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Seasonal changes in avian communities living in an extensively used farmland of Western Poland

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ABSTRACT

To study the seasonal changes in avian communities, we collected data in an extensively used farmland in Western Poland during 2006-2013. Generalized additive mixed models were used in order to study the effects of seasonality and protected areas on the overall bird species richness. A similarity percentage analysis was also conducted in order to identify the species that contribute most strongly to dissimilarity among each bird according to the phenological season. Furthermore, the differences in bird communities were investigated applying the decomposition of the species richness in season, trend, and remainder components. Each season showed significant differences in bird species richness (seasonality effect). The effect of the protected areas was slightly positive on the overall species richness for all seasons. However, an overall negative trend was detected for the entire period of eight years. The bird community composition was different among seasons, showing differences in terms of dominant species. Greater differences were found between breeding and wintering seasons, in particular, the spatial pattern of sites with higher bird richness (hotspots) were different between breeding and wintering seasons. Our findings showed a negative trend in bird species richness verified in the Polish farmlands from 2006. This result mirrors the same negative trend already highlighted for Western Europe. The role of protected areas, even if slightly positive, was not enough to mitigate this decline process. Therefore, to effectively protect farmland birds, it is necessary to also consider inter-seasons variation, and for this, we suggest the use of medium-term temporal studies on bird communities' trends.

KEYWORDS

birds, farmland, seasonality, trend, dominant species, SIMPER, Poland

INTRODUCTION

Agricultural habitats constitute one of the most important ecosystem elements throughout most of the world, including Central Europe (for humans, agriculture, birds and research) (Pain & Pienkowski 1997; Bignal & MaCracan 2000). By definition, agricultural areas are constructed by human activity and these landscapes have been subject to rapid and large-scale changes during recent decades, caused mainly by the intensification and mechanization of agricultural activities (Chamberlain et al. 2000; Donald et al. 2001; 2006). Agricultural intensification mainly occurs at two different spatial scales: the local scale – for example, increased use of agrochemicals or pesticides (Geiger et al. 2010), and the landscape scale – for example, destruction of semi-natural and marginal habitats, decreasing habitat variability, increasing monoculture patches, etc. (Benton et al. 2003; Morelli 2013a). The intensification of agro-ecosystems has been followed by an unprecedented decline of biological diversity; this effect has been most profoundly observed in birds (Donald et al. 2006; Pe'er et al. 2014). Bird diversity generally decreases with increased farming intensity (with increased nutrient and pesticide inputs, increased use of machinery and an overall increase in productivity) (Donald et al. 2001; Kleijn et al. 2009); however, this relationship is characterised by strong differences at continental and regional scales (Tryjanowski et al. 2011).

For these reasons, the conservation and restoration of biodiversity in agricultural landscapes have been the foci of recent conservation issues (Bennet et al. 2006). Common Agricultural Policies (CAP) in the European Union have highlighted the negative trend that affects biodiversity, and have entrusted each European country with responsibilities to tackle biodiversity loss (Baldock et al. 1993; De la Concha 2005; Onate 2005; Pe'er et al. 2014). For example, the farmers are encouraged to conserve biodiversity through the preservation of semi-

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natural landscape features and by encouraging extensification (greening) of farming systems (Pain & Pienkowski 1997; Kleijn & Sutherland 2003). However, to enable these measures to be effective in slowing down biodiversity decline, there is urgent need to develop measures for evaluating high nature value farmlands (HNV) and to maintain and protect these types of landscapes (Andersen et al. 2003; Baldock et al. 2004; Morelli et al. 2014).

