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Research article

Solar parks can enhance bird diversity in agricultural landscape

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ABSTRACT

Solar photovoltaic power parks are a relatively new anthropogenic habitat that will become more widespread in the future. The greatest potential for solar photovoltaic power production is on arable land and grassland. Knowledge on the impacts of solar parks on biodiversity is scarce and spatially limited. We investigated the impact of ground-mounted solar parks on species richness, abundance, Shannon diversity and composition of bird communities in Slovakia (Central Europe), taking into account pre-construction land cover, elevation and landscape context. We recorded breeding, foraging or perching birds on 32 solar park plots and 32 adjacent control plots (two hectares each) during single breeding season. We found that solar parks supported higher total bird species richness and diversity, and richness and abundance of invertebrate-eaters, and that the abundance of ground-foragers was higher in solar parks developed on grassland than in grassland control plots. Ordination analysis showed that solar parks had a different composition of bird communities and thus increased overall species diversity and beta diversity in the agricultural landscapes studied. Plot type and landscape context accounted for most of the variation in bird community composition. Black redstart, European stonechat, white wagtail and Eurasian tree sparrow were identified as indicator species for solar parks. The observed pattern could be due to the higher structural diversity of solar parks. The solar parks studied were designed and managed exclusively for electricity production. It can therefore be assumed that solar parks designed and managed in synergy with a stronger focus on wildlife would have an even greater positive impact on bird diversity in an agricultural landscape.

1. Introduction

Global energy production is highly dependent on fossil fuels, contributing significantly to greenhouse gas emissions, while energy consumption is expected to increase in the coming years. Due to concerns about the finite supply of fossil fuels, global climate change and energy security, the projected increase in electricity generation is expected to come primarily from renewable sources (EIA, 2021).

Worldwide, the installation of photovoltaic power systems has increased exponentially in recent years (Dhar et al., 2020). The negative environmental impacts of solar energy systems include visual pollution (del CarmenTorres-Sibille et al., 2009), land occupancy and habitat loss (Capellán-Pérez et al., 2017; Dhar et al., 2020; Tawalbeh et al., 2021), in addition to the production of hazardous contaminates, pollution of

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water resources and emission of air pollutants during the manufacturing process and recycling of photovoltaic waste and disposed modules (Tawalbeh et al., 2021). The transition to renewables will intensify the global competition for land (as their power density is lower than that of fossil fuels); thus solar energy may occupy up to 2.8% of the total land area in the European Union by 2050 (van de Ven et al., 2021).

The most robust data on interactions between wildlife and renewable energy facilities are available for wind energy facilities, particularly for birds and bats (Smith and Dwyer, 2016). Research on the environmental or biodiversity impacts of solar power facilities is scarce and geographically limited mainly to the south-western US, in arid desert habitats (Dhar et al., 2020; Gibson et al., 2017; Hernandez et al., 2015; Kosciuch et al., 2020; Lovich and Ennen, 2011; Smith and Dwyer, 2016).

The potential for solar photovoltaic power production is greatest over cropland, grassland, permanent wetlands, mixed forests and barren terrains (Adeh et al., 2019). The impact of the construction of solar parks (also known as solar power plant, photovoltaic power plant, photovoltaic power station) on biodiversity depends on the conservation value of the land (Cameron et al., 2012; Hernandez et al., 2015; Milbrandt et al., 2014). Bird species richness on arable land is lowest compared to other habitat types in Central Europe (Reif et al., 2023). Agriculture is considered to be, and is likely to remain, the main driver of terrestrial biodiversity loss due to management intensification and cropland expansion combined with habitat loss (Ekroos et al., 2016; Gonthier et al., 2014; Kehoe et al., 2017; Powers and Jetz, 2019; Robinson and Sutherland, 2002; Sala et al., 2000). Decline of common farmland birds' breeding populations across Europe is continuous (EBCC/BirdLife/RSPB/CSO, 2022). Decline of bird species associated with farmland have been greater than those of grassland species (Reif and Hanzelka, 2016), insectivorous species have declined more than herbivorous birds (Bowler et al., 2019) and ground-nesting bird species have declined more than birds nesting on woody vegetation (McMahon et al., 2020). Declines in species richness and/or abundance of farmland birds in agricultural landscapes have been attributed to a variety of factors acting simultaneously (Reif, 2013; Stanton et al., 2018). It is mainly due to reduced crop and land cover diversity (e.g. Denac and Kmecl, 2021; Jerrentrup et al., 2017; Pickett and Siriwardena, 2011; Robinson et al., 2001; Sanderson et al., 2013), higher cover of crop species with high and dense swards, such as maize and rapeseed (Busch et al., 2020; Reif and Hanzelka, 2020), higher mowing frequency or more livestock on grassland (McCracken and Tallowin, 2004; Reif, 2013), high fertiliser use (Reif and Hanzelka, 2020) and pesticide use (e.g. Moreau et al., 2021).

Species diversity is positively related to the complexity of agricultural landscapes (Benton et al., 2003; Estrada-Carmona et al., 2022; Gonthier et al., 2014; Landis, 2017). The lower management intensity in solar parks compared to cropland can increase plant diversity and thus provide a refuge for species from the surrounding human-used areas (Uldrijan et al., 2021, 2022). Photovoltaic panels alter vegetation species composition under panels (Lambert et al., 2023; Uldrijan et al., 2021, 2022). Greater botanical diversity supports greater invertebrate diversity, so wildlife and vegetation can interact positively on solar farms (Blaydes et al., 2021). Solar parks increase the structural complexity and heterogeneity of microhabitats at multiple scales: the construction supporting the solar panels and the panels themselves provide nesting and perching sites for birds and can protect them from aerial predators (Nordberg et al., 2021); solar panels also increase local moisture and thermal heterogeneity, leading to increased biodiversity (Dhar et al., 2020; Nordberg et al., 2021). Solar parks can act as habitat islands, providing shelter that can be reduced or destroyed in degraded environments (Nordberg et al., 2021; Sinha et al., 2018). There are few studies (reports and reviews) from the UK and Germany that have demonstrated positive effects of solar parks on biodiversity (Badelt et al., 2020; Montag et al., 2016; Parker and McQueen, 2013; Peschel, 2010; Peschel et al., 2019; Taylor et al., 2019). However, to the best of our knowledge, only two studies have been published in the primary

peer-reviewed literature that have investigated the effects of a solar park on birds using a systematic, repeatable and standardised sampling protocol. These were conducted in the USA (DeVault et al., 2014; from an aviation safety perspective) and in the semi-arid region of South Africa (Visser et al., 2019; from a biodiversity conservation perspective).

