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Effect of habitat structure and crop diversity on common and threatened birds breeding in semi-natural field margins

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Abstract. Field margins are inherent elements of European agricultural landscapes, thought to be crucial for maintaining a high biodiversity level. The interactions between the structure of field margins and biota have been recognized, yet the understanding of the importance of various components of the margins and adjacent areas is still incomplete. The aim of our study was therefore to determine the relative importance of structural features of the margins and diversity of adjacent crops for birds breeding in field margins. The study was carried out in 70 field margins covered with semi-natural vegetation, situated in SW Poland. Both the number of species and bird density were most strongly positively related to the development of tree and shrub layers, while presence of ditches and percentage of reed cover (positive effects) had much less importance. Analyses conducted at the species level revealed the complexity of bird-habitat interactions resulting from various requirements of individual species. Overall, for 22 abundant species and for the threatened species, the development of the shrub layer turned out to be a particularly important feature of field margins positively associated with occurrence of e.g. *Emberiza citrinella*, *Linaria cannabina* and *Streptopelia turtur*. Other significant positive effects had the development of the tree layer (e.g. *Turdus merula* and *Turdus philomelos*), presence of ditch (e.g. *Acrocephalus palustris*, *Sylvia communis*), and number of gaps in woody vegetation (e.g. *Lanius collurio*). The diversity of adjacent crops had positive effects only to some threatened species (e.g. *L. collurio* and *E. calandra*). Abundances of common and threatened birds were not correlated, which reflects different habitat demands of these two groups. Because of diverse bird-habitat relationships, maintaining a variety of field margins (in particular the shrubby ones), should be accepted as a rule in biodiversity-oriented management of agricultural landscapes.

Key words: semi-natural habitats, breeding birds, habitat characteristics, hedgerows, threatened species, heterogeneous landscape

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INTRODUCTION

The loss of habitat heterogeneity is thought to be a key factor driving widespread decline in biodiversity in agricultural landscapes (Ryszkowski et al. 2002, Benton et al. 2003, Cormont et al. 2016). Key components of this heterogeneity are various non-farmed habitats, such as field margins or other microhabitats (Tryjanowski et al. 2014), which increase the number of ecological niches and encourage species richness and abundance. The significance of field margins overgrown with semi-natural communities of perennial plants has been shown for a range of taxa (Wilson et al. 1999, Hinsley & Bellamy 2000, Marshall & Moonen 2002, Herzon & Helenius 2008), with birds being particularly well studied. In the European agricultural landscapes, the field margins are inhabited by diverse bird assemblages, as regards the abundance, ecological requirements and threat status (Green et al. 1994, Parish et al. 1994, Sparks et al. 1996, Kujawa 1997, Jobin et al. 2001, Wuczyński et al. 2011). Due to clear between-species differences in habitat selection and resource requirements, various associations between bird occurrences and margin attributes are expected. Indeed, the effects of field margin characteristics on bird assemblages have been identified in previous studies (Green et al. 1994, Parish et al. 1995, Kujawa 1997, Hall et al. 2018), usually highlighting the importance of plant cover structure and dimensions (width and length) of the field margins (Kujawa 1997, Hinsley & Bellamy 2000, Graham et al. 2018).

However, our understanding of the significance of various components of the field margins for birds is still incomplete, for several reasons. Firstly, most earlier studies concentrated on selected types of field margins, probably reflecting regional traditions in farmland management and corresponding landscape features. For example, research conducted in Western Europe usually focused on hedgerows (Green et al. 1994, Parish et al. 1995) and in Central and Eastern Europe — on tree belts (Balát 1986, Tryjanowski et al. 2009, Mérő 2010). Studies involving a wider spectrum of field margins, for example diverse multi-layer vegetation along drainage ditches, rich herb communities in baulks, or spontaneous gappy shrubs along field roads (Dajdok & Wuczyński 2008), are scarce.

Secondly, it has been shown that the structure of the surrounding habitats, including crop types, influences the diversity of birds associated with the field margins (Hinsley & Bellamy 2000, Le Cœur et al. 2002). Especially the ecotonal bird species, common in such habitats, use the resources of both the field margins and the adjacent areas. However, the context of the surroundings is rarely considered in field margin studies (Green et al. 1994, Parish et al. 1994, 1995) and the knowledge on the importance of interactions between field margins and adjacent cultivated fields for bird abundance in field margins is presumably insufficient.

Inadequate understanding of the field margins ecology also results from differences in biogeographic conditions, and socio-economic and historical circumstances of the various study areas. In particular, agricultural landscapes in Central and Eastern European countries (CEE) differ markedly from those in the early members of EU (Northern and Western Europe — NWE), which also implies the differences in bird assemblages (Reif et al. 2008, Sutcliffe et al. 2015, Cormont et al. 2016). Lower levels of agrochemical inputs, mechanization and productivity in CEE result in less than half yields per hectare than those of NWE. Moreover, large number of small farms in CCE, compared to large industrial units that dominate in NWE, promote mixed farming and mosaic landscape structures, with an overall positive effects on biodiversity (Tryjanowski et al. 2011, Sutcliffe et al. 2015). More recently however, CEE countries follow standards and economic indicators of the old EU members with detrimental effects on biodiversity that also include declines in bird populations.

Finally, due to variety of field margins and diverse ecological demands of the associated bird species, one may expect large variability in the influence of field margins properties across species and conservation targets. For example, do the field margin characteristics that promote higher species richness also promote higher abundance of threatened species? Are the abundances of the threatened ecotonal species breeding in field margin affected by the structure of adjacent habitats? This is important when management and conservation prescriptions are to be formulated. The recommendations often refer to the conservation priority species, regularly supported by field margins (Wuczyński et al. 2014), thus requirements of these species should be better documented and considered.

We have previously shown the value of seminatural field margins typical of Central European agroecosystems for the overall bird communities and for the occurrence of threatened birds, vascular plants, and bryophytes (Wuczyński et al. 2011, 2014). In this paper we enlarge this scope and highlight in more detail the relationships between breeding birds and habitat structure in diverse field margins, ranging from herb communities to dense shrub and tree belts. The specific objectives of this paper are to: 1) determine the relative importance of structural properties of the field margins for breeding birds at the community and species levels; 2) examine whether the diversity of habitats surrounding the field margins affects species richness and density of birds breeding in the field margins; 3) examine whether the occurrence of conservation priority species depends on the same habitat features that contribute most to the overall species richness and abundance of birds.

MATERIAL AND METHODS

Study area

A total length of 35 km of field margins was studied, divided into 70 linear sample plots, located in an agricultural landscape of the Sudetes Foreland (SW Poland) (Fig. 1). The plots were 500 m long sections of field margins as defined by Marshall & Moonen (2002), i.e. the areas between adjacent

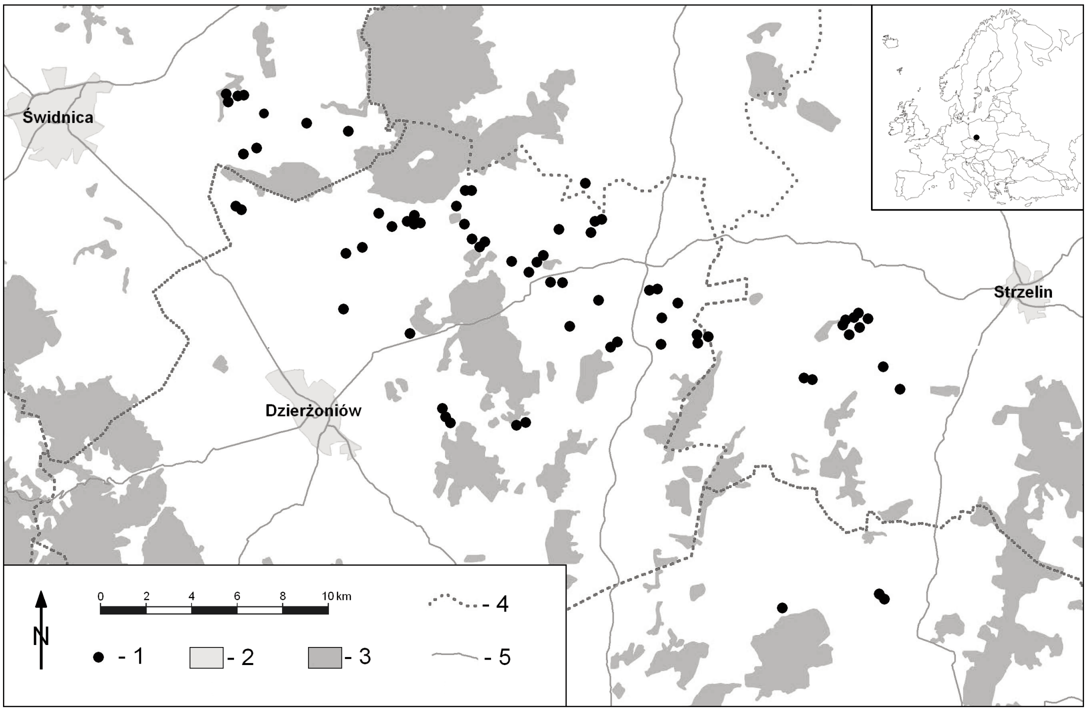

Fig. 1. Distribution of studied field margins. Explanations: 1 — location of the margin, 2 — main towns, 3 — forests, 4 — administrative borders, 5 — main roads.

