The role of churches in maintaining bird diversity: a case study from southern Poland

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Abstract

With the human population increasing there have been losses in biodiversity. A common feature of mankind is religious beliefs with various associated positive and negative consequences for biodiversity. Religion also has associated religious sites, many of which have a long history. The role of churches in benefitting biodiversity has not received attention. To examine the impact of churches we measured the taxonomic, phylogenetic and functional diversity of birds around Christian churches and compared this with matched farmsteads. We surveyed 101 churches and equal number of farmsteads in villages of southern Poland. We measured structural and compositional characteristics (e.g. number of trees, shrubs, number of buildings and height) at both churches and farmsteads. General additive models, ordination and rarefactions methods were used in data analysis. Species richness, abundance and phylogenetic diversity were each higher at churches than at farmsteads. The species composition differed between building types but functional diversity was similar at both types of buildings. Bird species richness and abundance were correlated with the church's age. Previous studies showed village farmsteads supported high species diversity, thus our current findings that churches are richer show they may increase bird diversity in studied villages. We suggest that the green surroundings and tall towers create strong environmental gradient that enhances species richness, functional and phylogenetic diversity. There are over ten thousand churches in Poland, and similar places of worship are present in many religions, thus this habitat may be important for sustaining local taxonomic, functional and phylogenetic biodiversity in different global areas.

Key words: Christianity, Culture, Ecosystem Services, Evolution, Religion

1. Introduction

Current human activity leads to habitat loss, land degradation, pollution, urban sprawl and the spread of invasive species, which collectively heavily impact biodiversity (McKee et al. 2003, Cardinale et al. 2012, Miraldo et al. 2016, Waters et al. 2016). Some species can adapt to these highly modified environments living alongside humans, while other species are unable to adopt to use such artificial landscapes (Erwin 2008, Parhar & Mooers 2011, Miraldo et al. 2016). With perishing species the unique biotic features and links with other species are lost (Barnosky et al. 2011). Thus, the biodiversity loss may diminish functional and phylogenetic diversity (Barnosky et al. 2011, Pimm et al. 2014).

The scientific community has sought to identify processes lying behind the worldwide decline of biotic diversity and means to stop them (Sutherland et al. 2009, Pimm et al. 2014). However, much less attention has been paid to the understanding of the opposite phenomenon: human alterations to ecosystems that prove to have benefits for biodiversity. Some man-made landscape transformation have offered alternative new habitats for several species with local high species diversity and functional complexity (Lenda et al. 2012, Moroń et al. 2014, Maclagan et al. 2018). As a consequence in highly modified regions a substantial proportion of biodiversity may be associated with these modern landscapes (Martínez-Abraín & Jiménez 2016). Conservation and management may need to be adjusted to these specific conditions.

Traditional cultural landscapes of Europe have centuries-long evolution as tightly coupled social-ecological systems (Plieninger & Bieling, 2012, Fischer et al., 2012). In such landscapes the ecosystem services are co-produced by environmental friendly (often traditional) agricultural and forestry practices and rich natural capital. This results in ecosystems and landscapes with outstanding biodiversity, commonly referred as high nature value landscapes (Hartel et al. 2013, 2014). For instance, traditional villages were identified as hot-spots of bird diversity in agricultural systems in Central Europe (Rosin et al. 2016, Šálek et al. 2018). Thus, long-term survival of different species together with their functional and phylogenetic diversity is now strictly associated with human culture and infrastructure development (Rosin et al. 2016, Šálek et al. 2018).

Religious beliefs are a universal feature of human culture across the globe (Botero et al. 2014). The relation between faith, religious groups and wildlife has become a growing research topic with the prospect of enhancing future nature conservation (Palmer & Finlay 2002, Wild & McLeod 2008, Frascaroli 2013, Shepheard-Walwyn & Bhagwat 2018). Religion may contribute to nature conservation in two major ways: indirectly by influencing attitude of people towards nature or directly by enforcing protection of areas that are devoted to the spiritual cult (Dudley et al. 2009, Frascaroli 2013). The latter can be important as the conservation benefits of sacred sites have been documented in several religions (Dudley et al. 2009). For example, sacred natural sites in Ethiopia (Reynolds et al. 2017), Italy (Frascaroli 2013), Greece (Avtzis et al. 2018) have been identified as important for the conservation of animal and plant species. Plant species richness was higher at Tibetan scared sites than at randomly chosen sites in mountains of Northwest Yunnan (Anderson et al. 2005), while supplemental feeding used as religious practice in such sites increased reproductive performance of the endangered and endemic buff-throated partridge *Tetraophasis szechenyii* (Yang et al. 2016). Unlike in Asia and Africa, in Europe the link between religion and nature has being remaining underexplored, perhaps because some view Christianity as anti-naturalistic (Frascaroli 2013).