To assess the impact of solar parks on birds in a Central European agricultural landscape (Slovakia), we compared 32 pairs of solar parks and control plots to test the hypothesis that solar parks will have higher species richness, abundance, diversity and different composition of bird communities than adjacent agricultural habitats. The number of species and individuals should be higher in solar parks than in agricultural habitats, as there is usually higher habitat heterogeneity (Denac and Kmecl, 2021; Reif et al., 2023; Wuczyński, 2016). We also predicted that insectivorous birds, ground-nesting birds and ground-foragers would become more common in solar parks because intensification of agriculture - e.g. use of chemicals, disturbance regime (ploughing, mowing), crop type with high and dense sward, etc. - has a negative impact on prey abundance, detectability and accessibility, and thus on bird abundance (Butler and Gillings, 2004; Guerrero et al., 2012; Hološková et al., 2023; Hoste-Danylow et al., 2010; Schaub et al., 2010; Stanton et al., 2018; Wilson et al., 2005). Finally, due to similarity of habitat characteristics, we expected that differences between solar parks and agricultural habitats might be more pronounced on arable land than on grassland.

2. Materials and methods

2.1. Study area

We collected data on plots at 32 localities in Slovakia (48.11626N, 17.37053E–48.93580N, 21.87151E; Fig. 1) during breeding season of 2022. The localities were located in Pannonian and Alpine biogeographical regions – in Pannonian Basin and Western Carpathian Mts. Climatic conditions in Slovakia range from oceanic in the western part to continental in the eastern part of the country. The mean annual temperature of the studied localities ranges from 5.3 to 10.2 °C, and precipitation ranges from 503 mm to 921 mm (Fick and Hijmans, 2017). The elevation of the localities ranges from 95 to 858 m a.s.l. The main land cover classes in the area within 500 m radius around the centre of each plot were arable land (mean, range: 60.6, 0–100%), artificial areas (12.4, 0–56%), forests (6.3, 0–55%), agricultural and natural areas (10.0, 0–70%) and grasslands (10.5, 0–92%) (European Union, Copernicus Land Montag et al., 2016, European Environment Agency (EEA); Supplementary material S1: Table S1.1).

2.2. Study design

At each locality, a pair of plots – a solar park and a control plot – was sampled. We selected ground-mounted photovoltaic power plants (i.e. fenced area of a power plant) with an area of at least 2 ha (i.e. with a capacity over approximately 0.90 MW in Slovakia); hereafter solar parks. The distribution and capacity of photovoltaic power plants in Slovakia was obtained from the Regulatory Office for Network Industries of Slovakia (ÚRSO SR). All of the studied solar parks had fixedtilt solar racks, one of which also had panels mounted on biaxial trackers, and were developed at least 8 years before we sampled the bird communities (Supplementary material S1: Fig. S1.1). The paired control plots in the adjacent farmland were then selected using historical images in Google Earth Pro 7.3.6.9345 (© 2022 Google LLC). The control plots were always in the land cover type that would have been present at the site of solar park if the solar park had not existed (arable land or grassland sensu lato, see below) and had as similar topographic conditions as possible (slope gradient and position). In addition, the local habitat structure (namely the presence of woody vegetation) in vicinity of the solar parks and the control plots was similar (to avoid or minimise confounding effects of local habitat structure on bird communities), so



Fig. 1. The distribution of the studied localities (n = 32 paired plots) in Slovakia, Central Europe.

that the main difference between the paired plots was the presence of a solar park. We therefore assume that the conservation value of the control plots did not differ from the conservation value of the sites where the solar parks were developed. The minimum edge-to-edge distance between paired plots was at least 500 m to help minimise spatial dependence; the maximum distance between paired plots was 1500 m.

In this study, we investigated 17 solar parks developed on arable land and 15 parks developed on grassland. We identified two categories of land cover on the study plots: arable land and grassland. By arable land, we mean cultivated land used for annually harvested nonpermanent crops and temporary fallow land (one control plot). By grassland we mean permanent grassland used for hay production or as pasture, abandoned grassland, arable land abandoned for more than 13 years (one control plot) and land with ruderal vegetation (one control plot) – without or with sparse woody vegetation on less than 10% of the area.

2.3. Bird surveys

Bird species and the number of adult individuals were recorded on the sampled plots using the line transect method (Bibby et al., 2000). The size of the plots was 2 ha. In the solar parks, transects were placed along a fence and birds were only recorded on one side of the transect - i. e. within the solar park, including the fence. In the control plots, both sides of the transect were surveyed. Thus, the width of the transect surveyed was 50 m in the solar parks and 100 m in the control plots. The length of the transect therefore differed between the plot types (400 m in the solar parks and 200 m in the control plots). All birds seen or heard on the plot during survey were recorded, except those that flew over. From 20 April to 10 June 2022 (breeding season), two 20-min surveys with binoculars were conducted on each plot at a slow walking pace, with at least 10 days between visits to the same plot. Surveys were carried out under good weather conditions (no rain, no strong wind) from sunrise to 10 a.m. and from 5 p.m. to sunset (Morelli et al., 2022), with at least one visit in the morning. The maximum number of the two visits in each plot was used to calculate bird abundance and diversity (Bibby et al., 2000).

2.4. Bird classification

Bird species were classified according to long-term (1980 (-1998) -2021) and ten-year (2012–2021) population trends using the latest version of the trends of common birds in Europe (EBCC/BirdLi-fe/RSPB/CSO, 2022).

