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Villages and their old farmsteads are hot spots of bird diversity in agricultural landscapes

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Summary

1. To counteract the decline of farmland biodiversity in Europe, it is crucial to recognize habitats that are hot spots. Old rural settlements (e.g. villages) may be such important habitats, although these presumably biodiversity-rich habitats have received little attention. Socio-economic changes in central-eastern Europe since 1989 mean that old homesteads and farmsteads are being replaced by new ones.

2. We investigated bird species composition, richness and abundance at three spatial scales (single rural property, village and landscape) in the farmland of Poland to test: (i) their association with age (built before vs. after 1989) and type of property (farmstead vs. homestead), (ii) their relationship with the increasing share of new homesteads at the village scale and (iii) the difference in diversity between the village environment and four other environments (open fields, forest–field ecotones, forests and towns) at the landscape scale.

3. At the single property scale, 15 out of 33 species preferred old farmsteads, while only one species preferred new homesteads. Old properties hosted a higher number of species and individuals than new ones, and farmsteads hosted a higher number of species than homesteads.

4. At the village scale, bird species richness and abundance were markedly negatively associated with the proportion of new homesteads. At the landscape scale, species composition differed between villages and the other environments, and villages had the highest average bird abundance.

5. *Synthesis and applications*. Rural villages and old farmsteads are important habitats for many farmland birds; thus, the increasing number of new homesteads not associated with farmland production will likely lead to a substantial further decline of farmland bird numbers and biodiversity. To counteract this process, we recommend (i) implementing educational programmes to develop rural residents' awareness about the importance of farmsteads and homesteads for biodiversity, (ii) including villages and farmsteads and consideration of bird-friendly habitats within these as part of EU conservation policies and (iii) compensating for changes in the structure of rural villages by increasing the amount of similar alternative habitats in the surrounding landscape.

Key-words: agricultural landscapes, biodiversity, building, community, farmland, farmland birds, heterogeneity, landscape transformation, social changes

Introduction

Despite a number of countermeasures, biodiversity loss in European agricultural landscapes is still present, although with a less marked negative trend (Krebs *et al.* 1999; Chamberlain & Fuller 2000). This farmland biodiversity decline tends to be associated mainly with agricultural intensification and landscape homogenization over large spatial scales (Chamberlain & Fuller 2000; Donald, Green & Heath 2001; Herzon *et al.* 2007). To counteract this

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decline, it is crucial to identify the farmland habitats and farming practices that have benefited farmland biodiversity for centuries, such as traditional tilling and harvesting methods, field margins, mid-field ponds (Fuller, Hinsley & Swetnam 2004; Josefsson *et al.* 2013). These elements are key drivers of local biodiversity in arable-dominated landscapes, and thus, their protection and restoration are usually included in agri-environmental schemes. However, rural settlements, such as single farmsteads and old villages (i.e. the economic and sociocultural centres of farmland) are usually not acknowledged as important habitats and a source of farmland biodiversity (but see Ahnström, Berg & Söderlund 2008; Hiron *et al.* 2013). Still, traditional settlements with their buildings, farmyards and gardens provide a range of microhabitats for farmland biodiversity in general, which includes breeding and foraging farmland bird species (Donald, Green & Heath 2001; Hiron *et al.* 2013).

Rural settlements are widely distributed across the agricultural landscapes of Europe, although their structure varies across the continent. In central-eastern Europe, rural settlements are largely concentrated in villages (Rey & Bachvarov 1998). In other parts of Europe, such as Sweden and England, villages occur, but most farms are isolated and evenly scattered across the landscape (Hiron *et al.* 2013). In western Europe, several parts of the rural landscapes have been strongly affected by the urbanization starting after the Second World War. New houses are built that differ functionally and structurally from the old ones (Antrop 2004), thus providing birds with fewer potential sites for nesting and foraging. Today, the western European countryside is largely characterized by a high proportion of modern settlements, mainly used only for living and not linked to farming (e.g. in the UK, Belgium, Netherlands; Antrop 2004; Sweden; Hiron *et al.* 2013).