In the European tradition, Christian churches are often cultural as well as religious centres, especially in rural areas, and for that reason are surrounded by special care, worship and regularly persist for centuries, often through political conflicts and wars (Frascaroli 2013, Klima 2011). Many churches are historic buildings that are closely related to the cultural heritage of the village and surrounding locations (Bartnik 1987). Churches are usually located centrally in a location, differ from other buildings as churches are usually the largest and tallest man-made structures in a village. Therefore, churches are sites with strong environmental gradient consisting of tall "rocks" and a green surrounding with several vegetation layers. Such strong gradient of conditions may increase available niches and boost species diversity (Amarasekare 2003, Nord & Forslund 2015). Moreover, due to consistent management, the structural complexity at churches is long-persisting thus may serve as suitable persistent environments for many taxa. The structure of the church buildings (high towers, holes) and churchyards (numerous trees and shrubs) can be refugia for different taxa. Although in landscapes of Europe churches are a distinctive and common landscape feature, there is no work showing their natural role for bird communities. They are, therefore, a good subject to study the relationship between religious-cultural heritage and natural values.

The aim of this study is to understand the associations between sacral buildings – Christian churches with their surrounding - and taxonomic, phylogenetic and functional diversity of bird communities in Poland. Birds are group well known in term of biology, phylogeny and functional traits and are good indicators of environmental health (Gregory et al. 2005, Skórka et al. 2013). The relatively high species richness of Polish rural landscape, resulting from extensive agriculture and land-use heterogeneity (Tryjanowski et al. 2011) provide the opportunity to track the responses of a wide diversity of bird species. First, we correlated taxonomic, phylogenetic and functional diversity of bird communities at churches and churchyards with characteristics of these objects, to identify main drivers of multilevel bird diversity in sacred buildings. Next, we related bird communities found at churches to those occurring at agricultural farmsteads (village buildings and their yards) – known to be remarkably rich in bird species within rural habitats (Rosin et al. 2016, Šálek et al. 2018). We hypothesized that churches have similar or higher abundance and number of species than farmsteads, both at local spatial scales, but also when species turnover among sites is taken into account. Furthermore we could examine whether bird communities at churches are taxonomically, phylogenetically and functionally more diverse than bird communities at farmsteads. We expected that because churches are buildings with more complicated structure and have a different and more developed vegetation in their surrounding than farmsteads. These features should increase bird diversity indices at churches compared with farmsteads. We also compared qualitative and quantitative composition of bird communities at churches with those at farmsteads.

2. Material and methods

2.1. Study area

This study was performed in southern Poland in 2016 (Fig. 1). This region is dominated by extensive agriculture; all surveyed sites were located in villages surrounded by open landscape, dominated by arable fields (mainly potatoes, cereals, cabbage) with low (<10%) proportion of permanent grasslands and midfield woodlots. We selected 101 churches and the same number of farmsteads. We consider churches as the area with a Christian temple and its surrounding delineated by a fence which both constitute a functional unit where people gather, pray and worship (Fig. S1 in Supplementary material 1). Mean distance between nearest churches was 3836 m. The criterion of selection was that the church was located within the village. Rural reference farmsteads were selected within a radius of 200 meters from the church so removing the role of differences in landscape composition confounding analyses of differences in bird species number and composition between the two types. In this study farmsteads were defined as in Rosin et al. (2016): they were village residential buildings, their yards and other structures therein (e.g. shed, stable) used for agricultural production, and delineated by a fence (Figs S1-S8, Supplementary material 2). Farmsteads did not include open farmland usually located outside villages. The relative location of farmsteads to churches was randomly distributed (Fig. S2 in Supplementary material 1). We choose to compare churches with farmstead because both represent similar habitats within villages. Churches and farmstead are composed of buildings and neighbouring yards and they are delineated by a fence. Farmsteads are a building type prevailing in Polish villages and they were identified as a habitat with the highest bird species richness and abundance compared to other building types in villages (Rosin et al. 2016). Thus, the comparison between churches and farmstead is very conservative in terms of finding possible differences in diversity indices and species composition, and this comparison is not as commonplace as the relating bird communities at churches with very different habitats such as open fields, grasslands or forests.

2.2. Bird surveys

Bird counts were performed twice in a season in all 202 sites (101 churches and 101 farmsteads). The first survey was in the period between 15th April and 15th May; the second survey was between 16th May and 15th June. Counting started from just after dawn (one hour after sunrise) until 11 a.m. local time. When counting birds an observer slowly walked around the church or farmstead and noted all birds that resided in the building and its surroundings. The area of church and farmstead was delineated by fence (a typical feature of every property in the study area, Fig. S1 in Supplementary material 1). Each survey at one church or farmstead lasted for 10 minutes. Surveys were done during good weather (no rain and wind below Beaufort scale 3).

2.3. Measuring habitat variables

For each location (church or farmstead) we noted its area (encompassed by a fence, Fig. S1 in Supplementary material 1). In case of churches we measured several additional parameters that were later correlated with bird abundance and diversity: age, number of trees (including their age category), number of shrubs. For each church we determined whether it was built from brick or wood, its height (m), the number of towers, presence of a separate bell tower, presence of rectory within a church and the extent of the property area that was concreted (in %). Number of church renovations in past 10 years was noted. Moreover, for each church we noted distance to the nearest town (> 10 000 inhabitants) and village human population size (retrieved from: https://bdl.stat.gov.pl/BDL/start). For farmsteads we also noted structural composition similarly to churches but we did not relate these variables with bird data in this paper.

