The effect of stand-level habitat characteristics on breeding bird assemblages in Hungarian temperate mixed forests

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Abstract: The effects of stand structure, tree species composition, proportion of habitat types and land use history on breeding bird assemblages in temperate mixed forests in Western Hungary were studied. The species richness, the abundance and the composition of the whole breeding bird assemblage and of some groups formed on the basis of nesting site and rarity were examined. Stand structural variables had the highest impact on the breeding bird assemblage, while tree species composition, the varying proportion of vegetation types and land use history had no significant effect. In the case of the species richness, the abundance and the composition of the whole assemblage, the most important variables were the mean diameter of trees, the vegetation cover of the forest floor and the dead wood volume. The explained variance in the linear models of different groups varied between 20% and 60%, and the relative importance of these three variables also differed considerably. These results indicate that forest management may considerably influence the diversity and the composition of birds, as all the structural elements affecting birds deeply depend on it. Within the shelterwood management system, the elongation of the rotation and regeneration periods, and the relatively high proportion of retention tree groups after harvest could contribute to the conservation of forest birds. Our results also showed that for the forest bird communities, both the prevalence of big trees and the presence of a dense understory layer are important. Management regimes which apply continuous forest cover might be more appropriate for providing these structural elements simultaneously on small spatial scales, and for the maintenance of a more diverse bird community, thus healthier forest ecosystems.

Nomenclature: Hagemeier and Blair (1997) for birds.

Abbreviation: DBH–Diameter at the Breast Height

Introduction

The effects of management-related habitat variables (e.g., structural and compositional characteristics) on bird assemblages are widely studied. There is a lot of interest in the conservation of birds, as they are especially popular, relatively easy to detect and very sensitive to the quality of their habitats (Fuller 1995). As a result, studies of birds are widely used for creating habitat indices to follow up the quality of numerous habitat types and to monitor the effects of their management (Gregory and van Strien 2010). However, the relationships between stand-level forest characteristics and birds are mostly explored in the boreal and hemiboreal zones of Europe (e.g., Virkkala and Liehu 1990, Jansson and Angelstam 1999, Mikusinski et al. 2001, Rosenvald et al. 2011). With the exception of a few analyses (e.g., Moskát et al. 1988, Moskát 1991, Moskát and Waliczky 1992), the studies from the temperate zone mainly focus on the Atlantic region (Donald et al. 1998, Hewson et al. 2011), where both forest cover (Food and Agricultural Organisation of the United Nations, 2009) and forest naturalness (e.g., Mikusinski and Angelstam 1998)

are lower than in Central Europe, so the main factors limiting bird assemblages are probably also different. A sad actuality of our study is that - according to The Pan European Common Bird Monitoring Scheme - forest indicators, based on population changes of common forest birds, show a definite decline in most European regions (EBCC 2015).

Most forest bird species use a relatively small area (less than 1 ha) for feeding and sufficing their needs in the breeding period (Fuller 1995). Thus, it seems obvious to study bird-environment relations at a local scale as well. The results of such studies are well applicable for forest conservation practice, as the size of the management units typically fits to this scale. However, there is an ongoing debate among conservation biologists on whether landscape-level (Mitchell et al. 2001, Loehle et al. 2005, Mitchell et al. 2006) or stand-level (Hagan and Meehan 2002, Poulsen 2002) variables are more important for forest bird assemblages. The answer is inconsistent, and the comparison of landscape and stand-level effects is difficult as in most of the studies, rough landscape variables are available from a coarser level, while the more detailed compositional or structural variables are only avail-

able from a finer stand-level. Thus, in many cases it is debatable whether the results refer to the effect of the level of the study, or to the different resolution of data.

Many studies have examined the relative importance of two main aspects of woodland habitats on bird communities: tree species composition and stand structure. Except for a few studies (e.g., James and Wamer 1982, Moskát 1988, Cushman and McGarigal 2004, Hewson et al. 2011), most of these works point out that bird assemblages are determined by habitat structure rather than tree species composition (e.g., MacArthur and MacArthur 1961, Moskát and Székely 1989, Virkkala 1991, Wilson et al. 2006, Archaux and Bakkaus 2007, Muller et al. 2010). However, the interpretation of these findings is often not easy, as structural and compositional variables are related to each other (Hewson et al. 2011). In addition, researchers usually select only a few potential explanatory variables describing the structure and composition of habitats, which makes the interpretation and the comparison of these studies difficult.