In contrast, central-eastern Europe still has a large number of old traditional villages and single old farmsteads conducting small-scale farming (Tryjanowski *et al.* 2011; Dmochowska 2014), but these presumably important habitats for farmland biodiversity are at risk. Old farmsteads (linked to agricultural production) and homesteads (used mainly for living) are disappearing and being replaced by new homesteads. This is an effect of the rapid socio-economic changes occurring after the fall of communism in 1989 that has had vast consequences for the functioning of agriculture and rural settlements in central-eastern Europe (Stoate *et al.* 2009; Hartel *et al.* 2014). In Poland, the largest country located in the middle of the region, the number of active farmsteads dropped by 29% between 1990 and 2010 and the area of abandoned farmland increased from 1 to 14% between 1990 and 2002 (Dmochowska 2014). However, the number of people living in rural areas remained roughly the same, albeit with some regional variation (Bański & Wesołowska 2010). Similar changes were also evident in, for example the Baltic countries, Czechoslovakia and Hungary (Kok 1999; Bičík, Janoušek & Kabrda 2015). At the same time, individual economy and standard of living increased markedly in rural areas in Poland between 1988 and 2013 (Bański & Wesołowska 2010). In Hungary and Poland, there has been a movement from the cities to nearby rural areas (Kok 1999) and 300 000 new houses were built in Polish rural areas between 1989 and 2001, often replacing old houses. However, only 18% of them were farmsteads designed for food production (Wesolowska 2006), while the remaining settlements were new non-producing homesteads. These new housing types substantially differ in structure from old homesteads and farmsteads built before 1989 (Bański & Wesołowska 2010), thus potentially changing the required conditions for farmland birds linked to old traditional villages and rural properties. Although there are studies suggesting the importance of human settlements and especially farmsteads for the diversity of farmland birds in intensive farmlands of western Europe (Grüebler, Korner-Nievergelt & Von Hirschheydt 2010; Hiron *et al.* 2013), data are largely lacking for the more species-rich parts of eastern Europe. Furthermore, few studies have contrasted the biodiversity of villages to other built-up (towns) or non-built-up (open fields, forest–field ecotones, forests) environments of the urban–rural landscape gradient.

Spatial and temporal patterns of biodiversity in farmlands suggest that at the local scale, biodiversity is mostly shaped by the disturbance rate and land management intensity (Kleijn & Sutherland 2003), whereas at larger spatial scales, habitat heterogeneity is important (Tscharntke *et al.* 2005; Kleijn *et al.* 2011). Thus, to better understand the role of different types of rural settlements for birds, various spatial scales should be considered. Consequently, we investigated the importance of villages and the type and age of property for bird species composition and abundance at three spatial scales in Poland: single rural property, village and landscape. At the property scale, we investigated whether bird species composition, richness and abundance associate with the age (built before vs. after 1989) and type (farmstead vs. homestead) of the property. At the village spatial scale, we assessed the relationship between the increasing share of new homesteads in a village and bird species richness and abundance. At the landscape scale, we investigated whether species composition, richness and abundance of birds in villages differed between four other environments (open fields, forest–field ecotones, forests and towns) at the urban–rural landscape gradient.

Materials and methods

STUDY DESIGN

Poland has a size of 314 000 km^2 and is dominated by agricultural land, which covers over 60% of its area. Agriculture is relatively extensive and over 1·5 million farms exist, of which more than 77% are smaller than 10 ha (Dmochowska 2014). Bird inventories were made in two regions of Poland, Wielkopolska and Małopolska, located in western and southern Poland (Fig. S1, Supporting information). Both areas are important agricultural regions and the dominant types of agriculture are cereal crop farming and cattle and pig farming (Dmochowska 2014). The studies were conducted at three spatial scales: single rural property, village and landscape.

Single rural property scale

We define 'property' as a house with all its associated elements (listed below), such as lawns, trees, barns, surrounded by a fence (see Table S1 and Fig. S2). This survey compared species composition, richness and abundance of four types of rural properties with different functions (farmsteads or homesteads) and age (built before or after 1989). Consequently, we distinguished: old farmsteads, new farmsteads, old homesteads and new homesteads.

Properties were randomly selected in villages. Only those properties which allowed us access were included in the study. Properties that did not provide permission were substituted with others. Altogether, 78 properties were surveyed (19 old farmsteads, 22 old homesteads, 20 new farmsteads and 17 new homesteads). Additionally, the presence of the following 17 elements associated with the property was noted: pigsty, hen house, cowshed, stable, barn, granary, domestic pigeon loft, bird feeders, outbuilding, garage, garden plot, orchard, lawn, number of trees, bushes, dogs and cats. The coverage of forest, grassland and settlements within a 500 m radius from the surveyed site were computed and used in further modelling.

Rural properties were surveyed in 2011, and during each survey, 10-min careful observations of each property were conducted. Each sample unit was surveyed twice form April to June with a 30-day interval between counts. Counts were made from dawn to 11 a.m. during favourable weather conditions, and the final number of avian individuals was based on the maximum number of observations during the two visits. We used all observations of all individuals recorded in the area, but we excluded individuals that were not associated with the habitats in any way, such as flocks of geese or gulls passing through the area at high altitudes. These rules were applied to surveys performed at the village and landscape scales as well.

Village scale

This part of the study analysed the relationship between the increasing share of new homesteads in a village and the occurrence of birds (species richness and abundance). We selected 30 villages differing in their share of new homesteads, from 5 to 40%, to enable the further analysis of this gradient (see Fig. S2 for the appearance of two contrasting villages). Additionally, we calculated the coverage of forests, grassland and human settlements within a 1 km radius around the transects. The values of these variables were kept as constant as possible, but we included them in the statistical models because of their potential effects on the birds. This part of the study was performed only in the Małopolska region, where many villages are large and properties are clustered along roads.

Birds were counted in 2011 along 1-km-long transects ($n = 30$). The width of the sampling area was 50 m on each side of the established transect. This width enabled good visibility and included all of the buildings within the farmsteads and homesteads along roads. The observer walked at a pace of 100 m per 5 min.