2.4. Data handling

We used six measures of bird diversity, calculated separately for each among 202 local bird communities: two related to taxonomic diversity, one connected with phylogenetic diversity and three related to functional diversity. We omitted owls from our analyses because we did not perform dedicated surveys to detect these nocturnal species.

Taxonomic diversity was expressed as species richness (SpecRich) and total abundance (Abund). The latter is important for functional diversity as well (Magurran 2004). Species richness and abundance were expressed as the maximal number (over two surveys) of recorded bird species and individuals at each site.

In order to understand bird communities in terms of phylogenetic diversity, we used the mean phylogenetic distance between taxons (PhyloDist) score as a measure of the species uniqueness (Frishkoff et al., 2014, Isaac et al., 2007). The advantage of this index is that it is usually weakly dependent on the number of species (Fig. S3 in Supplementary material 1). The bird phylogenetic tree (Jetz et al. 2012) was created in nexus format online (http://birdtree.org; see Fig. S4 in Supplementary material 1) and was used to calculate PhyloDist via package "picante" (Kembel et al. 2010) in R (R Core Team 2017).

The biodiversity metrics based on species-trait approaches are focused on functional aspects of biodiversity (de Bello et al., 2010). In this study we used functional richness (FuncRich), functional evenness (FuncEven) and functional divergence (FuncDiverg) calculated using the avian traits that relate to species function in the ecosystem based on life-histories, foraging, breeding and dispersal ecology (Huang et al., 2015, Morelli et al. 2017). FuncRich, FuncEven, FuncDiverg are much more sensitive to community assembly rules than species richness (Mouchet et al. 2010). The traits table used for the calculations consisted of 14 variables (see Table S1 in Supplementary material 1 for list of variables with considered levels for each): brain mass, body mass, maximum lifespan, age at first reproduction, sexual dimorphism, incubation time, clutch size, number of broods per year, mode of development, food categories, foraging microhabitat, nesting microhabitat, migration mode and sociality during the breeding period. Mode of development, food categories, nesting habitat, migration mode, sociality were all coded as categorical binary variables (e.g. whether colonial was coded as either as 0 or 1). This enabled us to include in analyses some plasticity in traits (e.g. the great tit *Parus major* breeds both in tree holes and various man-made structures). Functional richness (FuncRich) was represented by the volume of multidimensional functional space occupied by a species assemblage (Villéger et al., 2008). Functional evenness (FuncEven) describes regularity of the distribution of species abundance in the volume of traits. Functional divergence (FuncDiverg) measures how abundances tend to be on the outer margins of the functional space while controlling for functional richness (Villeger et al. 2008, Mouchet et al. 2010). High levels of functional divergence will be associated to a high degree of niche differentiation among species within communities; the most abundant species are very dissimilar and weakly compete. Functional traits calculations were weighted by species abundance. Functional diversity indices were calculated using the 'FD' package for R (Laliberté et al., 2015).

2.5. Statistical analysis

First, we correlated variables describing environment and structure of churches and the six bird diversity indices (SpecRich, Abund, PhyloDist, FuncRich, FuncEven and FuncDiverg). For this purpose we used generalized additive models (GAM) implemented in the "mgcv" package (Wood 2006) in R (R Core Team 2017) with Poisson (SpecRich), negative binomial (Abund) and Gaussian (remaining indices) error distribution. In the GAMs longitude and latitude were fitted as the interaction of regression splines to control for the spatial autocorrelation of the data, so part of the variation of response variable is being explained by geographical location. The area of studied churches was introduced and fitted with a regression spline to account for possible nonlinear species-area relationships.

Next, we compared the six measures of bird diversity between churches and farmsteads. Generalized additive mixed models (GAMMs,) were used for the comparison but in these GAMMs village identity was introduced as a random factor (fitted with ridge penalty spline). All remaining model parameters were the same as in GAMs. We also performed above GAMMs that included distance to the nearest town and village human population size to test if differences between churches and farmsteads are consistent across the rural-urban gradient.

We compared bird composition and abundance occurring in farmsteads and churches. For this purpose we used detrended correspondence analysis (DCA) implemented in the "vegan" package (Oksanen et al. 2013) in R. Using the permutation test, we checked whether the distribution of loadings of particular counts along the first two DCA axes differed between churches and farmsteads, which would indicate different bird communities in these two habitats. We also compared structural (number of buildings, trees, shrubs, presence of gardens etc.) and functional complexity (number of farm animals, number of cats and dogs) between farmsteads and churches. For this purpose we used the analysis of similarity (ANOSIM), analysis of percentages (SIMPER) and DCA implemented in the "vegan" package (Oksanen *et al*. 2013) in R. We also used chi-square test to check if the frequency of churches with records of cats and dogs differ from farmsteads. We identified species characteristic for churches (and farmsteads) by using indicator species analysis implemented in “indicspecies” package (De Caceres & Legendre 2009) in R. The statistical significance of association between species and habitat type was achieved via 999 permutations. Finally, we also scaled up the variation in alpha taxonomic diversity for both churches and farmsteads, and calculated a rarefied gamma diversity (i.e. species richness pooled across sites). We used a sample-based rarefaction accompanied by 95% confidence intervals (CIs) computed in the ‘iNEXT’ package (Hsieh et al. 2016) in R.