Conservation policies are widely employed in the agro-ecosystems, yet they appear to have little impact on biodiversity (Vickery et al. 2004; Grodzińska-Jurczak & Cent 2011). In farmland at least, even current conservation criteria are based mainly on species occurrence data obtained during the breeding period (Virkkala & Rajasarkka 2007; Herrando et al. 2009), whilst seasonal changes and shifts from wintering to breeding grounds are generally not taken into account, thus potentially neglecting conservation criteria. This is especially true in birds, where mainly the breeding grounds are taken into account when establishing priority conservation areas (O'Dea et al. 2006; Virkkala & Rajasarkka 2007; Herrando et al. 2009). Some generalizations are therefore impossible, because information about all components of species range in farmland birds is required, but strongly limited. Furthermore, the majority of papers only focus on one season, for example breeding (Berg 2002; Wuczyński et al. 2011) or winter (Tryjanowski 1995; Kasprzykowski & Goławski 2012), and only consider both periods in order to evaluate the effectiveness of conservation reserves (Marfil-Daza et al. 2013). Moreover, the data on spring and autumn migrations, as well as the post-breeding dispersal period, are mainly limited to single species (Tryjanowski et al. 2011; Herzon et al. 2014).

The majority of farmland bird species belong to a group of common species (sensu: Gaston & Fuller 2008), and form a background for whole communities in agro-ecosystems (Ryszkowski et al. 2002). Therefore, the information on dominant species among seasons should allow us to understand the biological functioning in bird communities in farmland and help formulate effective conservation strategies and target specific species.

In this study, we explored seasonal changes in the pattern of hotspots of species richness, and determined the dominant bird species for each phenological period, and additionally, we also tested if the trend in farmland bird richness in Western Poland is reflecting the overall trends for Europe.

1. MATERIALS AND METHODS

1.1. Study area

The study was conducted in the agricultural landscape of Western Poland, near Odolanów (51°34'N, 17°40'E). The study area is an extensively used agricultural landscape and comprises a mosaic of regularly, but not intensively, mowed meadows and extensively used pastures, flooded naturally during early spring (44%), arable fields (42%, mostly of rye and oat, less of wheat,

barley or maize), midfield woodlots of different ages (6%), scattered trees and discontinuous linear habitats, mainly mixed rows of trees and shrubs, (see details in Hromada et al. 2002). Uncultivated areas and fallow lands occupy 2% and rural settlements nearly 6% of the total area. The protected areas in the study area have a total surface of 18000 ha, covering 48% of total area. The Polish protected areas are classified into two categories: grounds covered by landscape park 'Dolina Baryczy' and areas protected by Natura2000, both partially overlapped (Grodzińska-Jurczak & Cent 2011). Each sample site was classified as 1, when inside a protected area, and 0 when outside the protected areas network. The seasonal changes in temperature and rain throughout the entire study period are shown in Figure 1. Weather conditions are clearly seasonal and the annual maximum temperature coincides with post breeding. A similar pattern also exists for rainfall.

1.2. Bird data collection

To obtain the bird data, five-minute point counts were carried out on 64 sample sites each month during eight years from 2006 to 2013 (with the exception of June 2006 and October 2012, when data were not collected due to logistical problems). Every single site was separated at a distance of at least 300 m from each other, in order to avoid double counting of same individuals (more details in Jankowiak et al. 2015). Each point count differed within the habitat types but all were located in open space landscapes. All counts were performed from half an hour after sunrise until 4.5 hours after sunrise, and only during favourable weather conditions (i.e., no rain and snow or strong wind). The point counts provide highly reliable estimates of relative population density and are recognised as a standardized and practical method to compare bird communities between different habitats and times (Bibby et al. 1992; Voříšek et al. 2008).

Study year was divided into five periods (seasons), considering the phenology of bird species: i) breeding season: April through June; ii) post-breeding season: summer, July through August; iii) autumn migration: September through November; iv) wintering: December through February; v) spring migration: March. For some comparisons, we used only the breeding season and the wintering season. Dominant species were defined as the most frequent species for each season. Species richness is a basic surrogate for the more complex con-
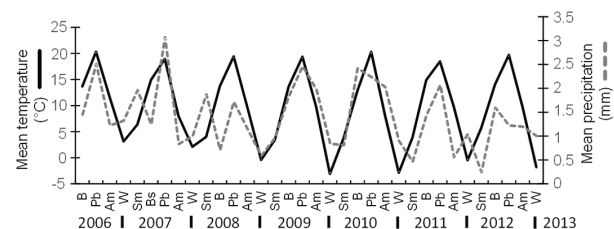