Landscape scale

This part of the study assessed the differences in bird communities, species richness and abundance among five main environments: village (up to 2000 inhabitants with a linear and compact distribution of buildings), fields (crop fields and grasslands as one habitat type; larger than 30 ha), the ecotone between the forest and field (having at least 30 ha of agricultural land and 30 ha of forest), forest (larger than 30 ha) and towns (>20 000 inhabitants). The counts were performed in the Małopolska and Wielkopolska regions. The environments were chosen randomly from those that fulfilled the criteria of sufficient area or limits for number of inhabitants.

Field investigations were undertaken in 2013 using transect inventories; transects were placed randomly in the environments. However, as all settlements in villages are located along roads, transects in villages and other environments were shifted to the nearest street or road. The minimum distance between adjacent transects was 1 km. Birds were counted along 122 transects (25 in villages, 25 in fields, 25 in ecotones, 23 in forests and 24 in towns), each 500 m long with a survey area of 100 m on each side. The observer walked at an average speed of 250 m per 5 min.

DATA ANALYSIS

Single rural property scale

The effect of property type and age in villages on species composition and abundance of birds was investigated with the help of redundancy analysis (RDA). First, we checked whether the four property categories (old and new farmsteads, old and new homesteads) determine the occurrences and abundances of the 17 property elements recorded at each site (see above for the full list of the elements). This was studied with RDA, where property category was used as an explanatory variable and the elements as response variables. The 'vegan' package (Oksanen *et al.* 2013) implemented in R (R Core Team 2014) was used for this purpose. Next, using RDA, we looked for the association between abundances of particular bird species and category of property. In this analysis, abundances of bird species were response variables and type of property was used as explanatory variable and the area of each property as a condition (to partial out this effect). The linearity assumption between the dependent and independent variables was unimportant in this case because the model included only orthogonal factors. The canonical correspondence analysis provided very similar results, but we opted for RDA due to the short gradients measured by the detrended correspondence analysis (DCA). The permutation tests with 9999 permutations were used to verify the obtained patterns in RDAs.

Generalized additive models (GAMs, Wood 2006) were used to test the effect of type (farmstead vs. homestead) and age (old vs. new) of property, as well as the interaction of these two factors on bird species richness and abundance using Poisson and negative binomial distributions, respectively (models 1 and 2, respectively) and log link functions. The 'mgcv' package (Wood 2006) implemented in R was used for all the GAMs (models 1–6).

Additionally, coverage of grassland, forest and settlements within a 500 m radius from the property was included as covariates and area of each property (log-transformed) as an offset. Longitude and latitude were fitted as the interaction of cubic regression splines to control the spatial autocorrelation of the data, so that part of the variation of response variable is being explained by geographical location.

Village scale

GAMs were used to test the effect of the proportion new homesteads in a village on bird species richness and abundance using Poisson and negative binomial distributions, respectively (models 3 and 4). In each model, we also included three landscape characteristics within 1 km from the transect: coverage of grassland, forest and human settlements. The number of all properties recorded in a transect (log-transformed) was included as an offset to control for the effect of property density in a village. The coordinates of each sampling transect were included as the interaction of cubic regression splines.

Landscape scale

We used DCA to compare bird communities (abundances of all species observed were included) recorded in the five studied environments. With the help of the permutation test, we checked whether the distribution of loadings of particular counts along the first two DCA axes differed between villages and other environments.

Differences in the mean number of species and mean number of individuals recorded in the five environments were investigated with GAMs with Poisson error distribution as well as negative binomial distribution, respectively (models 5 and 6). Environment type was included as a fixed categorical factor (with five levels), whereas the coordinates of each sampling transect were included as the interaction of cubic regression splines in order to control the effect of spatial autocorrelation.

Model selection

We used a multimodel inference (Burnham & Anderson 2002) to identify the models best describing the data at each spatial scale (single property, village, landscape). For this purpose, Akaike's Information Criterion (AICc) was calculated for each possible model with the help of the 'MuMIn' package (Bartoń 2014). Models with delta AICc < 4 (Burnham & Anderson 2002) were assessed to be worth considering in the set of competing models and conditional model averaging (averaged over the models where the parameter appears; Bartoń 2014) was performed within that set. Averaged parameter estimates were presented as a final result of the modelling.

Results

SINGLE RURAL PROPERTY SCALE

Inventories at the spatial scale of single farmstead/homestead within villages recorded 927 individuals of 33 species (Table S2). The property types differed in terms of the occurrence of several habitat elements as shown by the RDA (Fig. 1a). Elements related to animal and crop production, such as pigsty, barn, cowshed, were all associated with farmsteads and seemed to be weakly correlated with the age of the property. Also, domestic pets, cats and dogs, were most commonly observed in both old and new farmsteads. New homesteads were associated mainly with garages and lawns, while no elements appeared to be exclusively associated with old homesteads.