In this study, we examined the effects of stand structure, tree species composition, the proportion of different land cover types, and the land use history on breeding bird assemblages at stand-level in Central European mixed deciduous-coniferous forests. The comparatively moderate sample size (35 plots) allows for the use of relatively detailed and comprehensive explanatory variables. We hope that this versatile study approach is really suitable to explore the main factors affecting bird communities in this region, at least at the studied stand-level. We also investigated the relative importance of each examined environmental aspect for birds. Another specialty of our study is that land use history – which forms part of our examinations – is a scarcely studied aspect of the environment for birds in this region. As in this study our main purpose was to explore the relative importance of these environmental aspects for the whole breeding bird community, above all, the species richness and the abundance of birds were examined. However, for a deeper understanding of how the environmental variables affect bird communities, some groups of breeding birds were also included in the analysis. As one of the main characteristics that determines the requirements of bird species for their environment is the nesting site (e.g., Newton 1994), the species richness and the abundance of two rough categories (cavity and non-cavity nesters) based on this were examined. In addition, we expected that the needs of rare species could point out some of the main limiting factors for birds in the region, thus, the species richness and the abundance of two man-made groups (common and rare birds) were also analysed. Our study was carried out in the temperate zone of Europe, in the **highly (?)** forested Őrség region in Western Hungary. This region is especially suitable to examine the effects of the different aspects of forest quality, as it hosts a great compositional and structural variation of forests, under similar geological conditions (Tímár et al. 2002).

Methods

Study area and plot selection

The study was carried out in Őrség, Western Hungary (Fig. 1, N 46° 51'-55' and W 16° 07'-23'). In the region the elevation is 250-300 m above sea level, with the topography consisting of hills and small valleys. Annual precipitation is 700-800 mm, and mean annual temperature is 9.0-9.5 °C (Dövényi 2010). The soil is acidic and nutrient-poor in this region. Therefore, extensive forms of agriculture (such as mowing and grazing in meadows) and forestry are prevalent. Forest cover of the region is approximately 60% (Gyöngyössy 2008). The forests of the region are generally mixed, both tree species composition and stand structure show large variations among the stands (Tímár et al. 2002). The main tree species (*Quercus petraea* L. – sessile oak, *Quercus robur* L. – pedunculate oak, *Fagus sylvatica* L. – beech, *Pinus sylvestris* L. – Scots pine) occur in different proportions in the stands, and the number and the proportion of non-dominant tree species (*Carpinus betulus* L. – hornbeam, *Picea abies* Karst. – Norway spruce, *Betula pendula* Roth – birch, *Populus tremu-*
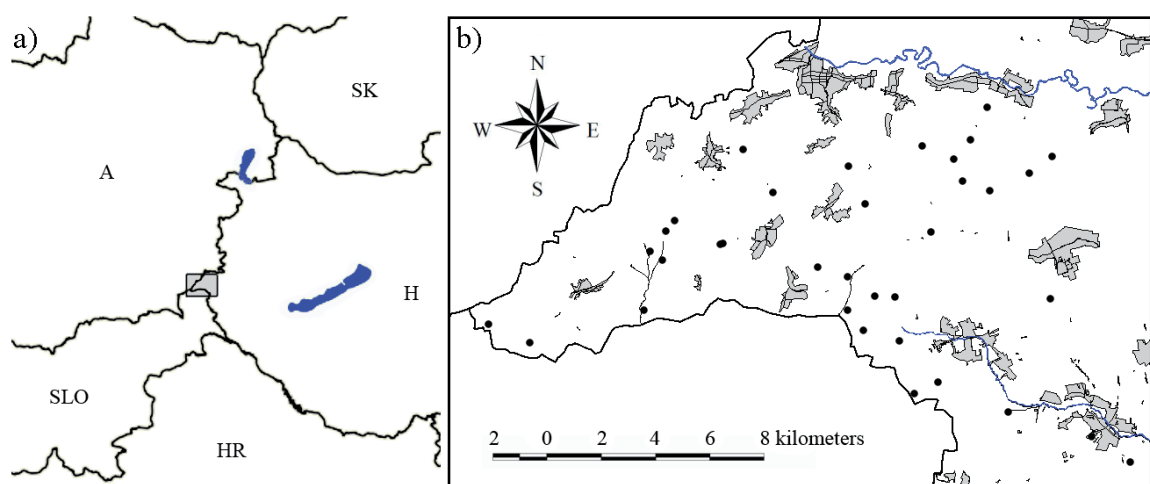
Figure 1. Geographical position of **a**) the study area in the region and **b**) the 35 plots (full circles) included in the analysis. Main rivers and lakes of the region are shown for an easier orientation. A: Austria, H: Hungary, HR: Croatia, SK: Slovakia, SLO: Slovenia.

Table 1. Potential explanatory variables included in the analyses. Proportion of habitat types and historical variables were calculated from 100 m radius circle of plots.