Figure 1. Seasonal changes in weather conditions (mean temperature and precipitation) for the entire period of study. Abbreviations: B: Breeding, Pb: Post-breeding, Am: Autumn migration, W: Wintering, Sm: Spring migration.

cept of ecological diversity (Magurran 2004; Morelli 2013b). For each sample site, the species richness was calculated as the number of heard and observed bird species. Abundance of birds is the number of different individuals per species recorded in each site. The mean number of bird species per site is estimated monthly and seasonal, by dividing total number of species recorded by the number of sample sites visited during the same period. Yearly mean values of species were obtained by combining these seasonal values.

1.3. Statistical analysis

A preliminary graphical exploration of seasonality and trend of overall bird species richness during the period from 2006 to 2013 was performed by the decomposition with 'stl' function (seasonal decomposition of time series by Loess) (Cleveland et al. 1990). The seasonal component is found by Loess smoothing the seasonal sub-series; then the seasonal values are removed and the remainder are smoothed to find the trend (Cleveland et al. 1990).

The generalized additive models (GAM) method is a flexible and effective technique for conducting nonlinear regression analysis in time-series studies (Hastie & Tibshirani 1990). Here, a Generalized Additive Mixed Model (GAMM) was applied in order to analyse the population trends and seasonality effect in bird communities using the time series survey data (2006–2013). We used the package `mgcv` (Wood 2004; 2006) and the variations in bird species richness (response variable) among years (trend) and seasons (seasonality). In order to avoid over fitting problems, the smoothing parameters were set automatically under the degrees of freedom offered by the data. The sample sites were considered as random factors, while the protected area was used as the predictor and month as the smoother. In order to take into account the fact that each site was counted every month in different years, a spatio-temporal correlation argument was added to the model structure. A quasi-poisson error distribution was assumed for the model. The equation of full model was:

Bird species richness = s(month) + protected area, random = list(sample site = ~1), correlation = corExp(form = ~ factor(month*year) | sample site), family = quasi-poisson

In order to study the differences in bird communities among seasons, dissimilarity measures were calculated by means of the 'vegan' package (Oksanen 2014) in R. The function 'meandist' was used to calculate a matrix of mean within-cluster dissimilarities (diagonal) and between-cluster dissimilarities (off-diagonal elements), and an attribute n of grouping counts. Then, a dendrogram based on the within-group and between-group dissimilarities was drawn. The relative frequency of each species was calculated, and differences in species composition and relative frequency of the 10 most abundant species between the seasons were also determined.

Some analyses were only performed for the breeding and wintering seasons, because these are the most different phenological seasons for birds. The spatial congruence between breeding and wintering seasons in terms of species richness were explored graphically using the delta species richness. Delta species richness based on seasonal differences was estimated as the absolute value of the difference between average bird species richness for breeding and wintering at each sample site. These values were used to map and visualize the mismatch areas considering the inter-season differences. A similarity percentage (SIMPER) analysis was conducted to identify the species that contribute most strongly to the dissimilarity between the two seasons. SIMPER (Clarke 1993) is based on the decomposition of the Bray-Curtis dissimilarity index. The contribution is the percentage for each of the most influential species accounting for the dissimilarity between the two seasons (Clarke & Warwick 2001). The SIMPER function performs pairwise comparisons of groups of sampling units and finds the average contributions of each species to the average overall Bray-Curtis dissimilarity (Warton et al. 2012). All statistical tests were performed with R software (R Core Team 2016).

2. RESULTS

We recorded a total of 1,882 observations of 179 species during the eight years of study. From the total of bird species observed, 492 observations of 160 species were collected during the breeding seasons, compared to 522 observations of 92 species collected during the wintering seasons (Table 1). 69% of sample sites were recorded inside the network of Polish protected areas.

