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The use of socio-economy in species distribution modelling: Features of rural societies improve predictions of barn owl occurrence

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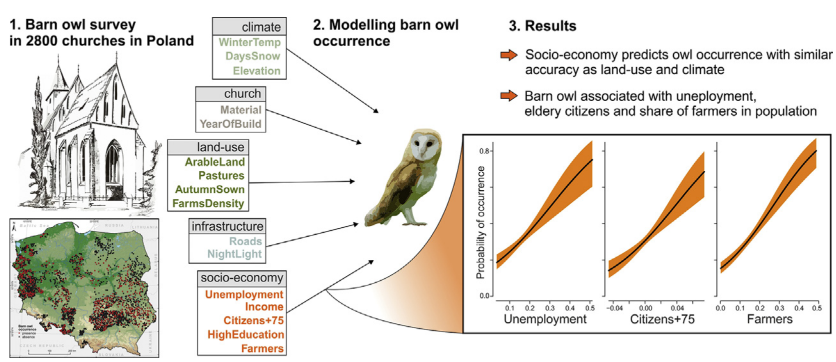
HIGHLIGHTS

- Barn owl prefers grasslands, fields, old churches and regions with mild climate.
- Socio-economy (unemployment, income, etc.) also predicts barn owl occurrence.
- Socio-economy may add overlooked information that links to farmland biodiversity.

GRAPHICAL ABSTRACT



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ABSTRACT

Variation of habitats and resources important for farmland birds seems to be only partly captured by ordinary statistics on land-use and agricultural production. For instance, densities of rodents being prey for owls and raptors or structures of rural architecture providing nesting sites for many species are central for bird diversity but are not reported in any official statistics. Thus, modelling species distributions, population abundance and trends of farmland birds may miss important predictive habitat elements. Here, we involve local socio-economy factors as a source of additional information on rural habitat to test whether it improves predictions of barn owl occurrence in 2768 churches across Poland. Barn owls occurred in 778 churches and seemed to prefer old churches made of brick located in regions with a milder climate, higher share of arable land and pastures, low road density and low levels of light pollution. Including data on local unemployment, the proportion of elder citizens, commune income per citizen, the share of citizens with high education and share of farmers among working population improved the model substantially and some of these variables predicted barn owl occurrence better than several land-use and climate data. Barn owls were more likely to occur in areas with high unemployment, a higher proportion of older citizens in a local population and higher share of farmers among working population. Importantly, the socio-economy variables were correlated with the barn owl occurrence despite all climatic,

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infrastructure and land-use data were present in the model. We conclude that the socio-economy of local societies may add important but overlooked information that links to spatial variation in farmland biodiversity.

1. Introduction

In the Anthropocene, the area of undisturbed natural environments has been considerably reduced across the whole globe. In many regions, vast areas of natural habitats (e.g. forests and grasslands) have been lost and replaced by new land-uses managed by humans such as farmland and urban areas (Antrop, 2004). Currently, farmlands are the most extensive habitat for biodiversity in Europe, harboring, for example, more than one half (250 species) of European bird species, of which 50% have suffered steep population declines (Krebs et al., 1999; Donald et al., 2001; Wretenberg et al., 2006). The important reason for this decline is believed to be driven by reduced amount of residual habitats at the field level (field verges, grasslands, rock outcrops, infield islands, wetlands) and a generally reduced habitat heterogeneity at the landscape level (e.g. Emmerson et al., 2016; Šálek et al., 2018b). Some recent studies also suggest additional influences of changes in human settlements as old farms and human settlements are important nesting habitats for many species but these are now renovated or replaced by new ones (Hiron et al., 2013; Rosin et al., 2016, 2020; Šálek et al., 2016, 2018a; see also Skórka et al., 2018).

Data on residual farmland habitats and habitat elements important for farmland birds are, however, not easily captured by ordinary statistics (e.g. the Corine Land Cover data, or national agricultural land-use statistics), as such habitats are generally not monitored because they are too small and play a marginal role in food production. Similarly, the age and structure of buildings and the availability of different microhabitats linked with rural architecture (see examples in Rosin et al., 2016, 2020) are usually not covered by official statistics in an accessible way. Thus, current state and changes in the availability of these residual habitats in agricultural landscapes remain largely unknown, and thus making the protection and management of farmland birds difficult. However, one may consider social and economic characteristics at administrative level (e.g. commune or parish, continuously collected at such spatial scales in many countries) as a potential indicators of residual habitats, vegetation heterogeneity and habitat structures (e.g. Hope et al., 2003).

In theory, socio-economic statistics may give additional information on general levels of agricultural intensification, amount of residual farmland habitats and residual habitat elements, type and age of human settlements at the landscape scale, as socio-economy commonly varies between regions, and thus could be linked to corresponding variation in biodiversity (e.g. Rosin et al., 2020). Furthermore, local socio-economy (e.g. average age of citizens, wages, degree of unemployment, etc.) may also give additional information on general levels of landscape and habitat heterogeneity. For example, old farmers in poor regions may be more likely to continue small-scale extensive farming with traditional crops. Moreover, we expect more abandoned farms in poor regions (e.g. Wretenberg et al., 2007), which can partly increase landscape heterogeneity and furthermore be of direct use for wildlife (Mainwaring, 2015), including birds (Wretenberg et al., 2007). In rich regions, however, we expect a higher share of young farmers renovating their homesteads, modernising farming practices and implementing large-scale intensive farming. Therefore, we also expect a loss of residual habitats and habitat elements and, as a result, a loss in landscape heterogeneity. Such broad associations between socio-economy and agricultural intensification was already suggested in Donald et al. (2001) comparing bird population declines and level of agricultural intensification across European countries. However, empirical evidence linking socio-economy and biodiversity are lacking.