3. Results

We recorded 5,687 individuals of 75 bird species in churches and farmsteads combined (Table S2 in Supplementary material 1). In churches, 68 species were recorded, with 50 in farmsteads. The most common species was house sparrow *Passer domesticus*, with 728 individuals followed by starling *Sturnus vulgaris* with 527, and jackdaw *Corvus monedula* with 395. The structure of dominants, however, differed between churches and farmsteads (Table S2 in Supplementary material 1). Sixteen species were represented by a single individual. Churches also differed structurally and functionally from farmsteads (ANOSIM: R statistic = 0.396, $p = 0.001$), especially in respect to the building age, height, presence of farm animals and number of trees and shrubs (Fig. S5 in Supplementary material 1).

In churches, bird diversity was associated with several architecture characteristics (Table 1). Species richness and abundance were significantly higher in old churches but these indices were lower in wooden churches (Table 1, Fig. S6 in Supplementary material 1). Number of trees and the number of shrubs weakly positively correlated with bird abundance and functional divergence, respectively (Table 1). Height of the church positively correlated with bird abundance, phylogenetic diversity, functional richness and functional divergence (Table 1). Presence of a separate bell tower was positively associated with bird species richness and bird abundance (Table 1, Fig. S6 in Supplementary material 1). Cover of concreted area was negatively correlated with phylogenetic diversity (Table 1). Occurrence of church renovations in previous 10 years had no effect on species richness, abundance nor phylogenetic diversity but it was negatively associated with functional richness (Table 1).

As compared to farmsteads, churches hosted significantly higher number of species and abundance of birds (Fig. 2, Table 2). Mean phylogenetic distance was also higher at churches than at farmsteads (Fig. 2. Table 2). However, indices of functional diversity (functional richness, functional evenness and functional divergence) were similar at churches and at farmsteads (Fig. 2, Table 2). All these differences remained significant if we included the proximity of towns and village population size (Table S3 in Supplementary material 1).

The DCA showed that the bird community surrounding churches was significantly different from that recorded at farmsteads: the two clouds of points representing the two habitats showed little overlap (Fig. 3). Thirteen species were present just in churches while eight species were present just in farmsteads (e.g. grey wagtail *Motacilla cinerea*, grey partridge *Perdix perdix*). Indicator species analysis showed that seven species were characteristic of churches: swift *Apus apus* (estimate = 0.773, p = 0.001), house martin *Delichon urbicum* (estimate = 0.575, p = 0.001), blackcap *Sylvia communis* (estimate = 0.451, p = 0.002), common redstart *Phoenicurus phoenicurus* (estimate = 0.407, p = 0.002), spotted flycatcher *Muscicapa striata* (estimate = 0.403, p = 0.003), feral pigeon *Columba livia f. domestica* (estimate = 0.375, p = 0.011) and short-toed treecreeper *Certhia brahydactyla* (estimate = 0.270, p = 0.050). None of species was selected as the indicative species in this analysis for farmsteads.

The two types of building compared were also different in term of species turnover among sites, which was higher in case of churches. Consequently, expected cumulative number of species was significantly higher for churches as compared to farmsteads (confidence intervals for these two curves did not overlap; Fig. 4). Moreover, rarefaction curves for churches and pooled data (i.e. churches and farmsteads pooled) had very similar slope, thus suggesting high dissimilarity of bird assemblages among different churches.

4. Discussion

This study shows that churches may be sites that increase local bird diversity in villages of southern Poland. The tall and old churches, with separate bell towers, host the highest bird diversity. These results correspond with earlier findings that churches may provide good breeding sites for some bird species, such as barn owl and common kestrel (Gorczewski et al. 2007). .Moreover, bird assemblages found at churches are distinct as compared to those found in farmsteads and are richer in species, whether measured as alpha or gamma diversity. Farmsteads have been recently identified as a habitat with the highest number of bird species in villages (Rosin et al. 2016) but churches were not included in that analysis. Our results suggest that churches may be sites with local high bird diversity in rural landscapes; their value may be even more important since there are over 10 000 churches in Poland (Klima 2011).

4.1. Factors affecting bird diversity at churches

Not all churches, however, are equally good for birds and several structural components of a church and its surrounding are correlated with bird diversity indices. Species richness and abundance increased with age of a church, which is most likely caused by increasing number of nesting cavities. Moreover, older churches are usually historical buildings, thus are often under legal protection, which constrains renovations and modifications. Many adjacent trees to these churches are equally old and sometimes formally protected as natural monuments; such ancient trees are important for providing nesting locations, especially holes (Cockle et al. 2011). Conversely, some old churches are made of wood that is negatively associated with bird species richness (lack of species preferring rock-like habitats). Moreover, very old churches are usually not as tall as those built in the 20th century that perhaps may reduce importance of very old objects for birds. Height of a church positively affected abundance, phylogenetic diversity, functional richness and functional divergence with latter indicating that most abundant species occur at the extremities of the functional character range (Mason et al. 2005). Churches are typically the tallest buildings in a village (Supplementary material 2). Several bird species from different families prefer such tall structures, especially the common kestrel *Falco tinnunculus,* jackdaw *Corvus monedula,* swift *Apus apus* and feral pigeon *Columba livia* and some of these species may breed colonially, which makes them the dominant species at some churches. Colonial species may also explain positive effect of church height on functional divergence. Also, the presence of separate bell tower, which is usually tall, was positively linked with species richness and abundance. Species especially the common house martin, feral pigeon and wood pigeon *Columba palumbus* used this structure to locate their nests therein. Separate bell towers are usually closed for people thus provide undisturbed nesting locations.