To assess the impact of the solar park environment on the birds' functional traits, we considered three functional traits: Nesting place hole, arboreal (open or closed), on the ground directly or in tussock very close to ground; foraging strata - ground, bushes or trees, aerial; and diet - seeds/plants, invertebrates, vertebrates/carrions, mixed diet (Supplementary material S2: Table S2.1). We assigned all recorded bird species by (i) nesting place by using the classification of Storchová and Hořák (2018) and by (ii) diet and (iii) foraging stratum by using the classification of Wilman et al. (2014; EltonTraits 1.0). We merged several original nesting place categories - open arboreal nests and closed arboreal nests, nests on the ground directly with a nest in a tussock very close to the ground but not directly on the ground, hidden in surrounded vegetation. We classified common cuckoo (Cuculus canorus) as a species with "arboreal nest" as defined in Storchová and Hořák (2018); rock pigeon (Columba livia) as a species with hole nest. We merged also three categories from the original classification for the foraging stratum (Wilman et al., 2014) – foraging in the understory below 2 m, at mid to high levels and in the canopy in trees or bushes, and in or just above the tree canopy - into one category (bushes or trees). We classified northern house-martin (Delichon urbicum) as a species foraging in the aerial stratum; barn swallow (Hirundo rustica) as a species foraging in the aerial stratum; carrion crow (Corvus corone) as a species foraging on the ground; great spotted woodpecker (Dendrocopos major) and Eurasian golden oriole (Oriolus) as species foraging in bushes or trees. In total, 24 species were assigned 1 category for the foraging stratum category, 26 species two categories and 3 species three categories (Table S2.1).

2.5. Environmental conditions and landscape context

On the solar park plots, we assessed management of vegetation in the solar park in area around the photovoltaic panels (mowing (n = 31) or grazing (n = 1)) and especially noted the management of vegetation under the photovoltaic panels (no management (n = 7), cutting (n = 22),

grazing (n = 1) or herbicide use (n = 2)). The control plots on arable land were planted with cereals, rape, maize, soya beans, sunflowers and potatoes.

We used a digital elevation model with a resolution of 90 m (Jarvis et al., 2008) to determine the elevation of the plots. We used the European Corine Land Cover classification (raster map, version 2020_20u1, 100 m resolution; European Union, Copernicus Land Montag et al., 2016, European Environment Agency (EEA)) to characterise the landscape context within 500 of the centre of each plot. This distance is arbitrary and is intended to reflect the influence of the landscape context, which can affect the composition of bird communities in plots. We grouped most Corine level 3 land cover classes into several categories: Discontinuous urban structures, Industrial or commercial units, Road and rail networks and associated land. Mineral extraction sites and Sport and leisure facilities were grouped under "Artificial areas". Non-irrigated arable land was not grouped ("Arable land"). Fruit trees and berry plantations, Complex cultivation patterns and Land principally occupied by agriculture with significant areas of natural vegetation were grouped as "Agricultural and natural areas". Broad-leaved, Mixed and Coniferous Forests were grouped under "Forests". Pastures, Natural grasslands and Transitional woodland-shrub forest classes were grouped as "Grasslands". Software QGIS 3.28.3 (QGIS Development Team, 2022) was used for the landscape description and for creation of map (Table S1.1, Fig. 1).

2.6. Data analysis

All statistical analyses were performed using R 4.2.2 (R Core Team, 2022) statistical software in RStudio (RStudio, 2022). For each plot, we calculated the species richness, abundance and diversity of all bird species, species richness and abundance of declining farmland bird species (i.e. with a ten-year declining population trend and a long-term declining population trend), ground-nesters, invertebrate-eaters and ground-foragers, i.e. 13 response variables. Thus as response variables, we used categories of species traits associated with open habitat. Plot level Shannon diversity index was calculated using the package vegan (Oksanen et al., 2022). To test the effect of land cover of the control plots, we use the variable "previous land cover", which indicates the type of land cover that was present in the area of the solar park before it was built. Thus, while previous land cover for solar parks represents past land cover, for control plots it represents current land cover (i.e. at least since 2010).

We fitted generalized linear mixed models (GLMM) for response variables with count data and linear mixed model (LMM) for Shannon diversity to assess differences between plot types (solar park/control plot; nominal fixed factor). The models also included the interaction between the type of previous land cover (arable land/grassland; nominal fixed factor) and plot type, as we expected a stronger discrepancy between solar parks and control plots on arable land. For all GLMMs, the locality ID was used as a random factor to account for the nonindependence of the observations, i.e. paired-plot design of our study. For each response variable in GLMMs, we used a series of models with different error distribution structures (Poisson, negative binomial with variance = $\mu(1 + k)$ and negative binomial with variance = $\mu(1 + \mu/k)$, each with and without zero inflation). We then selected the model with the lowest AIC as the final model, provided it met the model assumptions. We performed diagnostics (uniformity and dispersion tests, outliers) of the GLMMs and LMM using the simulateResiduals function of the DHARMa package (Hartig, 2022). We used the R packages glmmTMB (Brooks et al., 2017) and lme4 (Bates et al., 2015) to fit the models. We used the function Anova from the R package car (Fox and Weisberg, 2019) to compute analysis-of-variance tables of type III for the objects of the models. The pseudo- R^2 for the analysed models was calculated using the function r. squaredGLMM (the delta method was used to derive the variance at the observation level) from the R package MuMln (Bartoń, 2022); the marginal R^2 , which represents the variance explained by fixed factors, and conditional R^2 , which represents the variance explained by the whole model including random effect, are presented in the paper. We calculated summary statistics of variables according to a grouping variable (plot type) using the describeBy function from the package psych (Revelle, 2022).