The aim of this study was to investigate whether socio-economic statistics add to explain observed spatial variation of a farmland breeding species. To answer that we focus on one iconic bird species of rural landscapes – the barn owl (*Tyto alba*). The barn owl is an avian predator specialising on small mammals in open farmlands and it is known to use buildings, especially churches, for nesting (Barn Owl Trust, 2012). Its population has declined dramatically in many European countries during the last decades (Toms et al., 2001; Martinez and Zuberogoitia, 2004; Poprach, 2017). The occurrence of barn owls was surveyed in nearly 2800 churches in Poland and we linked it to two categories of variables: ordinary climate and land-use (including infrastructure) variables and socio-economic statistics at the commune level. First, we investigated the importance of climate, land-use, church architecture and infrastructure-associated data for explaining variation in the presence of barn owls. Based on previous studies we hypothesized that this species prefers: regions with a less severe winter climate, churches located in agriculture-dominated landscape, and old churches over new ones (Altwegg et al., 2006). Second, we investigated the links between socio-economic statistics at the commune level (age structure of citizens, economy and education levels) as predictors of barn owl occurrence. We expected socio-economic variables to also be good predictors of barn owl occurrence, as we assumed that these statistics would cover the type of unmanaged grassland habitat mainly used by this species (i.e. tall grass habitats such as residual grasslands and abandoned grasslands). Finally, we tested whether adding socio-economy data into a model already containing climate, land-use, and infrastructure-associated variables improved the predictive power of the models. We hypothesize that socio-economy may contain additional information on habitat quality which is not reflected by land-use, climate or infrastructure that may improve model performance and the predictions of presence vs. absence.

2. Materials and methods

2.1. Barn owl survey

The Polish population of the barn owl is estimated at 1000–1500 breeding pairs (Chodkiewicz et al., 2015) and has been declining for decades (Tomiałojć and Stawarczyk, 2003), most likely due to reduced amount of safe nesting places, changes of agricultural landscapes and increased mortality due to collisions with vehicles (Rivers, 1998; Gomes et al., 2009). The barn owl survey was performed as a part of the project "Conservation of barn owl in sacral buildings in Poland" led by the Wildlife Society "Stork" in the years 1998–2002 (http://www.bocian.org.pl/plomykowka-o-projekcie). The barn owl survey aimed to cover as many churches as possible but in some cases the surveyors did not manage to contact people taking care of the church or were not allowed by them to perform the inventory. The project covered the whole country, however only results from ca. half of the regions were finally available for analyses (see Fig. 1 for the final coverage). As churches are generally most important breeding places of Polish barn owls (Jermaczek et al., 1995; Indyk et al., 1996; Żurawlew, 2013), we assume substantial proportion of its population was covered by the survey.

During the survey, contracted observers visited churches and inspected all possible places available for barn owls in towers and attices. They searched for birds (dead or alive) and remains of pellets and feathers. A church was classified as currently occupied if birds were observed or fresh signs of their presence were recorded, i.e. fresh pellets, feathers, eggshells, indicating that the church is currently

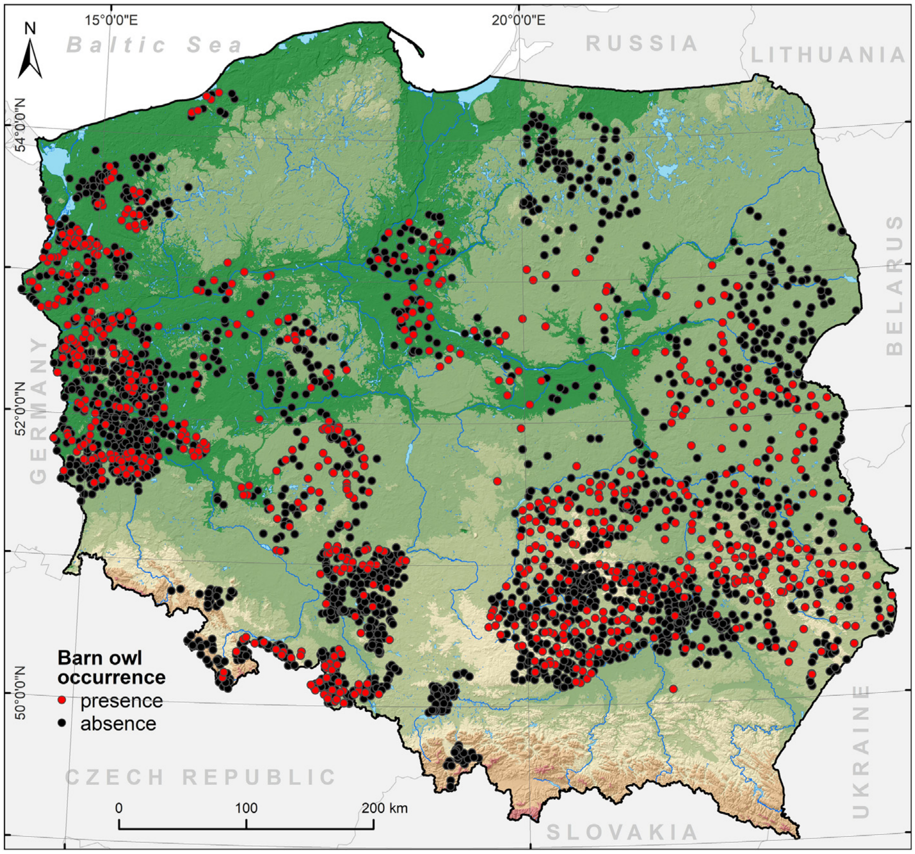

Fig. 1. Distribution of 2768 churches in Poland surveyed for the barn owl occurrence.

