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Birds wintering in heterogeneous farmland of Poland: weather-dependent temporal changes in abundance and habitat associations

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Abstract. Bird communities wintering in the mosaic-like farming landscapes of SW Poland were studied to assess drivers of intra-seasonal changes in numbers and habitat associations of birds. During two severe winters (November–March) the complete area search method was applied to count birds and link their occurrence with weather and habitat in six plots (320 ha in total). A modelling approach was used to test birds' responses to environmental factors at community and species levels. These farmlands were inhabited by diverse and dense populations of wintering birds, including a significant proportion of species of conservation concern. Bird numbers revealed decreasing trends, with winter- and species-specific fluctuations, affected in particular by snow cover. The lowest population indices were recorded in mid-winter (February) and remained low until mid-March. Field margins (6.6% of the total area) supported 35.6% of individuals and 55.0% of flocks. The preference for field margins over other farmland habitats was particularly prominent during severe weather conditions. Our results suggest that during severe winters, complex farmlands are important areas for birds, enhancing their known importance to breeding birds. Intense snowfall in mid-winter rather than temperature drops lead to immediate population declines, aggravating the effects of natural food depletion. Adverse weather keeps populations at low levels until mid-March, despite the influx of spring migrants. Behavioural adjustments to winter conditions elicit the characteristic habitat distribution of birds, exposing the crucial importance of non-cropped landscape elements. In particular, the variety of field margins significantly contributes to the persistence of internationally important populations of farmland birds in Poland.

Key words: agriculture, winter ecology, field ornithology, phenology, Farmland Bird Indicator

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INTRODUCTION

The communities of wintering birds in transitional regions like Central Europe are very unstable, since they comprise a mixture of sedentary, migratory and wintering species and are highly susceptible to fluctuating weather conditions. These can change rapidly, thus affecting food availability, which is believed to be the main driving factor of bird occurrence in winter (Butler et al. 2010, Newton 2013, Ponce et al. 2014). A high level of adaptability allows birds to respond immediately to a changing environment by adjusting their behaviour or moving to more profitable habitats or regions (Santos et al. 2014). These complicated relationships mean that the functioning of bird assemblages wintering in a temperate climate is a highly dynamic phenomenon within a season and between seasons, but also between adjacent regions (Brauze & Zieliński 2006, Zuckerberg et al. 2011). The vertical distribution of January isotherms in Europe, perpendicular to the main overland migration routes of birds, may result in quite different abundances and composition of bird assemblages in areas separated by just a few hundred kilometres (Jankowiak et al. 2015, Tryjanowski et al. 2015).

In agricultural landscapes the temporal and spatial patterns of bird occurrence is further complicated by the unequal habitat heterogeneity, a proxy for land use (Geiger et al. 2010, Myczko et al. 2013). Complex landscapes with retained traditional practices support particularly large and diverse populations, serving as a model for other areas and conservation goals (Concepción et al. 2012, Morelli 2013, Hartel et al. 2014). However, the term "landscape complexity" is vague, changing gradually, and in modern agriculture the borderlines between complex and simplified farmlands have become blurred, making the results of field studies unique (Kleijn et al. 2009). It is therefore advisable to collect many sets of ornithological data from various landscapes so as to better understand the patterns of bird occurrence. Insufficient knowledge of the ecology of wintering farmland birds — apart from its inherent complexity — is also due to highly disproportional research efforts. Firstly, the majority of studies of farmland birds to date have concentrated on the breeding season, sometimes considered as being more important for population persistence; secondly, many winter studies have focused on management and conservation, while neglecting natural ecological processes; finally, the bulk of the relevant literature comes from the most highly developed regions such as Western Europe. The last-mentioned is of particular importance, because there is growing evidence that neglecting other regions, especially those with an incomparably richer biodiversity and different land use practices, may give a distorted picture of the true ecological processes in farming ecosystems (Báldi & Batáry 2011, Tryjanowski et al. 2011, Sutcliffe et al. 2015).

Population parameters vary in the course of the winter in response to weather conditions and bird phenology. The number of species is usually more stable than the abundance of birds, although both parameters reveal generally decreasing trends in successive months owing to food depletion and poor overwinter survival. These patterns may be regionally specific: for example, they were distinct in the harsh conditions of east-central Poland, where bird communities are mainly migratory and many local breeding species leave for the winter (Goławski & Kasprzykowski 2010), but less pronounced in the mild winters of the UK, with its high number of winter immigrants (Gillings et al. 2008b). It would be interesting to know how the assemblages of birds change in areas with intermediate weather conditions and species composition, such as SW Poland. One may also expect these changes to be species-dependent: sedentary species should react in a different way to weather deterioration or changing daylight from migrants. These responses may be particularly interesting in late winter (February–March), when food resources are severely depleted, food demand is still high, bird assemblages are augmented by early migrants, but the harsh weather continues. Some evidence suggests that certain species, like granivores, experience the greatest food stress precisely in late winter (Robinson & Sutherland 1999). This 'hungry gap' (sensu Siriwardena et al. 2008) may therefore be responsible for the high winter mortality of these birds and more generally for their widespread population declines; unfortunately, however, there is only limited evidence regarding bird abundances in late winter.

Birds are unequally distributed over farmlands in winter. The preferential use of the seed-rich cereal stubbles is particularly well recognised, the retention of over winter stubbles is therefore an advocated conservation measure (Moorcroft et al. 2002, Hancock & Wilson 2003, Henderson et al. 2004). Moreover, emphasis is often put on the relationship between stubbles and granivores (Gillings et al. 2008a), grasslands and insectivores (Barnett et al. 2004), and the importance of various non-cropped habitats for the majority of species. Nevertheless, there is insufficient knowledge on how the various habitat types change in relative importance during the winter and how external conditions influence their importance. The habitat associations of wintering birds are particularly poorly understood in the rich farmlands of Central and Eastern Europe (Kasprzykowski & Goławski 2012). Specifically, the importance of field margins, the most common form of non-cropped, semi-natural habitats in low intensity farmlands, and the periods when their significance to wintering birds is greater compared to other habitats, have not been quantitatively assessed before.

The present study investigated the occurrence of bird communities in the heterogeneous farmland of SW Poland over the course of two winters. It aimed to provide a better grasp of the complicated interrelations between the requirements of bird communities and species, the fluctuations of the weather extending into late winter, and the availability of various habitats in the mosaic-like farming landscapes of a Central European country. The specific aims of the study were: (i) to assess the numbers and species richness of wintering birds and to monitor the changes in the abundance of the total community and the most numerous species during the winter months, (ii) to evaluate the main drivers of these changes, especially the response of birds to fluctuations in weather conditions, and (iii) to examine the birds' use of the main habitat types in farmland and changes in their relative importance during winter.

METHODS

Study sites

The fieldwork took place between November and March 2003/2004 and 2004/2005 on six study plots covering 320.2 ha (ranging in area from 48.1 to 60.9 ha, with a mean of 53.4 ha) of the Sudeten Foreland in SW Poland (coordinates of the centre of the area 50°48′N, 16°41′E). The plots were situated in mosaic-like agricultural landscapes representing traditional, low-intensity arable farming and matching the High Nature Value Farmland Type 2 (Paracchini et al. 2007). The plots were covered by small, privately owned fields (0.1 ha up to several hectares), seven mid-field copses (mean area 0.36 ha, range 0.03–0.96 ha), some permanent fallow land, and a network of linear, semi-natural field margins. During the growing season the main crops were winter- and spring-sown cereals (mainly wheat, barley and rye), oilseed rape, maize and root crops, including potatoes and sugar beet. In winter, the area given over to cereals made up 44.4% of the total (mean of the two winters), plough fields 25.1%, oilseed rape 7.4%, grasslands 4.1%, cereal stubbles and maize stubbles 1.0 and 1.2%, respectively, and other crops 0.3%. Altogether, crops covered 83.5% of the area. The remaining non-cropped habitats were permanent fallows covered by dense perennial vegetation with such dominating species as *Elymus repens*, *Tanacetum vulgare*, *Artemisia vulgaris* (8.8%), field margins (6.6%), and other habitats, i.e. mid-field copses, small, old orchards and a pond (1.1%).

This study focused specifically on field margins, as they are common in the Polish landscape, and on their consequent importance for biodiversity. In the study plots they were permanent semi-natural habitats usually associated with functional landscape features (roads and ditches), and covered with lush spontaneous vegetation. The herbaceous layer covered nearly 100% of the margin area and was mainly composed of perennial native species, including several sections of ditches that were dominated by the Common Reed *Phragmites australis*. Shrubs occurred in the majority of the field margins and were characterized by a variety of species composition and spatial architecture. Spiny species, mostly *Rosa* spp. and *Crataegus* spp. were associated with drier margins, whereas the shrub species along ditches were mainly *Salix* spp. and *Sambucus nigra*. Occasionally, *Prunus spinosa* formed dense thickets. Although trees were associated mainly with the mid-field copses, some field margins also included trees, usually solitary. On four study plots occurred remnants of old fruit tree lines formed by *Prunus avium* or *Malus* sp. Considering all plots the number of mature trees (≥ 30 cm diameter at breast height) totally amounted to 435 specimens, mostly of deciduous species. The mean ± SD density of the field margins was 13.7 ± 1.9 km/km^2 (Wuczyński 2016), and the mean ± SD width was 8.0 ± 2.8 m (based on measurements of 10 field margins situated within the study plots, corresponding to the mean width of a larger sample of 70 field margins in the Sudeten Foreland, amounting to 11.7 m, and described by Wuczyński et al. 2011). Field margin lengths and all the other data on landscape structure were processed by GeoMedia Professional 5.2 GIS software (http://www.intergraph.com). For a further description of the study plots, including their location presented with Google Earth KMZ file and associated breeding bird communities, see Wuczyński (2016). Note that only the category of shrubby mosaic plots described in that paper are equivalent to the plots presented here.