To associate bird community composition to solar parks or control plots, elevation and landscape context, we used distance-based redundancy analysis (dbRDA) with the package vegan (Oksanen et al., 2022). In dbRDA, we used the Bray-Curtis dissimilarity index (beta diversity) as a response variable for bird species composition. Abundance data were transformed using a logarithmic transformation (base 2). For plots with no recorded species (one solar park and 4 control plots), we added a very small number (0.0001) to each species value in the dataset. As explanatory (constraining) variables, we used plot type, type of previous land cover type and its interaction with plot type, elevation, and landscape context, i.e., cover by artificial areas, arable lands, agricultural and natural areas, forests and grasslands within a 500 m radius around the centre of each plot. Continuous explanatory variables were scaled and centered. Next, we partitioned the variation in multivariate bird abundance with respect to the explanatory variables grouped into four sets: (i) plot type, (ii) previous land cover type, (iii) elevation, and (iv) landscape context (the cover of artificial areas, arable land, agricultural and natural areas, forests and grasslands). For variation partitioning, we used the varpart function from the R package vegan. We assessed the significance of unique contributions of the sets of variables using partial dbRDAs. Within the solar parks, association between management under the photovoltaic panels (no management/managed) and the bird communities was tested with dbRDA.

Permutational multivariate analysis of variance (PermANOVA) was performed using the adonis2 function in the R package vegan to associate plot type and subtype – solar park, control–arable land and control–grassland – to bird communities (Bray-Curtis distances calculated from log2-transformed abundances), followed by a multilevel pairwise comparison using the wrapper function pairwise. Adonis (Martinez Arbizu, 2020) with adjusted P-values.

Finally, we conducted an indicator species analysis using the R package indicspecies 1.7.12 (De Caceres and Legendre, 2009) to determine species particularly associated with solar parks or control plots (arable land or grassland). Correlation indices (point biserial correlation coefficients) were used as association indices (the argument func = "r.g" in the function multipatt). To inspect the predictive values of the species significantly associated with the plot groups, indicator value indices ("IndVal.g") were then used, indicating (A) the probability of the surveyed plot belonging to the target plot group if the species was found (species specificity or positive predictive value) and (B) the probability of finding the species in plots belonging to the plot group for the species (species fidelity or sensitivity).

The R packages tidyverse 1.2.1 (Wickham et al., 2019), ggrepel 0.8.1 (Slowikowski, 2023), dplyr 1.1.1 (Wickham et al., 2023) and ggplot2 3.3.2 (Wickham, 2016) were used for plotting results of this study.

3. Results

3.1. Bird diversity

In total, we recorded 624 individuals and 53 bird species during the visits with maximum counts per species (Table S2.1). Twenty species were recorded on a single plot only. Eight species were classified as farmland bird species of a declining 10-year trend, 13 species of a declining long-term trend, and 23 species were classified as invertebrate-eaters, 16 as seed-eaters, 17 as ground-foragers, 14 as ground-nesters (Table S2.1). Mean species richness at plot level was 4.7 per 2 ha (SD = 2.9, range = 0–12), mean total abundance at plot level was 9.8 per two ha (SD = 7.5, range = 0–34), mean Shannon diversity at plot level was 1.203 per two ha (SD = 0.705, range = 0–2.302), The most abundant species were the Eurasian tree sparrow (*Passer montanus*,

n = 73), common starling (*Sturnus vulgaris*, n = 64), European stonechat (*Saxicola rubicola*, n = 57), common wood-pigeon (*Columba palumbus*, n = 44) and Eurasian skylark (*Alauda arvensis*, n = 41); the most often occurring species were European stonechat (frequency = 43.8%), Eurasian skylark (31.3%), white wagtail (*Motacilla alba*, 28.1%), redbacked shrike (*Lanius collurio*, 25.0%) and Eurasian tree sparrow (25.0%) (Table S2.1).

3.2. Effect of solar parks

There were 353 individuals of 41 species recorded in the solar parks and 271 individuals of 40 species in the control plots. Thirteen unique species were recorded on plots in solar parks, 12 on control plots (Table S2.1).

There were statistically significant differences between the solar parks and the control plots in total bird species richness, Shannon diversity, and invertebrate-eaters species richness and abundance (Table 1, Table S1.2 and Table S1.3). These variables were higher in the solar parks than in the control plots (Fig. 2). A significant interaction between plot type and previous land cover on the abundance of the ground-foragers was found (Table 1), their number was lower in control plots on grassland than in solar parks developed on grassland (Fig. S1.2, Table S1.2). Otherwise, there was no significant interaction between plot type and previous land cover, indicating that the type of land cover on a site prior to solar park development had no influence on the differences between solar parks and control plots (Table 1). The variability of the response variables explained by the fixed factors in the (G)LMMs ranged from 4 to 18% (Table 1). Total bird abundance, species richness and abundance of farmland birds with declining 10-year trend and with declining long-term trend, the ground-nesters species richness and abundance, and ground-foragers species richness did not differ significantly between solar parks and control plots.

The explanatory variables (plot type, previous land cover, elevation and landscape context) explained 14.3% of the variation (R_{adi}^2) in bird community composition (dbRDA, $F_{9, 54} = 2.1051$, P < 0.001; Table S1.4). The proportion of inertia constrained by the explanatory variables was 26.0%; total inertia = 23.042. The first two axes explained 11.8% (CAP1) and 4.4% (CAP2) of the bird community composition. The first axis separated the solar parks from the control plots, while the second axis further subdivided the bird communities by separating the control plots on arable lands from the control plots on grasslands and spread the communities along the gradients of elevation, cover of arable land, forests and grasslands (Fig. 3). European stonechat, Eurasian tree sparrow, black redstart (Phoenicurus ochruros), white wagtail, and redbacked shrike were most strongly associated with solar parks. Eurasian skylark, common pheasant (Phasianus colchicus) and common wood-pigeon occurred most frequently on control plots on arable land at lower elevations in a landscape dominated by arable land, while mistle thrush (Turdus viscivorus) and fieldfare (Turdus pilaris) occurred most frequently on control plots on grasslands (Fig. 3). The variation partitioning revealed that the largest fractions of variation in community composition were explained by plot type and landscape context, although half of the contribution of landscape context was shared with other variables, mainly previous land cover and elevation (Fig. 4). The pure effect of previous land cover alone was not significant ($F_{1, 55} =$ 1.2773, P = 0.167) (Table S1.4).

Management under the photovoltaic panels influenced bird community composition in the solar parks and explained 3.4% of community variability ($F_{1,30} = 1.7811$, P = 0.048).