occupied by the barn owl. If no signs were recorded, the church was classified as unoccupied. Also, if only very old signs were present, like old pellets or skeletons of barn owls, a church was categorised as unoccupied, as pellets may persist several years in dry conditions (Poprach, 2010). In total, 2768 churches were surveyed and used in the analyses of the present study. The majority of the inspected churches were situated at least 3 km apart (mean = 3755 m; range = 42–28,199 m; SD = 2702 m), which exceeds the radius of an ordinary barn owl home-range (1–2 km, Taylor, 1994.

2.2. Environmental and socio-economic data

Sixteen environment characteristics belonging to five groups were considered as explanatory variables potentially explaining barn owl occurrence (Table 1). First, we used information on climatic (temperature and snow) and terrain conditions (elevation), as the barn owl may suffer from harsh winter conditions (Marti and Wagner, 1985; Newton et al., 1997; Šálek et al., 2019). Second, church architecture (material and age) was considered as an indicator of building availability for breeding and roosting (Poprach, 2010). Third, variables concerning land-use were gathered as indicators of foraging grounds and prey density (Wendt and Johnson, 2017). As barn owls may suffer from road mortality (Šálek et al., 2019) and avoid illuminated areas and buildings (Barn Owl Trust, 2012), we also included infrastructure variables: road density and light pollution. Finally, we used five socio-economic characteristics: unemployment, the age structure of local society, commune income per citizen, level of education and share of farmers in the community.

All the 16 considered environmental characteristics were gathered by observers during the barn owl survey or measured using GIS tools based on open geospatial data available for the study period (e.g. satellite imagery, datasets derived from national or European government agencies; see Table S.1 for data sources). Most of the variables were calculated within a circle of 1500 m radius from a church to refer to the average size of the barn owl home-range (Taylor, 1994). The spatial data processing and calculations were performed using ArcGIS 10.4 software and “raster” package in R (R Core Team, 2019; Hijmans, 2019).

2.3. Statistical analysis

We used generalized linear models (GLM) to investigate the link between the occurrence of the barn owl in surveyed churches and 16 explanatory variables listed in Table 1. We used binomial GLMs implemented in “mgcv” package (Wood, 2017) in R with the barn owl occurrence as a response variable (1 – present, 0 – absent) and each church as a single data record (2768 churches in total). We checked the spatial dependency of residuals for the full model with spline correlograms (“ncf” package in R; Bjornstad, 2019) analysing correlation between the residuals and spatial distance between data points. The correlation was generally low (below 0.2) and not significant (i.e. $p > 0.05$, 95% confidence intervals largely overlapping zero, see Fig. S.1) thus we conclude that there is a weak spatial dependency among churches and our models do not suffer from spatial pseudoreplication.

First, we performed 16 univariate models (separate GLM for each explanatory variable) and compared their performance with AIC and leave-one-out cross validation (LOOCV). The LOOCV procedure was as follows: from all 2768 churches we selected all with barn owl present ($n = 778$) and a random sample of 778 churches with barn owl absent (out of 1990 churches with barn owl absent). As an effect, in this new

Table 1
List of environmental variables considered in barn owl occurrence modelling. For each variable its character (continuous vs. categorical) and basic description are listed, details are given in Table S.1.

#	Variable	Description
	Climate and terrain	
1	WinterTemp	Continuous. Average multi-annual temperature in January (in Celsius degrees).
2	DaysSnow	Continuous. Number of days with snow cover.
3	Elevation	Continuous. Elevation above the sea level (in m) at the church location.
	Church architecture	
4	Material	Categorical. Material from which the church was built: wood vs. brick.
5	Year(OfBuild)	Categorical: old (before 1945) vs. new (after 1945).
	Land-use	
6	ArableLand	Continuous. Area of arable land (in ha) within 1500 m radius of the church.
7	Pastures	Continuous. Area of pastures (in ha) within 1500 m radius of the church.
8	AutumnSown	Continuous. Share of autumn-sown crops in the total crop area within 1500 m radius of the church.
9	FarmDensity	Continuous. Number of farms per 1 ha of farmland within 1500 m radius of the church.
	Infrastructure	
10	Roads	Continuous. Total length (in m) of roads within 1500 m radius of the church.
11	Nightlight	Continuous. A remote sensing measure of light pollution.
	Socio-economy	
12	Unemployment	Continuous. Proportion of registered unemployed in the total working-age population within 1500 m radius of the church.
13	Citizens+75	Continuous. Proportion of citizens ≥75 yrs. of age in the total population within 1500 m radius of the church.
14	Income	Continuous. Commune income (in PLN) per citizen within 1500 m radius of the church.
15	Education	Continuous. Proportion of higher educated citizens in the total number of economically active population within 1500 m radius of the church.
16	Farmers	Continuous. Proportion of farmers in the total number of actively working citizens within 1500 m radius of the church.

data subset ($2 \times 778 = 1556$) the presence to absence ratio was 1:1, so the probability for correct church classification to occupied vs unoccupied by random was 50%. This data subset was next used in LOOCV: a single observation *n* was excluded and used for validation, while remaining observations (i.e. 1556–1 = 1555) were used for GLM fit. Next, on the basis of this GLM, a prediction was made for the excluded observation *n*. The difference between predicted probability of barn owl occurrence (assumed 1 if probability >0.5, and 0 if <0.5) and observed (actual value of observation *n*), averaged across all 1556 observations, is an approximately unbiased estimate for the model classification error (James et al., 2013). The procedure (starting from taking a random sample of 778 unoccupied churches) was repeated 10 times for each among 16 explanatory variables, resulting in 248,960 models in total (i.e. 16 explanatory variables × 10 random church samples × 1556 models leaving a single observation out).