The number of trees increased the abundance of birds. Trees provide nesting sites (holes, branches), shelter and foraging ground for many birds such as tits, woodpeckers and treecreepers (Snow & Perrins 1998). The number of shrubs weakly positively correlated with functional divergence. Increasing functional divergence suggests a higher degree of niche differentiation (Mason et al. 2005) and lower resource competition between birds occurring at churches with abundant shrubs. It is possible that that dense shrubs may increase abundance of dominant species that have specific functional features (e.g. they forage and breed mostly in shrubs) and thus increase the value of the index at churches. Interestingly, church renovations had statistically non-significant effect on species richness, abundance nor phylogenetic diversity but was negatively associated with functional richness. Also, cover of concreted area around churches was negatively correlated with bird phylogenetic diversity. Church renovations are usually associated with the increase of the cover of concreted area around these buildings. This indicates that church renovations may be disadvantageous for bird species with unique evolutionary histories and features. For example swifts and kestrels often disappear from renovated buildings if holes in walls or roofs are bricked over (Sumasgutner et al. 2014, Shaub et al. 2017).

4.2. Taxonomic, phylogenetic and functional diversity

We used several biodiversity indices, because conservation of biodiversity is fundamentally about the maintenance of living variation, at all levels from genes to ecosystems. It is therefore important to evaluate several aspect of diversity, not just species lists. In our data phylogenetic and functional diversity are moderately or weakly linked with species richness and abundance thus suggesting that species-rich sites do not have to be rich in term of functions and phylogeny (Fig. S3 in Supplementary material 1).

We demonstrated that bird communities at churches were more phylogenetically diversified than those at farmsteads. This indicates that bird species associated with churches represents often different evolutionary histories, most probably because fairly different habitats are available in churches (e.g. ‘rocky’ towers and forest-like groups of old trees). These habitats are inhabited by species from different bird orders (Apodiformes, Columbiformes, Falconiformes largely occupy towers while Piciformes and Passeriformes are mainly associated with trees). Phylogenetic diversity is more linked with functional diversity than species richness (Forest et al. 2007). However, we found that functional diversity indices at churches were as high as at farmsteads. High functional diversity is important because studied churches are located in rural landscapes. Studied villages were mostly inhabited by farmers and high bird functional diversity provides various ecosystem services, such as pest control, seed dispersal and nutrient cycling (Zhang et al. 2007, Raffaelli & Frid 2010, Skórka et al. 2013).

Considering role of churches in conservation of birds in southern Poland one should also evaluate possibility that churches are ecological traps. However, we think this is unlikely. First, diversity of birds increased with age indicating there is temporal stability in environmental conditions (Fjeldsaå & Lovett 1997). Second, we observed only 12 cats at 12 churches but we observed 28 cats in 23 farmsteads ($\chi^2 = 4.182$, df = 1, p = 0.041). Cats are major bird predators (Krauze-Gryz et al. 2016). We observed 39 dogs at 35 churches and 85 dogs at 61 farmsteads ($\chi^2 = 13.419$, df = 1, p < 0.001). This suggests that the predatory pressure and disturbance are lower at churches than in farmsteads.

4.3. Religion and conservation of biodiversity

Studies show a relationship exists between biological diversity and cultural diversity (e.g. Sutherland 2003, Pretty et al. 2009, Martin et al. 2016). A greater involvement of religious communities in the conservation discourse, and a greater inclusion of conservation issues in religious ethics, could be beneficial for biodiversity (Mikusiński et al. 2014). Religion can also improve biodiversity by providing ethical and social models for living respectfully with nature (Negi 2005, West et al. 2006). Our findings suggest a role of local pastors in sustaining biodiversity values at churches and their surroundings in southern Poland. Providing advice based on evidence-based conservation (e.g. Sutherland et al. 2018) interpreted for local conditions would seem a clear conservation priority. This could assure more biodiversity-friendly management of the church and surroundings. Workshops targeting parish-rectors about the value of sacred places for biodiversity conservation could also be valuable. Furthermore with 90% of Polish citizens declared Catholics and a widespread tradition of attendance at church (Klima 2011) there is also the opportunity to increase ecological knowledge among people.

New churches are being still often built, older are reconstructed or renovated. Thus, we suggest that tradition of building high towers and separate bell towers was kept as this seems to positively affect birds and may create unique value of churches as the landmarks in agricultural landscapes of southern Poland. At newly constructed churches planting trees and shrubs at the expense of concreted places are recommended to increase bird diversity. However, our study is geographically limited thus relating our findings and recommendations to other regions and countries should be done with caution. Moreover, we compared churches with just farmsteads. In order to better evaluate the importance of churches for biodiversity, comparisons with other habitats (e.g. parks, woodlands, fallows, orchards) and building types (e.g. single houses, other temples) across range of different landscapes are necessary in future studies. We believe that our case study presents results that may encourage more thorough research at larger scales on the role of sacred sites and religious beliefs in sustaining biodiversity in different parts of the world.