Weather conditions

Both winters under study were relatively severe, snowy and long compared to "normal" winters in SW Poland, but with a number of weather fluctuations (Fig. 1). The average daily temperatures for the period 1 November–31 March were 1.9 °C ± 5.5 SD in 2003/2004 and 1.5°C ± 4.5 SD in 2004/2005 ($t = 0.80$, $df = 301$, $p = 0.423$), the average depth of the snow cover was 2.9 cm ± 5.3 SD and 5.4 cm ± 8.5 SD ($t = -3.13$, $df = 301$, $p = 0.002$), the number of days with snow cover was 62 and 60, and the total precipitation was 136.6 mm and 196.8 mm, respectively. All these data, as well as the mean 24-hour ambient temperatures and the depth of the snow cover for the days of the bird counts (the figures used in the linear models, see below) were provided by the weather station in the village of Sieniawka (50°46′N, 16°46′E), situated in the study area. These data indicate that both winter seasons were quite similar regarding weather conditions, except that there was slightly more snow in the second winter. An important difference concerned the onset of the main, long-lasting deterioration in the weather, which happened at the very end of December in 2003/2004, but almost a month later in 2004/2005. This difference strongly affected patterns of bird occurrence. In both winters the severe conditions extended into the first half of March (Fig. 1).

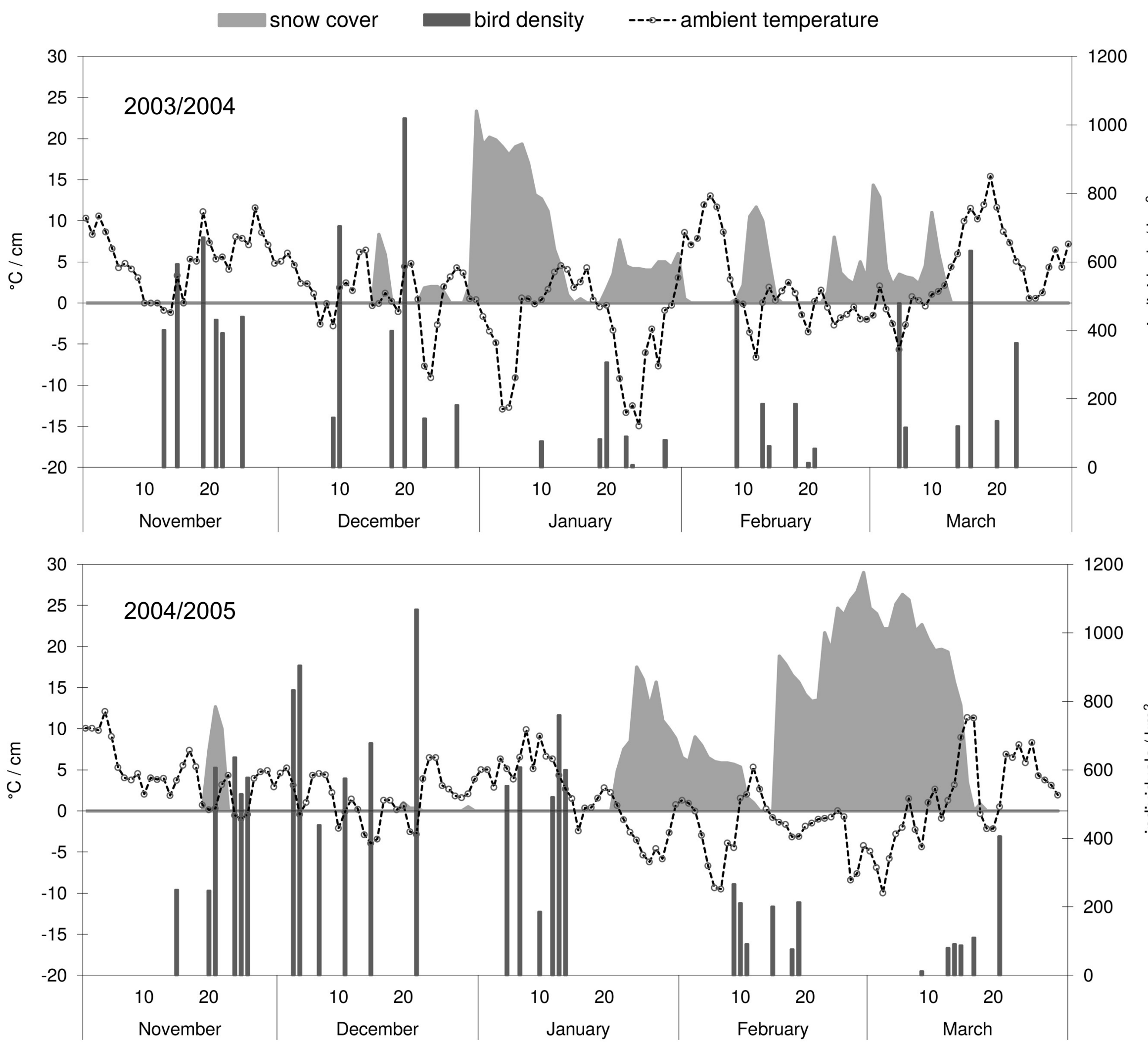


Fig. 1. The densities of birds obtained in six study plots (320.2 ha in total) during individual counts in the winters of 2003/2004 and 2004/2005. The position of the bars on the x-axis shows the distribution of counts within particular months. The weather conditions in the course of the winters are illustrated by the depth of snow cover and the mean 24-hour ambient temperature.

Field procedures
Counts of birds of all species were made on one occasion per month in each study plot, making a total of 60 counts over two winters. The complete area search method (Wilson et al. 1996) was applied: the observer, equipped with binoculars, walked over all parts of the plot along field edges or parallel transects crossing large fields, and counted all the birds present. Shorter transects and a slower pace was used when walking along well vegetated habitats, especially field margins and mid-field copses. The plots were surveyed at a rate of about 10 ha per hour. Double counting of birds was minimized by the observer taking into account birds that were flushed to other fields or to other habitats. Visits were made on days with good visibility, but not in the first or last hours of daylight so as to avoid counting birds flying to or from roosts (Sutherland et al. 2004). In each month the order of plots and census routes within the plot were altered to minimize any effects of time of day or weather on the detectability and presence of birds. All the counts were done by one person (AW).

Prior to the counts in each year, detailed maps of each study plot were prepared and each field and other patch of different land use was given a unique number. Land use was further checked on a field-by-field basis during the bird surveys but this changed little during winter. Laminated sketches of the maps including the patch numbers were used during the fieldwork. Each bird or the number of birds in each discrete flock were recorded separately for each species and were assigned to the field (=patch number) in which they were first detected. Birds recorded in field margins extending along several fields received additional notation to make the location precise. Birds observed flying were counted without any patch number or ignored if clearly not associated with the study plot.

Analysis

The field data were the basis for calculating the following population indices, used in the subsequent analysis: number of species, number of flocks, total density (density = number of individuals per km^2), and density of FBI species, i.e. the group of species used in Poland for calculating the European Farmland Bird Indicator. Moreover, the percentages of species, flocks, individuals, and individuals of FBI species were applied to examine the relative importance of habitat types for birds. All the indices were first calculated at the count level, so that one individual count from the total of 60 counts was taken to be the base unit in most analyses.

We used several indices in order to obtain a more comprehensive picture of bird communities wintering in SW Poland. Apart from the parameters customarily used, such as species richness and bird density, we modelled the occurrence of flocks and FBI species. The number/percentage of flocks was used to overcome a common problem when dealing with winter bird data, namely, that many species show some degree of flocking, and that individuals in flocks cannot be treated as independent data points (Buckingham et al. 1999). The number of flocks is defined as the number of non-zero (1–n) counts of a given species seen on one habitat patch during one visit. The group of FBI species was evaluated separately to assess the importance of the winter farmlands we investigated for birds of conservation concern in Europe. This group consists of 22 species in Poland (Chylarecki et al. 2018), 11 of which were recorded in our study.

The statistical analysis covered two problems: one aimed to assess the environmental factors that affect the indices of wintering bird communities, while the other looked at the habitat associations of bird communities. Generalized linear mixed models (GLMM) were used to evaluate the response of bird indices calculated for individual counts to three categorical variables — year (2003/2004 and 2004/2005, random effect), month (5 months, November–March, fixed effect) and study plot (6 plots, random effect) — and two continuous variables — snow depth and ambient temperature, which were weakly correlated ($r= 0.25$, $p = 0.053$). Owing to the high heterogeneity of the residual variance in all models concerning bird density, the response variable was log-transformed. The interactions between the continuous variables were checked, but as they were insignificant in most models and the sample sizes were relatively small, the analysis was confined to the main effects. The significances of the fixed variables were checked using the Wald test (F statistics), while the random effects were tested with likelihood ratio tests (Chi squared statistics) (Bolker et al. 2009). Since consecutive winter months cannot be treated as independent, classical post-hoc tests are inadvisable. To analyse between-month differences in bird abundances, we therefore checked whether the estimated 95% confidence intervals overlapped, a method known to be robust with respect to data dependence and unequal variances, yet very conservative (Noguchi & Marmolejo-Ramos 2016).

To test for habitat use, bird occurrence was summarized in four broad habitat types covering all habitats in the landscape studied: crop fields, field margins, permanent fallows, and other non-cropped habitats. In order to assess the influence of the habitat, another set of GLMMs were calculated, which included habitat type (fixed categorical variable) and area of habitat type (continuous variable, included in models that do not involve densities). To meet the assumptions of the GLMM model, habitat area was log-transformed. Also, bird density was log-transformed in models involving this response variable, following prior removal of null observations. The method of non-overlapping confidence intervals was used to check between-habitat differences in bird indices averaged over two winters. The same method was also used to test for between-habitat differences in each month, i.e. percentages of bird indices were the response variables, and the indices were calculated for each month and each winter separately.