A pairwise comparison of plot types using PermANOVA ($R^2 = 0.11$, $F_{2, 61} = 3.8817$, P < 0.001) revealed the largest differences between the communities of the solar parks and those of the control plots on arable land ($R^2 = 0.12$, F = 6.5638, P = 0.003), smaller differences between the communities of the solar parks and those of the control plots on grasslands ($R^2 = 0.06$, F = 2.6972, P = 0.004), while the differences between the control plots on grassland and those of arable land were marginally

Table 1

Analysis of variance tests for the generalized linear mixed models and linear mixed model examining the effects of plot type (solar park or control plot), previous land cover (the land cover that would have been present if the solar park had not existed), and the interaction between plot type and previous land cover on bird species richness, abundance and diversity (n = 64). $R^2m/c = marginal/conditional pseudo-R^2$, Error structure: NB1 = negative binomial with linear parametrization, NB2 = negative binomial with quadratic parametrization, P = Poisson, G = Gaussian. The parameter estimates for each effect are presented in Table S1.2.

Response variable	Model term	χ^2	Р	R ² m∕ c	Error structure
Bird species richness	Intercept	47.688	<0.001	0.13/ 0.35	NB2
	Plot type	4.682	0.030		
	Previous	2.019	0.155		
	land cover				
	Plot type \times	0.186	0.666		
	Previous				
Dind abundance	land cover	150.007	-0.001	0.05/	NDO
Bird abundance	mtercept	158.837	<0.001	0.05/	INDZ
	Plot type	0.015	0.903		
	land cover	0.525	0.469		
	Plot type x	2 386	0 1 2 2		
	Previous	2.000	0.122		
	land cover				
Shannon diversity	Intercept	24.823	<0.001	0.15/ 0.34	G
	Plot type	8.170	0.004		
	Previous	2.078	0.149		
	land cover				
	Plot type \times	0.454	0.500		
	Previous				
Spacias richnoss of	Iana cover	0.050	0 800	0.007	D
farmland birds	intercept	0.059	0.808	0.00/	Р
with declining	Plot type	0.032	0.856	0.00	
10-vear trend	Previous	< 0.001	0.982		
	land cover				
	Plot type \times	< 0.001	0.985		
	Previous				
	land cover				
Abundance of	Intercept	6.704	0.010	0.02/	
with declining	Plot type	1 1 7 4	0.406	0.10	NB1
10-year trend	Previous	0.583	0.400		NDI
	land cover				
	Plot type \times	0.484	0.487		
	Previous				
	land cover				
Species richness of	Intercept	3.718	0.054	0.01/	Р
tarmland birds	Diot trees	0.077	0.790	0.01	
long-term trend	Provious	0.077	0.782		
iong-term trend	land cover	0.10/	0.744		
	Plot type ×	0.067	0.798		
	Previous				
	land cover				
Abundance of	Intercept	27.615	< 0.001	0.03/	NB2
farmland birds				0.14	
with declining	Plot type	0.581	0.446		
long-term trend	Previous	0.374	0.541		
	Plot type ~	0.004	0.952		
	Previous	0.004	0.932		
	land cover				
Ground nesters'	Intercept	3.358	0.067	0.01/	Р
species richness	-			0.11	
	Plot type	0.183	0.668		
	Previous	0.192	0.661		
	land cover	0.040	0.005		
	Plot type ×	0.043	0.835		
	land cover				

(continued on next page)

Table 1 (continued)

Response variable	Model term	χ^2	Р	R ² m∕ c	Error structure
Ground nesters' abundance	Intercept	16.580	<0.001	0.03/ 0.47	
	Plot type	1.185	0.276		Р
	Previous	0.109	0.742		
	land cover				
	Plot type \times	2.595	0.107		
	Previous				
	land cover				
Invertebrate-	Intercept	0.041	0.839	0.18/	Р
eaters' species				0.32	
richness	Plot type	6.501	0.011		
	Previous	3.620	0.057		
	land cover				
	Plot type \times	0.928	0.335		
	Previous				
	land cover	0.000	0.070	0.15 /	
Invertebrate-	Intercept	3.099	0.078	0.15/	
eaters' species	Diet true e	4 170	0 041	0.25	ND1
abundance	Plot type	4.173	0.041		ND1
	land covor	0.969	0.320		
		<0.001	0.080		
	Provious	<0.001	0.909		
	land cover				
Ground-foragers'	Intercept	5.779	0.016	0.04/	Р
species richness				0.04	-
	Plot type	0.800	0.371		
	Previous	0.101	0.750		
	cover				
	Plot type \times	0.068	0.795		
	Previous				
	cover				
Ground-foragers'	Intercept	32.715	< 0.001	0.08/	
species				0.39	
abundance	Plot type	0.000	1.000		Р
	Previous	0.700	0.404		
	land cover				
	Plot type \times	4.198	0.040		
	Previous				
	land cover				

Table 2

Distance-based redundancy analysis (dbRDA) model for bird community composition (Bray-Curtis dissimilarities) of solar parks and control plots.

Term	Sum of squares	F	Р
Plot type	1.9305	6.1114	0.001
Previous land cover	1.0469	3.3143	0.001
Elevation	0.6646	2.1038	0.020
Artificial areas	0.4744	1.5017	0.128
Arable land	0.6852	2.1691	0.018
Agricultural and natural areas	0.2657	0.8412	0.615
Forests	0.3275	1.0367	0.443
Grasslands	0.4042	1.2794	0.246
Plot type \times Previous land cover	0.1858	0.5883	0.851
Residual	17.0577		

non-significant ($R^2 = 0.06$, F = 1.8513, P = 0.068).

Black redstart, European stonechat, white wagtail and Eurasian tree sparrow were identified as species most strongly associated with solar parks; fieldfare was identified as indicator of control plots on grassland and Eurasian skylark as best indicator species for control plots on arable land (Table 3, Table S1.5).