Old properties hosted a higher number of species and individuals than new ones (Table 1, Fig. 2), while farmsteads hosted a higher number of species and individuals than homesteads. But these effects were not fully additive, hence the negative interaction between type and age of properties. The species composition of local bird

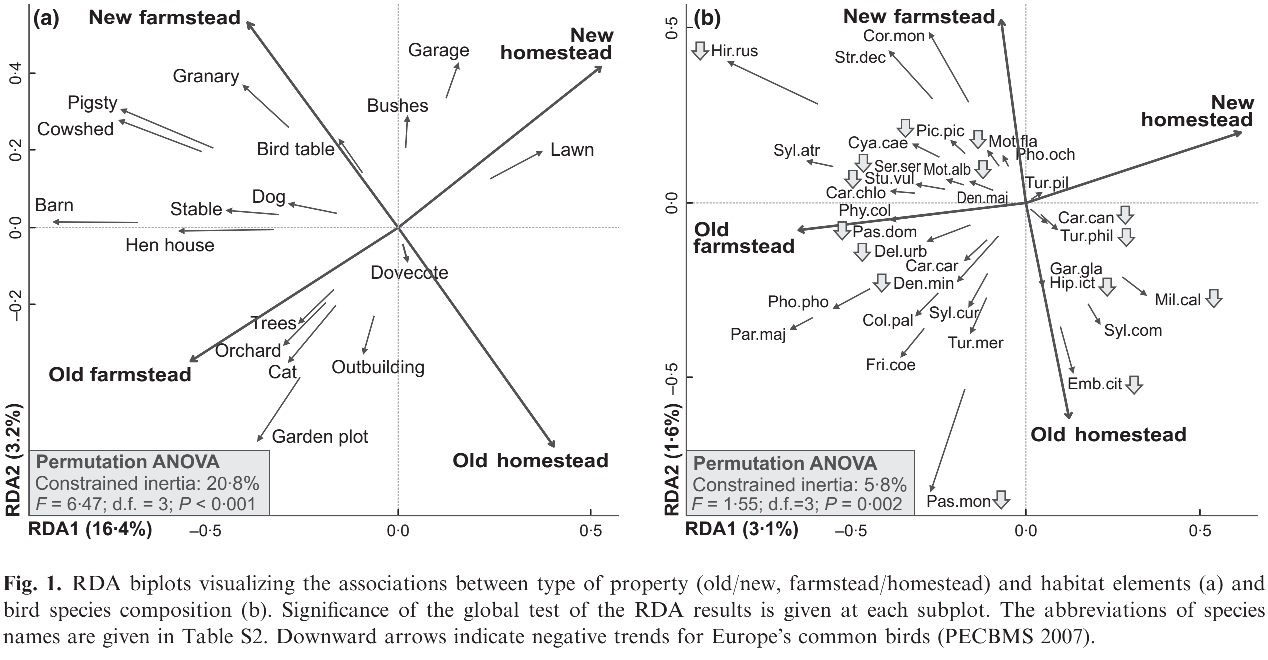

Fig. 1. RDA biplots visualizing the associations between type of property (old/new, farmstead/homestead) and habitat elements (a) and bird species composition (b). Significance of the global test of the RDA results is given at each subplot. The abbreviations of species names are given in Table S2. Downward arrows indicate negative trends for Europe's common birds (PECBMS 2007).

Table 1. Averaged parameter estimates (and 95% CIs) of the generalized additive models explaining species richness and total bird abundance at three spatial scales

Description	Predictor	Estimate	95% CI	
Model 1 (property scale)	Type = farmstead	**0.953**	**0.513;**	**1.393**
Species richness	Age = old	**0.813**	**0.402;**	**1.223**
ΔAICc Null = 44·9	Type * age	**−0.628**	**−1.100;**	**−0.156**
	% Grassland	0.844	−0.235;	1.924
	% Forest	0.936	−0.230;	2.102
	% Settlement	0.234	−0.428;	0.897
Model 2 (property scale)	Type = farmstead	**0.946**	**0.535;**	**1.356**
Total abundance	Age = old	**0.554**	**0.181;**	**0.927**
ΔAICc Null = 55·2	Type * age	−0.401	−0.910;	0.108
	% Grassland	1.075	−0.259;	2.409
	% Forest	0.535	−0.721;	1.791
	% Settlement	0.427	−0.265;	1.118
Model 3 (village scale)	% New homesteads	**−0.031**	**−0.041;**	**−0.021**
Species richness	% Grassland	−0.012	−0.033;	0.008
ΔAICc Null = 47·3	% Forest	−0.009	−0.026;	0.008
	% Settlement	−0.001	−0.028;	0.027
Model 4 (village scale)	% New homesteads	**−0.048**	**−0.058;**	**−0.038**
Total abundance	% Grassland	−0.009	−0.031;	0.013
ΔAICc Null = 46·0	% Forest	−0.006	−0.025;	0.012
	% Settlement	−0.024	−0.053;	0.005
Model 5 (landscape scale)	Env:Ecotone	**0.171**	**0.075;**	**0.267**
Species richness	Env:Forest	**−0.161**	**−0.267;**	**−0.055**
ΔAICc Null = 301·6	Env:Fields	**−0.423**	**−0.535;**	**−0.311**
	Env:Town	**−0.571**	**−0.693;**	**−0.449**
Model 6 (landscape scale)	Env:Ecotone	**−0.448**	**−0.777;**	**−0.118**
Total abundance	Env:Forest	**−0.843**	**−1.181;**	**−0.506**
ΔAICc Null = 36·6	Env:Fields	**−0.778**	**−1.108;**	**−0.449**
	Env:Town	−0.172	−0.510;	0.166