To evaluate the monthly fluctuations in bird numbers at species level, linear models (LM) were estimated for the 23 most numerous species, i.e. those with at least 50 individuals in two winters. Since the monthly number of individuals was low in most of these species, each model consisted of only two categorical variables — month and year, without interactions.

Most calculations were performed in R programming language (R Core Team 2018), using lme4 and lmerTest packages (Bates et al. 2015, Kuznetsova et al. 2017). Linear models performed at species level were calculated using Statistica version 10 software (StatSoft Inc. 2011). All tests of significance were at the $p < 0.05$ level.

RESULTS

Characteristics of the wintering bird community
Fifty-six species, with a total number of 11 370 individuals aggregated in 2073 flocks, and an average density of 356.6 ind./km^2 (mean of 60 counts), were recorded in the farmland studied (Table 1, Appendix 1). In separate counts, both species richness and bird abundance fluctuated highly, from a mere three species and four individuals, up to 23 species and 605 individuals in one plot. The two most numerous and frequent species were Yellowhammer *Emberiza citrinella* and Tree Sparrow *Passer montanus*, i.e. 51% of all the birds counted. Both these species, along with nine others, are FBI birds; hence, the group constituted a significant proportion of individuals (58.5%) and species (19.6%). Overall, sedentary birds, which are regionally common both in winter and during the breeding season, were numerically dominant. However, a significant proportion of species in the total community consisted of birds that rarely breed in farmland, including forest species (Siskin *Spinus spinus*, Jay *Garrulus glandarius*, Common Crossbill *Loxia curvirostra*, Kestrel *Falco tinnunculus*). Nine species, mainly migrants, were recorded only in March; all the March numbers represented 12% of birds. The total number of birds was 17% higher in the second winter, whereas the number of species was identical in both winters (47). Only one of the eight most common species (> 2% of individuals) — Tree Sparrow — was more numerous in 2003/04 (Appendix 1). There were six species of winter immigrants from the north amounting to 3.7% of individuals. In 2004/2005 the group of immigrants was also incomparably more numerous (413 individuals) than in the preceding winter (8 individuals) (Mann–Whitney U-test, $Z = -4.18$, $p < 0.0001$, $N_{2003/04} = N_{2004/05} = 30$ counts,). This pertains particularly to Brambling *Fringilla montifringilla*, regularly observed in 2004/05 but absent the year before, but also to Bullfinch *Pyrrhula pyrrhula*, Common Redpoll *Acanthis flammea* and Twite *Linaria flavirostris*.

Intra-seasonal changes in bird occurrence
The size of the bird assemblages and species richness fluctuated strongly over the two winters in response to weather conditions (Fig. 1, 2); in particular, compared with the relatively high numbers recorded in November and December, numbers in mid-winter were very much smaller. In 2003/04 this rather abrupt decline took place as early as January, following a sudden deterioration in the weather at the turn of the year, whereas in 2004/05 this decrease was delayed until February, since the weather did not deteriorate until late January. As a result, the biggest differences in bird numbers between the two winters were recorded in January, whereas the figures for February, averaged over the winters, were particularly low (Fig. 2). In both seasons, conditions remained harsh until about mid-March, so that the March bird numbers were still low.

These patterns of intra-seasonal changes were much the same with respect to the number of species, flocks, density and density of FBI birds, but the least pronounced in the number of species

Table 1. The characteristics of the total community of wintering birds and the European Farmland Bird Indicator species (FBI) encountered in the study plots over the two winters. See also Appendix 1 for more detailed information on particular species.

Variable	2003/2004	2004/2005	Total
Total No. of individuals	4730	6640	11370
No. of individuals per count	157.7 (4–490)	221.3 (6–605)	189.5 (4–605)
No. of flocks	938	1135	2073
No. of flocks per count	31.3 (4–82)	37.9 (4–76)	34.6 (4–82)
No. of species	47	47	56
No. of species per count	12.5 (3–22)	14 (3–23)	13.2 (3–23)
Density (ind./km^2)	299.6 (7.1–1019.1)	413.5 (11.4–1067.4)	356.6 (7.1–1067.4)
No. (%) of individuals of FBI species	3420 (72.3)	3237 (48.8)	6657 (58.5)
No. (%) of FBI species	10 (21.3)	10 (21.3)	11 (19.6)
No. of FBI species per count	2.8 (0–7)	2.6 (0–8)	2.7 (0–8)
No. of individuals of FBI species per count	114.0 (0–423)	107.9 (0–269)	111.0 (0–423)
Density of FBI species (ind./km^2)	218.1 (0–879.7)	202.0 (0–446.8)	210.0 (0–879.7)

