibility for their welfare and conservation. Threatened farmland bird species, especially the skylark and corn bunting, responded positively to WFS. We identified a high WFS proportion in the vicinity and the implementation in open landscapes as further key factors essential to exploit the full potential of this AES when focussing on the restoration of AES target farmland bird communities. This means that future AES programmes should be accompanied by communication and advice measures to increase the willingness of farmers to participate in AES programmes at landscape level. Farmers should also be motivated to create new WFS in the vicinity of established WFS before the funding period ends after five years to ensure habitat continuity.

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.2021.10.005.

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