Second, using data on all 2768 churches, we fitted two binomial multivariate GLMs: Reduced GLM and Full GLM. The former used 11 explanatory variables (all but socio-economy variables) while Full GLM took all the 16 explanatory variables into account. Some of the variables, however, were inter-correlated (e.g. nightlight depending on road length), we thus replaced three original variables with residuals from linear regressions: DaysSnow~WinterTemperature, Nightlight~Roads and Citizens+75~Farmers. Based on these regressions, three new variables were created (DaysSnow.resid, Nightlight.resid, Citizens+75.resid) which were introduced in both Reduced GLM and Full GLM instead of original variables (DaysSnow, Nightlight, Citizens+75). This enabled us to keep collinearity among the 16 variables low ($r < 0.56$ in all cases, Fig. 2) as variance inflation factor (VIF) for the model did not exceed 3.1, which is below the threshold of collinearity (i.e. 5.0 or 10.0, see James et al., 2013).

3. Results

3.1. Univariate models

Barn owl presence was recorded in 778 out of 2768 churches, i.e. 28.1% of all surveyed churches. Generally, the barn owl occurrence was significantly univariately associated with all except two variables considered (Fig. 3A). The barn owl occurrence was associated with low elevation and short snow cover duration. Both type of material and age of the church were correlated with barn owl occurrence: the species preferred old churches over new ones and those made of bricks over those made of wood. The presence of barn owls was also associated with three land-use characteristics (arable land, pastures and farm density). Both infrastructure characteristics, i.e. road density and night lights, were negatively associated with barn owl occurrence. All five socio-economic characteristics were significantly univariately correlated with barn owl occurrence: the species occurred more often at sites with lower income and lower education level, high unemployment, a high share of farmers and old citizens (Fig. 3A).

Among all 16 univariate models, seven were distinctly more parsimonious as measured by AIC (i.e. AIC score below 3250, see Fig. 3B). Three out of these seven models were based on socio-economy variables. The cross validation confirmed that univariate models containing socio-economic variables had relatively higher prediction accuracy in comparison to several models basing on land-use or climate variables, although models using the year of build, the proportion of arable land and night light pollution had highest predictive power exceeding 60% of correctly classified cases (i.e. true presences and true absences combined; Fig. 3C).

3.2. Reduced model vs. Full model

Five variables negatively correlating with barn owl occurrence in the univariate approach (Fig. 3) appeared to be non-significant in the full model (Table 2); namely elevation, roads density, light pollution, commune income and proportion of higher educated citizens. By contrast, winter temperatures and share of autumn-sown crops, which showed no univariate correlation with barn owl occurrence, became important in the Full GLM. Interestingly, farm density, which was an important negative predictor of the barn owl occurrence in univariate models, appeared to be a positive predictor of the species occurrence in Full GLM (most likely due to a strong correlation between farm density and light pollution).

Full GLM containing all five socio-economy variables was distinctly more parsimonious than the Reduced GLM which ignored socio-

	WinterTemp	DaysSnow.resid	Elevation	Material	Year	ArableLand	Pastures	AutumnSown	FarmsDensity	Roads	NightLight.resid	Unemployment	Income	CitizensPlus75.resid	HighEducation
DaysSnow.resid	0.00 1.000														
Elevation	−0.45 <0.001	0.52 <0.001													
Material	0.14 <0.001	0.06 0.002	−0.06 0.001												
Year	0.13 <0.001	−0.05 0.007	−0.13 <0.001	−0.11 <0.001											
ArableLand	0.01 0.480	−0.10 <0.001	−0.08 <0.001	−0.04 0.029	0.22 <0.001										
Pastures	−0.13 <0.001	−0.15 <0.001	−0.06 0.003	−0.03 0.087	0.01 0.437	−0.29 <0.001									
AutumnSown	0.46 <0.001	−0.03 0.068	−0.11 <0.001	0.08 <0.001	0.15 <0.001	0.25 <0.001	−0.20 <0.001								
FarmsDensity	−0.26 <0.001	0.15 <0.001	0.36 <0.001	0.03 0.142	−0.30 <0.001	−0.39 <0.001	0.02 0.387	−0.27 <0.001							
Roads	−0.05 0.015	0.07 <0.001	0.06 0.001	0.07 <0.001	−0.09 <0.001	−0.27 <0.001	−0.10 <0.001	−0.03 0.144	0.32 <0.001						
NightLight.resid	−0.02 0.255	0.15 <0.001	0.15 <0.001	0.01 0.513	−0.21 <0.001	−0.28 <0.001	−0.06 0.003	0.00 0.938	0.46 <0.001	0.00 1.000					
Unemployment	0.13 <0.001	0.00 0.849	−0.16 <0.001	0.14 <0.001	0.08 <0.001	0.00 0.889	0.00 0.970	0.07 <0.001	−0.14 <0.001	−0.16 <0.001	−0.15 <0.001				
Income	0.12 <0.001	0.04 0.040	−0.09 <0.001	0.04 0.033	−0.08 <0.001	−0.21 <0.001	−0.07 <0.001	0.04 0.019	0.11 <0.001	0.26 <0.001	0.28 <0.001	0.01 0.635			
CitizensPlus75.resid	−0.30 <0.001	0.18 <0.001	0.30 <0.001	−0.05 0.017	−0.07 <0.001	−0.18 <0.001	0.11 <0.001	−0.23 <0.001	0.20 <0.001	0.03 0.148	−0.02 0.392	−0.04 0.021	−0.10 <0.001		
HighEducation	0.07 <0.001	0.05 0.007	0.05 0.010	0.06 0.004	−0.17 <0.001	−0.35 <0.001	−0.11 <0.001	0.08 <0.001	0.41 <0.001	0.55 <0.001	0.49 <0.001	−0.21 <0.001	0.46 <0.001	0.01 0.639	
Farmers	−0.48 <0.001	−0.09 <0.001	0.06 0.003	−0.13 <0.001	0.09 <0.001	0.36 <0.001	0.09 <0.001	−0.18 <0.001	−0.30 <0.001	−0.24 <0.001	−0.34 <0.001	−0.18 <0.001	−0.28 <0.001	0.00 0.999	−0.54 <0.001