fields, covered by spontaneous semi-natural vegetation and usually including a functional component (ditch, road, disused railway track). The total length of field margins covered by the bird counts amounted to 35 km and was therefore sufficient to characterize relationships between bird occurrence and habitat structure. The mean width of the field margins was 11.7 m (range 4.9–29.0 m, SD = 5.1) including the functional component, if present. The sample plots were not contiguous, except for two plots which adjoined perpendicularly. The maximum distance between sample plots was 35 km. The average minimum distance between the midpoints of two neighbouring sample plots was 774 m (range 155–4177 m). Detailed description of the plots is given in Dajdok & Wuczyński (2008) and Wuczyński et al. (2011).

The landscape is dominated by small fields (0.1 ha up to several hectares) and comprises a network of semi-natural habitats. The main crops cultivated in the region are wheat, maize, rye and oilseed rape. The farming intensity is close to that observed in other CEE countries (Table 1).

The plots were selected to reflect the diversity of field margins in an agricultural landscape in Poland, and they included different combinations of functional components. In total, as many as 53 plots included a ditch, 24 — a road, 4 — a disused railway track, and 4 were without any additional elements.

The vegetation in the plots created a lush multi-layer plant cover. Altogether 533 vascular plant species were found in 70 field margins (Dajdok & Wuczyński 2008). The herb layer occurred commonly, mainly composed of perennial species (e.g. *Phragmites australis*, *Elymus repens*, *Arrhenatherum elatius*, *Urtica dioica*, *Artemisia vulgaris* and *Aegopodium podagraria*), and its percentage cover depended inversely on the density of trees and shrubs. Shrub layer in drier plots included spiny species, mostly *Rosa* spp. and *Crataegus* spp., while along ditches — mainly *Salix* spp. and *Sambucus nigra*. In some other plots, a

Table 1. The indicators (averaged for 2006–2007) of agriculture intensity in the study area, i.e. in Dolnośląskie Province (Central Statistical Office, http://www.stat.gov.pl) and CEE countries (Eurostat, http://ec.europa.eu/eurostat). Agricultural area per holding was estimated excluding the extreme value of 89.3 ha in Czech Republic.

Indicator	Study area	CEE countries
Nitrogen input (kg N/ha)	96.0	100.0
Cereal yields (dt/ha)	32.3	34.5
Agricultural area per holding (ha)	8.4	13.8

dense thicket was formed by *Prunus spinosa*. Most abundant species in the tree layer were *Salix fragilis*, *S. alba*, *Alnus glutinosa*, *Fraxinus excelsior* and *Quercus robur*.

Quantifying the habitat in the sample plots and in their neighbourhood

Habitat structure and plant cover features were quantified in one of the growing seasons of 2004–2007 using a set of variables (Table 2). Standard parameters, i.e. percentage cover of trees and shrubs, their height and number of species, were completed with some other features, unique to field margins, such as the total number of gaps in tree or shrub layer, and percentage cover of the surface without trees and shrubs (both quantifying habitat heterogeneity). Additionally, habitat diversity in adjoining fields was taken into account.

To quantify these variables a number of field measurements were conducted with the use of three different approaches — T, T3, and T5 (Table 2). T — some variables were quantified for the whole sample plot (500 m), i.e. list of plant species, neighbourhood features, the length of sections: with trees, with shrubs, and without trees and shrubs (an index of structural heterogeneity). The diversity index of crop fields (Shannon index H') in 200 m buffer zone adjoining each study plot was estimated on the basis of crop composition. Crop types that differed taxonomically or ecologically, such as winter and spring cereals, grasslands, legumes etc. were treated separately. The borders of individual fields were obtained from aerial photographs and their actual pattern and crop types were updated during field surveys. All spatial data were processed by the GeoMedia Professional software. T5 — the variables describing the structure of vegetation were quantified with the use of 10 m wide transects perpendicular to the field margin axis, encompassing the whole width of the margin, and located at 50, 150, 250, 350 and 450 m from the end point of a given plot. The height of trees and shrubs was measured with the use of SUNTO PM5/1520 Height Meter or with a scaled stick. The measurements were averaged and used for further analyses. T3 — the dominance of reed in plant cover (Reed in Table 2) was assessed with the use of phytosociological relevés (N = 913) in three transects located at 100, 250, and 400 m from the end point of a given plot. For each sample plot the coefficient of reed cover was calculated as a sum of mean cover reached by the reed in each of the relevés x 100/total number of relevés (van der Maarel 1980).

Two principal components were identified in the Factor Analysis, which represented 80% of the total variability: PC_Trees and PC_Shrubs, representing tree stand "richness" and shrub layer "richness", respectively (Table 3). The higher value of PC_Trees, the larger tree species richness, tree stand height and cover. The higher value of PC_Shrubs, the larger shrub species richness, shrub height and cover, combined positively with the field margin width.

The two PCs, four other features of the field margins (Ditch, Road, Gaps, and Reed), and crop diversity in the nearest neighbourhood (Crops) constituted a complete set of habitat variables which was used to explain the bird distribution and abundance. The pair-wise correlations between the variables were weak ($|r| < 0.30$) and mostly insignificant (Appendix 1).

Table 2. The variables used for quantifying the habitat structure and features of plant cover in sample plots and their neighbourhood. The column 'Approach' indicates whether the variable is a mean of measures conducted in five (T5) or three (T3) cross-section transects, or along the whole 500 m long section (T). See text for further details.

Abbreviation	Approach	Habitat variable (unit)	Range of values	Transformation function
Width	T5	Field margin width (m)	4.9–29.0	log
Ditch	T	Presence of ditch	Yes/No	–
Road	T	Presence of road	Yes/No	–
Tree_cover_length	T	Total tree stand length (m)	0–434	log
Tree_height	T5	Tree stand height (m)	0–17.2	–
Tree_species	T	No. of species in tree stand	0–10	log
Shrub_cover_length	T	Total shrub layer length (m)	0–494.5	–
Shrub_height	T5	Shrub layer height (m)	0–8.9	–
Shrub_species	T	No. of species in shrub layer	0–23	–
Gaps	T	Number of gaps in tree or shrub layer	1–45	–
Open_area	T	Open area cover (%)	0–100	arcsin
Reed	T3	Coefficient of reed cover in the margin	0–4133.3	–
Crops	T	Crop field diversity in plot neighbourhood (H')	0–1.9	–

Table 3. The results of Factor Analysis for the variables describing the structure of field margins. The loadings > 0.7 are marked bold.

Variable	PC_Trees	PC_Shrubs
Width	0.07	**0.75**
Tree_species	**0.91**	0.28
Tree_height	**0.91**	0.19
Tree_cover_length	**0.95**	0.25
Shrub_height	0.48	0.62
Shrub_species	0.19	**0.87**
Shrub_cover_length	0.37	**0.85**
Open area	-0.57	-0.69
Variance explained	3.30	3.08
Variance explained (proportion)	0.41	0.39

Bird surveys

Bird abundances were assessed with the use of a simplified version of the territory mapping method (Bibby et al. 2012). In both years (2006 and 2007), bird surveys were performed by experienced researchers (the authors — AW, KK and WG) from dawn until 10 am, three times per breeding season. The observer walked along the whole plot and marked birds on a map (scale 1 : 2000). Special attention was paid to simultaneous territorial records (e.g. singing) of males. Direct evidence of breeding (nests, birds carrying nesting material, food etc.) were gathered too. Duration time (min/plot) increased with the diversity of the vegetation within the sample plots and ranged between 20 min in herbaceous field margins to 60 min in tree lines. Various observation duration times did not affect the field survey results, as proved by insignificant Pearson correlation ($r = 0.14$, $p = 0.24$) between duration time and the residuals in model of the relationships between the bird density and habitat structure (for model details see the section "Factors affecting the variability in bird assemblage")

The number of breeding territories per plot was estimated on the basis of clusters of sightings combined with any data on direct evidence of breeding. In some cases (ambiguous observations), a range of possible values was defined, and the mean value was used for further analyses. The obtained number of territories was used for the estimation of the number of breeding pairs per year (mean value for two years) and the total number of species (for two years jointly). The number of territories was defined (by field map analysis) by one person only (AW) to minimize bias related to subjectivity. Because of atypical breeding system (brood parasite), *Cuculus canorus* was included in the number of species but excluded from the analyses of the number of breeding pairs.