Explanatory variables	Unit	Mean (Min.-Max.)
Tree species composition		
Tree species richness	pc./1600 m^2	5.6 (2-10)
Tree species diversity	-	0.9 (0.2-1.9)
Relative volume of beech	%	28.0 (0.00-94.3)
Relative volume of oaks	%	36.2 (1.2-96.5)
Relative volume of Scots pine	%	26.4 (0.00-78.6)
Relative volume of spruce	%	3.3 (0.0-49.6)
Relative volume of hornbeam	%	4.0 (0.0-21.8))
Relative volume of other non-dominant trees	%	2.0 (0.0-17.3)
Stand structure		
Mean DBH of trees	cm	26.3 (13.6-40.6)
Variation coefficient of DBH	-	0.5 (0.2-1.0)
Density of all trees	stems/ha	591 (219-1319)
Volume of dead wood	m^3/ha	22.8 (1.8-78.8)
Density of shrub layer	pc./ha	952 (0-4706)
Cover of floor vegetation	m^2/ha	741 (19-4829)
Cover of soil	m^2/ha	147 (8-472)
Cover of litter	m^2/ha	9366 (7814-9833)
Proportion of land cover types		
Proportion of beech forests	%	10.5 (0.0-100.0)
Proportion of oak forests	%	12.8 (0.0-100.0)
Proportion of Scots pine forests	%	26.8 (0.0-100.0)
Proportion of spruce forests	%	5.2 (0.0-12.5)
Proportion of young (<20 yr. old) forests	%	1.1 (0.0-15.7)
Proportion of non-forested areas	%	2.2 (0.0-59.1)
Diversity of land cover types	-	1.1 (0.1-1.9)
Land use history		
Proportion of forests in 1853	%	76.6 (24.0-100.0)
Proportion of meadows in 1853	%	7.3 (0.0-40.7)
Proportion of arable lands in 1853	%	16.2 (0.0-61.3)
Management types of the plots in 1853 (forest, meadow, arable land)	factor	-

la L. – aspen, *Castanea sativa* Mill. – chestnut, *Prunus avium* L. – wild cherry, *Acer spp.* – maple species) is also high. The great variation of tree species, which makes this area so suitable for the examination of the effects of forest composition, also has phytogeographic, geographic and historical reasons. Besides the traditional selective cutting in private forests, state forests have recently been managed in a more intensive shelterwood management system with a rotation period of 70-110 years (Tímár et al. 2002). For a more detailed description of site conditions and the history of this region, see Márialigeti et al. (2009) and Király and Ódor (2008).

Thirty-five forest stands (2-15 ha) were selected for the study in a stratified random sampling design (Lepš and Šmilauer 2003). The stratification was based on tree species composition: the stands represented the main tree species (oak species, beech, Scots pine) and their combinations equally. All the selected stands were older than 70 years, located on relatively plain areas and not directly influenced by water. Selected stands were not closer to each other than 500 m, to insure spatial independence.

Environmental data collection

In every selected stand, we designated a 40 m × 40 m plot that represented the average tree species composition and the structure of the stand and was as far from the edges as possible, in order to minimise edge effects. Tree species composition and stand structure were measured in these plots in 2006 and 2007. Species identity, height and diameter at breast height (DBH) were measured for each tree with DBH thicker than 5 cm, including snags. Average diameter and length of logs, thicker than 5 cm and longer than 0.5 m were recorded. Saplings and shrubs (every individual thinner than 5 cm DBH, but taller than 0.5 m) were counted, in order to estimate shrub layer density. The absolute cover of floor vegetation (herbs and seedlings lower than 0.5 m), open soil and litter were visually estimated. To describe the area surrounding each plot, the proportion of main forest types (beech, oak, pine and spruce, stand age older than 20 yr), clear-cuts (stand age younger than 20 year) and non-forested areas (settlements, meadows, arable lands) were estimated around the plots within a circle of 100, 200, 300, 400 and 500 m radius, using maps and the data of the Hungarian National Forest Service (National Food Chain Safety Office 2015). Previous data analysis showed that the larger surroundings have no sig-

nificant effect on any of the examined bird variables, so we used variables calculated from the smallest, 100 m radius, as it was the most effective for predicting birds. Land use history data were generated based on the map of the Second Military Survey of the Habsburg Empire from 1853 (Arcanum 2006). The presence of forests in the plots was estimated (as a binary variable), and the proportion of forested areas in the historical landscape (in a circle of 100 m radius) was calculated. All the included variables are shown in Table 1. For the diversity of tree species and land cover types, the Shannon index (Shannon and Weaver 1949) with natural logarithm was used, based on relative volume and relative cover values, respectively. Volumes of tree individuals were calculated by species specific equations from DBH and height variables (Sopp and Kolozs 2000). *Quercus petraea*, *Q. robur* and *Q. cerris* were merged as oaks, because *Q. petraea* and *Q. robur* could not clearly be distinguished in the region, and *Q. cerris* was very rare. Other rare tree species were merged as non-dominant trees. Logs and snags were also merged as dead wood during the analyses, because these two variables strongly and positively correlated with each other.

Bird data collection

Bird data collection was carried out in 2006, in the central areas of the 40 m × 40 m plots by double-visit fixed radius point count technique (Moskát 1987, Gregory et al. 2004). The first count took place between 15th April and 10th May, while the second was carried out between 11th May and 10th June. In all cases, at least two weeks passed between the two counts. In these periods, each survey was carried out for 10 minutes at dawn, between sunrise and 10.00 a.m. in the morning, if no strong wind was blowing (maximum 3 on the Beaufort-scale), and there was no rain. During each count, we noted all the birds seen or heard within a 100 m radius circle. As the detectability is different for every species, the proportion of the observed birds can differ among species, and our counts do not offer absolute abundances, but rather indicator-like measurements that are comparable between sites (Gregory et al. 2004). As birds of prey and corvids have larger territories than most of the forest bird species and the size of our stands, these species were excluded from the analysis. After choosing our plots as far from the edges as possible, and excluding the bird species whose territories do not fit with the size of our stands, we assume that the edge effect is minimal in our data. We also excluded cuckoo (*Cuculus canorus*) due to its special reproductive behaviour, so finally passerines, woodpeckers and columbiformes were included in the analysis. For each species, we used the maximum of the two counts for calculating our variables.