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Tables and figures

Table 1. The effect of environmental variables on bird diversity components at churches. GAM estimates of function slopes with standard errors (in brackets) are presented. Explanations: SpecRich – species richness, Abund – number of individuals, PhyloDist – mean phylogenetic distance, FuncRich– functional richness, FuncEven – functional evenness, FuncDiverg –functional divergence. Statistically significant effects are emboldened: *** - P <0.001, ** - P <0.01, * - P <0.05, ‘ – P < 0.10.

	Response variables					
Explanatory variables	SpecRich	Abund	PhyloDist	FuncRich	FuncEven	FuncDiverg
Intercept	**3.44 (0.39)*** **	**3.85 (0.57)*** **	**106.01 (18.88)*** **	33.47 (25.57)	**0.43 (0.17)***	**0.83 (0.13)*** **
Number of species	Not included	Not included	Not included	**2.13 (0.45)*** **	Not included	Not included
Construction year	**-0.0004 (0.0001)** **	**-0.0004 (0.0002)’**	-0.007 (0.008)	-0.009 (0.011)	0.00004 (0.00008)	-0.00002 (0.0006)
Material:wood	**-0.20 (0.11)’**	**-0.29 (0.16)’**	-1.84 (5.05)	3.54 (6.12)	0.01 (0.04)	0.04 (0.03)
Number of towers	0.04 (0.03)	-0.002 (0.045)	**2.64 (1.48)**’	2.35 (1.77)	-0.001 (0.014)	0.003 (0.010)
Separate bell tower: yes	**0.10 (0.06)’**	**0.17 (0.08)***	1.36 (2.62)	2.60 (3.8)	-0.012 (0.024)	0.008 (0.018)
Max. height	0.0007 (0.0029)	**0.011 (0.004)** **	**0.33 (0.14)***	**0.30 (0.16)’**	0.0001 (0.0004)	**0.002 (0.0004)***
Concreted area	-0.004 (0.003)	-0.002 (0.005)	**-0.36 (0.15)***	-0.16 (0.18)	0.001 (0.001)	-0.0005 (0.0018)
Number of trees	0.001 (0.002)	**0.004 (0.002)’**	0.01 (0.08)	0.07 (0.10)	-0.0003 (0.0008)	-0.003 (0.005)
Shrubs	0.0004 (0.0006)	-0.0007 (0.0009)	-0.03 (0.03)	-0.06 (0.04)	-0.0003 (0.0003)	**0.0004 (0.0002)’**
Church renovation	0.02 (0.06)	0.08 (0.08)	-1.82 (2.59)	**-5.45 (3.06)’**	0.38 (0.24)	-0.026 (0.018)
R^2_{adj} (%)	43.8	43.6	11.7	44.0	17.3	14.0

Table 2. The formal tests (GAMM) comparing bird diversity components at churches and farmsteads. Area of each building was included as a spline to control for the effect of area. Pair of buildings (a church and farmstead) in a village was assigned as random factor (modeled as the ridge penalty spline). Number of species was included as a covariate in GAMM for functional richness (FuncRich). Explanations: SpecRich – species richness, Abund – number of individuals, PhyloDist – mean phylogenetic distance, FuncRich – functional richness (square root transformed), FuncEven – functional evenness, FuncDiverg – functional divergence.

Explanatory variables	Intercept	SR	Building type: Church	s(Area)
SpecRich	3.14 (0.22)***	Not included	0.39 (0.04)***	Df=1.87***
Abund	3.80(0.27)***	Not included	0.50 (0.05)***	Df=1.86***
PhyloDist	103.53 (4.98)***	Not included	16.42 (2.03)***	Df=1.10
FuncRich	25.26 (9.37)***	2.00 (0.38)***	3.44 (3.28)	Df=1.00
FuncEven	0.54 (0.06)***	Not included	-0.002 (0.02)	Df=1.00
FuncDiverg	0.71 (0.01)***	Not included	0.01 (0.01)	Df=1.00