Statistical analysis

To normalize the data frequency distribution of measured variables, some of them were transformed (Table 2). Due to numerous significant correlations between habitat variables, their number was reduced with the use of the Factor Analysis (with rotation VARIMAX normalized). The number of principal components (PCs) was defined with the use of Kaiser's criterion. As the PCs are standardized variables, all the variables used in the analyses of the relationship between birds and habitat structure were standardized, too.

General Linear Model (GLM) and Generalized Linear Model (GLZ) were used to quantify the relationships between habitat structure and bird abundance or occurrences. Best models were selected with the use of the corrected Akaike Information Criterion (AICc). If there were more than one model for ΔAICc < 2 (difference between the AICc value of the best model and the AICc value for each of the other models), they were averaged with the use of R package MuMIn (Bartoń 2016). In order to minimize the spatial autocorrelation between sample plots, spatial covariance variable was added to the models using "spdep" R package (Bivand et al. 2013, Bivand & Piras 2015).

The bird species were classified into two groups: i) most common species ($n = 14$) — the species that occurred in at least 30% ($N > 20$) of sample plots; the response was the number of pairs per plot; ii) moderately common species ($n = 8$), i.e. found in 14–29% ($N = 10$–20) of field margins; their occurrence was included as a binary variable (absence/presence).

Moreover, to test the effect of habitat structure on the occurrence of birds of high conservation priority, a group of species defined as "threatened and conservation concern species" (TCCS) has been selected (Wuczyński et al. 2014). The group includes the species listed in Annex I of Bird Directive, in the European Red List of Birds (BirdLife International 2015), or species of European conservation concern (SPEC) by BirdLife International (2017).

In concordance with the frequency distribution of the explained variables the GLM and three variants of the GLZ were applied (Table 4). Tweedy distribution was used in the analyses related to the individual common species, as there was large proportion of abundances equal to zero.

Table 4. Model variants and Goodness-Of-Fit (GOF) measures applied in the analysis of the relationships between birds and habitat structure.

Type of model	Response variable	Assumed frequency distribution of the response variable	Applied link function	GOF
GLM	Total number of breeding pairs/plot (for community, *Emberiza citrinella* and *Acrocephalus palustris*)	Gaussian	Identity	R^2
GLZ	Number of species/plot (for community)	Poisson	Log	Pseudo-R^2
GLZ	Total number of breeding pairs/plot (for individual most common species)	Tweedy	Log	-
GLZ	Presence/absence in plot (for moderately common species)	Binomial	Log	Pseudo-R^2

In the case of two most common species, Yellowhammer *Emberiza citrinella* and Marsh Warbler *Acrocephalus palustris*, the GLM (with Gaussian distribution) was used. In the case of binomial distribution (logistic regression) the maximum number of variables in the model was set to 4; with bigger number of allowed variables the algorithm tended not to converge or returned very low significance level (> 0.98). Since all the predictors were standardized, their coefficients could be interpreted as a measure of relative effect size of predictors on response value. To assess coefficient significance, statistical significance and 95% confidence intervals (CI) were estimated. Additionally, in the averaged models the number of best models containing given predictor was defined, and the relative variable importance (RVI) of the predictors was estimated (Burnham & Anderson 2004).

Statistical analyses were performed using R packages (R Core Team 2016), Statistica 13.1 (Dell Inc. 2016), and PAST 3.11 (Hammer et al. 2001). In the multi-factor models the marginally significant effects ($p < 0.1$) were also presented with the intent to show a wide spectrum of possible bird-habitat relationships.

RESULTS

Composition of bird assemblage

The bird assemblage consisted of 50 breeding species (Table 5); and on average 11.8 species bred in one sample plot (range 5–25). On average, 1163 pairs were recorded (mean for 2006–2007), with the mean density of 33.2 pairs/km (from 14 to 90 pairs/km). The most abundant species (dominance > 5%) were Marsh Warbler (almost ¼ of all pairs), Yellowhammer, Red-backed Shrike *Lanius collurio*, Common Blackbird *Turdus merula*, Common Whitethroat *Sylvia communis* and Eurasian Blackcap *Sylvia atricapilla*.

Factors affecting the variability in bird assemblage

Three best models (ΔAICc < 2) fitted to explain variation in species richness contained four variables (Appendix 2). The averaged parameter estimates indicate that the number of species was most strongly and positively related to PC_Shrubs and PC_Trees (Fig. 2), whereas two other variables, i.e. spatial autocorrelation (Autocov) and presence of road (Road) were insignificant. The percentages of explained variance in the number of species were high for all best models ($R^2 = 0.76$).

Three best models of the relationships between bird density and habitat variables contained six variables and were fitted well to the observed bird density (adjusted pseudo-R^2 ranged from 0.93 to 0.96) (Appendix 3). In the averaged model the most important predictor variables were again PC_Shrubs, PC_Trees, and also Ditch and Reed (Fig. 3), according to model coefficients, statistical significance and RVI. Number of gaps affected bird abundance negatively. It is noteworthy that the effect sizes in both the number of species and bird density were highest in PC_Shrubs (Table 6 and 7), stressing the importance of shrub cover, rather than tree cover in field margins (Fig. 2, 3).

Factors affecting the variability in the most common bird species

For 14 the most common species the variables describing field margin structure were apparently more important than crop diversity in the adjacent areas (Fig. 4, Appendix 4). Overall, woody vegetation (PC_Trees and PC_Shrubs) was particularly important as revealed by the high

Table 5. Breeding bird assemblage in the studied sections of field margins. N — number of occupied plots, F — Frequency: S — most common species, i.e. occurred in N > 20 plots, D — moderately common species, i.e. occurred in 10–20 plots, % — dominance of the species. The TCCS (Threatened and Conservation Concern Species — marked in bold): SPEC — by BirdLife International (2017): 2, 3 — species which have an unfavourable conservation status in Europe, and whose global populations are concentrated (2) or not concentrated (3) in Europe. ETS — threat status of birds in Europe by BirdLife International (2017): VU (vulnerable), DC (declining), H (depleted); parentheses indicate that the status is provisional; categories of D and H are equivalent to the IUCN category of NT (Near Threatened). BD — species listed in Appendix I of Bird Directive. ERL — European Red List of Birds by BirdLife International (2015): VU (vulnerable).