Species richness and the abundance of the whole assemblage and of the different functional subsets based on nesting site and rarity were analysed (Table 2). For forest birds, we calculated species richness and the abundance of cavity-nesters and non-cavity nesters. In the group of cavity-nesters, primary cavity-nesters (woodpeckers) and secondary cavity-nesters (tits, flycatchers, etc.) were merged, as these two groups are closely related to each other. We also merged

bird species nesting in the canopy or on the ground, as the species richness and the abundance of these groups was too low for a separate analysis, and these two categories are not obviously separable (e.g., robin – *Erithacus rubecula*, wren – *Troglodytes troglodytes*). Grouping by rarity was based on the Hungarian population size of the species (Birdlife Hungary 2012); species with a maximum of 100,000 breeding pairs in Hungary were deemed rare. We found that this man-made criterion adequately separated the specialist, vulnerable forest species from the generalist species in the region.

Data analysis

The breeding bird community composition was analysed by principal component analysis, with detrended correspondence analysis as indirect and with redundancy analysis as direct ordination methods (Podani 2000). Species with a frequency lower than three were excluded from the analysis. Potential explanatory variables were standardized. Based on the principal component analysis, we found that neither plot nor bird data show aggregation, so the chosen ordination methods were adequate to explore the main connections in our data structure. Detrended correspondence analysis was used to reveal gradient length values along the axes. As they were lower than 2.5 standard deviation units, redundancy analysis was used as direct ordination method (ter Braak and Smilauer 2002, Lepš and Šmilauer 2003). Before the final model selection, the significant explanatory variables were selected from among the potential ones (Table 1) by manual forward selection. During the statistical selection, collinearity between the explanatory variables was checked by pairwise correlations (Appendix 1), and from strongly correlated variables (r>0.5, Spearman correlations), only one was used for modelling. The effect of explanatory variables was tested by F-statistics via Monte-Carlo simulation with 499 permutations. As the explained variance of the individual variables was relatively low, the accepted significance level was 0.1 (ter Braak and Smilauer 2002). The significance of the canonical axes was tested in a similar way. The significances of the canonical axes of redundancy analysis were also tested by Monte-Carlo simulations using F-statistics. As the longitudinal EOV (Hungarian National Grid System) coordinate had a significant effect on bird composition, it was included in the model as a covariate.

The relationships between the studied variables of bird assemblages (species richness and abundance of the whole assemblage and the analysed groups) and explanatory variables were revealed by general linear models (Faraway 2005, 2006), using Gaussian error structure and identity link function. For species richness variables, Poisson models were also tested, but both their diagnostics and their explanatory power were weaker, so all models presented here supposed Gaussian error structure. If necessary, logarithmic transformation was used, both on the bird and the explanatory variables, to achieve normality and for a better fit of the models. Before modelling, preliminary selection and data exploration were performed. Pairwise correlation analyses and graphical explorations were carried out between the dependent variables and the potential

Table 2. Common and scientific names, codes, group membership, Freq.=frequency (number of plots where a species is observed) and Abu.=abundance of the detected bird species. Grouping was carried out by nesting site (CN=cavity-nester and NCN=Non-cavity nester) and rarity (R=Rare and C=Common). Bird species are presented in taxonomical order. Codes of bird species are derived from the first three letters of their genus and their species names.