Table 1. Total number of observations, species recorded and average bird species per seasons in farmlands in Poland.

Parameter	Breeding	Post breeding	Autumn migration	Wintering	Spring migration
Total bird species recorded	160	138	118	92	81
Average bird species[1]	14.57	13.03	9.33	4.71	10.84
SD average bird species[1]	4.85	4.56	4.03	3.20	4.76
Observations[2]	492	389	403	522	76
Total sampled sites[3]	64	62	64	64	46

[1]Average bird species and SD values are referred to as bird species richness calculated for each season from 2006 to 2013 in the farmlands of Poland.
[2]Observations is the number of visits per season performed during whole study period.
[3]Total sampled sites is the number of sites visited at least once in each phenological season.

2.1. Seasonal variation in bird species richness

Mean species richness was different among years and months (Table 2, Figure 2). Table 3 presents parameter estimates, standard errors and significance for levels of the GAMM model performed on bird species richness. The diagnostics based on residuals showed no departures from the model assumptions, suggesting a good fit. The adjusted r-square of the model was 0.58. The effect of protected areas was slightly positive on the overall bird species richness (Table 3), and the effects of month was also a significant predictor of species richness (Figure 2). Overall, species richness was higher during the breeding season (mean per sample site: 14.6 species, SD: 4.8) than during the non-breeding season (minimum values for winter season mean: 4.7 species, SD: 3.2) (Table 1, 2). Each season showed differences in bird richness values, but the overall trend for all seasons during the full studied period was negative (Figure 3). The sites with greater bird species richness were different, varying through seasons and years, and these changes on the spatial distribution of the biodiversity are shown in Figure 4. The delta species richness identified the areas where the mismatch was higher and the areas where the mismatch was lower, between the breeding and wintering seasons (Figure 4).

2.2. Seasonal variation in bird assemblages

The differences between bird communities among seasons were initially quantified by mean of a dissimilarity matrix. The greatest distance was found between the breeding and wintering seasons, followed by the post breeding and wintering seasons (Figure 5). The differences between the breeding and wintering seasons were highlighted by SIMPER analysis, indicating that the average dissimilarity between both seasons was up to 63.7%. 19 species contributed more than 50% to the dissimilarity between these seasons (Table 4).

At least one of the ten most frequent bird species seen during the breeding season was present in 100% of the total observations recorded during this season. In comparison, at least one of the most frequently seen species during
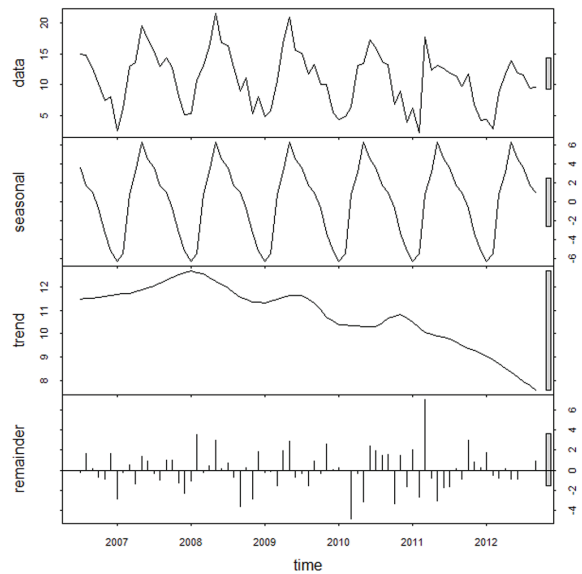
Figure 3. Seasonal variations on farmland bird richness and trend for the full period of study (2006-2013): applying the Seasonal-Trend Decomposition Procedure with 'stl' function. The species richness is decomposed in seasonal: trend: and remainder components. The seasonal component is estimated by taking the mean of all seasonal sub-series. The sum of the seasonal: trend: and remainder components equals the data series. The solid bars on the right hand side of the plot show the same data range: to aid comparisons.
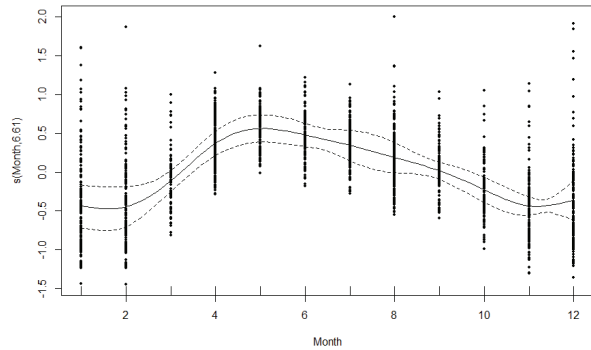