4. Discussion

To our knowledge, this is the first peer-reviewed original study investigating the impact of solar parks on bird diversity across a large number of sites (Harrison et al., 2017). In Central European agricultural landscapes, we found that the total bird species richness, Shannon diversity, species richness and abundance of invertebrate-eaters were higher in solar parks than in control plots. The abundance of ground-foragers was higher in solar parks developed on grassland than in grassland control plots; otherwise, previous land cover did not affect bird richness and abundance either alone or in interaction with plot type. We also found that solar parks increase bird beta-diversity by affecting the species composition of bird communities.

The higher total species richness and diversity observed in solar parks than in control plots could be due to their higher structural diversity. Habitat heterogeneity across multiple spatial and temporal scales is a key determinant of bird diversity (and other animal and plant taxa), with which habitat heterogeneity is positively associated (Andersen et al., 2023; Benton et al., 2003; Pickett and Siriwardena, 2011; Stein et al., 2014; Vickery and Arlettaz, 2012). In Central Europe (Czechia), cropland has the lowest bird species richness and beta diversity compared to the other main habitats (forests, urban areas, wetlands, grasslands); a similar pattern holds for the species-area relationship (Reif et al., 2023). Given the positive correlation between habitat structural diversity (complexity/heterogeneity) and the slope of the species-area relationship (Reif et al., 2023) as well as abundance (Pickett and Siriwardena, 2011), it can be expected that the difference between solar parks and control plots will become more apparent when larger area study units with are sampled.

Consistent with our predictions, we observed more invertebrateeating bird species and their higher abundance in solar parks than in control plots. Populations of insectivorous birds in Europe are negatively affected by agricultural intensification and loss of grassland habitat (Bowler et al., 2019). In addition to indirect effects of intensification, such as the homogenisation of farmland and the cultivation of crops with dense and tall sward (reduced food accessibility), agricultural intensification is thought to directly negatively affect the availability of food resources through the use of insecticides (Bowler et al., 2019; Busch et al., 2020; Reif and Hanzelka, 2020; Hološková et al., 2023; Moreau et al., 2022). In addition, the food availability for insectivorous birds in solar parks may be increased by photovoltaic panels, which inadvertently attract various species of water-seeking aquatic insects through the horizontally polarised light reflected by the panels (Horváth et al., 2010). It is important to note that here we have only classified species as invertebrate-eaters whose main diet consists of invertebrates (Wilman et al., 2014), but most of the species studied in our study supplement their diet or feed their nestlings with insects during the breeding season (Storchová and Hořák, 2018). Therefore, we can assume that solar parks may be even more important for birds during the breeding season.

Next, as predicted, we observed higher abundance of groundforagers within solar parks compared to grassland control plots, but contrary to our prediction, no effect of the solar park on species richness or abundance of ground-nesters. Vegetation structure, food availability and accessibility determine populations of ground-foragers and groundnesters in agricultural landscapes (Butler and Gillings, 2004; Hološková et al., 2023; Hoste-Danylow et al., 2010; Wilson et al., 2005). In grasslands, vegetation height is positively related to invertebrate abundance and biomass and negatively related to the number of foraging birds (Hoste-Danylow et al., 2010). The effects of vegetation characteristics on the selection of nesting habitat of ground-nesters are species-specific and thus influence the composition of bird communities. For example, the nesting habitat preferences of skylark are negatively correlated with sward height (Koleček et al., 2015), yellow wagtail (Motacilla flava) prefers crops with a height of 20–40 cm and a ground coverage of at least 60% (Kragten, 2011), European stonechat breeds in open habitats with extensive management, often with scrubby vegetation, its nest is built in grass, often growing underneath the bushes (Fuller and Glue, 1977), while the abundance of northern wheatear (Oenanthe oenanthe) is positively associated with the presence of bare ground and short vegetation as a nesting or foraging habitat (Kämpfer and Fartmann, 2019). Nesting habitat may not necessarily be identical to foraging habitat and can be shifted during the course of a single breeding season due to



Fig. 2. Boxplots of bird species richness, abundance and Shannon diversity of all species, species richness and abundance farmland birds with declining ten-year population trend and declining long-term population trend, ground-nesters, invertebrate-eaters, and ground-foragers in solar parks and control plots (2 ha in size). The asterisk indicates statistically significant differences between plot types (**P < 0.01, *P < 0.05) based on (G)LMMs (Table 1).

crop/vegetation development (e.g. Kirby et al., 2012; Koleček et al., 2015; Kragten, 2011).

Our results support previous observations from reports and preliminary studies of bird diversity at solar parks. In the UK, several (11) solar farms were found to have higher bird species richness than adjacent undeveloped sites. These solar parks were more important for declining bird species than control plots (Montag et al., 2016); in contrast, we observed no difference in declining bird richness and abundance between solar parks and control plots. Observations of birds of conservation concern in a small sample of solar parks were reported by Parker and McQueen (2013). Similar to our study, Montag et al. (2016) recorded predominantly higher bird abundance on solar park



Fig. 3. Distance-based redundancy analysis biplot of the association between bird community composition and solar parks and control plots (on arable land or grassland), elevation and landscape context – cover of arable land, artificial areas, forests, agricultural and natural areas, and grasslands. For clarity, only the labels of the species best fitted by the explanatory variables (>0.20 units on both axes) are displayed; continuous variables were scaled to the unit variance. Explanatory variables accounted for 14.3% of community composition (R_{adj}^2 ; P = 0.001; Table 2). The scale represents the Bray-Curtis dissimilarities. Species abbreviations are composed of the first four letters of the scientific genus and species name (see Table S2.1 for species list).

plots, although this was not statistically significant. An increase in species richness and constant or increased abundance was reported by about 70% and 85% of solar parks in Germany, respectively (Peschel et al., 2019). In Japan, bird species richness in solar parks did not differ from cropland, wetland and pasture and was lower than on abandoned farmland; total bird abundance did not differ significantly between solar farms and wetland, abandoned farmland and pasture, abundance on cropland was lower (Kitazawa et al., 2019). However, this pattern may be influenced by the small sample size used in their study, i.e., three

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solar farms (Kitazawa et al., 2019).