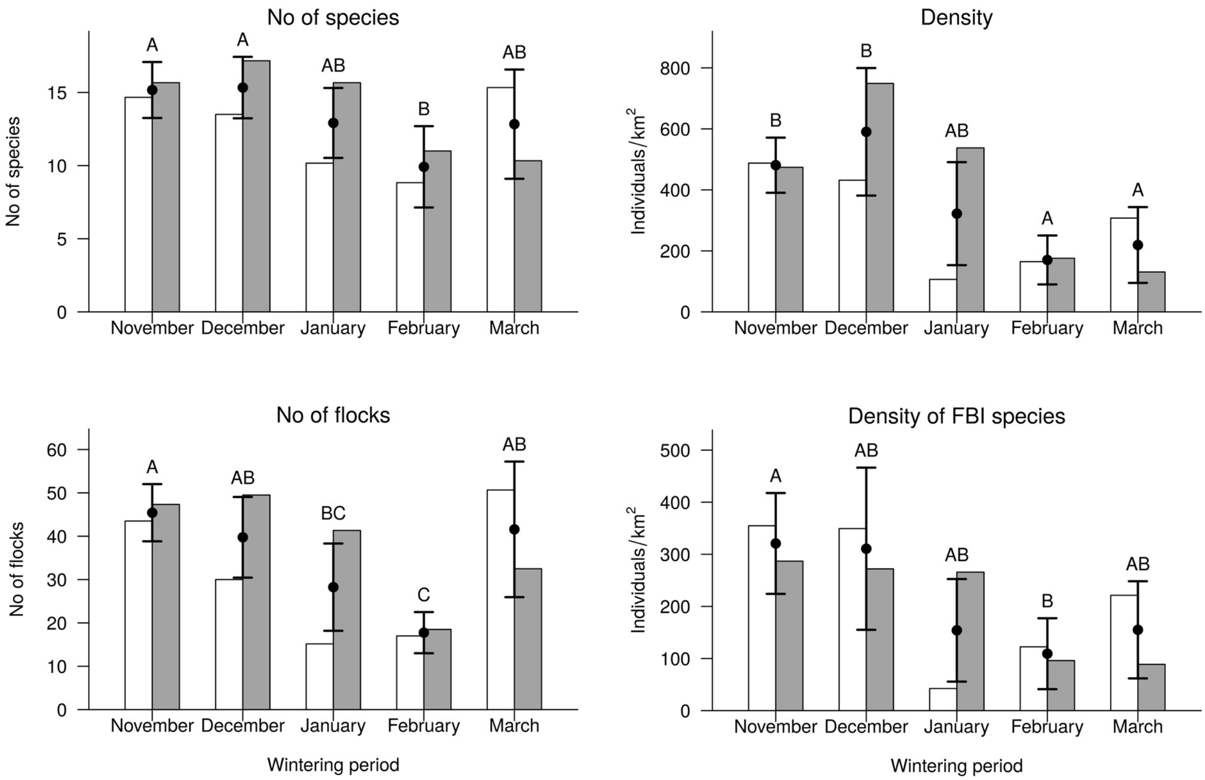


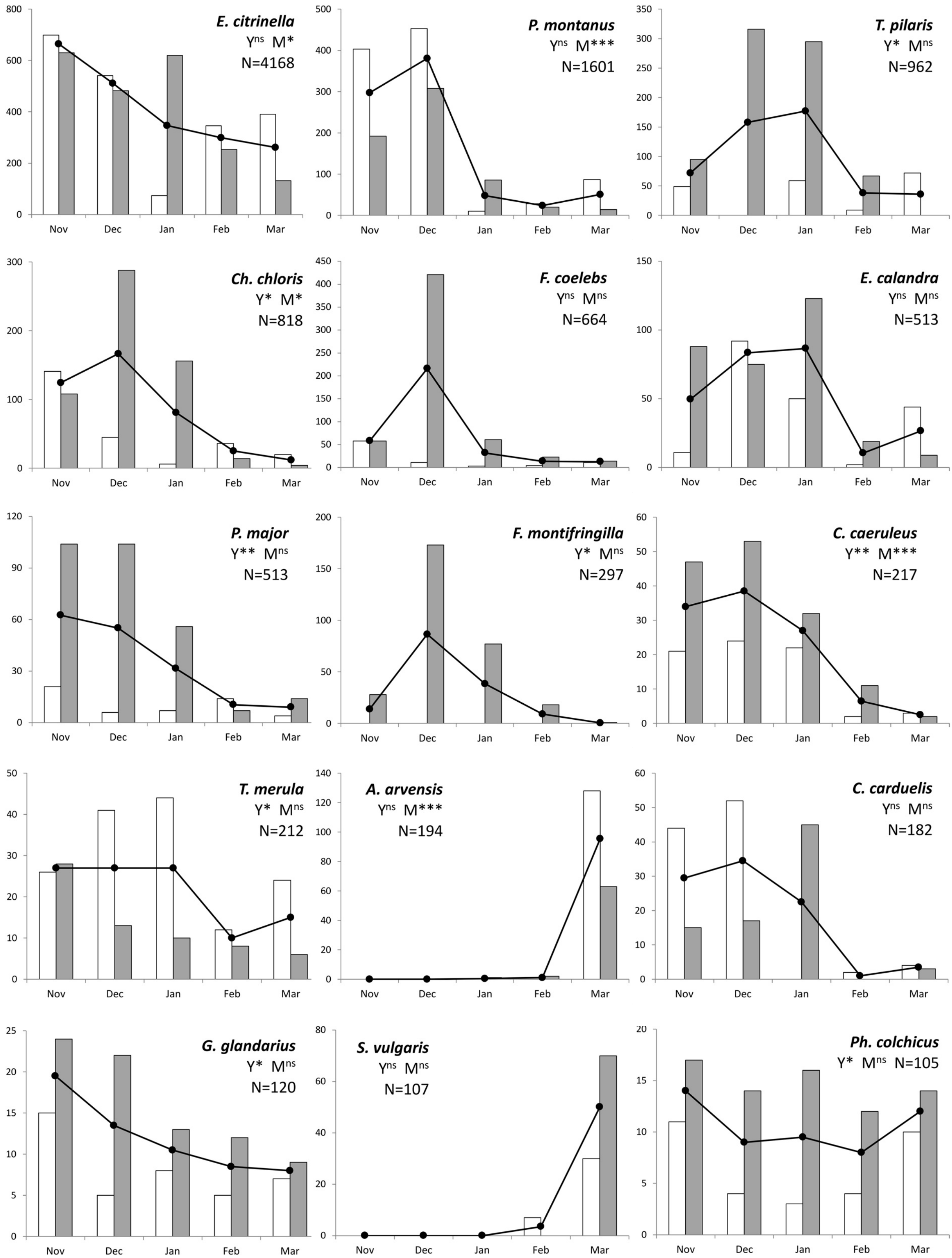
Fig. 2. Number of species, total density, number of flocks and density of FBI species recorded in the winter months of 2003/2004 (light bars) and 2004/2005 (dark bars). The bars represent the mean values from the six study plots in the respective winters; the dots and whiskers represent the means ± 95% CI (N=12) of the two winters. The various letters indicate statistically significant differences determined from the non-overlapping confidence intervals.

(Fig. 2). Data averaged over two winters revealed significant differences in all these parameters between November and February, and December and February (except the density of FBI species). A slight consistent increase in bird abundances in March was significant only with regard to the number of flocks.

The mean abundances of most species also decreased as the winter progressed, especially those of the most numerous species (Yellowhammer, Greenfinch *Chloris chloris*, Great Tit *Parus major*, Blue Tit *Cyanistes caeruleus*, Jay) (Fig. 3). Numbers of a smaller group of species, mainly sedentary ones, remained stable (Blackbird *Turdus merula*, Pheasant *Phasianus colchicus*, Buzzard *Buteo buteo*, Great Grey Shrike *Lanius excubitor*), while returning birds that had left for the winter (Skylark *Alauda arvensis*, Starling *Sturnus vulgaris*, Song Thrush *Turdus philomelos*) were recorded mainly in March. In contrast, the northern immigrants were occasionally observed in this month and peaked in numbers during mid-winter (Bullfinch, Brambling). Linear models applied at species level to assess the inter- and intra-seasonal changes in bird numbers confirmed the significant effect of month in six of the 23 most common species, and a marginally significant effect in one species (Great Tit, $p = 0.051$). Tree Sparrow and Blue Tit exhibited the most consistent decrease in numbers over both winters, whereas the spring arrivals displayed a consistent increase. The influence of year was significant in 10 species and marginally significant in one species (Siskin, $p = 0.071$).

Factors influencing bird abundance

GLMMs confirmed the importance of count data (month) and snow cover on the parameters of the bird communities (Tables 2, 3). Both variables had significant effects on each of the bird indices. The depth of snow cover was negatively correlated with bird densities (Fig. 4), species richness, number of flocks and numbers of FBI species, and had a much stronger effect than ambient temperatures, as revealed by the many times higher test statistics (Table 2). GLMMs also demonstrated the significant effect of year on total bird density and number of flocks, and a weak relationship with



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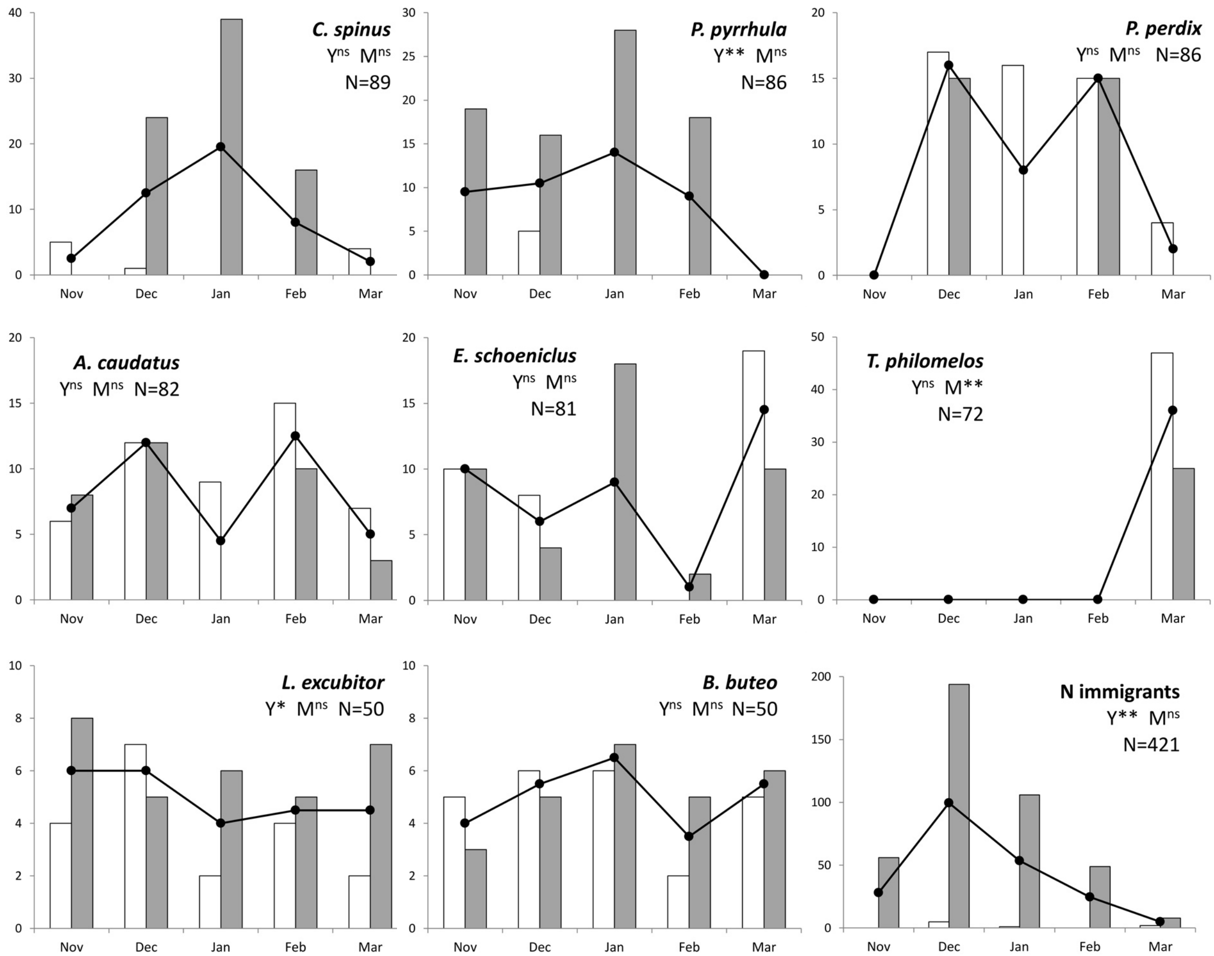

Fig. 3. Changes in abundance of the 23 most numerous species (sum of individuals in the two winters ≥ 50) and northern immigrants (six species, see Appendix 1) during the winter months. The bars represent the sum of individuals counted in six plots in 2003/2004 (white bars) and 2004/2005 (grey bars), and the curves represent the means of the two winters. Note that the scales of the vertical axis differ between charts. The results of the LM on the influence of year (Y) and month (M) on bird numbers are shown for each species. *** — $p < 0.001$. ** — $p = 0.01$. * — $p < 0.05$. ns — non significant.

the sample plot, which was related only to the number of flocks.

Habitat associations of wintering birds

Linear models that included habitat type as an independent variable confirmed the earlier findings on the importance of snow cover and count data, and the insignificant effects of ambient temperature and plot number on bird abundances (Table 4). By contrast, habitat type as well as the area of habitat type (when applicable) appeared to be particularly important in explaining the variability in bird communities ($p < 0.0001$ in all bird indices, Table 5). Birds were unequally distributed in the four habitat types (Fig. 5). Separated confidence intervals indicated that the field margins were particularly important, being associated with significantly higher numbers of species and flocks than the remaining habitats. Also, the total density and the density of FBI species were much higher in field margins than in crops and fallows, and were similar to densities in other non-cropped habitats. These comparisons should be treated with caution, however, owing to the strong effect of habitat area on density indices. Crop fields had similar numbers of species compared to fallows and other non-cropped habitats and similar densities to permanent fallows, but the average number of flocks was higher in crops than in these habitat types.