Figure 2. Plots of the smoother (month, for the seasonal effect) and their standard errors for the GAMM, accounting for the changes in bird species richness in the farmland birds of Poland.

Table 2. Average and SD of bird species richness per month and year in farmlands of Poland.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Average	SD
2006	-	-	-	13.00	19.66	-	14.93	14.84	12.68	10.20	7.44	8.07	12.60	4.02
2007	2.50	6.00	13.00	13.57	19.59	17.43	15.41	12.90	14.28	12.75	8.00	5.13	11.71	5.20
2008	5.25	10.66	13.09	15.93	21.50	16.8	16.31	12.74	9.00	11.08	5.20	8.00	12.13	4.94
2009	4.75	5.74	10.70	16.56	20.86	15.55	15.03	11.65	13.23	10.09	10.00	5.37	11.63	4.92
2010	4.29	4.81	6.28	13.06	13.45	17.28	15.96	13.66	13.26	6.76	8.96	3.84	10.13	4.83
2011	6.13	2.15	17.77	12.32	13.16	12.68	11.81	11.44	9.69	11.73	6.73	4.15	9.98	4.40
2012	4.40	2.83	8.68	11.75	13.80	11.87	11.6	9.44	9.54	-	4.65	3.84	8.40	3.83
2013	3.15	4.97	-	-	-	-	-	-	-	-	-	-		
Average	4.35	5.31	11.59	13.74	17.43	15.27	14.44	12.38	11.67	10.44	7.28	5.49		
SD	1.23	2.76	4.00	1.81	3.77	2.42	1.93	1.74	2.17	2.06	1.93	1.84		

Table 3. Results of the Generalized Additive Model (GAMM) explaining the bird species richness in farmlands of Poland from 2006 to 2013 in 64 sampled sites, in relation to month and protected areas. R-sq.(adj): 0.58, scale est.: 1.606, n: 1804.

Model				
Parametric coefficients	**Estimate[1]**	**SE[2]**	**t-value**	**P value[3]**
Intercept	2.153	0.025	86.121	<0.05***
Protected area	0.100	0.029	3.412	<0.05***
Approximate significance of smooth term	**edf[4]**	**res.df[5]**	**F**	**P value**
s(Month)	8.404	8.404	226.9	<0.05***

[1]Estimate: parameter estimates.
[2]SE: standard errors.
[3]Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.
[4]edf: estimated degrees of freedom.
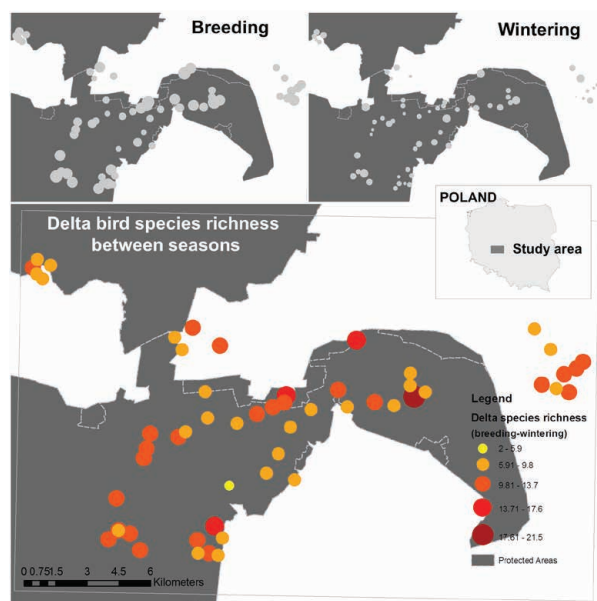[5]res.df: estimated residual degrees of freedom.