r value: −0.54
p value: <0.001

Fig. 2. Correlation matrix among 16 explanatory variables used in barn owl occurrence modelling. Note that DaysSnow.resid, Nightlight.resid and Citizens+75.resid are used instead of original variables (DaysSnow, Nightlight and Citizens+75 respectively) – see methods and Table 1 for details.

economy variables (ΔAIC = 104.2). Also, Full GLM had slightly higher accuracy as determined by the LOOCV procedure. Generally, overall prediction accuracy as determined by LOOCV was significantly higher for the Full GLM than for the Reduced GLM, although the difference was not large (difference = 2.2%, i.e. 67.8% vs 65.6%, see Table 2 and Fig. 4A). Both models better predicted observed presences (ca. 72% and 74% of observed presences were correctly classified by Full and Reduced GLM, respectively, Fig. 4C) than absences (63% and 56% of observed absences were correctly classified by Full and Reduced GLMs, respectively, Fig. 4B).

In the Full GLM three out of five socio-economy variables were statistically significant ($p < 0.05$), indicating some contribution of these variables to the model despite all remaining 11 variables that were already introduced (Table 2). The average income and share of citizens with high education were no longer significant (as compared to the univariate approach, see Fig. 3) but the barn owl occurrence was positively associated with unemployment, share of elderly citizens and share of farmers (Table 2). Restricting the Full GLM predictions to sites with old brick churches (i.e. the preferred nesting and roosting sites) and keeping all other environmental variables constant, showed that indeed, these three socioeconomic variables were strongly positively related to the probability of barn owl presence (Fig. 5). However, infrastructure variables (road density and residuals of light pollution) became non-significant after taking socio-economy into account while winter temperature appeared to be important in Full GLM.

4. Discussion

Barn owl occurrence in Polish churches was associated not only with landscape, habitat and climate characteristics, but also with church type and age and socio-economy of the local societies. Importantly, some socio-economic factors were still significant predictors of barn owl occurrence when church characteristics, all remaining land-use and climate variables were simultaneously considered. Thus, data on local societies – their age structure and economy – seem to provide additional relevant information in relation to measured environmental characteristics of where to predict presences or absences of breeding barn owls.

4.1. Climate and environmental factors predicting occurrence

The distribution of barn owls suggests that the species may be sensitive to cold winters with snow cover. In a Swiss study, it was also shown that adult mortality of barn owls increased in years with harsh winter climate and long snow cover (Altwegg et al., 2006). Although our results were partly dependent on the model used (Table 2), number of days with snow cover and possibly also low average winter temperatures were negatively associated with barn owl occupancy. As a result, barn owls were mainly absent in the north-eastern part of Poland, i.e. the part of the country with the coldest and most snow-rich winters