Common name	Latin Name	Code	Nesting Site	Rarity	Freq.	Abu.
stock dove	*Columba oenas*	*COLOEN*	CN	R	4	5
wood pigeon	*Columba palumbus*	*COLPAL*	NCN	C	12	12
turtle dove	*Streptopelia turtur*	*STRTUR*	NCN	C	3	3
wryneck	*Jynx torquilla*	*JYNTOR*	CN	R	1	1
grey-headed woodpecker	*Picus canus*	*PICCAN*	CN	R	1	1
green woodpecker	*Picus viridis*	*PICVIR*	CN	R	2	2
black woodpecker	*Dryocopus martius*	*DRYMAR*	CN	R	9	9
great spotted woodpecker	*Dendrocopos major*	*DENMAJ*	CN	C	18	18
lesser spotted woodpecker	*Dendrocopos minor*	*DENMIN*	CN	R	2	2
wren	*Troglodytes troglodytes*	*TROTRO*	NCN	R	7	8
robin	*Erithacus rubecula*	*ERIRUB*	NCN	C	30	52
blackbird	*Turdus merula*	*TURMER*	NCN	C	13	15
song thrush	*Turdus philomelos*	*TURPHI*	NCN	C	30	46
mistle thrush	*Turdus viscivorus*	*TURVIS*	NCN	R	8	11
blackcap	*Sylvia atricapilla*	*SYLATR*	NCN	C	14	20
chiffchaff	*Phylloscopus collybita*	*PHYCOL*	NCN	C	17	20
willow warbler	*Phylloscopus trochilus*	*PHYTRO*	NCN	R	2	2
goldcrest	*Regulus regulus*	*REGREG*	NCN	R	2	2
firecrest	*Regulus ignicapillus*	*REGIGN*	NCN	R	1	1
collared flycatcher	*Ficedula albicollis*	*FICALB*	CN	R	4	5
long-tailed tit	*Aegithalos caudatus*	*AEGCAU*	NCN	C	1	1
blue tit	*Cyanistes caeruleus*	*CYACAE*	CN	C	20	26
marsh tit	*Parus palustris*	*PARPAL*	CN	R	13	14
crested tit	*Parus cristatus*	*PARCRI*	CN	R	1	1
coal tit	*Parus ater*	*PARATE*	CN	R	5	6
great tit	*Parus major*	*PARMAJ*	CN	C	26	39
nuthatch	*Sitta europaea*	*SITEUR*	CN	C	14	14
treecreeper	*Certhia familiaris*	*CARFAM*	CN	R	16	18
short-toed treecreeper	*Certhia brachydactyla*	*CERBRA*	CN	C	3	4
golden oriole	*Oriolus oriolus*	*ORIORI*	NCN	C	6	6
starling	*Sturnus vulgaris*	*STURVUL*	CN	C	2	2
chaffinch	*Fringilla coelebs*	*FRICOE*	NCN	C	33	73
hawfinch	*Coccothraustes coccothraustes*	*COCCOC*	NCN	C	10	10

explanatory variables (Appendix 2). Intercorrelations among explanatory variables were also checked, to reduce collinearity (Appendix 1). Only the explanatory variables which significantly correlated with the dependent variables, had homogenous scatterplots, and low intercorrelations with other explanatory variables (r<0.5, Spearmann-correlations) were included into the model selection process. After the preliminary selection, 5-8 explanatory variables were chosen for the selection procedure of the regression models. Models were built with backward elimination, by log likelihood tests, using the Akaike Information Criterion (Faraway 2006). After that, deviance analysis with F-test (ANOVA) was used to examine the relative importance of the variables in the models, and the ones that did not significantly enhance the predictive power of the models were also excluded, in order to find the minimal adequate models. After modelling, the normality and variance homogeneity of residuals were checked. The spatial autocorrelation of the model residuals were tested by Moran I correlation coefficient along the spatial range 1-7 km (Moran 1950, Borcard et al. 2011). The residuals did not show spatial autocorrelation for any of the models (the Moran I values did not differ significantly from zero and did not show any trend along the studied spatial level).

For the multivariate analyses, Canoco for Windows 4.5 (ter Braak and Smilauer 2002) was used. Linear regressions and descriptive statistics were carried out with R 3.0.2 (R Core Team 2013). For the spatial autocorrelation analysis, the "spdep" package was used (Bivand and Piras 2015).

Results

In the 35 plots, 857 individuals and 37 bird species were recorded (Table 2). The mean species richness of plots was 9.4 (range 5-19), and the mean abundance of birds was 12.8 (range 6-23). Species richness and abundance of each bird group correlated strongly (r=0.90 for forest birds, r=0.94 for

Table 3. Explanatory variables of the redundancy analysis. The canonical axes explained 15.8% of variance (redundancy analysis is significant, F=1.877, p=0.001). For the included variables, explained variance (Variance %) and F-statistics (F-value and p) are shown.

	Variance (%)	F-value	p
Mean DBH of trees	6.3	2.30	0.008
Cover of floor vegetation	4.7	1.74	0.043
Relative Scots pine volume	3.9	1.47	0.098
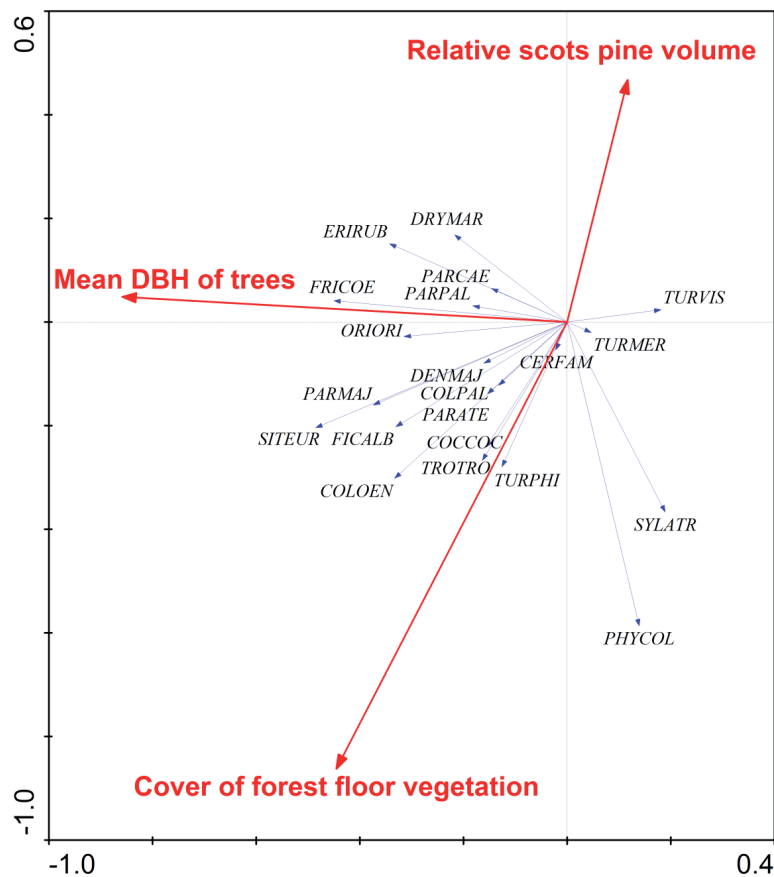
Figure 2. Ordination biplot of the first and second redundancy analysis axes, bird species and significant explanatory variables are shown. Codes of bird species are found in Table 2.