Figure 4. Spatial distribution of farmland bird richness in breeding and wintering seasons for the full period of study (2006-2013). The size of the grey circles is proportional to the values of bird species richness standardized for breeding and wintering records. The delta species richness identify the sample sites where the mismatch is higher and lower between breeding and wintering seasons. The size and colour (from yellow to dark red) of circles is proportional to the absolute value of the differences between the average species richness inter-seasons.
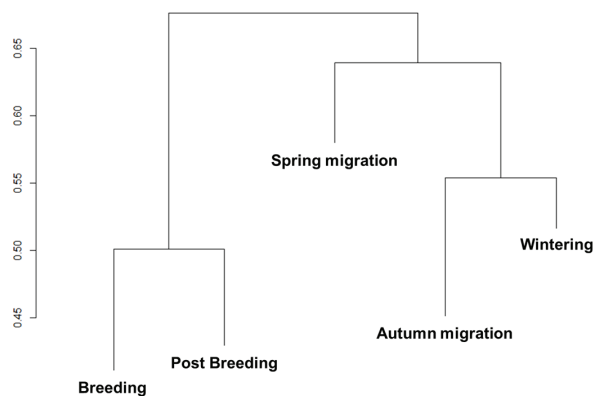

Figure 5. Cluster analysis of dissimilarities among seasons based on the bird community composition. Distances were calculated using the average values for seasons for the full period of study (2006-2013).

3. DISCUSSION

Agricultural intensification reduces biodiversity substantially at different scales, simplifies communities and leads to a loss of ecosystem services (Green et al. 2005). Negative factors that play an important role at the European scale and are also important in the study area include land-use change from meadows and pastures to arable fields, increased use of pesticides and fertilizers, and habitat fragmentation (Geiger et al. 2010; Kociolek et al. 2011; Tryjanowski et al. 2011). However, the local farmlands in Poland support extremely rich bird communities, which contrasts markedly to the farmland habitats in Western Europe (Skorka et al. 2006; Tryjanowski et al. 2011). There are probably different reasons for this high bird species richness. First, the study area is a place with extensive agriculture and is located in a complex landscape in a river valley, which attracts high numbers of the common species (Skorka et al. 2006) that play an essential role in the conservation of ecosystems (Gaston & Fuller 2008).

The indication of real importance of agro-ecosystems for the conservation can be neglected when the studies are focused only on breeding season (Herzon et al. 2014). For this reason, our study emphasizes the importance of intra-seasonal variation on the occupancy patterns for both breeding and non-

the wintering season was only present in 89.9% of the total observations recorded during this season. The Composition of top-ten most frequent species differed among breeding and nonbreeding seasons (Figure 6A). The dominant passerine species during the breeding season were Skylark, Yellowhammer and Corn Bunting, while the dominant species during the wintering season were Yellowhammer, Great tit and several corvid species including Jay, Raven and Magpie. The bird species most shared in multiple seasons were Yellowhammer and Great Tit (100% of the sharing among seasons for all study years), followed by Skylark, Starling and Chaffinch (80% of sharing). The composition of generalist or specialist dominant species was slightly more balanced during breeding than during the wintering season (Figure 6B).