We have also shown that solar parks affected the composition of bird communities in agricultural landscapes. Such a pattern was expected based on reports of the biodiversity of solar parks in the UK and Germany (Montag et al., 2016; Peschel, 2010; Peschel et al., 2019); bird surveys of photovoltaic installations at airports in the USA also showed some changes in bird communities – birds were more abundant in photovoltaic arrays than in airfields, but opposite was true for the number of bird species (DeVault et al., 2014). We also expected that the effects of the solar park to be more pronounced – the differences between the solar park and the control plot to be greater – if the solar park had been developed on arable land rather than grassland. PermANOVA confirmed our expectations for the composition of the bird communities. This pattern can be explained by the greater habitat similarity of solar parks with grassland control plots than arable land control plots. In addition to plot type (solar park and control plot), landscape context

Table 3

Indicator species of solar parks and control plots (arable lands or grasslands). The indicator value indices assess the predictive values of species as indicators of the conditions prevailing in the plot groups; the predictive value of the species is expressed by (A) the species specificity, i.e. the probability that the plot surveyed belongs to the target plot group if the species was found, and (B) the species fidelity, i.e. the probability of finding the species in plots belonging to the plot group for the species.

Plot type	Species	Statistic	Р	Specificity (A)	Fidelity (B)
Solar	Phoenicurus ochruros	0.428	0.0029	0.690	0.688
	Saxicola rubicola	0.412	0.0024	0.807	0.438
	Motacilla alba	0.368	0.0114	0.704	0.500
	Passer montanus	0.354	0.0115	0.875	0.375
Control –Grassland	Turdus pilaris	0.341	0.0192	0.796	0.333
Control –Arable	Alauda arvensis	0.419	0.0020	0.688	0.765



Fig. 4. Variation partitioning in bird community composition explained by four sets of variables – type of plot (solar parks or control plots), previous land cover (arable land or grassland), elevation, and landscape context (cover of arable land, artificial areas, forests, agricultural and natural areas, and grasslands). The partitioning was done using distance-based redundancy analyses based on the Bray-Curtis dissimilarity matrix. The numbers (%) refer to the adjusted coefficients of determination. Fractions with percentages in grey were not tested. ***P < 0.001, **P < 0.01, **P < 0.05.

(the proportion of landscape cover classes in the surrounding area) was also associated with bird community composition on the study plots. Bird community composition in the control plots was most strongly associated with the proportion of arable land (or grassland and forest) in the surrounding landscape. In contrast, bird community composition in solar parks was mainly related to the higher proportion of artificial land cover in the surrounding landscape (solar parks are also classified as artificial surfaces by Corine Land Cover) (Fig. 3). This can be explained by the degree of similarity between control plots and solar parks and habitats (land cover classes) in the surrounding landscape. Therefore, solar parks also meet the habitat requirements of bird species often associated with artificial environment, such as black redstart and white wagtail. This suggests that the solar parks studied may represent more distinct spatial units in the agricultural landscape (i.e., habitat islands) than the control plots (e.g. Tworek, 2002), especially when solar parks are surrounded by a matrix of more contrasting habitat types (Matthews, 2021). The importance of landscape context for local biodiversity has been widely recognised in recent decades (e.g. Guerrero et al., 2012; Mazerolle and Villard, 1999). As shown by the variation partitioning (Fig. 4), collinearity between the variables characterising landscape context and other variables, in particular the previous habitat type, the land cover of the control plots (Fig. 3), should be taken into account as it may confound the interpretation of the results. Thus, no statistically significant pure effect of previous land cover can be attributed to the similarity of the habitats on the control plots to the habitats prevailing in the surrounding landscape - within 500 m, the proportion of arable land ranged between 0 and 100%) and the proportion of grassland ranged between 0 and 92% (Table S1.1).

Black redstart, European stonechat, white wagtail and Eurasian tree sparrow were identified as indicator species for solar parks in our study. The high specificity and fidelity of the identified indicator species (Table 3) suggests that solar parks contained strong cues that are used by these species to select this habitat for breeding and foraging. All four species feed entirely or mainly on invertebrates; they forage on the ground, some of them also in short flight from the air (black redstart and white wagtail), but they also capture objects from walls, foliage, etc. by hovering nearby (black redstart). Black redstart and white wagtail inhabit also artificial and anthropogenic habitats similar to their natural habitats which always include bare patches (a rocky component or waterside) and very low vegetation cover; they nest in a hole or crevice in a variety of natural and artificial sites. The European stonechat inhabits habitats with low vegetation and scattered bushes, shrubs, stones, walls, fences, which are used as look-outs and song-posts; the species avoids tall and dense grass (book; book; Paquet and Keller, 2020; Storchová and Hořák, 2018). We observed that the support structures of the solar panels were used as nesting sites by the black redstart and the white wagtail, the Eurasian tree sparrow nested in the support structures of the panels made of pipes, while the stonechat nested in the uncultivated or extensive vegetation under the solar panels or next to the fence. These species used the solar panels and fence for perching and/or for foraging.

We also observed other species of conservation concern in the solar parks, e.g. European stonechat, red-backed shrike, lesser grey shrike (*Lanius minor*), whinchat (*Saxicola rubetra*), northern wheatear, European roller (Coracias garrulus) and grey partridge (*Perdix perdix*) – species that could benefit from solar parks in the agricultural landscape of central Europe. In contrast, the skylark, a species identified as an indicator for control plots on arable land, was more common on control plots than on solar parks. Observations from Germany suggest that close row spacing of photovoltaic plants may be negatively associated with skylark breeding density (Peschel et al., 2019), but this issue remains to be investigated.