The unequal importance of the different habitats became particularly clear when habitat availability was taken into account. Field margins covering a mere 6.6% of the area were occupied

Table 2. Results of GLMM on the influence of year (2003/2004 and 2004/2005), month (November–March), plot number (6 plots), depth of snow cover, and mean 24-hour ambient temperatures on species richness, total density, number of flocks in the total community of wintering birds, and the density of FBI species. Distribution families, link functions and model R^2 are presented alongside each response. Numerator degrees of freedom (ndf) and estimated denominator degrees of freedom (ddf) are given for the fixed effects.

Variable	Estimate	SE	ndf; ddf	F/Chi	p
Species richness					
(Poisson distribution, log link function; model R^2 = 0.356)					
Intercept	2.748	0.095			
Snow cover	-0.025	0.009	1; 50	10.074	**0.003**
Temperature	0.002	0.008	1; 53	0.093	0.762
Month	-	-	4; 47	4.192	**0.005**
Year	-	-	-	1.362	0.243
Plot number	-	-	-	0.049	0.825
Density (log-transformed), (ind./km^2)					
(Gaussian distribution, identity link function, model R^2 = 0.540)					
Intercept	482.567	95.148			
Snow cover	-13.836	5.734	1; 53	5.822	**0.020**
Temperature	7.416	5.925	1; 52	1.567	0.216
Month	-	-	4; 52	4.967	**0.002**
Year	-	-	-	4.136	**0.042**
Plot number	-	-	-	0.549	0.459
No. of flocks					
(Poisson distribution, log link function, model R^2 = 0.632)					
Intercept	3.824	0.129			
Snow cover	-0.053	0.006	1; 50	115.476	**0.000**
Temperature	0.019	0.005	1; 52	13.212	**0.001**
Month	-	-	4; 47	41.488	**0.000**
Year	-	-	-	41.516	0.000
Plot number	-	-	-	8.682	**0.003**
Density of FBI species (log-transformed), (ind./km^2)					
(Gaussian distribution, identity link function, model R^2 = 0.620)					
Intercept	5.654	0.473			
Snow cover	-0.159	0.032	1; 50	25.107	**0.000**
Temperature	0.074	0.033	1; 52	4.964	**0.030**
Month	-	-	4; 47	3.343	**0.017**
Year	-	-	-	2.086	0.149
Plot number	-	-	-	1.102	0.294

by 35.6% of individuals and 55.0% of flocks, whereas in crops that covered 83.5% of the area, the respective figures were 46.9% and 25.3%. This clearly indicates that field margins were preferentially occupied by birds, whereas crop fields were avoided, although birds tended to form larger flocks there.

The relative importance of the habitat types for birds changed during both winters, mainly in response to weather conditions. Field margins outnumbered the other habitats, in percentage terms, irrespective of the month and in most bird parameters, but especially in percentage of species and flocks (Fig. 6). The role of crop fields was better illustrated when the percentage of individuals and FBI individuals were considered. Especially during mild weather, the crop fields were occupied by comparable numbers of birds to those in the field margins. But when the weather deteriorated, the field margins were preferred to the crops, as seen in January–February 2004 and in March 2005. Owing to the small sample sizes in

Table 3. The effects of winter months on bird community indices. The values are the estimates ± SE obtained from the GLMMs presented in Table 2. The November data (used as controls) have been omitted from the table.

Community indices	December	January	February	March
Species richness	-0.02 ± 0.09	-0.14 ± 0.11	-0.32 ± 0.12	-0.06 ± 0.12
Density (log)	0.09 ± 0.33	-0.74 ± 0.33	-0.83 ± 0.34	-0.88 ± 0.34
No. of flocks	-0.15 ± 0.07	-0.45 ± 0.07	-0.66 ± 0.08	0.07 ± 0.07
Density of FBI species (log)	-0.19 ± 0.47	-1.52 ± 0.46	-0.69 ± 0.47	-0.52 ± 0.48

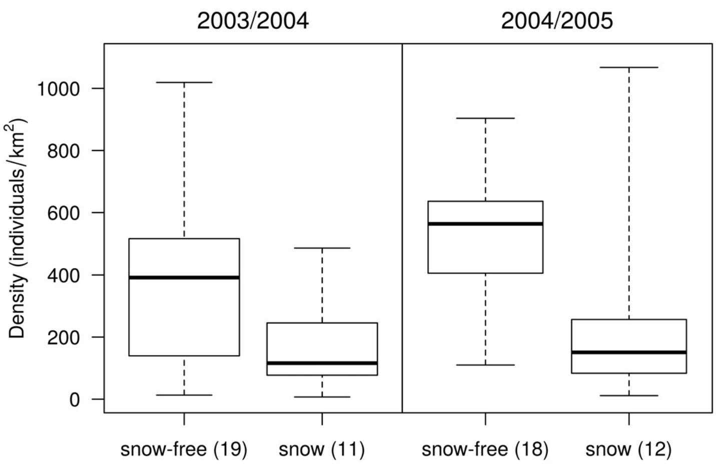

Fig. 4. Comparison of bird densities for conditions both with and without snow in the winters of 2003/2004 (Z = 1.89, p = 0.058) and 2004/2005 (Z = 2.73, p =0.006, Mann–Whitney U-test). The bars, boxes, whiskers, and dots represent the medians, first and third quartiles, non-outlier ranges, and the outliers, respectively. Number of counts for each group is presented in parentheses.

Table 4. Results of GLMM on the influence of year (2003/2004 and 2004/2005), month (November–March), plot number (6 plots), depth of the snow cover, mean 24-hour ambient temperatures, habitat type and area of habitat (log-transformed) on species richness, total density, number of flocks in the total community of wintering birds, and the density of FBI species. Distribution families, link functions and model R^2 are presented alongside each response. Numerator degrees of freedom (ndf) and estimated denominator degrees of freedom (ddf) are given for the fixed effects.

Variable	Estimate	SE	ndf; ddf	F/Chi	p
Species richness					
(Poisson distribution, log link function, model R^2 = 0.490)					
Intercept	1.240	0.142			
Snow cover	-0.038	0.008	1; 211	10.074	**0.000**
Temperature	-0.002	0.008	1; 211	0.093	0.761
Area (log)	0.602	0.127	1; 211	24.135	**0.000**
Habitat	-	-	3; 212	80.833	**0.000**
Month	-	-	4; 211	4.192	**0.000**
Year	-	-	-	8.117	**0.004**
Plot number	-	-	-	0.015	0.904
Density (log-transformed); (ind./km^2)					
(Gaussian distribution, identity link function, model R^2 = 0.569)					
Intercept	7.853	0.294			
Snow cover	-0.048	0.018	1; 97	6.690	0.011
Temperature	0.022	0.020	1; 174	1.192	0.277
Habitat	-	-	3; 175	58.438	**0.000**
Month	-	-	4; 173	4.220	**0.003**
Year	-	-	-	0.060	0.806
Plot numer	-	-	-	2.653	0.103
No of flocks					
(Negative binomial distribution, log link function, model R^2 = 0.543)					
Intercept	1.122	0.271			
Snow cover	-0.059	0.014	1; 211	23.223	**0.000**
Temperature	0.013	0.015	1; 201	1.458	0.229
Area (log)	1.052	0.271	1; 211	18.335	**0.000**
Habitat	-	-	3; 210	51.590	**0.000**
Month	-	-	4; 208	8.461	**0.000**
Year	-	-	-	4.695	**0.030**
Plot number	-	-	-	0.171	0.679
Density of FBI species (log-transformed); (ind./km^2)					
(Gaussian distribution, identity link function; model R^2 = 0.500)					
Intercept	7.301	0.307			
Snow cover	-0.041	0.027	1; 134	2.300	0.132
Temperature	0.019	0.023	1; 135	0.655	0.420
Habitat	-	-	3; 135	32.676	**0.000**
Month	-	-	4; 135	4.299	**0.003**
Year	-	-	-	0.000	1.000
Plot number	-	-	-	2.475	0.116

Table 5. Results of GLMMs describing the effect of habitat type on bird community indices. The values are the estimates ± SE obtained from the models, which included the year, month, depth of snow cover, mean 24-hour ambient temperatures, plot number, and area of habitat (log-transformed) as independent variables (see Table 4 for the full models). Data from the other non-cropped habitats, used as a control in the GLMMs, have been omitted from the table. Numerator (ndf) and estimated denominator (ddf) degrees of freedom, F-ratios and associated significance levels (p) are given in the last two columns.

Community indices	field margins	crops	fallows	ndf; ddf	F; p
Species richness	0.3 ± 0.16	-1.88 ± 0.43	-0.93 ± 0.19	3; 212	80.83; p < 0.000
Density (log)	-0.29 ± 0.25	-2.73 ± 0.26	-2.05 ± 0.27	3; 175	58.44; p < 0.000
No. of flocks	0.55 ± 0.29	-2.78 ± 0.9	-1.39 ± 0.37	3; 210	51.59; p < 0.000
Density of FBI species (log)	-0.25 ± 0.27	-2.18 ± 0.28	-1.59 ± 0.34	3; 133	32.68; p < 0.000

these analyses (N=6) and conservative testing based on 95% confidence intervals, only a few differences in bird abundances between field margins and crops were significant. Fallows and other non-cropped habitats were used by birds with a similar, low intensity throughout both winters.

DISCUSSION

Our results demonstrate that during severe winters, complex farmlands are inhabited by diverse and dense populations of birds, including a significant proportion of species of conservation concern. The populations exhibit overall decreasing trends as the winter progressed, with abrupt decreases in mid-winter in response to intense snowfalls. The non-cropped landscape elements, but in particular the field margins, decide on distribution of birds over farmland, probably enhancing their over wintering survival. We used a rare window of opportunity to collect data in extreme winters, rarely seen in recent years, with harsh weather extending till mid-March.