Species	N	F	No. of breeding pairs		Pairs	%	TCCS species			
			2006	2007	per 10 km		SPEC	ETS	BD	ERL
Acrocephalus palustris	64	S	275.5	291	80.9	24.4				
Emberiza citrinella	**67**	**S**	**166**	**203**	**52.7**	**15.9**	**2**			
Lanius collurio	**56**	**S**	**73**	**91.5**	**23.5**	**7.1**	**2**	**(H)**	**+**	
Turdus merula	56	S	67	88	22.1	6.7				
Sylvia communis	60	S	67	72.5	19.9	6.0				
Sylvia atricapilla	27	S	53.5	66	17.1	5.1				
Turdus philomelos	44	S	43	50	13.3	4.0				
Sylvia nisoria	**39**	**S**	**38**	**43**	**11.6**	**3.5**			**+**	
Carduelis chloris	31	S	28	35	9.0	2.7				
Fringilla coelebs	24	S	27	34.5	8.8	2.6				
Phasianus colchicus	41	S	27.5	26	7.6	2.3				
Emberiza calandra	**26**	**S**	**25**	**27.5**	**7.5**	**2.3**	**2**	**(DC)**		
Emberiza schoeniclus	22	S	26	17.5	6.2	1.9				
Sylvia curruca	27	S	24	19.5	6.2	1.9				
Sylvia borin	12	D	17	19	5.1	1.5				
Linaria cannabina	**20**	**D**	**10.5**	**11.5**	**3.1**	**0.9**	**3**	**DC**		
C. coccothraustes	16	D	7	13	2.9	0.9				
Alauda arvensis	**16**	**D**	**5**	**13.5**	**2.6**	**0.8**	**3**	**(H)**		
Saxicola rubicola	11	D	8	9.5	2.5	0.8				
Acrocephalus scirpaceus	7		4	13	2.4	0.7				
Acrocephalus arundinaceus	7		8.5	6	2.1	0.6				
Sturnus vulgaris	**8**		**4**	**10**	**2.0**	**0.6**	**3**	**DC**		
Hippolais icterina	7		6.5	7	1.9	0.6				
Saxicola rubetra	**11**	**D**	**8**	**5.5**	**1.9**	**0.6**	**2**			
Parus major	10	D	4	7.5	1.6	0.5				
Oriolus oriolus	7		4.5	4.5	1.3	0.4				
Phylloscopus collybita	5		5	3.5	1.2	0.4				
Motacilla flava	**8**		**3**	**5**	**1.1**	**0.3**	**3**			
Cyanistes caeruleus	7		3	5	1.1	0.3				
Locustella naevia	8		5	2.5	1.1	0.3				
Carduelis carduelis	7		3.5	3.5	1.0	0.3				
Turdus pilaris	5		4	3	1.0	0.3				
Columba palumbus	9		3	3.5	0.9	0.3				
Passer montanus	**6**		**3.5**	**3**	**0.9**	**0.3**	**3**	**(DC)**		
Perdix perdix	**9**		**3.5**	**3**	**0.9**	**0.3**	**2**	**VU**		
Streptopelia turtur	**10**	**D**	**4.5**	**1.5**	**0.9**	**0.3**	**1**	**DC**		**VU**
Locustella fluviatilis	4		2.5	3	0.8	0.2				
Prunella modularis	6		2.5	3	0.8	0.2				
Lanius excubitor	**4**		**2.5**	**2**	**0.6**	**0.2**	**3**	**(H)**		**VU**
Luscinia megarhynchos	4		0.5	4	0.6	0.2				
Muscicapa striata	**2**		**1.5**	**3**	**0.6**	**0.2**	**2**	**H**		
Acrocephalus schoenobaenus	3		0	4	0.6	0.2				
Anas platyrhynchos	3		2.5	1	0.5	0.2				
Dendrocopos major	3		0	3	0.4	0.1				
Garrulus glandarius	3		1	1.5	0.4	0.1				
Buteo buteo	2		0	2	0.3	0.1				
Emberiza hortulana	**1**		**0**	**1**	**0.1**	**0.0**	**2**	**(H)**	**+**	
Serinus serinus	**1**		**1**	**0**	**0.1**	**0.0**	**2**			
Pica pica	1		0.5	0	0.1	0.0				
Cuculus canorus			Breeding, not counted							
Total			1080	1246	332.3	100				

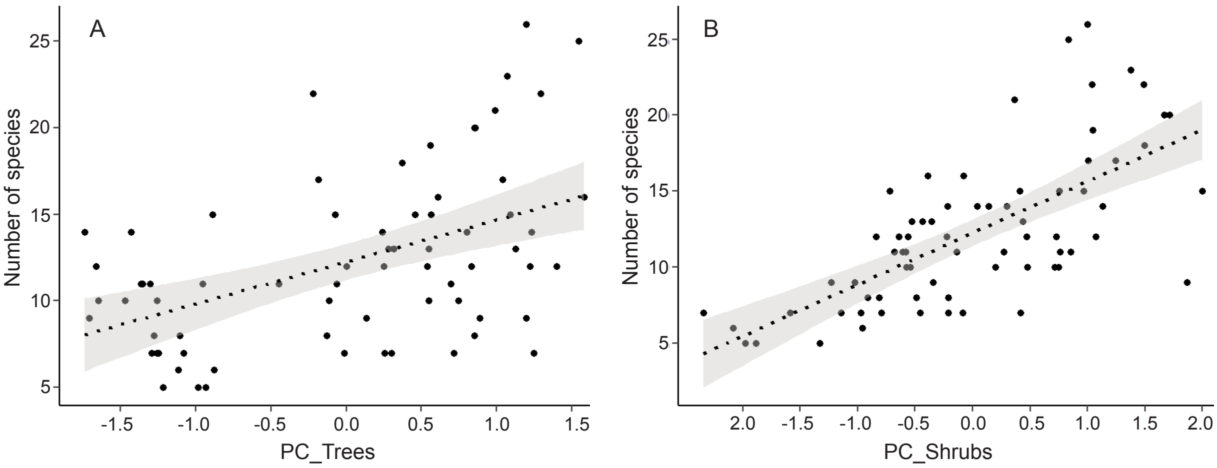

Fig. 2. Relationships between the number of bird species per plot and PC_Shrubs and PC_Trees as significant factors in multivariate averaged model described in Table 6.

number of significant relationships, high values of most coefficients, and a total of RVI's values (Fig. 5). Only Marsh Warbler and Common Pheasant *Phasianus colchicus* were not related significantly with these variables. Marginally significant relationships ($p < 0.10$) regarded Red-backed

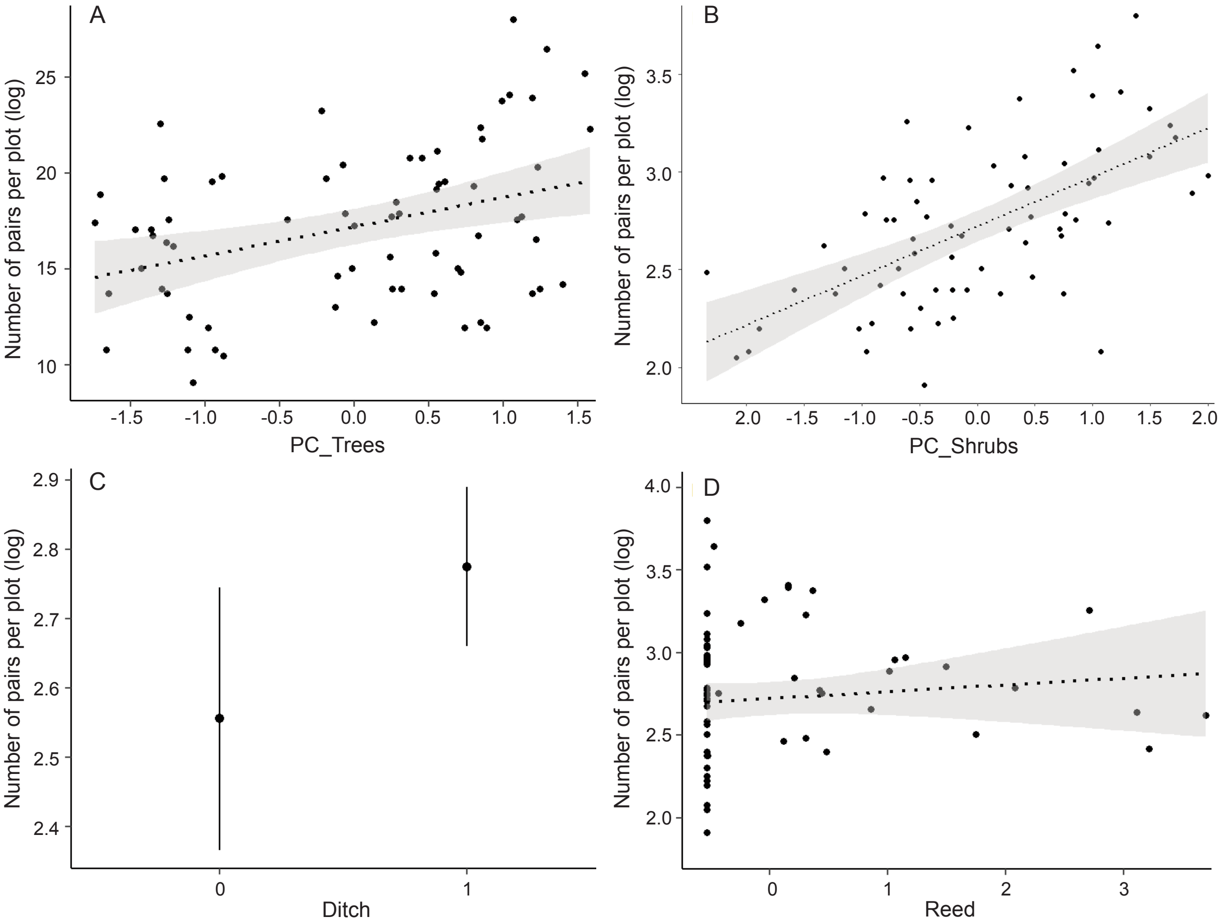

Fig. 3. Relationships between the bird abundance (number of breeding pairs per plot) and PC_Shrubs, Ditch, PC_Trees and Reed as significant factors in multivariate averaged model described in Table 7. The mean bird abundance with 95% CI is presented for Ditch.