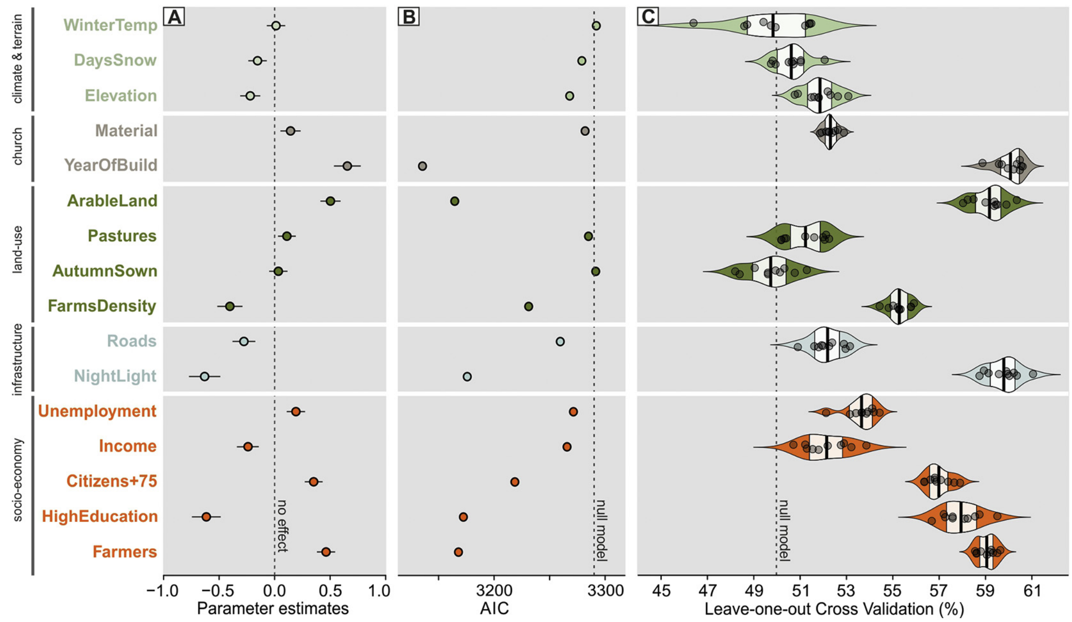

Fig. 3. Performance of 16 univariate GLMs (using 16 explanatory variables, listed on the left) explaining barn owl occurrence in 2768 churches in Poland. For each model parameter estimate of the explanatory variable (with 95% CI) is given (panel A), accompanied by AIC values (B) and LOOCV (C) indicating share (%) of correctly classified churches. Panel C shows kernel density (irregular violins), 95% highest density interval based on 1000 iterations (white belt), mean (vertical thick line) and empirical LOOCV scores from 10 randomizations (points).

(Fig. 1). This is also suggested by barn owl distribution data in Poland (Tomiałojć, 1972).

As in previous habitat association studies on barn owls, our study showed the importance of arable land and pastures for predicting presence of barn owls in the rural landscape. Especially grasslands are known to be important foraging areas, as these are important habitats for shrews, voles and mice (i.e. the main food of barn owls; Bond et al., 2005; Frey et al., 2011; Kitowski, 2013; Kross et al., 2016; Balestrieri et al., 2019). Loss of semi-natural or rough grassland habitats have therefore been viewed as an important driver of observed population declines of barn owls in many regions (Colvin, 1985; De Bruijn, 1994; Hodara and Poggio, 2016). Loss of grasslands and grassland habitat elements of the farmland (e.g. field edges, infield islands, open ditches) is generally linked to an increased agricultural intensification (Matson et al., 1997) and intensive agricultural landscapes are also often characterised by a high share of autumn-sown crops (Donald et al., 2001; Wretenberg et al., 2007). In our study, autumn-sown crops were also most common in arable-dominated areas with lower representation of pastures and few, possibly large-scale, farms (see correlations in Fig. 2). With these associations in mind, it comes as no surprise that the presence of breeding barn owls were negatively associated with areas of autumn-sown crops. Last, the probability of the presence of barn owls was negatively related to the dense network of roads and light pollution. High traffic may be associated with increased owl mortality caused by accidents with cars or because effects of noise pollution reducing foraging success (Fajardo, 2001; Hindmarch et al., 2012; Šálek et al., 2019; Silva et al., 2019).

Table 2
Summary of two GLM models explaining barn owl occurrence in 2768 churches in Poland. Socio-economy is excluded from Reduced GLM while taken into account in Full GLM. Significant results ($p < 0.05$) are marked in bold, the performance of each model is given at the bottom: AIC score and leave-one-out cross validation (LOOCV).

Explanatory variable	Reduced GLM			Full GLM		
	Estimate	SE	p-Value	Estimate	SE	p-Value
Intercept	**−3.11**	**0.22**	**<0.001**	**−3.18**	**0.23**	**<0.001**
Climate and terrain						
WinterTemp	0.003	0.06	0.956	**0.45**	**0.08**	**<0.001**
DaysSnow.resid	**−0.22**	**0.06**	**<0.001**	**−0.32**	**0.06**	**<0.001**
Elevation	0.002	0.07	0.973	0.04	0.08	0.643
Church characteristics						
Material: brick	**0.85**	**0.16**	**<0.001**	**0.84**	**0.16**	**<0.001**
YearOfBuilt: before1945	**1.48**	**0.16**	**<0.001**	**1.52**	**0.16**	**<0.001**
Land-use						
ArableLand	**0.51**	**0.06**	**<0.001**	**0.47**	**0.06**	**<0.001**
Pastures	**0.22**	**0.05**	**<0.001**	**0.18**	**0.05**	**<0.001**
AutumnSown	**−0.12**	**0.05**	**0.031**	**−0.12**	**0.06**	**0.036**
FarmsDensity	0.14	0.08	0.096	**0.28**	**0.09**	**0.001**
Infrastructure						
Road	**−0.33**	**0.08**	**<0.001**	−0.15	0.09	0.087
NightLight.resid	**−0.34**	**0.07**	**<0.001**	−012	0.08	0.123
Socio-economy						
Unemployment	Not included			**0.31**	**0.06**	**<0.001**
Income	Not included			−0.06	0.06	0.324
Citizens+75.resid	Not included			**0.27**	**0.05**	**<0.001**
HighEducation	Not included			0.08	0.10	0.416
Farmers	Not included			**0.68**	**0.08**	**<0.001**
AIC	2940.2			2836		
LOOCV	65.6%			67.8%		

Although several land-use variables were of importance for predicting barn owl occurrence, the presence of old churches was one of the most important predictors of them all (Table 2). Especially, old brick churches are characterised by numerous holes and cavities that may be of great importance as roosting sites and nesting sites for this species (Skórka et al., 2018). In general, safe roosting and nesting sites in buildings, such as barns, houses, towers and especially churches (Barn Owl Trust, 2012) seem to be a prerequisite for the occupancy of barn owls in rural landscapes (Toms et al., 2001; Wendt and Johnson, 2017). Therefore, except in very harsh climatic regions, the combination of foraging habitats with available prey and high-quality nesting and roosting sites may be the major drivers of habitat suitability for barn owls (for similar results based on demography, see Bond et al., 2005).