cavity-nesters, r=0.82 for non-cavity nesters, r=0.87 for common forest birds and r=0.97 for rare birds). As both the proportion of explained variance and the relative importance of explanatory variables differed in species richness and abundance models, here we present both models for forest birds and the analysed groups.

Environmental drivers of bird species composition

The first three axes of principal component analysis explained 45.1% of species variance, while the three canonical axes of redundancy analysis explained 15.8% of it (Table 3, Fig. 2). The mean DBH of trees was the most influential variable for the community composition, but the effect of floor vegetation cover and relative Scots pine volume was also considerable. The first axis was determined mainly by mean DBH of trees, correlating negatively with it, while the second axis correlated negatively with the cover of floor vegetation and positively with relative Scots pine volume. Although our variables had a moderate power in explaining canonical axis

of redundancy analysis, the revealed effects could explain the position of many species along these two axes. All of the primary (great spotted woodpecker – *Dendrocopos major,* black woodpecker – *Dryocopus martius*) and secondary (treecreeper – *Certhia familiaris,* stock dove – *Columba oenas,* collared flycatcher – *Ficedula albicollis,* coal tit – *Parus ater,* great tit – *Parus major,* marsh tit – *Parus palustris,* blue tit – *Cyanistes caeruleus,* nuthatch – *Sitta europaea*) cavity-nesters had negative scores on the first axis, as they need large trees for nesting and feeding. On the contrary, many thrushes and warblers (chiffchaff – *Phylloscopus collybita,* blackcap – *Sylvia atricapilla,* blackbird – *Turdus merula,* song thrush – *Turdus viscivorus*) got negative values on the second axis, showing that they need forests with denser floor vegetation. It should be noted that none of the species have high scores either on the first or on the second axis. This could be related to the fact that Scots pine volume had a negative effect on most of the bird species. In addition, nearly all of the forest bird species had a positive relationship either with the mean DBH of trees or with the cover of floor vegetation.

Table 4. Explanatory variables of the general linear models. For the presented models, adjusted coefficient of determination (R^2) or direction of the parameters of the variables (Sign), explained variances (Var) and significance (F-statistics, n=35, ˙ p<0.1, * p<0.05, ** p<0.01, *** p<0.001) are shown.

Explanatory variables	Sign	Var (%)	Explanatory variables	Sign	Var (%)
Abundance of forest birds; $R^2=0.590$			*Species richness of forest birds; $R^2=0.397$*		
Mean DBH of trees	+	29.4***	Mean DBH of trees	+	19.5**
Cover of floor vegetation	+	19.5***	Cover of floor vegetation	+	13.7*
Volume of dead wood	+	10.0**	Volume of dead wood	+	6.5˙
Abundance of cavity-nesters; $R^2=0.530$			*Species richness of cavity-nesters; $R^2=0.429$*		
Mean DBH of trees	+	35.5***	Mean DBH of trees	+	26.5***
Volume of dead wood	+	17.5***	Volume of dead wood	+	16.3**
Abundance of non-cavity nesters; $R^2=0.364$			*Species richness of non-cavity nesters; $R^2=0.189$*		
Cover of floor vegetation	+	28.2***	Cover of floor vegetation	+	18.9**
Cover of soil	+	8.1˙			
Abundance of common forest birds; $R^2=0.501$			*Species richness of common forest birds; $R^2=0.288$*		
Mean DBH of trees	+	23.8***	Mean DBH of trees	+	15.6*
Cover of floor vegetation	+	21.0**	Cover of floor vegetation	+	13.2*
Relative volume of oaks	+	5.4˙			
Abundance of rare forest birds; $R^2=0.294$			*Species richness of rare forest birds; $R^2=0.298$*		
Volume of dead wood	+	12.0*	Volume of dead wood	+	11.8*
Mean DBH of trees	+	9.6*	Relative volume of oaks	-	11.0*
Relative volume of oaks	-	7.9˙	Mean DBH of trees	+	6.9˙

Environmental drivers of bird species richness and abundance variables

In each group, the same explanatory variables were significant in species richness and abundance models, but the coefficients of determination (R^2) were higher for abundance than for species richness variables (the differences were approximately 15%, Table 4). Our models explained very different proportions of variation (from 20% up to 60%).