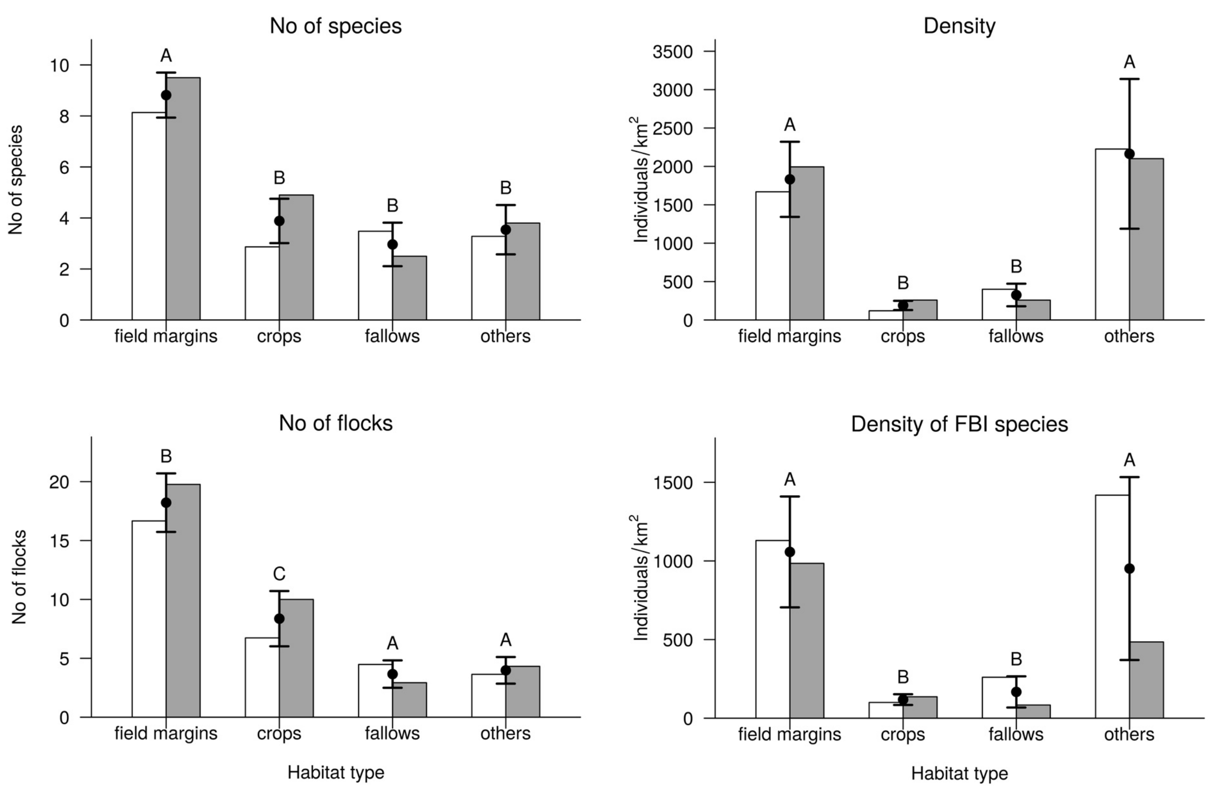

Fig. 5. Number of species, total density, number of flocks and density of FBI species recorded in four habitat types in the winters of 2003/2004 (light bars) and 2004/2005 (dark bars). The bars represent the mean values from the 30 counts in respective winters; the dots and whiskers represent the means ± 95% CI (N=60) of the two winters. The various letters denote statistically significant differences as revealed by non-overlapping confidence intervals in paired comparisons between habitat types. The figures were calculated based on 11085 individuals and 1988 flocks that could be assigned to any habitat (97.5% and 95.9%, respectively).

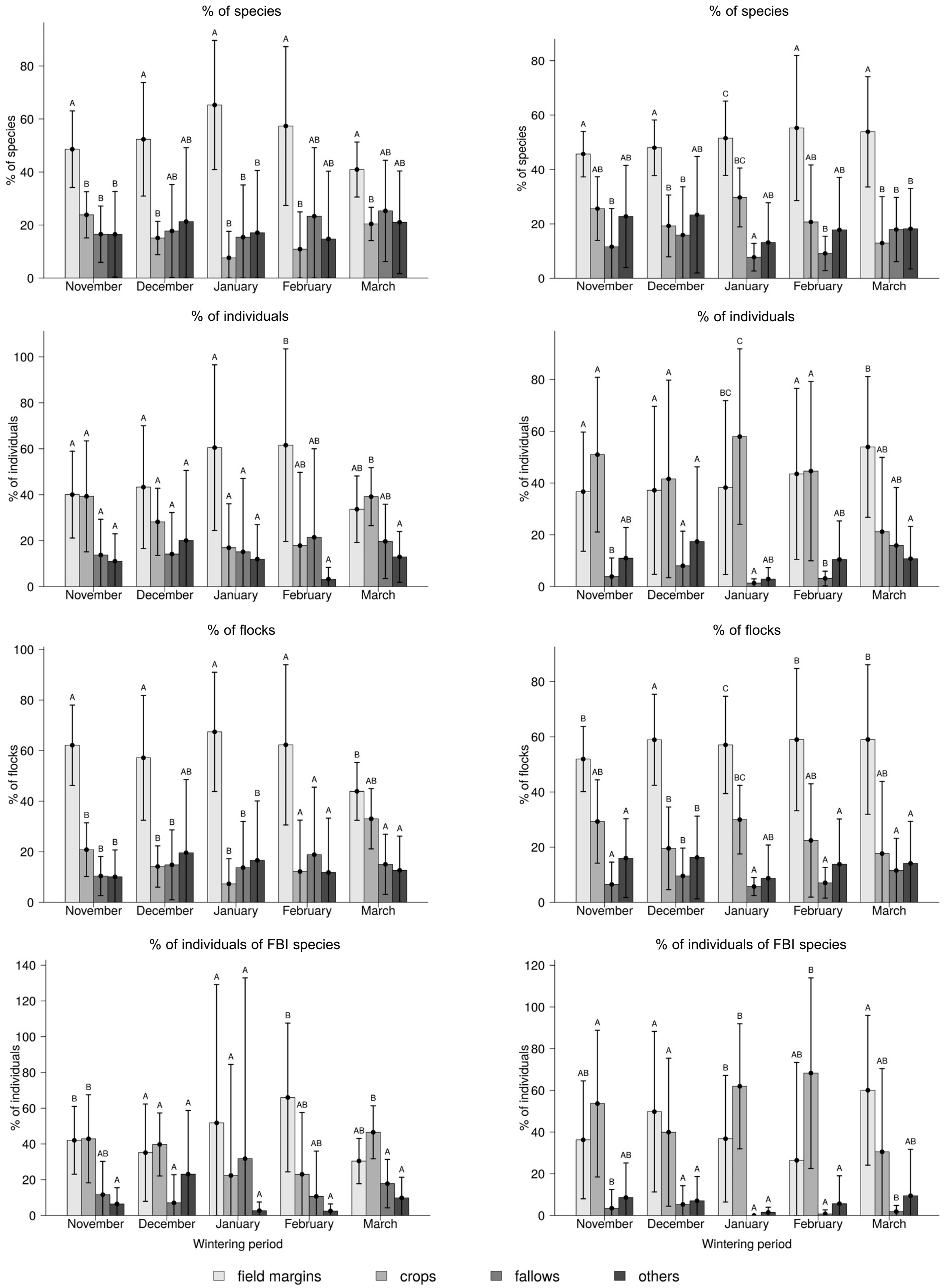

Fig. 6. The effects of winter months and habitat types on the percentage of bird species, individuals, flocks and individuals of FBI species. The bars and whiskers represent the bird indices ± 95% CI (N=6) in four habitat types averaged over six plots in the consecutive winter months in 2003/2004 (left-hand plots) and 2004/2005 (right-hand plots). The various letters denote statistically significant differences as revealed by non-overlapping confidence intervals in paired comparisons between habitat types in each month.

Interestingly, adverse conditions kept populations at low levels until mid-March, despite the influx of spring migrants. Moreover, the data have been collected at the moment of Poland's EU accession, thus, before the subsequent changes in regional farmland. From conservation perspective, such data may be useful, serving as a model of bird communities once wintering in an example of low-intensity agriculture, disappearing in Central Europe and elsewhere.

Characteristics of the wintering bird community
Although direct comparisons are difficult because of differences in weather, methodology or habitat structure between the study areas, the number of 56 species and density of 357 ind./km^2 must be regarded as high compared to other European studies, including elsewhere in Central Europe (reviewed in Goławski & Kasprzykowski 2008). Species richness was also high when compared with the 40 species recorded during the breeding season in the same plots (Wuczyński 2016). A high degree of landscape heterogeneity coupled with natural combinations of species of different origin and habitat associations during winter were probably responsible for the bird indices obtained.

The total abundance was higher in the second winter 2004/2005, possibly due to the longer period of mild weather (till the end of January), and the larger area of attractive field types, especially maize stubble. The vast difference in numbers of the northern immigrants, that were almost lacking in the first winter, was probably due to phenomena operating at multiple spatial scales, especially a different weather between the two winters in Scandinavia and northern Russia. Overall, the between-season differences make one aware of the importance of the characteristics of individual winter seasons for bird populations and the need for repeated multi-season field studies (Hancock et al. 2009).