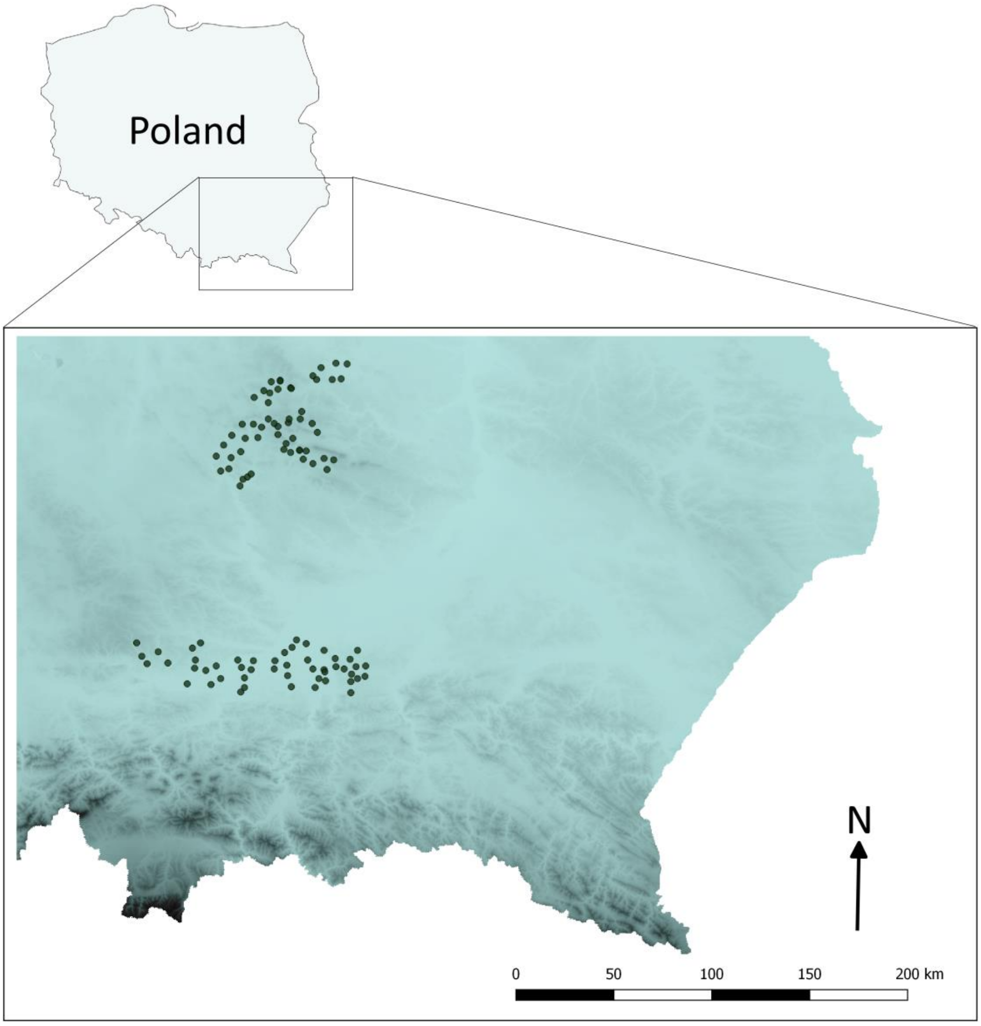

Fig. 1. Map of the study area. Dots indicate studied objects (pairs of church and farmstead).