For each set of models, ΔAICc of the null model is given, parameters not overlapping zero are marked in bold. Environment type parameter (models 5, 6) is relative to the baseline category – village.

communities in villages was related to the type and age of the properties (Fig. 1b). Only one species was positively associated with new homesteads, while many species (including those declining in Europe) showed a positive association with old farmsteads and, to some extent, old homesteads and new farmsteads (Fig. 1b).

VILLAGE SCALE

Both species richness and abundance in villages (see Table S3 for details) were dependent on the share of new homesteads in the village: birds declined markedly with an increased proportion of new homesteads in a village (Table 1). For example, species richness declined from 20 to 25 species in villages with about 10% of new homesteads to less than 10 species in villages with 40–50% of new homesteads (Fig. 3). Similarly, the total abundance of birds was about three times higher in old villages (i.e. 10% of new homesteads) as compared to the ones with more than 30% of new homesteads. No significant relationships with birds were found with the studied characteristics of the landscape around villages (Table 1).

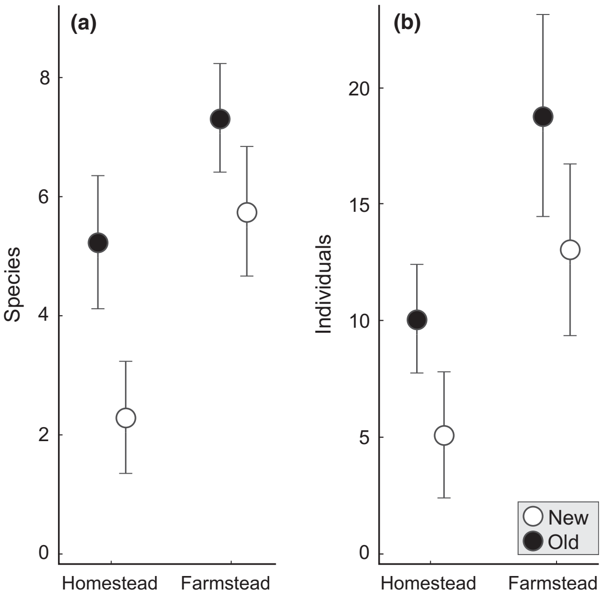

Fig. 2. Mean (and 95% CIs) number of bird species (a) and abundance (b) recorded during 10-min counts in rural properties of different type and age.

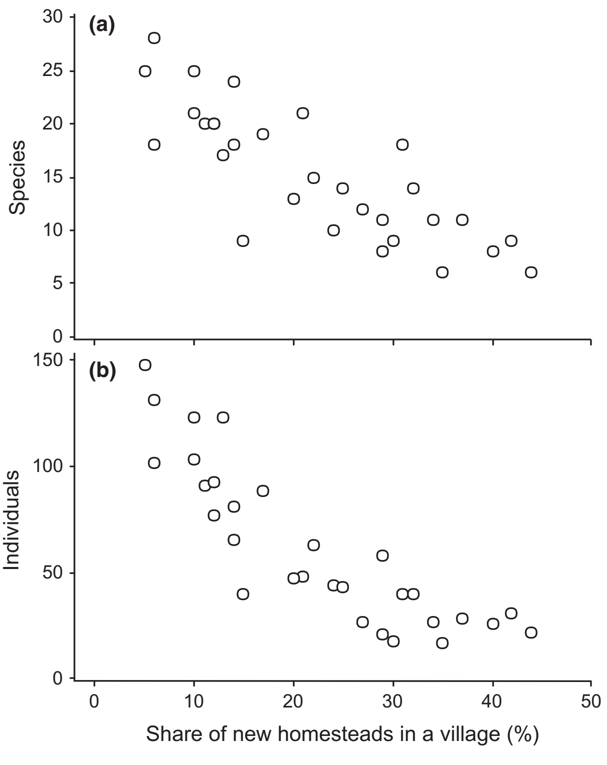

Fig. 3. Correlations between the percentage of new homesteads of all rural properties in villages and the number of species (a) and abundance (b) of birds in village transect surveys.