Table 6. Averaged model of relationships between the number of species per plot and habitat variables, defined with the use of GLZ and AICc for best model selection (see section "Methods" for methodological details, and Appendix 2 for the details of best model subset). Pred. stat. — predictor statistics, p — statistical significance, CI — 95% confidence interval, RVI — relative variable importance, No. models — the number of models that contain given predictor.

Pred.stat.	Predictors				
	Intercept	Autocov	Road	PC Trees	PC Shrubs
p	< 0.0001	0.31	0.40	< 0.0001	< 0.0001
Value	2.50	-0.01	-0.06	0.20	0.29
CI	(2.27;2.72)	(-0.04;0.01)	(-0.21;0.09)	(0.13;0.28)	(0.22;0.36)
RVI		0.28	0.23	1	1
No. models		1	1	3	3

Shrike and Barred Warbler *Sylvia nisoria*, and only Reed Bunting *Emberiza schoeniclus* was affected negatively. Two other variables, appearing in the models relatively frequently as significant, i.e. Ditch and Reed, affected bird species bidirectionally (Ditch: positive significant effects for two species and negative for five species, Reed: positive for two, and negative for four species). Other habitat variables appeared in the models less frequently. Three species were related (positively) to crop diversity around field margins (Crop), i.e. Red-backed Shrike, Corn Bunting *Emberiza calandra* and Barred Warbler. Interactions between land diversity and the variables of field margins had little significance. Finally, in relatively high number of seven species their abundances were positively spatially correlated (Fig. 4).

Factors affecting the variability in the moderately common species

Similarly to the commonest species, the occurrence of those moderately common species was particularly related to woody vegetation (Fig. 6, Appendix 5). Seven of eight species were affected significantly by PC_Shrubs (two, i.e. Skylark *Alauda arvensis* and European Stonechat *Saxicola rubicola* — negatively), and four species — by PC_Trees (Skylark and European Stonechat — negatively). In six species the habitat diversity around field margins (Crop) was included into the best model, however only in Whinchat *Saxicola rubetra* the effect (negative) was significant. Unexpectedly, the crop diversity tended to affect most species (5/8) negatively. The significance of the other variables was small, reflected by low RVI values (<0.5), and low number of models containing the variables (one model in most cases) (Appendix 5). In three species the autocovariance was included in the best models, with significantly positive effects on Whinchat and Turtle Dove *Streptopelia turtur.*

The effect of habitat structure on the occurrence of conservation priority species

Bird assemblage included 16 species classified as the TCCS (Table 5), including 8 species abundant enough (i.e. recorded in at least 10 plots) to test which habitat variables affected their occurrence (Table 8). Most species (6/8, five — positively) were affected by PC_Shrubs, whereas only four species showed relationships with PC_Trees. Half species were negatively affected by reed cover (Reed), and two of these species (Red-backed Shrike and Barred Warbler) were also negatively affected by the presence of ditch (Ditch). Land diversity around field margins (Crops) favoured three species (Red-backed Shrike, Barred Warbler and Corn Bunting) and was negatively related with

Table 7. Averaged model of relationships between the number of breeding pairs per plot and habitat variables, defined with the use of GLZ and AICc for best model selection (see section "Methods" for methodological details, and Appendix 2 for the details of best model subset). Pred. stat. — predictor statistics, p — statistical significance, CI — 95% confidence interval, RVI — relative variable importance, No. models — the number of models that contain given predictor.

Pred.stat.	Predictors						
	Intercept	Autocov	Ditch	Gaps	PC Trees	PC Shrubs	Reed
p	< 0.0001	0.266	0.034	0.063	0.0001	< 0.0001	0.046
Value	2.47	0.16	0.18	-0.06	0.13	0.28	0.07
CI	(1.91;3.02)	(-0.12;0.45)	(0.01;0.35)	(-0.13;0.00)	(0.06;0.20)	(0.22;0.35)	(0.00;0.14)
RVI		0.27	1.00	0.76	1	1	0.69
No. models		1	3	2	3	3	3

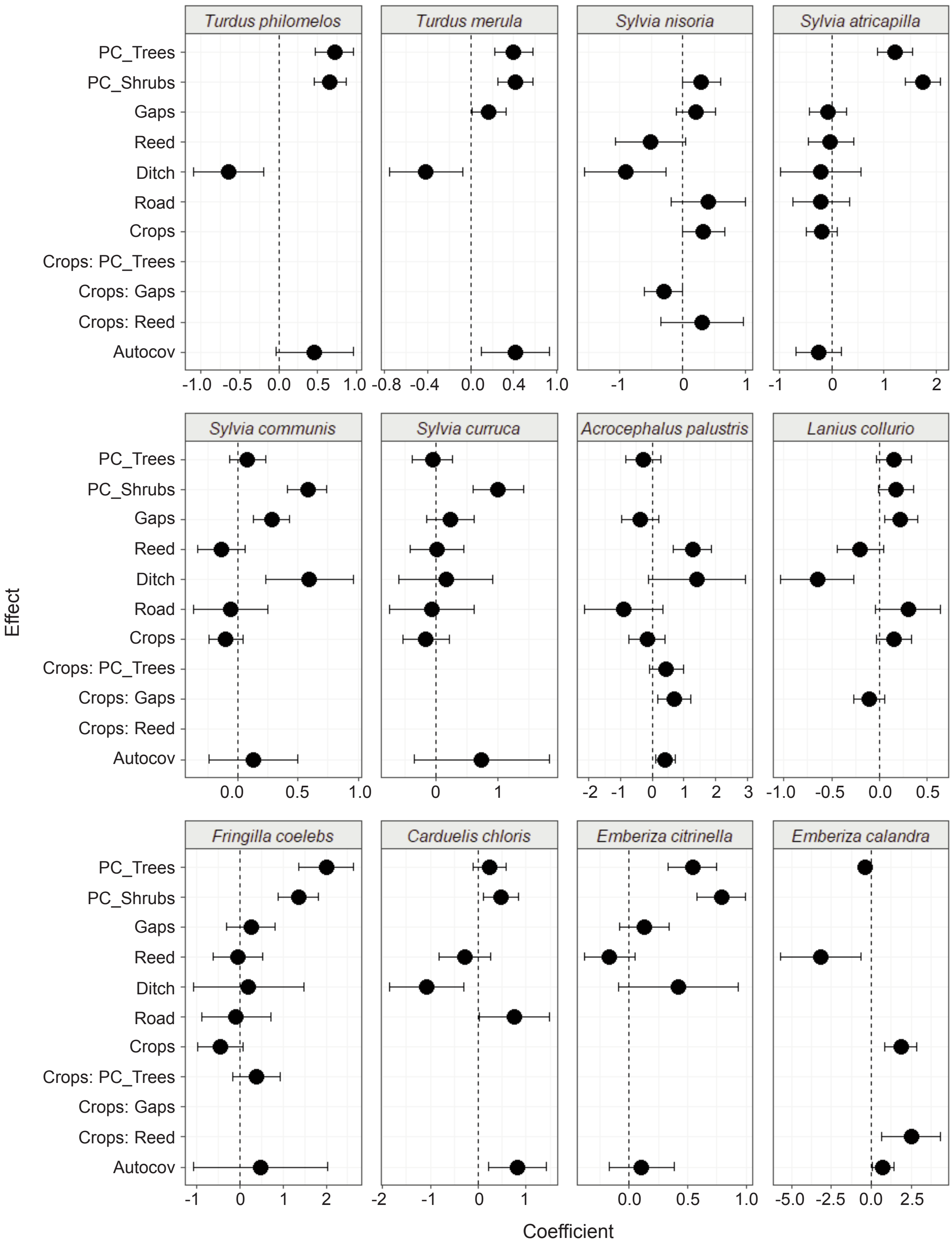

Fig. 4. The coefficients (with 95% CI) in the averaged model of the relationships between the number of breeding pairs per plot and habitat variables for the most common bird species, i.e. those that occurred in at least 20 of sample plots. The model is defined with the use of the GLZ and AICc for best models selection (see Methods for details). The *Emberiza schoeniclus* and *Phasianus colchicus* are not included as the CI length was very large (> 6000 in case of two coefficients in *E. schoeniclus*) or p > 0.1 for all the habitat variables (for *P. colchicus*). The relative variable importance (RVI) and the number of the best models that contain given variable are presented in Appendix 4.