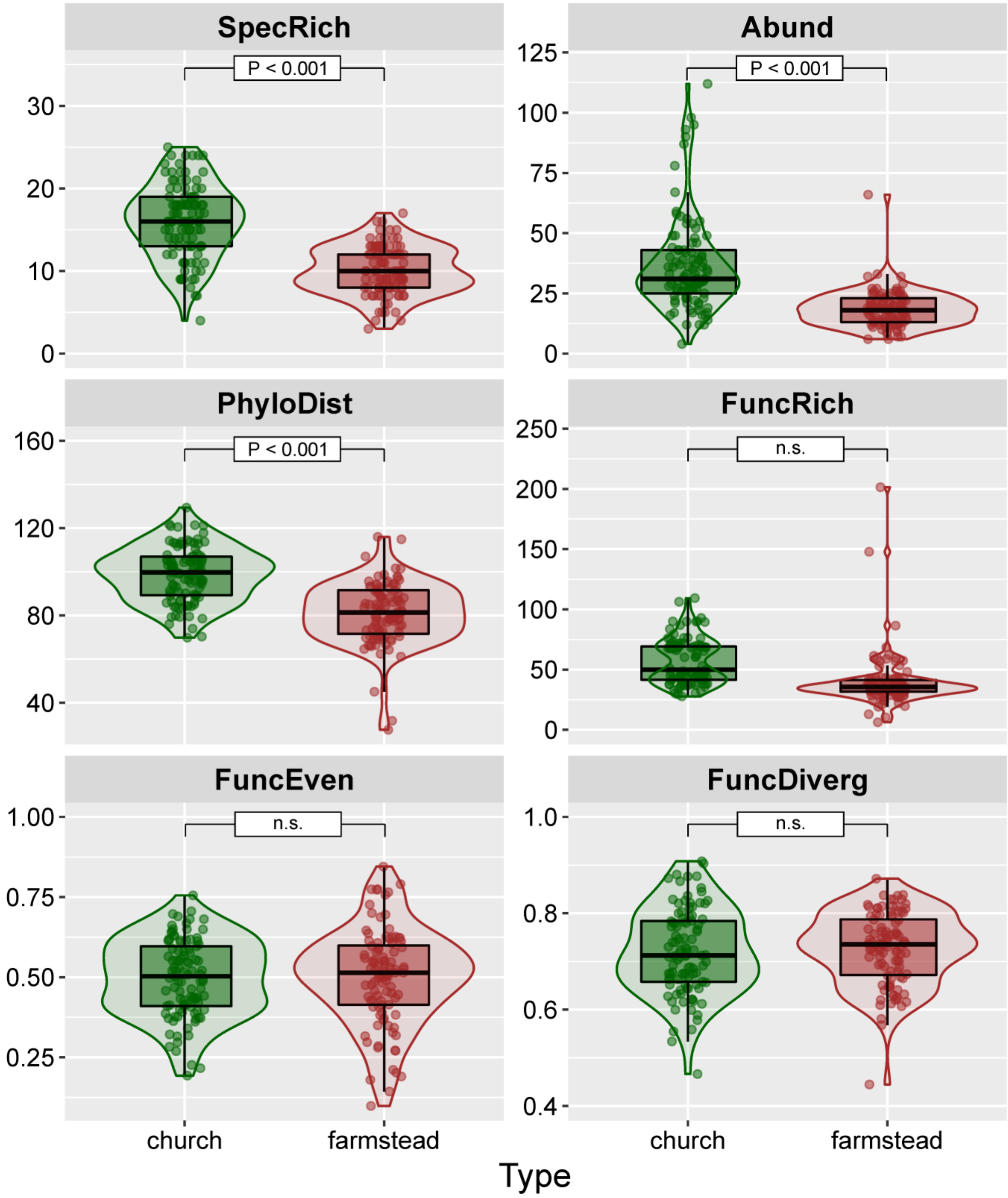

Fig. 2. The comparison of bird diversity indices between churches and farmsteads: SpecRich – species richness, Abund – number of individuals, PhyloDist – mean phylogenetic distance, FuncRich – functional richness, FuncEven – functional evenness, FuncDiverg – functional divergence. Boxplots show medians with 2nd and 3rd quartile. Density of points is also shown. Results of general additive mixed model controlling for spatial autcorrelation and area (and species richness in case of FuncRich). Explanations: n.s. – statistically non-significant difference.

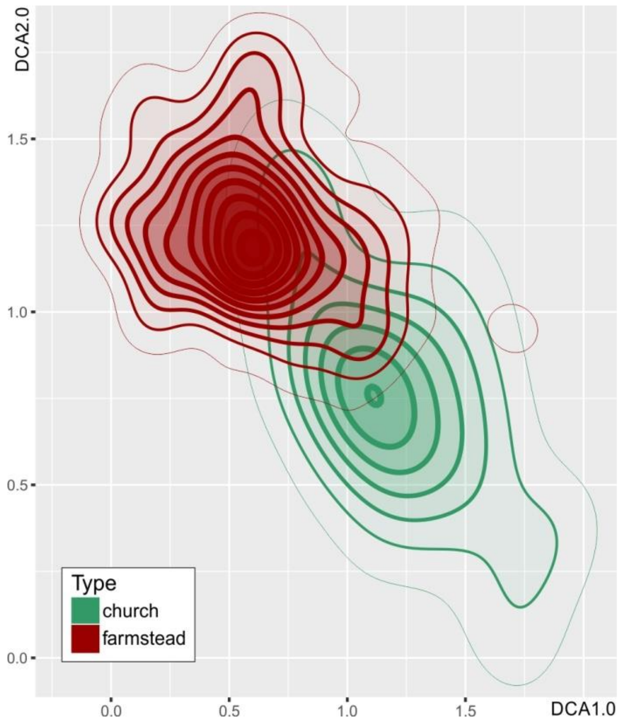

Fig. 3. Dissimilarities between bird communities at churches and farmsteads depicted via kernel density estimations of site-specific scores of species along the two first axes of DCA.

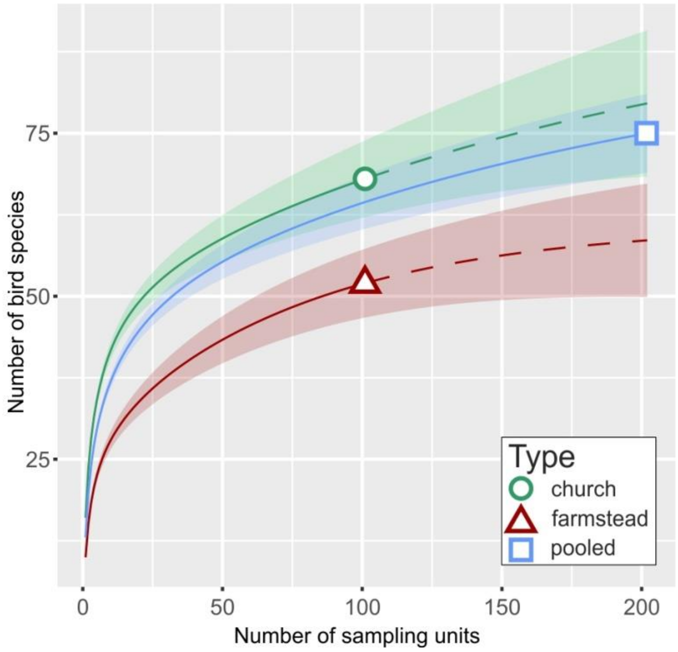

Fig 4. Sample-based rarefaction curves (with 95% confidence intervals) for number of species at churches and farmsteads. Pooled rarefaction is also shown.