However, note that our study is only based on inventories of churches with or without roosting and breeding barn owls. Absence of barn owls may not necessarily mean there are no breeding pairs in the church neighbourhood as barn owls breed at other sites as well (e.g.

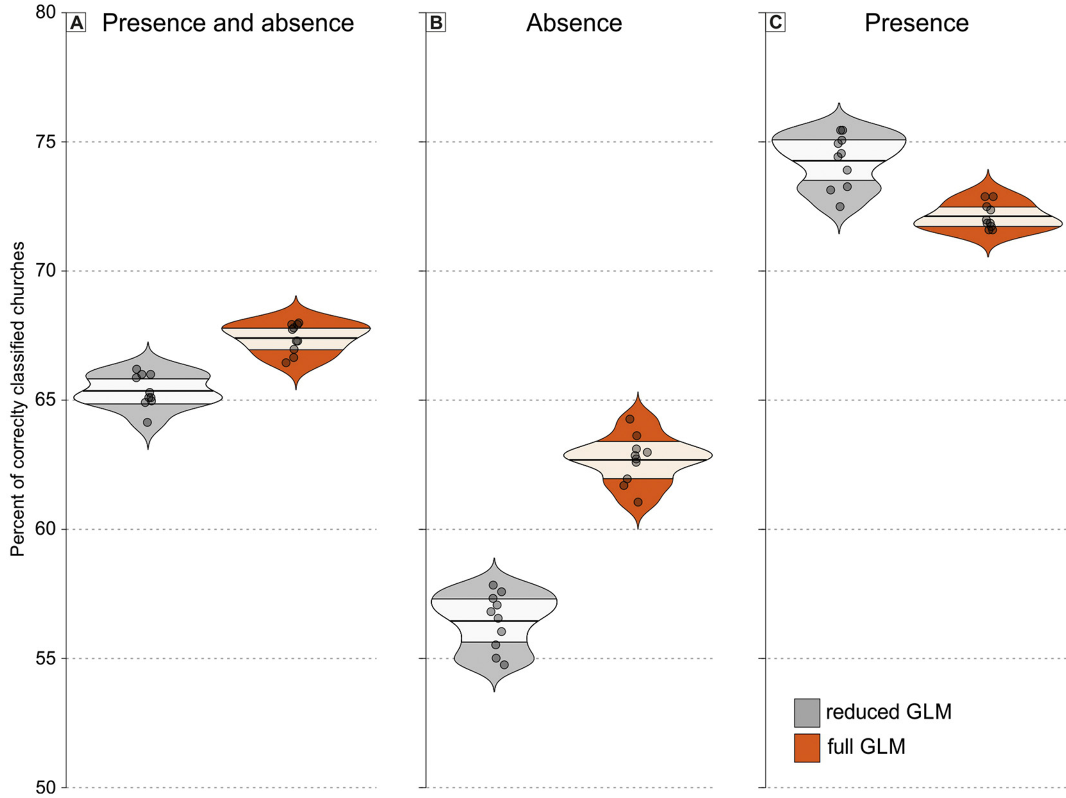

Fig. 4. Results of leave-one-out cross validation (LOOCV) for Reduced and Full GLMs summarised in Table 2. Overall LOOCV score is shown (subplot A), percent of correct classification of absences (B) and presences (C) of the barn owl. Circles show results for 10 subsampling from the pool of unoccupied churches (see methods), vertical thick lines represent means, white horizontal bands represent 95%CI and violins show kernel density estimations.

barns, attices; Krupiński, 2006). The question is then whether there are many such false absences (i.e. undetected pairs) in our data and whether these may affect our results of relationships with environmental and socio-economic variables. First, other studies show that churches are generally preferred as breeding sites in Poland as about 60–80% of all pairs breed in churches (Jermaczek et al., 1995; Indyk et al., 1996; Gorczewski et al., 2004; Żurawlew, 2013) and churches are also used as roosting sites for pairs breeding in the close neighbourhood. Second,