Table 4. Summarized results of SIMPER analysis for the cumulative contribution of the dominant influent bird species to the overall dissimilarity (63.7%) between the bird communities of breeding and wintering seasons from 2006 to 2013 in farmlands of Poland

Specie	Common names	Contribution (%)[1]	Ratio[2]	Av.a[3]	Av.b[3]	CumSum (%)[4]
Alauda arvensis	Skylark	4.47	5.83	94.78	5.98	6.99
Sturnus vulgaris	Starling	2.73	4.02	62.56	7.92	11.27
Miliaria calandra	Corn bunting	2.27	3.30	68.85	15.07	15.51
Fringilla coelebs	Chaffinch	2.27	2.44	57.83	12.90	19.06
Emberiza citrinella	Yellowhammer	1.83	1.54	87.37	55.43	21.92
Turdus philomelos	Song thrush	1.77	2.53	36.77	2.10	24.69
Oriolus oriolus	Golden oriole	1.57	3.68	32.93	0.00	27.00
Motacilla alba	Pied wagtail	1.50	3.64	30.78	0.48	29.51
Turdus merula	Blackbird	1.49	2.75	36.49	6.86	31.85
Hirundo rustica	Barn swallow	1.44	2.15	29.55	0.48	34.10
Phylloscopus trochilus	Willow warbler	1.41	2.99	29.13	1.68	36.00
Phasianus colchicus	Pheasant	1.34	1.62	32.93	6.05	38.40
Lullula arborea	Wood lark	1.21	2.48	24.66	0.48	40.31
Anthus pratensis	Meadow pipit	1.19	1.46	28.06	4.36	42.17
Vanellus vanellus	Lapwing	1.19	3.82	24.47	0.71	44.04
Columba palumbus	Wood pigeon	1.17	3.67	24.01	0.71	45.87
Lanius collurio	Red-backed shrike	1.15	2.18	23.38	0.00	47.67
Cuculus canorus	Cuckoo	1.15	3.48	24.44	0.00	49.00
Sylvia communis	Whitethroat	1.07	1.94	23.08	0.00	51.23

[1]Contribution (%) is the percentage of contribution for each species on the dissimilarity between the two seasons.
[2]Ratio is the average to SD ratio.
[3]Av.a, Av.b are the average abundance of each species per group (seasons: breeding and wintering respectively).
[4]CumSum is the ordered cumulative contribution on the total dissimilarity, expressed as percentage.

breeding bird species. Our findings clearly show how the avian communities change seasonally in the continental temperate zone: from very rich during the breeding season to less rich and complex during winter. This seems obvious considering the high proportion of breeding migratory species (Tworek 2002, 2003; Skorka et al. 2006). Our findings are aligned with the fact that, for different phenological seasons, different bird species form the base of avian communities (Tworek 2002), reflected by the changes in seasonal dominance of some bird species (Figure 6A). A novel finding is that we found both changes between years in the community parameters and changes in the geographic position of important areas for bird richness, among seasons. In farmland, these fluctuations can be at least partially related to human activity, for example seasonal farming activities like ploughing, sowing or harvesting (Pain & Pienkowski 1997). Regarding the year-to-year changes, we observed a very clear oscillation pattern of seasonal changes in the number and composition of species, repeated very conservatively during the study period spanning over 8 years. Furthermore, in addition to the seasonality effect, our findings showed