Intra-seasonal changes and drivers of bird occurrence
Bird densities clearly decreased over both wintering periods, reaching a threefold difference between the lowest (February) and highest (December) 2-year monthly means, or a 100-fold difference between the min-max counts in each season. This pattern seems to be typical of temperate zones such as Poland (Tryjanowski 1995, Goławski & Kasprzykowski 2010). In regions with milder winters, such as Hungary (Field et al. 2007), northern Italy (Fedrigo et al. 1989) or the UK (Gillings et al. 2008a, Siriwardena et al. 2008), decreases are less clear or bird abundances remain more or less stable throughout the winter, probably due to immigration and a lower mortality rate.

A distinctive feature of the count data presented here was the suddenness of changes in bird abundances, related to the occurrence of snow cover (Fig. 1, 2). In the linear models the depth of snow cover had a strong negative effect on bird assemblages, causing significant and long-lasting drops in numbers and species richness. In contrast, ambient temperature was not a significant variable in most models, although it is regularly used to explain dynamics in animal populations. This suggests that it is actually the snow which really affects wintering bird communities, and in snow-rich regions at least, this variable cannot be disregarded or used interchangeably with temperature.

The occurrence of birds was also significantly affected by month, suggesting the influence of other, time-dependent factors, particularly the direct effect of food supply (Hammers et al. 2015, Báldi et al. 2016). It has long been known that in Central Europe, mid-January is a period when small passerines, especially the seed-eaters, typically abandon foraging grounds in fields in response to the depletion of seed resources (Witkowski 1964, Górski 1976). During winter, seeds gradually become depleted through being eaten, germination, decomposition and incorporation into the soil (Robinson & Sutherland 1999, Perkins et al. 2008, Powolny et al. 2018). The detrimental effect of snow may therefore mask more general population processes in wintering birds. In fact, sudden snowfalls may simply bring forward or put off the unavoidable time when birds largely retreat from previously occupied wintering areas in farmland.

These statements apply in particular to seed-eaters, and may also be applicable to our data, since granivores were dominant in the bird assemblage. Changes in the abundance of other species (Fig. 3) showed that they did not fluctuate in synchrony, illustrating different wintering strategies and responses to the same winter conditions. Moreover, our data were collected in winters characterized by rather severe weather, typical of the past decades. It would be interesting to re-evaluate the occurrence of wintering birds in Central European modern farmland during snow-free winters characteristic of recent years and to check more widely how the assemblages of birds have responded to recent climatic changes (Maclean et al. 2008).

Habitat associations of wintering birds

Bird distribution was highly uneven among the habitats. In a small percentage of the overall study area (16.5%), the three non-cropped habitats were occupied by most wintering species and half the individuals. The role of field margins was particularly evident (see below) but also, as expected, birds frequently occupied "other" habitats, including small non-linear patches, such as mid-field copses and old orchards of known importance for biodiversity (Myczko et al. 2013).

The importance of fallow land for wintering birds is also acknowledged (Wuczyński 2005, Šálek et al. 2018), yet not confirmed in our study. Their relatively infrequent occupation reflected the age and vegetation structure in the majority of fallows, which were old, permanent and covered by dense perennial vegetation hindering access to food sources. In contrast, young fallows were characterized by a high abundance and occupancy of many species, but such fallows were uncommon in our study plots. A similar contrasting use of old and young fallows was noted in another region of SW Poland (Orłowski 2006). Interestingly, in E Poland old fallows were preferentially occupied (Kasprzykowski & Goławski 2012), as did semi-natural grasslands (virtually similar to old fallows) in West Hungary (Báldi et al. 2016). The discrepancies may reflect regional differences in habitat choice by wintering birds and different proportions of granivores that utilise seeds still on the plant, such as Twite, Goldfinch *Carduelis carduelis*, or Linnet *Linaria cannabina*, that were relatively uncommon in our study.

In proportion to their area, open cultivated fields were avoided by birds, however, the proportion of individuals and FBI species within crop fields was still high, and the preferences for given field types were visible. Cereal and maize stubbles were frequently occupied, confirming their acknowledged role, mainly by seed-eaters (Buckingham et al. 1999, Moorcroft et al. 2002, Hancock & Wilson 2003). Interestingly, cereal stubbles were occupied mainly by Yellowhammers and Greenfinches (92.9% and 4.2% of individuals, respectively, 7 species in total), while maize stubbles were occupied by a wider range of 14 species in a more equal dominance structure, Chaffinch *Fringilla coelebs* being the most numerous species (25.7%). These differences may be due to the different habitat structure and available food composition in the two types of stubbles.

Even if winter cereals and winter rape were clearly avoided across winters, in the early winter months (November, December) cereals were frequently used by foraging flocks, utilizing sprouting plants. Wilson et al. (1996) found a similar pattern of avoidance of winter cereals, but in early winter many species foraged in freshly sown fields. It is unclear what parts of plants attract birds most in that growth phase: grain scattered during sowing, sprouting grains rising through the soil surface, or young shoots. In a study of the winter diet of Yellowhammers in Poland, grains of wheat were the staple diet (97%) of this species in managed fields, whereas green plant material was only occasionally consumed (Orłowski et al. 2014).

Importance of field margins for wintering avian communities

Several studies indicated the crucial value of semi-natural margins to breeding populations and to overall biodiversity (Wuczyński et al. 2014, Sutcliffe et al. 2015, Haddaway et al. 2018). Yet the role of field margins for wintering birds has rarely been assessed in quantitative terms, especially in the complex farmlands of Central Europe (Kujawa 1995, Geiger et al. 2010, Kasprzykowski & Goławski 2012). Being a distinct landscape feature, these margins are potential biodiversity hotspots in winter farmland, providing food, sheltering sites and connectivity among larger patches. It is likely that during severe weather, field margins provide sufficient cover against predators and cold, and some feeding opportunities. This applies particularly to the baccivorous (berry eating) species (Graham et al. 2018), insectivorous birds that rely on overwintering arthropods (Mestre et al. 2018), but also to ground-feeders, thanks to the relatively low snow-depth under woody cover and diverse vegetation (Marshall 1989, Hinsley & Bellamy 2000).

In this study almost 4000 individuals were observed in field margins, i.e. over 35% of the birds recorded, despite field margins covering only 6.6% of the area. By comparison, a survey conducted during the breeding season in the same plots showed that the proportion of pairs breeding in field margins reached 50.3% (Wuczyński 2016). That statistic alone demonstrates that field margins are decisive as regards abundance and diversity in farmland bird communities. Our data also confirm that field margins provide birds with the best support among farmland habitats during adverse weather, as indicated by the mutual proportions of birds observed in field margins and cropped fields. Both habitats had roughly equal shares of individuals in "normal" winter conditions, however, as the weather deteriorated, the margins started to play an important role in retaining bird communities, whereas the importance of crops gradually decreased, especially when covered with snow. The winter-lowest densities and species numbers were recorded in midwinter of 2003/2004 and in March 2005 (Fig. 1, 2). Interestingly, in both cases the highest percentage of bird parameters were observed in field margins (Fig. 6).

These processes should be seen in the context of adjustments to winter survival (Salewski et al. 2013). Mortality in birds occurs mostly in response to prolonged periods of continued, adverse conditions, rather than short-term extreme episodes (Robinson et al. 2007). Moreover, it has been suggested that birds may be more affected by the harsh conditions that occur near the end of winter, when most food has been eaten, than near the start when food is still abundant (Siriwardena et al. 2008, Powolny et al. 2018). The prolonged periods of adverse weather, noted above, were the ones in which birds had to face particularly bad conditions and probably suffered an increased mortality rate. The preferential use of field margins during these periods suggests that this habitat probably provides birds with the best support among farmland habitats during adverse weather: birds remaining in farmland respond to weather extremes by moving to these non-cropped habitats, so long as they are available.

CONCLUSION

This study highlights several aspects of winter ecology of farmland birds, including a key role of landscape complexity, especially the field margins, in maintaining avian biodiversity. While numerous studies have emphasized the need for retention of a variety of field margin types in agricultural landscapes, we believe this study to be one of the few to confirm the idea based on winter data, and collected in complex farmlands. We suggest that the network of various field margins retained within the Polish farming landscape makes a substantial contribution to the occurrence of internationally important populations of wintering farmland birds.

However, it might be expected that the importance of non-cropped habitats relative to that of crop fields will decrease, as a result of current changes in agri-ecosystems, especially reduced landscape heterogeneity. In the plots described in this paper, many of the semi-natural habitats have disappeared since the completion of our study, and average field sizes have increased, a process that is taking place right across the country and elsewhere in Europe. This suggests that biodiversity components, including wintering birds, are now relatively more dependent on cultivated areas than they used to be. Emphasis should therefore be placed on improving the value of the cropped area, especially by reducing field sizes, if biodiversity conservation is a priority (Butler et al. 2007, Fahrig et al. 2015, Josefsson et al. 2017). It should nevertheless be noted that crop heterogeneity will not necessarily benefit the avian community if the retention of semi-natural habitats between crops is absent (Castro-Caro et al. 2015, Wilson et al. 2017).