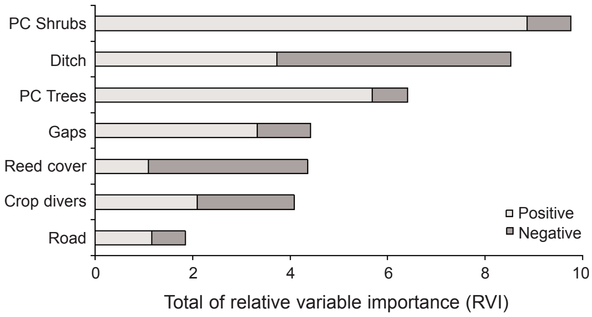

Fig. 5. The relative importance of seven habitat variables for abundances of the 14 most common bird species. The bars represent the totals of the relative variable importance's values from Appendix 4, with the division into variables with positive and negative effects.

one species (Whinchat). Finally, occurrences of two TCCSs (Red-backed Shrike and Skylark) showed positive correlations with the presence of road.

Because of the small number of affected species, there was also a limited facility for testing the differences in proportion of positive/negative effects between TCCS and Non-TCCS. However, weak correlations in species richness ($r = 0.13$, $p = 0.29$) and density ($r = 0.09$, $p = 0.47$) between both groups, lead to the expectation that also responses to habitat features can be different in TCCS and Non-TCCS. Indeed, the results show that the impact of habitat variables across species was bidirectional. While there was a high prevalence of positive effects in Non-TCCS (25 vs 8, especially due to PC_Trees and PC_Shrubs), a more balanced proportion of positive and negative effects was noted in TCCS (16 positive vs 13 negative) (Table 9). However, the difference in the proportions (25/8 vs. 16/13) was not significant (Fisher exact test, $p = 0.11$). It shows that TCCS and Non-TCCS are affected by similar set of habitat variables, although they act differently in both groups. The most pronounced differences in terms of the direction of effects related to the reed cover, development of the tree layer, and the crop diversity.

DISCUSSION

Habitat variables affecting bird assemblage and individual species

We examined how compositional features of the field margins and diversity of adjacent crops affect birds breeding in field margins. As expected, the two variables quantifying the structure of woody vegetation influenced birds most strongly at both an assemblage and species level. Interestingly, we also found that the development of the shrub layer (PC_Shrubs) was more important than that of the tree layer (PC_Trees). This finding contradicts conventional presumptions that all kind of patches covered by arboreal vegetation, both linear and surface (tree lines, woodlots, parks) are of higher importance for biodiversity than the non-afforested habitats. The high importance of shrubs compared to trees may be specific to agricultural landscapes and the associated bird assemblages. These assemblages include high proportion of species typical for field-forest mosaic for which the shrubby field margins are most suitable.

Various features of woody vegetation are known to affect bird abundance: the height and width, age, species composition and spatial distribution (Hinsley & Bellamy 2000, Graham et al. 2018). However, it is usually difficult to identify the effect of each parameter independent of correlation with other structural features. In general, it

Table 8. The significant and marginally significant ($p < 0.10$) effects of habitat variables on threatened and conservation concern species (TCCS). All positive (+) and negative (–) effects from Fig. 4 and 6 are presented. Crops:Gaps etc. means interaction between Crops and other variables.

Species	Auto-cov	Ditch	Road	Gaps	Reed	PC Trees	PC Shrubs	Crops	Crops: Gaps	Crops: Reed	Crops: PC Trees	Crops: PC Shrubs
Emberiza citrinella				+	–	+	+			–		
Lanius collurio		–	+	+	–	+	+	+				
Sylvia nisoria		–			–		+	+	–			
Emberiza calandra					–	–		+		+		
Linaria cannabina							+			–		
Alauda arvensis			+			–	–					
Saxicola rubetra	+			–				–	–			
Streptopelia turtur	+						+					

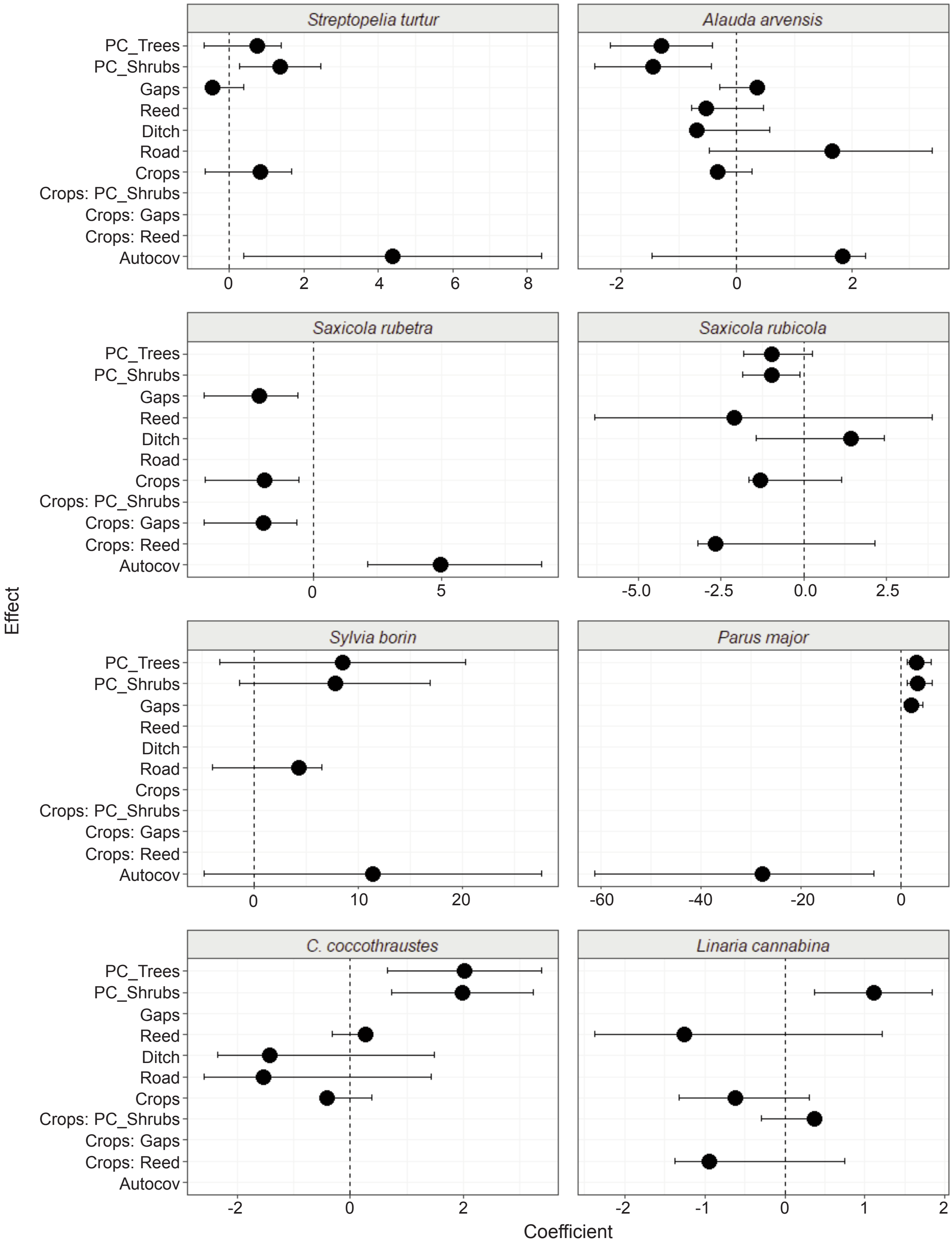

Fig. 6. The coefficients (with 95% CI) in the averaged model of the relationships between the occurrence of species in plots and habitat variables for moderately common species, i.e. those that occurred in 10–19 of sample plots. The model is defined with the use of GLZ and AICc for best models selection (see Methods for details). The relative variable importance (RVI) and the number of the best models that contain given variable are presented in Appendix 5.