Mean DBH of trees had the strongest positive effect on both the abundance and the species richness of forest birds. We also found significant and positive effects of floor vegetation cover and dead wood volume on these variables. These three variables were the major determinants of bird assemblages in this region, but their importance differed between all the groups of forest birds. Significant effects of some other variables (soil cover for non-cavity nesters and oak volume for rare and common forest birds) were also discovered with less importance.

For cavity-nester species, the mean DBH of trees and dead wood volume seemed to have a strong and positive effect, while floor vegetation cover did not seem to be important to them. On the contrary, for non-cavity nesters this was the most important explanatory variable beside soil cover. Both variables had a positive effect on none-cavity nesters.

Common forest birds were positively related to the mean DBH of trees and the cover of floor vegetation, while the relative volume of oaks also had a positive, but much weaker effect. On the other hand, the most important positive effect on rare forest birds was the volume of dead wood. The mean DBH of trees positively influenced this group, but its effect was much weaker on them than on the common forest birds.

In addition, relative oak volume had a marginally positive effect on rare forest bird abundance and species richness.

Discussion

Effectiveness of our variables

The explained variance of the selected environmental variables was much higher for regression models than for redundancy analysis. We assume that different bird species have numerous different specific needs which are difficult to represent in two or three axes of a redundancy analysis. However, in general linear models, aggregated bird community variables masked these specific effects, and we could manifest the few main factors that affect bird occurrences at community level.

Relative importance of different aspects of environment

We found that the proportions of land cover types had no significant effect on forest breeding bird communities. Although in many studies landscape variables were found to be at least as important to birds as stand-level variables, in Őrség this is not an unexpected result. Here, the landscape is highly forested and, as other studies also showed (Hagan and Meehan 2002, Batáry et al. 2010), landscape-level variables can become important if the availability of potential habitats in the landscape is low. However, if the landscape-level availability of habitats is high, the quality of local stands is more determining. Besides, other attributions of the landscape could have effects on bird community (e.g., patch size through side-effect, Moskát and Báldi 1999), but in such a forested area we presume that these effects are not influential.

The rough land use history variables included in our studies did not have effects on the breeding bird communities either. This result is reconcilable with the fact that birds are among the most reactive organism groups, as they are able to occupy suitable habitats expeditiously (Gregory et al. 2004), in contrast with most herbs and many groups of animals (e.g., Ehrlén and Eriksson 2000, Fournier and Loreau 2001, Endels et al. 2004). As dispersal is typically not limited for this group, it is expected that they can reach the suitable habitats. In addition, we would like to note that land use history could have an indirect effect on bird communities, through its long-term effects on stand structure and composition, and other variables of land use history, that are not examined here, could also have an effect on bird communities.

In accordance with most studies (e.g., MacArthur and MacArthur 1961, Muller et al. 2010), forest structural variables were found to be the major determinants of forest bird communities, whereas compositional variables had only marginal effects. The studied stands have a great variation in both groups of variables. Nevertheless, we have to notice that these two aspects of forests conversely affect each other (Moskát et al. 1988, Hewson et al. 2011), so at least indirect impacts of the composition are presumable.

Stand structural variables affecting breeding bird communities

Our study showed that only some of the many potential variables had effects on the forest breeding bird community. Apart from some variables that had smaller effects on one or two functional groups of forest birds (soil cover for ground-nesters and oak volume for some other groups), most of the variance was explained by three structural variables: mean size (DBH) of trees, cover of floor vegetation and volume of dead wood. These variables explained both total species richness and total abundance, and also played a determining role in explaining the variance of all analysed groups of birds. It is notable that these three structural variables had the same and positive manner for all analysed groups, but the strength of their effect differed extremely.

The most important variable affecting forest bird community in the Őrség region was the mean size (DBH) of trees. This is in agreement with numerous publications (e.g., Angelstam and Mikusinski 1994, Donald et al. 1998, Hewson et al. 2011), but in our case the importance of this variable is a little surprising as all of our stands are relatively old, older than 70 years. However, the lack of over-mature trees is typical in this region due to selective cutting regimes performed by farmers in previous centuries, which fact may partly explain the local importance of this variable (e.g., Tímár et al. 2002). The probable reason for this phenomenon is that both the amount of invertebrates (especially insects) and the number of potential nesting sites increase at an accelerating rate with the size of trees (e.g., Lencinas et al. 2008, Bereczki et al. 2014). This is confirmed by the fact that the importance of this variable was largest for cavity-nesters, the group containing species feeding and nesting in the canopy, in branches or trunks (woodpeckers, treecreepers, nuthatch and tits, e.g., see in Fuller 1995).