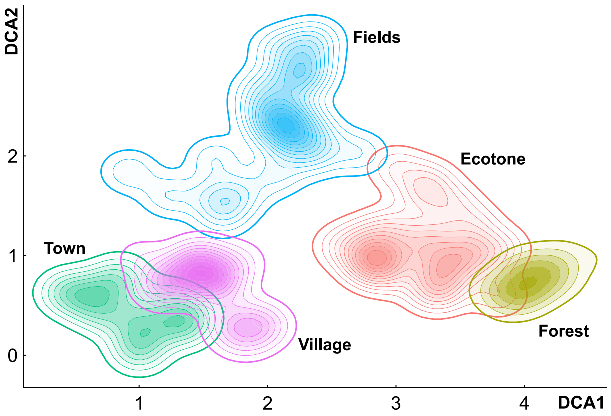

Fig. 4. Similarities between bird communities from the five environments expressed as two-dimensional kernel density estimations of site-specific scores of species along the two-first axes of DCA.

LANDSCAPE SCALE

During the study, we recorded 135 bird species of a total abundance equalling 11 974 individuals, including species declining in Europe (Table S4). DCA revealed a clear separation of bird communities in the five environments (Fig. 4). Forest and town environments were the least similar in terms of the qualitative and quantitative characteristics of the bird community. Although the bird community of the village environment was similar to the one of the town, it also shared some of the community of the open farmland (i.e. fields, see first DCA axis; Fig. 4). The village environment differed significantly from all other environment types along the first DCA axis (permutation test for density comparison, $P < 0{\cdot}01$ in all cases) and along the second DCA axis with the exception of forest (permutation test, $P = 0{\cdot}055$). Thus, the village environment was clearly a distinct environment in terms of bird species composition with several species observed exclusively in this habitat (e.g. barn owl *Tyto alba*, long-eared owl *Asio otus*; Table S4).

Local species richness and total abundance (i.e. per transect) differed between the five environments (Table 1). The average local number of species was the highest in the forest–field ecotone, followed (in decreasing richness) by village, forest, farmland field and urban environments. The highest average abundance, however, was recorded in the village and the lowest in the forest and field environments (Fig. 5).

Discussion

Our multiscale study suggests that villages play an important role in the conservation of farmland bird diversity in central-eastern Europe. First, at the spatial scale of single rural property, we showed that species richness and abundance of birds was highest at farmsteads and old homesteads, whereas it was lowest in new homesteads. Secondly, by comparing different villages, we showed that increasing proportion of new homesteads strongly negatively correlated with species richness and abundance of birds in villages. This suggests that the recent replacement of old farmsteads and homesteads with new ones may greatly reduce bird diversity in villages. Thirdly, when comparing bird diversity among the five broad categories of environments in the agriculturally dominated landscapes of Poland, villages were identified as bird diversity hot spots, especially for farmland birds. Below we discuss the effects of local habitat elements on local species richness and abundance and how these local effects drive the distinct differences in species diversity observed among villages and environments.

LOCAL EFFECTS: AGE AND TYPE OF RURAL PROPERTIES

The local conditions of farmsteads and old homesteads benefit high bird diversity due to their complex and heterogeneous local habitat structures, which are important for nesting and foraging. For example, old roof tiles, chimneys and beams are used as nesting sites by at least 10 species observed in villages, while the commonly occurring old broad-leaved deciduous and fruit trees in gardens usually have numerous cavities offering breeding sites for another 15 species. In our inventory of single farmsteads and homesteads, nine out of 11 species nesting in cavities or at houses were more common at old sites than new ones. Also, several open nesting species requiring dense shrubs and trees for safe nesting sites were more common in old farmsteads and homesteads compared with new ones. Furthermore, ponds, gardens, farm animals and farm residues (e.g. grain, manure) and associated ruderal

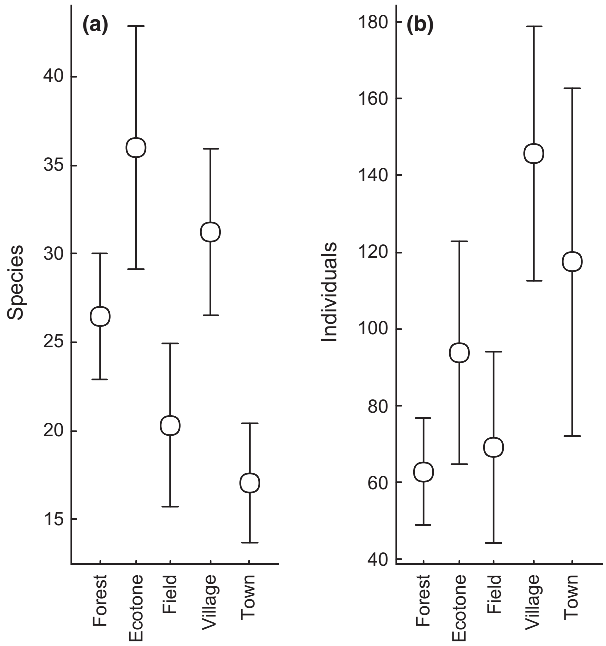

Fig. 5. Mean (with 95% CIs) number of bird species (a) and number of individuals (b) recorded in transects in the five compared environments.

ground vegetation provide a wide range of food and foraging microhabitats for several of the species found at farmsteads compared with homesteads (Cannon *et al.* 2005; Ahnström, Berg & Söderlund 2008; Šálek *et al.* 2015). These additional food sources probably caused the species richness at new farmsteads to be higher than expected by only the age of the property (i.e. 2–3 times higher number of species and individuals as compared to new homesteads). Moreover, in farmsteads, some birds may remain undetected inside barns and cowsheds; thus taking detectability into account, the importance of farmsteads could even increase. New homesteads, on the other hand, were structurally simple, due to the trend of keeping the environs of the house open (e.g. lawns, stone or gravel) with single shrubs or trees.