The impacts of solar energy development on biodiversity depend on the conservation value of the habitat in which the facilities are developed (Cameron et al., 2012). Impacts can be negative, mainly due to destruction and modification of wildlife habitat (Hernandez et al., 2015;

Kim et al., 2021; Lovich and Ennen, 2011). Thus, negative impact of solar park on bird species richness and density was observed in South Africa (Visser et al., 2019). In the UK, the installation of solar parks is seen as an opportunity for biodiversity enhancement (Harrison et al., 2017; Montag et al., 2016; Taylor et al., 2019), and is the case in Germany (Badelt et al., 2020; Peschel, 2010; Peschel et al., 2019). While bird species richness was lowest on croplands compared to other habitat types in Czechia (Reif et al., 2023), the opposite was observed on croplands in central Italy (Morelli et al., 2018). These differences can be attributed to the landscape heterogeneity of the studied farmland areas (Clough et al., 2020; Martin et al., 2019): While farmland in Italy is very heterogeneous, the opposite is true for Czechia and Slovakia, where the average field size is among the largest in the European Union (Hološková et al., 2023; Reif et al., 2023). Therefore, in landscapes characterised by intensive agriculture with habitats of low conservation value, the impact of solar parks on bird diversity may be positive.

There is also a recognised potential impact of solar park development on birds – the potential for collision mortality. There is limited information from studies monitoring mortality (Kosciuch et al., 2020; Visser et al., 2019), so generalisations about the direct impacts of solar parks on birds are currently limited (Kosciuch et al., 2020). Some observations of stranded, injured or deceased water-associated and water-obligate birds led to the hypothesis of the "lake effect", which states that solar arrays are mistakenly perceived as water bodies by these birds and therefore attract those (Kagan et al., 2014). This bird behaviour has also been observed in relation to other man-made objects (Bernáth et al., 2001; Horváth et al., 2009). It appears that bird mortality associated with solar parks is lower than other anthropogenic sources of bird mortality, but due to lack of data and monitoring challenges, further empirical studies are needed to better understand the risk of solar energy development to birds (Kosciuch et al., 2020; Visser et al., 2019).

The management of the solar parks studied only considered the operational aspects of the facilities (keeping the panels free of debris, reducing shading from vegetation). The vegetation between the rows of solar panels and around the solar panels was usually mowed regularly (at least twice a year); the vegetation under the panels was usually cut, treated with herbicides or not maintained at all (see Materials and methods, Environmental conditions and landscape context). We have shown that even the management of the vegetation under the panels, expressed by a simple binomial variable (managed/unmanaged), influences the composition of bird community in the solar parks. We suggest that a more detailed assessment of the structure of solar parks could shed more light on the factors underlying bird community composition in solar parks. Solar farms are thought to offer opportunities to simultaneously promote and conserve biodiversity, in addition to the economic benefits of renewable energy production (Randle-Boggis et al., 2020; Nordberg et al., 2021). Evidence-based management recommendations for solar parks to promote pollinator biodiversity have recently been published (Blaydes et al., 2021). Similarly, solar parks can be designed and managed to provide suitable habitat for target species by focusing on their habitat requirements, for example using restoration ecology (see Hale and Swearer, 2017; McAlpine et al., 2016). For example, the colonisation of a solar park by tawny pipit (Anthus campestris), northern wheatear and Eurasian hoopoe (Upupa epops) had been encouraged by habitat improvement, installation of artificial nesting sites and appropriate site management that provided foraging substrate in a solar park in Germany (Peschel, 2010; Peschel et al., 2019). Factors that may influence the composition of the bird communities in a solar park include land cover (e.g. bare ground, sparse vegetation, rocky surface), type and intensity of vegetation management (grazing, moving, herbicide application; removal of mown vegetation), vegetation composition, solar park design (i.e. type of support structures of solar modules – profile shape and height of racking systems, row spacing, park area) (e.g. Hoste-Danylow et al., 2010; Montag et al., 2016; Nordberg et al., 2021; Peschel, 2010; Peschel et al., 2019). Thus, it is likely that solar parks designed and managed in

synergy with a greater focus on wildlife would increase the positive impacts of solar parks on avian biodiversity in agricultural landscapes (e.g. Bennun et al., 2021; BRE, 2014; SolarPower SolarPower Europe, 2022). Further research is needed to assess the impacts of the above factors on birds, which could help in the design of solar parks to achieve synergies between commercial and conservation outcomes (Moore-O'Leary et al., 2017; Nordberg et al., 2021).

5. Conclusion

In conclusion, we have found that solar parks can play a positive role in promoting bird diversity in a homogeneous and intensively managed agricultural landscape and thus represent landscape features that can increase bird species richness and diversity and change the composition of bird communities in such a landscape as a by-product of electricity production. It is important to note that the solar parks in our study were designed and managed for renewable electricity production only. Therefore, it can be assumed that the biodiversity benefits would be even greater if they were managed synergistically with a stronger focus on wildlife (i.e. in line with the habitat requirements of the target species of conservation concern) (e.g. Fahrig et al., 2019; Šálek et al., 2018). We surveyed the study plots during the breeding season. As food availability and accessibility is low in winter, it can be assumed that solar parks can have a positive impact on farmland birds outside the breeding season, as they can serve as stopover, foraging and roosting sites during migration and wintering (Šálek et al., 2022), as the ground under the solar panels can remain snow-free in winter (Peschel, 2010). It needs to be investigated whether solar parks do not act as ecological traps for some bird species (Hale and Swearer, 2017), for example nests of species nesting on solar panel support structures could be more easily preyed upon by nest predators such as stone martens or red squirrels.

Research data

The data that support the findings of this study are available from the corresponding author upon request.

CRediT authorship contribution statement

Benjamín Jarčuška: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. Monika Gálffyová: Investigation, Writing - review & editing. Richard Schnürmacher: Investigation, Writing - review & editing. Michal Baláž: Investigation, Writing - review & editing. Michal Baláž: Investigation, Writing - review & editing. Miloslav Mišík: Investigation, Writing review & editing. Matej Repel: Investigation, Writing - review & editing. Miroslav Fulín: Investigation, Writing - review & editing. Dušan Kerestúr: Investigation, Writing - review & editing. Zuzana Lackovičová: Investigation, Writing - review & editing. Marian Mojžiš: Investigation, Writing - review & editing. Matej Zámečník: Investigation, Writing - review & editing. Peter Kaňuch: Investigation, Methodology, Writing - review & editing. Anton Krištín: Investigation, Methodology, Writing - review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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