an overall negative trend in bird species richness for the full period of study. This negative trend reflects the biodiversity decline already known for the wider European situation (Butler et al. 2010; Laaksonen & Lehikoinen 2013). The changes in land-use (in terms of composition and configuration) are among the most recognized drivers of biodiversity changes, and for this reason many strategies in the last decades have been focused on the preservation of landscape heterogeneity and promoting multifunctional landscapes (Foley et al. 2005; Ekroos et al. 2016). However, in the farmland studied, previous research comparing the land cover variables between 2005 and 2010 has already demonstrated that there were no significant differences (Jankowiak et al. 2015). Then, we can assume that the changes observed in the overall bird richness are not a direct consequence of only land use changes. We can hypothesize a series of drivers working together to cause an overall decline of biodiversity in European patterns: from more low changes in land uses, undetected on the basis of land use mapping, to the effects of climate change. Additionally, even if the study period is too short to support ideas on long-term changes in farmland
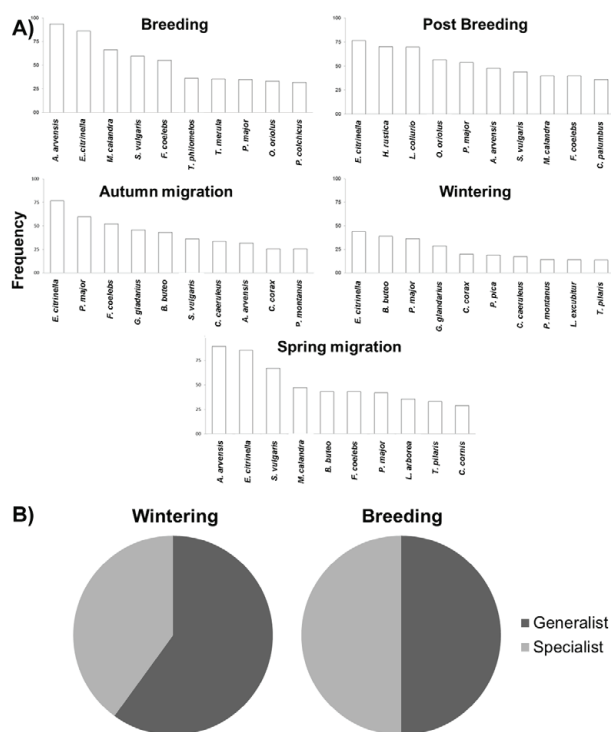
Figure 6. A) Bird assemblages and relative frequency of species during the different seasons for the full period of study (2006-2013). Only the ten most frequent bird (dominant species) are shown. B) Composition of ten dominant bird species for breeding and wintering season: in terms of habitat generalist or specialist species

bird communities, some changes in community structures are visible, such as the higher domination of species connected with dry arable fields (skylark, corn bunting, yellowhammer and yellow wagtail), than wet meadows (lapwing, meadow pipit).

On the other hand, a slight but positive effect of protected areas on the overall species richness was found in the farmlands in Poland. This is an important aspect that can encourage planning based on the use of network of protected areas as conservation tool (Grodzińska-Jurczak & Cent 2011). However, considering that the spatial pattern of a site with higher average bird richness (congruence analysis) differed between breeding and wintering season, we suggest that for effective protection of bird diversity, more attention should be paid to the changes in seasonal communities' composition in farmlands. In this regard, the delta species richness was able to

identify areas where the bird richness congruence was higher between breeding and wintering seasons. We suggest that this procedure can constitute a useful tool to focus attention on inter-seasonal hotspots, areas where more attention is necessary for conservation efforts. We suggest that there is an urgent need to incorporate such data into effective conservation planning. It is crucial to take this into account due to the fact that bird richness values are not similar between seasons, and therefore, represent unique seasonal communities with particular requirements to be protected. Moreover, the evaluation of importance of farmlands using only species richness can underestimate threats. The reason for this being that diversity is smaller in the winter season, but species are under more threat in winter than in spring. Additionally, the typical bird communities for each season can reflect differences in terms of composition between generalist and specialist species, which suggest deep implications for conservation with regard to functional diversity aspects of the communities (Petchey & Gaston 2006).

Summarizing, further studies should combine direct measures of species richness, functional diversity, and the conservation status of each species, as well as seasonal changes in the biodiversity patterns. Only by doing this will it be possible to effectively manage conservation of declining populations of farmland avian species. To ensure effective protection, it is necessary not only to preserve habitats used during breeding, but also during migration and wintering seasons (Studds & Marra 2005), periods which can be spatially separated. Our findings provide more evidence about the need for a spatio-temporal modelling approach (Santos et al. 2016) when studying farmland areas. Further studies should pay more attention to seasonal changes (dominant species), as well as the long-term perspective (overall trend).

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