However, domestic cats, dogs, rats, magpies and crows are also positively associated with such human settlements and are likely to increase the risk of predation to both adults and nest contents (Sims *et al.* 2008), especially of ground nesting species (Söderström, Pärt & Rydén 1998). The occurrence of dogs, cats and magpies was linked to farmsteads, that is the most bird-rich local habitats, and was probably the main cause for the lack of ground nesters in bird communities at farmsteads and other village properties (see also Hiron *et al.* 2013 for a similar result).

SCALING UP PATTERNS: VILLAGES AND SURROUNDING LANDSCAPES

Species richness and abundance of birds were much higher in old traditional villages compared with modernized villages (i.e. those with a high proportion (>30%) of newly built homesteads). This is in line with the finding that local scale factors of farmsteads and homesteads at least partly relate to bird communities at the larger spatial level of villages. The correlation of the proportion of new homesteads with bird diversity was dramatic, with a 60–70% decline in the number of species and total number of individuals when the proportion of new homesteads increased from less than 10% to more than 30%. This strong effect of village modernization suggests the influence of additional factors than just the local ones related to single farm- and homesteads.

The village with its different types of buildings, gardens, ponds, grass strips and ruderal vegetation patches is a highly heterogeneous environment both in terms of structure and habitat composition. It is therefore likely that bird species diversity at the village spatial scale is not only the result of local processes at the homestead/farmstead scale, but that habitat heterogeneity at the larger spatial scale of the whole village has additional effects on species richness (cf. positive effects of landscape heterogeneity; Fahrig *et al.* 2011). Also, the composition and structure of the surrounding agricultural landscape likely affect bird diversity in the villages (Grüebler, Korner-Nievergelt & Von Hirschheydt 2010). Although some of these landscape effects (coverage of grassland, forest and human settlements in the surrounding area) were accounted for and appeared to have no association with bird diversity in villages, it is possible that other landscape characteristics (e.g. use of pesticides) vary among villages and thus affect species richness at the village scale.

AT THE REGIONAL SCALE: VILLAGES AS ENVIRONMENTAL HOT SPOTS

The rural village environment was also a bird diversity hot spot at the regional scale, and the DCA suggested that the bird communities of villages were distinct in their community composition and structure. For example, ground nesting bird species were depauperated in villages and cities. A similar lack of ground nesting species was also found in the peri-urban areas of Sweden (Hedblom & Söderström 2010). Compared with fields and forest–field ecotones, villages had higher abundances of many aboveground nesting farmland bird species, probably because nesting substrates could be limited in the open farmland. Furthermore, villages are located as ‘islands’ in the open agricultural landscape and are close to the food sources of many species. Similarly, Hiron *et al.* (2013) showed that farmsteads could be an important nesting habitat for farmland birds, especially in the intensively farmed open plains, where alternative nesting substrates are largely lacking. Thus, the local bird communities of villages are very rich in species and individuals, but they differ in composition to the bird communities in other rural environments (Meffert & Dziock 2013).

Despite the differences in bird assemblages between villages and crop fields, several species used both environments. For example, the white stork *Ciconia ciconia*, barn owl, barn swallow *Hirundo rustica* and many others are mutually dependent on both fields and grasslands for foraging and buildings for nesting (e.g. Ambrosini *et al.* 2002). It is inconsistent, therefore, to put considerable effort on the restoration of extensive agricultural land use through, for example, agri-environment schemes (Żmihorski *et al.* 2016) while ignoring the availability of nesting places in villages. Thus, we suggest that rural villages are important but neglected environments for the bird diversity of farmland and that changes in the habitats and structures of villages could add to the observed farmland bird declines in Europe.

SOCIO-ECONOMIC CHANGES AND THEIR CONSEQUENCES TO VILLAGES

After 1989, the rapid and marked socio-economic changes in central European countries resulted in changes to rural landscapes similar to those that have occurred in large parts of central and northern Europe during the last 50 years (Antrop 2004). Agriculture was modernized and intensified, causing a dramatic loss of semi-natural and natural habitats, as well as a general reduction in the heterogeneity of croplands with a resulting reduction in farmland biodiversity (Krebs *et al.* 1999; Chamberlain & Fuller 2000). At the same time, urbanization has increased, resulting in the growth of the human population living in cities at the expense of populations living in rural areas (Antrop 2004). As a consequence, villages, or at least parts of villages, are being abandoned in some regions (Dmochowska 2014), while in other regions, for example close to cities, a new group of inhabitants have moved in, namely commuters (Wesolowska 2006). The expansion of cities may negatively affect nearby villages (the 'urban shadow' effect) which still have a rural appearance, but have become functionally urbanized (Antrop 2004). Regardless of the finding that not only active farms benefit birds (Hiron *et al.* 2013), saving the visually intact traditional style of rural settlements is not enough, as many birds rely on the functions of rural villages. Therefore, the expansion of cities to the adjacent rural landscape may lead to the taxonomic homogenization of the avifauna (Clergeau *et al.* 2006; Meffert & Dziock 2013) and thus may decrease polarization of bird communities between villages and towns.