Table 9. Number of TCCS (threatened and conservation concern species) and Non-TCCS species affected positively (Pos) and negatively (Neg) by individual habitat variables (summary of Fig. 4 and 6). Crops:Gaps etc. means interaction between Crops and other variables.

	Effect	Ditch	Road	Gaps	Reed	PC Trees	PC Shrubs	Crops	Crops: Gaps	Crops: Reed	Crops: PC Trees	Crops: PC Shrubs	Total
TCCS	Neg	2	0	1	4	2	1	1	1	1	0	0	13
	Pos	0	2	2	0	2	5	3	1	1	0	0	16
Non-TCCS	Neg	3	0	1	0	2	2	0	0	0	0	0	8
	Pos	2	1	3	2	6	10	0	1	0	0	0	25

seems that in the case of farmland birds, the vertical differentiation of field margins, e.g. the number of vegetation layers, is most important, whereas the plant species composition plays a secondary role (Wuczyński et al. 2011).

Our results indicate that the presence of drainage ditches was also an important determinant of the bird assemblages, however the impact of ditches was ambiguous. Ditch presence positively affected bird density but not species richness. Besides, a high percentage cover of reeds, usually associated with ditches, encouraged the abundance of birds (reeds were present in 25 of 53 plots with a ditch and in only one of 17 plots without a ditch). The latter relationship resulted clearly from the impact of individual, specialized bird species, such as Marsh Warbler and Reed Bunting, known to reach high densities in rush vegetation (Cramp & Simmons 2004). However, within intensively farmed landscapes these birds are uncommon and their populations rely heavily upon the vegetation of wet drainage ditches. Thus field margins consisting of ditch and performing several agricultural functions (water retention, purification, nutrient cycling), also contribute to the presence of an ecological group of wetland birds, otherwise rare in cropped areas. Overall, our results support claims that the widespread presence of the surface drainage ditches, that are one of the distinguishing features of the Polish agricultural landscape (Herzon & Helenius 2008), significantly contributes to the persistence of internationally important farmland bird populations (Dajdok & Wuczyński 2005, Marja et al. 2013).

Out of the 22 analysed species, 21 showed any responses to the habitat variables. However, no fixed set of habitat characteristics were found to benefit all taxa. The results reflect diverse biological requirements of individual species and complexity of bird-habitat interactions. It is noteworthy that variables associated with the structure of field margins turned out to be much more significant than the diversity of adjoining crops. Indeed, we found only a weak link between the crop diversity and the occurrences of individual bird species (Corn Bunting), and the lack of relation to the entire bird assemblage. We therefore could not confirm one of our hypotheses that the diversity of the surrounding agricultural habitats affects the communities of birds breeding in field margins (see Green et al. 1994, Kujawa 2006, Skórka et al. 2013 for analogous conclusion). The tenuous dependency of birds on crop heterogeneity may indicate a considerable distinctness of fields and field margins and associated faunas, and an asymmetric contribution of both habitats to the biodiversity of agrocenoses. With their relatively small area, the field margins play a decisive role in the overall richness of agricultural land and it is rather that these margins affect the biodiversity of adjoining fields (Marshall & Moonen 2002), and not vice versa.

The effect of habitat structure on the occurrence of threatened birds

Despite their small relative area and a strong pressure from agrotechnical practices, field margins serve as refuge habitats for threatened species, that occurred in as many as 95.7% of margins (Wuczyński et al. 2014). Most habitat variables had either positive or negative effects highlighting their varying conservation importance for threatened birds (Table 8). The development of the shrub layer was visibly positive for the TCCS (except Skylark) confirming that the field margins with an intermediate volume of woody vegetation can act as refuge habitats of endangered species in agro-ecosystems (Wuczyński et al. 2014). It also suggests that some other elements of agricultural landscapes, like patches of semi-natural vegetation at pylons (Tryjanowski et al. 2014) or along railways can play a positive role for TCCS, especially when overgrown with some shrubs and trees.

The presence of road, the number of gaps expressing a mosaic layout of vegetation, and diversity of adjacent crops were also positively correlated with the abundances of TCCS, whereas the dominance of reeds and presence of ditch had negative effects. The latter conclusion, related to Red-backed Shrike and Barred Warbler, might be confusing since both species frequently bred in field margins having a ditch, if accompanied by any bushes. Although wide, water-filled ditches overgrown with reeds were avoided by both species, these ditches were usually devoid of woody vegetation necessary for nest construction. This means that the actual role of ditches with respect to threatened birds may be positive but requires another habitat variables quantifying their structure. At a landscape scale various wetlands are known to be particularly important for overall species richness and habitat specialists, including endangered birds (Skórka et al. 2006).

Mostly negative responses of TCCS to the development of the reed cover and tree layer and positive responses to crop diversity complies with the characteristics of the TCCS group. The group consists predominantly of species associated with a traditional agricultural landscape or more specifically, with the field-forest mosaic. Homogenization of farmland, e.g. by replacing shrub lines with tree lines or by increasing reed cover, can therefore have negative effects on populations of the TCCS (Doxa et al. 2012, Morelli & Tryjanowski 2017). In contrast, such homogenization can favor habitat generalists, like many forest birds (Chylarecki et al. 2018), or species reaching high densities in uniform habitats, such as Marsh Warbler in reed dominated field margins.

CONCLUSIONS

Several conclusions of this study can be helpful in ecological optimization of agricultural landscape. It seems that habitat-scale measures regarding the structure of field margins can be effective in farmland conservation, as indicated by the numerous relationships with species abundances. The measures, such as the internal proportion between open and wooded sections in linear habitats, are also relatively easy to implement, compared to management conducted on a landscape scale.

For breeding birds, including endangered and conservation concern species, the most important feature of field margins has proven to be the mere presence of shrub layer, and to a lesser extent the tree layer. The internal structure of these layers (the proportion of trees and shrubs, species composition, distribution patterns) is presumably less important. Unfortunately, shrubs and trees are now disappearing at an unprecedented rate in farmlands driven by the CAP's regulations (Pe'er et al. 2014) and also fairly liberal environmental regulations in Poland (Biernacka & Kronenberg 2019). Since our study was conducted before changes triggered by Poland's EU accession, the data may serve as a model of bird communities inhabiting well vegetated field margins once typical for low-intensity farmlands.

Finally, there is no common pattern of the relationship between the habitat structure and the presence of several dozen bird species. The spectrum of relationships is as wide as the ecological requirements of these species. This means that reconciling these requirements in relation to the variety of bird species (and thus to the other taxa living in the agricultural landscape) is possible only by maintaining the mosaic of field margins displaying a high structural diversity (Hall et al. 2018). This result supports a general hypothesis on the role of landscape structure for biodiversity (Tscharntke et al. 2012), that the negative local impact of high habitat fragmentation on biota may be compensated by dissimilarities of local assemblages of species related to the high differences in the landscape structure.

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STRESZCZENIE

[Wpływ struktury siedliska i urozmaicenia przyległych upraw na gniazdowanie pospolitych i zagrożonych ptaków w liniowych środowiskach marginalnych]