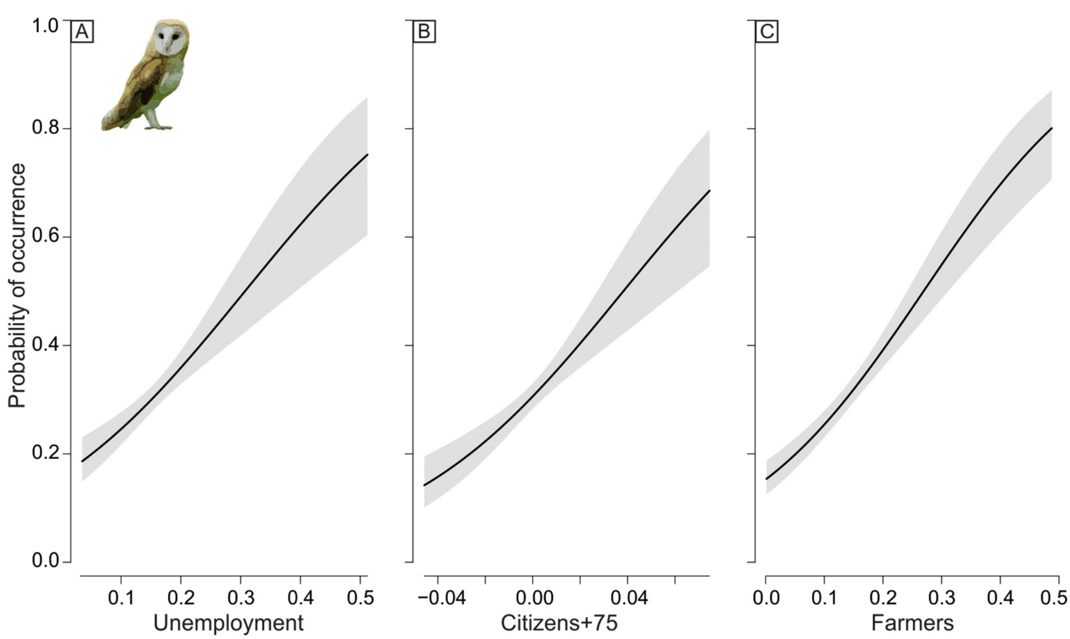

Fig. 5. Predicted probability of the barn owl occurrence (95% CI shaded) in relation to proportion of registered unemployed in the total working-age population (A), proportion of citizens ≥75 yrs. of age in the total population (B; residuals, see methods) and proportion of farmers among working population (C). Based on the Full GLM model (Table 2). Predictions are made for old churches (YearOfBuild<1945) made of brick (Material: brick) while all remaining explanatory variables are kept in their means.

the broad distribution of absences found in this study (North-Eastern Poland; Fig. 1) corresponds to other published distribution data based on ordinary inventories (Tomiałojć, 1972; Tomiałojć and Stawarczyk, 2003). Third, the habitat relationships predicting known occurrence of barn owls in our study largely follow predictions based on the known biology of the species. We are therefore confident that our results largely hold, although the parameter estimates may be more uncertain because of the occurrence of false negatives.

4.2. Socio-economy and occurrence of barn owls

Although the inclusion of socio-economic variables greatly improved the model fit, the cross-validation only suggested a small improvement of a few percent in term of correct predictions (Table 2). Actually, the full model including socio-economy variables mainly improved the percentage of correctly classified absences (from 56% to 63%) while the predictions of presences were roughly equal. However, when restricting the predictions to old brick churches and accounting for all other land-use and climatic factors, the additional effects of three socio-economic variables on the probability of owl presences were enormous (Fig. 5). Clearly, socio-economic variables captured important unmeasured environmental variables with great importance for the occurrence of barn owls.

First, the proportion of citizens being farmers (when accounted for the general area of arable land and pastures) indicate small-scale farming and many small farm properties with possibly abundant numbers of rodents benefitting from farm residues, patches of wastelands and grassy field edges connected to small scale farming at the commune level (Gomez et al., 2015). Unemployment and the share of old citizens were also strongly and independently (in relation to other variables) positively associated with the probability of the presence of barn owls. Although these socio-economic variables may be related to landscape structure and composition beneficial for barn owls, we believe it may be linked to the economy of parishes and whether they can afford to renovate old churches or not. Unemployment and old citizens mean that many parishes in these communes have a poor economy, thus may not afford to do full renovation of their old churches. In rich communes with low levels of unemployment and few retired people, the economy of parishes is also better and many churches are consequently renovated causing a dramatic reduction in the availability of safe roosting and nesting sites for birds (cf. Rosin et al., 2020; see also Skórka et al., 2018).

4.3. Management implications

Our findings indicate the need to save nesting sites for barn owls in churches. The characteristics of churches that barn owls prefer (i.e. holes and cavities for safe nesting and roosting) should be maintained and the national guidelines for church renovations should be corrected accordingly, so that owls are not excluded when churches are refurbished.

Habitat and land-use variables alone may not fully cover the variation in habitat quality important from the perspective of wildlife species living in anthropogenic environments. As already reported for the barn owl, landscape features may only moderately predict its occupancy (Frey et al., 2011; Hindmarch et al., 2012). We show that socio-economic data may contain additional relevant information on habitats for wildlife which is not present in widely used official statistics concerning land-use, agricultural production and habitat configuration.

In a broader perspective, our results show that biodiversity may often be associated with a specific subset of local societies in term of their socio-economic status (several studies reported similar patterns in urbanised landscapes: Shaw et al., 2008, Luck et al., 2012; Chamberlain et al., 2019, see also Torralba et al., 2018), which potentially has important consequences concerning biodiversity conservation possibilities and strategies. From the perspective of a “living rural landscape” and nature conservation in farmlands, high biodiversity values and occurrence of species with conservation concern in economically poor and less developed regions opens up for the opportunity of synergies in rural development and nature conservation. In these regions, nature conservation could be developed with benefits to local citizens through e.g. increased nature tourism and a sustainable agriculture.

5. Conclusions

The present study shows that spatial distribution pattern of barn owls in Poland correlates with climate, land-use, road density and light pollution, which confirms numerous previous findings. Importantly, the barn owl distribution is also explained by local socio-economy factors: unemployment, the proportion of elder citizens, commune income per citizen, the share of citizens with high education and share of farmers among working population. We, therefore, conclude that social and economic characteristics of local societies should be more often considered as drivers of biodiversity patterns in human dominated landscapes, while the mechanism behind these correlations and its consequences need further investigations.

CRediT authorship contribution statement

Michał Żmihorski: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Marek Kowalski:**Investigation.**Jan Cichocki:**Investigation.**Sławomir Rubacha:**Investigation.**Dorota Kotowska:**Writing - original draft, Visualization.**Dominik Krupiński:**Investigation.**Zuzanna M. Rosin:**Writing - original draft.**Martin Šálek:**Writing - original draft.**Tomas Pärt:**Conceptualization, Writing - original draft, Writing - review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

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