Besides the mean size of trees, the cover of floor vegetation seemed to be the other determinant of forest breeding bird assemblages. The importance of understory layers for forest birds is well known. Many studies showed the significance of the shrub layer on birds (e.g., Moskát and Fuisz 1992, Hagan and Meehan 2002, Melles et al. 2003, Fernandez-Juricic 2004, Wilson et al. 2006), but fewer underlined the importance of floor vegetation as ours did (e.g., Donald et al. 1998, Hewson et al. 2011). As many of the common forest birds nest and/or feed on the ground or close to it (e.g., thrushes, warblers, wren, robin, blackcap, blackbird), this result is not unexpected. We additionally noted that the cover of floor vegetation had the greatest predictive power for non-cavity nesters, the group containing most of the above species. Conversely, the fact that the shrub layer was not a relevant factor for any of the studied bird groups is a little bit surprising, although many of the discussed species feed and some of them even nest in this layer. The effectiveness of floor cover in predicting the abundance and species richness of birds related to understory layers may be partly caused by an indirect effect. In this project, some light measurement methods were used to estimate direct and indirect light conditions in the understory (Tinya et al. 2009), but we did not use these variables during the analyses of bird data, as they are expected to have only indirect effect on them at the most. Bird species related to understory layers are presumed to be sensitive to the heterogeneity and density of foliage in the understory which primarily depend on light conditions and canopy openness. The reason for the importance of floor cover for birds may be that ground vegetation is a good indicator of foliage density in the understory (besides, it is important for many birds in itself). This concept was partly confirmed by the fact that the cover of floor vegetation correlated significantly with the mean relative diffuse light at 1.3 m height (r=0.52, p=0.001, Spearman correlation), but the cover of shrub layer did not (r=0.19, p=0.283, Spearman correlation, Tinya et al. 2009). The shrub layer could be strongly affected by management (Tímár et al. 2002), but the foliage density (partly caused by nearby trees) can sensitively respond to the light conditions, similarly to floor vegetation. Further research is needed for the verification of this theory, but in this way, the floor vegetation could be a useful indicator of habitat quality for forest birds.

The third component of forest structure, which has a smaller, but also significant effect on breeding bird community, was the volume of dead wood. The importance of dead wood for woodpeckers and some other forest bird species is well known (Angelstam and Mikusinski 1994, Fuller 1995, Rosenvald et al. 2011). However, it is notable that the effect of dead wood was marginal for the total bird community, while this was the most important effect for rare birds. Although this variable had the smallest effect from among the three discussed above, this fact underlines that dead wood can be one of the key factors in the conservation of vulnerable forest birds. Conversely, the fact that many birds related to dead wood are rare shows that this can be one of the major

limits of their presence in Hungary (e.g., many of the wood-peckers that need dead trees for predation and/or nesting: grey-headed woodpecker – *Picus canus*, green-woodpecker – *Picus viridis*, black woodpecker – *Dryocopos martius*, lesser spotted woodpecker – *Dendrocopos minor*, or middle spotted woodpecker – *Dendrocopos medius*, which is so rare that we did not find it in our plots). There is relatively little information available on the dead wood volumes of forests in Hungary, but in most of the studied stands, its amount reaches only 20-40% of the supposed natural reference of this forest type (Hanski and Walsh 2004, Christensen et al. 2005).

We would like to note that from this work it cannot be diagnosed whether the abundance or the species richness of a bird group is more affected by the explanatory variables, as these characteristics are highly correlated to each other. However, the higher variance explanation of abundance models shows that our relatively simple structural variables may primarily determine the abundance of breeding birds by controlling the amount of available food for them (Holmes and Schultz 1988, Bereczki et al. 2014). In this case, the reason for the lower variance explanation of the species richness models could be that the specific needs of forest specialists are not so easily examined by our variables. Moreover, these specialists with their different needs were pooled in our bird groups, as here our aim was to analyse the whole bird community.

Our study also showed that different groups of forest birds can be sensitive to completely different aspects of the environment. Thus, it is strongly recommended to examine at least a few functional groups of forest birds in ecological researches, as the only use of total species richness and abundance may hide the needs of some specific groups (see also Mag et al. 2012).

Implications for forest conservation and management

We found that for different groups of forest birds, completely different aspects of forest structure may be important. Thus, to ensure the diversity of forest bird assemblages at the landscape-level, forest management should strive to develop the diversity of structurally different stands. Within the prevalent shelterwood management regimes, the elongation of rotation and regeneration periods and the relatively high proportion of retention tree groups after forest harvest could contribute to the conservation of forest birds, as these interventions lead to a higher proportion of old trees and dead wood in the landscape. Our results also showed that for many groups of birds, more than one aspect of the forest structure is important (e.g., they need both large trees and dense understory). Management regimes operating with continuous forest cover might be more appropriate in providing these structural elements simultaneously at fine spatial level and maintaining diverse forest bird communities, thus healthier forest ecosystems.

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Electronic supplementary material

Appendix 1. Correlation coefficients among environmental variables.

Appendix 2. Correlation coefficients between bird community and environmental variables.

The files may be downloaded from www.akademiai.com.