Obrzeża pól są nieodłącznym elementem krajobrazów rolniczych i mają kluczowe znaczenie dla utrzymania wysokiego poziomu różnorodności biologicznej. Do tej pory rozpoznano różne interakcje między strukturą występujących tam pasm roślinności śródpolnej (dalej: pasm śródpolnych) a fauną i florą, ale zrozumienie znaczenia poszczególnych cech tych środowisk oraz wpływu przyległych pól uprawnych na różnorodność biologiczną pasm śródpolnych jest wciąż niepełne. Celem badań było określenie znaczenia poszczególnych cech pasm śródpolnych i różnorodności przyległych upraw dla ptaków lęgowych, których zagęszczenia były ocenione za pomocą uproszczonej metody kartograficznej. Badania przeprowadzono w południowo-zachodniej Polsce (Fig. 1), w regionie o podobnie intensywnej gospodarce rolnej, jak w innych krajach środkowo-wschodniej Europy (Tab. 1). Wyznaczono 70 powierzchni badawczych (odcinków pasm śródpolnych o długości 500 m każdy), ze zróżnicowaną roślinnością półnaturalną — od zbiorowisk roślin zielnych, poprzez zbiorowiska z dominującymi krzewami, po gęste szpalery drzew. Na części powierzchni obecne były drogi, kanały lub rowy melioracyjne. Cechy struktury środowiska pasm śródpolnych i zróżnicowania terenów sąsiednich oceniono za pomocą szeregu zmiennych (Tab. 2 i 3), a analizę statystyczną przeprowadzono głównie przy użyciu uogólnionego modelu liniowego (GLZ) (Tab. 4). Zgrupowanie ptaków składało się z 50 gatunków, w tym 16 o wysokim priorytecie ochronnym (TCCS) (Tab. 5). Zarówno liczba gatunków, jak i łączne zagęszczenie ptaków, były najsilniej i pozytywnie związane z obfitością drzew i krzewów, natomiast obecność rowu melioracyjnego oraz stopień pokrycia trzciny miały wpływ mniejszy i również dodatni (Tab. 6 i 7, Fig. 2 i 3). Analizy przeprowadzone na poziomie gatunkowym ujawniły złożoność interakcji między ptakami a strukturą środowiska. Ogólnie, zarówno dla 22 gatunków licznych, a także dla TCCS szczególnie ważną cechą okazała się obfitość warstwy krzewów (Fig. 4, 5 i 6). Ponadto pozytywny wpływ na występowanie wielu gatunków miały: obfitość drzew (np. dla *Turdus merula* i *Turdus philomelos*), obecność rowu melioracyjnego (np. dla *Acrocephalus palustris*, *Sylvia communis*), a także liczba luk w warstwie drzew i krzewów (np. dla *Lanius collurio*). Ptaki TCCS były pozytywnie zależne przede wszystkim od obfitości krzewów (5/8 analizowanych gatunków), połowa spośród analizowanych gatunków (4/8) zależała negatywnie od stopni pokrycia trzciny, a trzy z nich (*L. collurio*, *S. nisoria* i *E. calandra*) — pozytywnie od różnorodności upraw w sąsiedztwie (Tab. 8). Biorąc pod uwagę cały zestaw zmiennych środowiskowych o istotnym statystycznie wpływie na zagęszczenie ptaków, gatunki TCCS charakteryzowały się zbliżonym udziałem oddziaływań negatywnych i pozytywnych, podczas gdy w grupie gatunków pospolitych oddziaływania pozytywne stanowiły większość (ok. ¾) (Tab. 9). Zagęszczenie łączne ptaków z gatunków pospolitych oraz zagęszczenie łączne ptaków TCCS nie były ze sobą skorelowane, co wskazuje na odmienne wymagania siedliskowe tych dwóch grup. Ze względu na silnie zróżnicowane relacje między ptakami a strukturą siedlisk podstawą działań zorientowanych na ochronę lub zachowanie różnorodności biologicznej na terenach rolniczych powinno być utrzymywanie obrzeży pól różnorodnych pod względem występującej tam roślinności.

Appendix 1. Pearson's coefficients in the correlations between numeric habitat variables. * — $p < 0.05$.

	PC_Trees	PC_Shrubs	Gaps	Reed	Crops
PC_Trees	x	0.00	-0.13	-0.05	0.17
PC_Shrubs		x	0.13	-0.22	0.13
Gaps			x	-0.26*	0.09
Reed				x	-0.13

Appendix 2. Best models of the relationships between the number of species per plot and habitat variables, defined with the use of GLZ and AICc for best model selection. Explanations: adjR^2 — adjusted R^2, df — degrees of freedom, AICc — corrected Akaike Information Criterion (see Methods for details).

Intercept	Autocov	Road	PC Trees	PC Shrubs	adjR^2	df	AICc	Akaike weight
2.45			0.20	0.28	0.76	3	339.3	0.49
2.61	-0.01		0.21	0.29	0.76	4	340.5	0.28
2.47		+	0.20	0.29	0.76	4	340.8	0.23

Appendix 3. Best models of the relationships between the number of breeding pairs per plot and habitat variables, defined with the use of GLZ and AICc for best model selection. Explanations: adjR^2 — adjusted R^2, df — degrees of freedom, AICc — corrected Akaike Information Criterion (see Methods for details).

Intercept	Autocov	Ditch	Gaps	PC Trees	PC Shrubs	Reed	adjR^2	df	AICc	Akaike weight
2.59		+	-0.06	0.13	0.29	0.07	0.96	7	20.5	0.48
2.16	0.16	+	-0.06	0.12	0.28	0.06	0.97	8	21.6	0.27
2.56		+		0.13	0.29	0.08	0.93	6	21.9	0.24

Appendix 4. The number of best models (see section Methods for details), that contain given predictor (top row at given species, e.g. 4, 5, 5, etc. for *A. palustris*), and relative variable importance (bottom row at given species, e.g. 0.84, 1.00, 1.00 for *A. palustris*) in the subset of best models of the relationships between the number of breeding pairs per plot and habitat variables for the most common bird species, i.e. those that occurred in at least 20 of sample plots. The TCCS are marked in bold. Statistically significant relationships at $p < 0.10$ are marked in grey. Positive effects are darker. Crops:Gaps etc. means interaction between Crops and other variables. The data in the table supplement the results of the analyzes presented in Fig. 4.

Species	PC Trees	PC Shrubs	Gaps	Reed	Ditch	Road	Crop divers	Crops: PC_Trees	Crops: PC_Shrubs	Crops: Gaps	Crops: Reed	Autocov
Phasianus colchicus	1	1	1	1	1	1	1					8
	0.09	0.09	0.09	0.09	0.09	0.12	0.09					1.00
Turdus philomelos	2	2			2							1
	1.00	1.00			1.00							0.57
Turdus merula	2	2	1		1							2
	1.00	1.00	0.32		0.68							1.00
Sylvia nisoria		6	1	9	12	3	8			4	1	
		0.57	0.07	0.74	1.00	0.20	0.71			0.31	0.06	
Sylvia atricapilla	7	7	1	1	1	1	1					1
	1.00	1.00	0.11	0.10	0.11	0.12	0.14					0.14
Sylvia communis	1	6	6	1	6	1	1					1
	0.15	1.00	1.00	0.22	1.00	0.09	0.19					0.11
Sylvia curruca	1	8	1	1	1	1	1					1
	0.10	1.00	0.11	0.10	0.10	0.10	0.11					0.11
Acrocephalus palustris			4	5	5	2	2			2		5
			0.84	1.00	1.00	0.30	0.44			0.44		1.00
Lanius collurio	5	6	1	7	19	5	6			17		
	0.28	0.35	0.04	0.33	1.00	0.27	0.30			0.93		
Fringilla coelebs	9	9	2	1	1	1	3	1				1
	1.00	1.00	0.19	0.08	0.08	0.08	0.35	0.09				0.09
Carduelis chloris	1	4		1	5	2						5
	0.17	0.85		0.14	1.00	0.46						1.00
Emberiza citrinella	11	11	11	9	6		7	3	3		7	
	1.00	1.00	1.00	0.76	0.56		0.56	0.20	0.19		0.56	
Emberiza calandra	1			3			3				3	1
	0.43			1.00			1.00				1.00	0.30
Emberiza schoeniclus	1	6	2	7	7	1	1					1
	0.19	0.90	0.25	1.00	1.00	0.12	0.09					0.14

Appendix 5. The number of best models (see section Methods for details), that contain given predictor (top row at given species, e.g. 2, 5, 1, etc. for *S. turtur*), and relative variable importance (bottom row at given species, e.g. 0.48, 1.00, 0.11 etc. for *S. turtur*) in the subset of best models of the relationships between the number of breeding pairs per plot and habitat variables for the moderately common species i.e., those that occurred in 10–20 of sample plots. The TCCS are marked in bold. Statistically significant relationships at $p < 0.10$ are marked in grey. Positive effects are darker. Crops:Gaps etc. means interaction between variables. The data in the table supplement the results of the analyzes presented in Fig. 6. Two species, i.e. *P. major* and *S. rubetra*, are not included as the models for the species were single best models (not averaged).

Species	PC Trees	PC Shrubs	Gaps	Reed	Ditch	Road	Crops	Crops: PC_Shrubs	Crops: Gaps	Crops: Reed	Autocov
Streptopelia turtur	2	5	1				3				5
	0.48	1.00	0.11				0.61				1.00
Alauda arvensis	7	7	1	2	1	6	1				1
	1.00	1.00	0.11	0.28	0.09	0.88	0.10				0.21
Saxicola rubicola	4	5		3	2		1			1	
	0.80	1.00		0.57	0.35		0.20			0.20	
Sylvia borin	1	2				1					2
	0.29	1.00				0.71					1.00
C. coccothraustes	6	6		1	2	2	1				
	1.00	1.00		0.10	0.30	0.37	0.13				
Linaria cannabina		5		2			4	1		1	
		1.00		0.46			0.82	0.15		0.33	