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STRESZCZENIE

[Ptaki zimujące w urozmaiconym krajobrazie rolniczym Polski: wpływ warunków pogodowych na wewnątrzsezonowe zmiany liczebności i wybiórczość środowiskową]

Praca przedstawia wyniki ilościowych badań ptaków zimujących w mozaikowatym krajobrazie rolniczym południowo-zachodniej Polski. Zaprezentowano wewnątrzsezonowe zmiany liczebności na poziomie zespołów i gatunków, czynniki determinujące te zmiany oraz rozmieszczenie ptaków w czterech środowiskach tworzących zimowy krajobraz rolniczy (gruntach ornych, ugorach, liniowych i powierzchniowych środowiskach marginalnych), z podkreśleniem znaczenia środowisk liniowych, tzw. pasm śródpolnych. Comiesięczne liczenia prowadzono przez dwa sezony zimowe 2003/2004 i 2004/2005 w okresie listopad — marzec (łącznie 60 liczeń), na sześciu powierzchniach próbnych o średniej wielkości 53.4 ha (łącznie 320,2 ha), określając liczebność, skład gatunkowy, wielkość stad oraz środowiska występowania ptaków. Równolegle prowadzono codzienne pomiary temperatury powietrza oraz pokrywy śniegowej charakteryzujące zmienne pogodowe potencjalnie determinujące występowanie ptaków. Oba sezony okazały się stosunkowo surowe (nie spotykane w późniejszych latach), z raptownym załamaniem pogody w styczniu lub lutym i utrzymywaniem się warunków zimowych do połowy marca (Fig. 1). Zgromadzone wyniki analizowano za pomocą modeli liniowych na poziomie gatunkowym oraz na poziomie zespołu ptaków, posługując się czterema wskaźnikami różnorodności: liczbą gatunków, liczbą stad, zagęszczeniem ogólnym oraz zagęszczeniem gatunków wykorzystywanych w Polsce

do obliczania wskaźnika zmian liczebności ptaków krajobrazu rolniczego (FBI, Farmland Bird Indicator).

Wyniki ujawniły duże bogactwo gatunkowe i liczebność ptaków zimujących w badanych agrocenozach. Stwierdzono 56 gatunków oraz 11370 osobników w średnim zagęszczeniu 356,6 os./km^2, a także 2073 stada ptaków (Tab.1). Liczebność była wyższa w drugim sezonie, co mogło wynikać z dłużej trwających korzystnych warunków pogodowych oraz większego udziału zasobnych pokarmowo struktur, zwłaszcza ściernisk po kukurydzy. Ilościowo dominowały ptaki osiadłe, regionalnie liczne na obszarach rolnych także w sezonie lęgowym, z najliczniejszymi trznadlem i mazurkiem (łącznie 51% zespołu) (Zał. 1). W konsekwencji, duży udział osobników (58,5%) i gatunków (19,6%) miały ptaki z koszyka FBI. Grupa sześciu inwazyjnych gatunków z północy stanowiła 3,7% osobników, w tym głównie jer.

Wielkość zgrupowania w ciągu zimy zmniejszała się, największe liczebności występowały w listopadzie i grudniu, następnie notowano gwałtowny spadek w środku zimy, w styczniu lub lutym, zależnie od terminu zaostrzenia pogody. Interesującym wynikiem było utrzymywanie się niskiej (nieistotnie wyższej niż w lutym) liczebności ptaków do połowy marca, tj. do chwili ustąpienia typowo zimowej pogody, mimo rozpoczęcia wiosennej migracji przez wczesne gatunki. Zaprezentowany wzorzec wewnątrzsezonowego zmniejszania liczebności utrzymywał się niezależnie od badanego wskaźnika różnorodności, w przypadku liczby gatunków był wyrażony najsłabiej, zaś liczba stad była jedynym wskaźnikiem, którego wzrost w liczeniach marcowych był istotny (Fig. 2). Analizy dotyczące 23 najbardziej rozpowszechnionych gatunków pokazały, że zmniejszanie liczebności dotyczyło większości gatunków, w tym najliczniejszych. Inne, głównie osiadłe ptaki miały wyrównaną liczebność przez całą zimę (kos, bażant, myszołów, srokosz), zaś gatunki północne cechowała wyższa liczebność w środku sezonu (jer, gil) (Fig. 3).

Wartości statystyk uzyskane w uogólnionych mieszanych modelach liniowych GLMM wskazywały, że pokrywa śniegowa oraz miesiąc były najważniejszymi determinantami liczebności ptaków w każdym z czterech badanych wskaźników różnorodności zespołu. Śnieg miał zdecydowanie większy negatywny wpływ niż temperatura powietrza (Fig. 4). Efekt roku zaznaczył się istotnie w przypadku zagęszczenia oraz liczby stad ptaków, zaś zmienną o najsłabszym wpływie był numer powierzchni badawczej (Tab. 2, 3).

Modele GLMM uwzględniające dodatkowo typ środowiska wskazywały, że również ta zmienna miała silny wpływ na występowanie ptaków ($p < 0.0001$ przy każdym parametrze zespołu, Tab. 4 i 5). Ptaki wybiórczo zasiedlały poszczególne środowiska, unikając dominujących powierzchniowo gruntów ornych, zaś preferując środowiska marginalne (Fig. 5). W pasmach śródpolnych, zajmujących zaledwie 6,6% powierzchni, stwierdzono 35,6% osobników oraz 55,0% stad. W szczególności w okresach zaostrzenia warunków pogodowych pasma stawały się główną ostoją ptaków w krajobrazie rolniczym (Fig. 6).

W przeciwieństwie do informacji z sezonu lęgowego, dane ilościowe o zimowaniu ptaków w środkowoeuropejskich agrocenozach o cechach tradycyjnych są wciąż nikłe. Zaprezentowane nowe materiały z Polski, zgromadzone tuż przed zmianami jakie dla obszarów rolnych oznaczała akcesja do UE, wskazują, że urozmaicone agrocenozy są zasiedlane przez bogate zespoły ptaków oferując warunki do przetrwania nawet stosunkowo surowych zim. Intensywne opady śniegu w środku sezonu, a nie wahania temperatury, prowadzą do załamania liczebności ptaków i mogą utrzymywać populacje na niskim poziomie do połowy marca, mimo napływu wiosennych migrantów. Przetrwaniu krytycznego okresu sprzyja heterogeniczność krajobrazu wpływająca na specyficzne międzyśrodowiskowe rozmieszczenie ptaków. Szczególne znaczenie mają przy tym środowiska półnaturalne, zwłaszcza sieć pasm śródpolnych, wciąż powszechna w krajobrazie rolniczym Polski i warunkująca obecność licznych populacji ptasich, w tym gatunków zagrożonych w Europie.

Appendix 1. Total winter counts of 56 bird species encountered in six study plots in SW Poland, the percentage of the total number of individuals (%) and the frequency of occurrence (% of visits, N=60) of each species. The species have been arranged according to the decreasing sum of individuals over two winters. * — species encountered only in March; FBI — European Farmland Bird Indicator species; NORTH — winter visitors from the north.

Species	FBI / NORTH	2003/2004	2004/2005	Total	%	Frequency
Emberiza citrinella	FBI	2051	2117	4168	36.66	90.0
Passer montanus	FBI	981	620	1601	14.08	80.0
Turdus pilaris		189	773	962	8.46	43.3
Chloris chloris		248	570	818	7.19	75.0
Fringilla coelebs		87	577	664	5.84	66.7
Emberiza calandra	FBI	199	314	513	4.51	35.0
Parus major		52	285	337	2.96	70.0
Fringilla montifringilla	NORTH	0	297	297	2.61	25.0
Cyanistes caeruleus		72	145	217	1.91	73.3
Turdus merula		147	65	212	1.86	76.7
Alauda arvensis	FBI	128	66	194	1.71	16.7
Carduelis carduelis		102	80	182	1.60	46.7
Garrulus glandarius		40	80	120	1.06	63.3
Sturnus vulgaris	FBI	37	70	107	0.94	8.3
Phasianus colchicus		32	73	105	0.92	50.0
Spinus spinus		10	79	89	0.78	18.3
Pyrrhula pyrrhula	NORTH	5	81	86	0.76	26.7
Aegithalos caudatus		49	33	82	0.72	21.7
Perdix perdix		52	30	82	0.72	11.7
Emberiza schoeniclus		37	44	81	0.71	30.0
*Turdus philomelos**		47	25	72	0.63	8.3
Lanius excubitor		19	31	50	0.44	66.7
Buteo buteo		24	26	50	0.44	58.3
Linaria cannabina	FBI	4	42	46	0.40	10.0
Dendrocopos major		12	17	29	0.26	40.0
Cocc. coccothraustes		23	2	25	0.22	20.0
Acanthis flammea	NORTH	2	20	22	0.19	6.7
Accipiter gentilis		10	9	19	0.17	28.3
Accipiter nisus		7	10	17	0.15	26.7
Trog. troglodytes		7	9	16	0.14	21.7
Poecile montanus		10	6	16	0.14	16.7
Linaria flavirostris	NORTH	0	14	14	0.12	3.3
Falco tinnunculus	FBI	8	1	9	0.08	13.3
*Saxicola rubicola**	FBI	7	0	7	0.06	3.3
Certhia familiaris		3	3	6	0.05	10.0
Ardea cinerea		4	2	6	0.05	8.3
Anthus pratensis	FBI	1	5	6	0.05	6.7
*Anas platyrhynchos**		6	0	6	0.05	1.7
Loxia curvirostra		0	6	6	0.05	1.7
*Vanellus vanellus**	FBI	4	1	5	0.04	3.3
Corvus corax		2	1	3	0.03	5.0
Turdus viscivorus		3	0	3	0.03	5.0
Passer domesticus		0	3	3	0.03	3.3
Dendrocoptes medius		1	1	2	0.02	3.3
Dryobates minor		2	0	2	0.02	3.3
Erithacus rubecula		1	1	2	0.02	3.3
*Columba palumbus**		0	2	2	0.02	1.7
Asio otus		1	0	1	0.01	1.7
Buteo lagopus	NORTH	1	0	1	0.01	1.7
Circus cyaneus		1	0	1	0.01	1.7
*Prunella modularis**		1	0	1	0.01	1.7
*Phyll. collybita**		1	0	1	0.01	1.7
Sylvia communis	FBI	0	1	1	0.01	1.7
Falco columbarius	NORTH	0	1	1	0.01	1.7
*Pica pica**		0	1	1	0.01	1.7
*Motacilla alba**		0	1	1	0.01	1.7