Together with the generally positive socio-economic changes taking place in central-eastern Europe (including increasing financial support to agriculture by the Common Agricultural Policy within the EU), replacing old farmsteads and homesteads with new ones in villages has rapidly increased in recent years (Hartel *et al.* 2014). The EU Rural Development Programmes allocate enormous financial support for farm modernization (in Poland ca. 4 billion EUR for 2014-20); the Water Framework Directive (Directive 2000/60/EC) and standards of Good Agricultural and Environmental Conditions (Council Regulation 73/2009) regulate the storage of manure and silage within farmsteads, while the directive on the energy performance of buildings (Directive 2010/31/UE) delimits the architecture of new settlements. In the light of our study, these legislative acts are likely to negatively affect traditional villages.

THE FUTURE OF BIRD DIVERSITY IN VILLAGES

With both a change in the modernization of villages and the intensification of agriculture in the surrounding landscapes, many bird species may be punished twice as both breeding and foraging habitats for several species may deteriorate. However, it is possible that villages could become more important as breeding habitats for several farmland species when farming activities are intensified (Hiron *et al.* 2013). The net result of the contemporary changes to agricultural landscapes and village heterogeneity on bird diversity in the rural landscapes of central-eastern Europe will therefore be hard to predict and is presently not known. However, it is alarming to observe that several of the bird species in greatest decline are also those species that we found to be largely confined to rural villages (e.g. house sparrow *Passer domesticus*, tree sparrow *P. montanus*, barn swallow; PECBMS 2007; Ahnström, Berg & Söderlund 2008), suggesting that changes to the village environment may strongly affect the population trends of these species.

Socio-economic changes in rural areas highlight the inherent contradictions between biodiversity maintenance, benefitting from old architecture and traditional agricultural practices on the one hand and new, comfortable buildings for improving people's lives on the other. However, these two purposes do not necessarily have to be considered mutually exclusive. This problem reflects the broad and lively debate on the tangible and intangible non-monetary values of natural and cultural ecosystems (Rotherham 2015). Old settlements and traditional farming practices are undoubtedly an important part of biocultural heritage and play a role in the maintenance of local biodiversity, culture, traditions and regional identity (Rotherham 2015). Moreover, the traditional, idyllic appearance and biodiversity of old villages may be a source of aesthetic and leisure satisfaction (Hartel *et al.* 2014). Thus, traditional farming landscapes may be managed because of their intrinsic value (Rotherham 2015), but as socio-economic change is unavoidable, it is also desirable to work out new strategies to both promote human settlements for 'a living rural landscape' and rural biodiversity (Fischer, Hartel & Kuemmerle 2012; Hartel *et al.* 2014).

IMPLICATIONS FOR CONSERVATION AND POLICIES

It is essential to acknowledge old villages and farmsteads as crucial habitat for populations of many declining species. Biodiversity enhancement within rural settlements may be supported by public educational programmes developing the awareness of people that some simple practices, such as providing artificial nesting sites, planting native trees, maintaining orchards, can benefit biodiversity. Such informational programmes have been successfully implemented, for example, in the UK with 'British Garden Birds' (www.garden-birds.co.uk) and in Australia with the 'Living smart' (www.livingsmart.org.au) programmes. Finally, as today's schemes for biodiversity conservation in European farmlands (e.g. the EU Direct Payments or Rural Development) largely ignore biodiversity linked to built-up areas (Fischer, Hartel & Kuemmerle 2012), we suggest that these conservation schemes need to be changed to include villages and farmsteads as part of conservation policies. One way to do this is to try to promote the maintenance of biodiversity-friendly rural architecture (e.g. complex structure, availability of farm building interiors for birds) and the structure of the surroundings of a house (e.g. presence of old trees, orchards, gardens) through the use of subsidies when renovating and modernizing the properties. Another idea is to change the available tools of biodiversity conservation in the European farmland (AES, EFA) such that changes in the structure of villages are compensated by increases in the amount of similar alternative habitats (e.g. mid-field trees, shrubs, ponds) in the surrounding landscape.

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Data accessibility

Data are available from Dryad Digital Repository http://dx.doi.org/10.5061/dryad.7sj32 (Rosin *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Distribution of the study plots.

Fig. S2. Appearance of typical rural properties and villages investigated in the study.

Table S1. Description of studied rural property types.

Table S2. List of bird species recorded in four types of rural properties.

Table S3. List of bird species recorded at the village scale.

Table S4. List of bird species recorded in the five main environments.