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5

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

8

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10

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16

17 **Keywords:** Bird community, Land use history, Species richness, Stand composition, Stand
18 structure, Vegetation type.

19

20 **Abstract:** The effects of stand structure, tree species composition, proportion of habitat types
21 and land use history on breeding bird assemblages in temperate mixed forests in Western
22 Hungary were studied. The species richness, the abundance and the composition of the whole
23 breeding bird assemblage and of some groups formed on the base of nesting site and rarity

24 were examined. Stand structural variables had the highest impact on the breeding bird
25 assemblage, while tree species composition, the varying proportion of vegetation types and
26 land use history had no significant effect. In the case of the species richness, the abundance
27 and the composition of the whole assemblage, the most important variables were the mean
28 diameter of trees, the vegetation cover of the forest floor and the dead wood volume. The
29 explained variance in the linear models of different groups varied between 20% and 60%, and
30 the relative importance of these three variables also differed considerably. These results
31 indicate that forest management may considerably influence the diversity and the composition
32 of birds, as all the structural elements affecting birds deeply depend on it. Within the
33 shelterwood management system, the elongation of the rotation and regeneration periods, and
34 the relatively high proportion of retention tree groups after harvest could contribute to the
35 conservation of forest birds. Our results also showed that for the forest bird communities, both
36 the prevalence of big trees and the presence of a dense understory layer are important.
37 Management regimes which apply continuous forest cover might be more appropriate for
38 providing these structural elements simultaneously on small spatial scales, and for the
39 maintenance of a more diverse bird community, thus healthier forest ecosystems.

40

41 **Nomenclature:** Hagemeyer and Blair (1997) for birds.

42

43 **Introduction**

44

45 The effects of management-related habitat variables (e.g., structural and compositional
46 characteristics) on bird assemblages are widely studied. There is a lot of interest in the
47 conservation of birds, as they are especially popular, relatively easy to detect and very
48 sensitive to the quality of their habitats (Fuller 1995). As a result, studies of birds are widely
49 used for creating habitat indices to follow up the quality of numerous habitat types and to
50 monitor the effects of their management (Gregory and van Strien 2010). However, the
51 relationships between stand-level forest characteristics and birds are mostly explored in the
52 boreal and hemiboreal zones of Europe (e.g., Virkkala and Liehu 1990, Jansson and
53 Angelstam 1999, Mikusinski et al. 2001, Rosenvald et al. 2011). With the exception of a few
54 analyses (e.g. Moskát et al. 1988, Moskát 1991, Moskát and Waliczky 1992), the studies from
55 the temperate zone mainly focus on the Atlantic region (Donald et al. 1998, Hewson et al.
56 2011), where both forest cover (Food and Agricultural Organisation of the United Nations,
57 2009) and forest naturalness (e.g., Mikusinski and Angelstam 1998) are lower than in Central
58 Europe, so the main factors limiting bird assemblages are probably also different. A sad
59 actuality of our study is that - according to The Pan European Common Bird Monitoring
60 Scheme - forest indicators, based on population changes of common forest birds, show a
61 definite decline in most European regions (PECBMS 2010).

62

63 Most forest bird species use a relatively small area (smaller than 1 ha) for feeding and
64 sufficing their needs in the breeding period (Fuller 1995). Thus, it seems obvious to study
65 bird-environment relations at a local scale as well. The results of such studies are well
66 applicable for forest conservation practice, as the size of the management units typically fits
67 to this scale. However, there is an ongoing debate among conservation biologists on whether

68 landscape-level (Mitchell et al. 2001, Loehle et al. 2005, Mitchell et al. 2006) or stand-level
69 (Hagan and Meehan 2002, Poulsen 2002) variables are more important for forest bird
70 assemblages. The answer is inconsistent, and the comparison of landscape and stand-level
71 effects is difficult as in most of the studies, rough landscape variables are available from a
72 coarser level, while the more detailed compositional or structural variables are only available
73 from a finer stand-level. Thus, in many cases it is debatable whether the results refer to the
74 effect of the level of the study, or to the different resolution of data.

75

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

87

88 In this study, we examined the effects of stand structure, tree species composition, the
89 proportion of different land cover types, and the land use history on breeding bird
90 assemblages at stand-level in Central European mixed deciduous-coniferous forests. The
91 comparatively moderate sample size (35 plots) allows for the use of relatively detailed and
92 comprehensive explanatory variables. We hope that this versatile study approach is really

93 suitable to explore the main factors affecting bird communities in this region, at least at the
94 studied stand-level. We also investigated the relative importance of each examined
95 environmental aspect for birds. Another specialty of our study is that land use history – which
96 forms part of our examinations – is a scarcely studied aspect of the environment for birds in
97 this region. As in this study our main purpose was to explore the relative importance of these
98 environmental aspects for the whole breeding bird community, above all, the species richness
99 and the abundance of birds were examined. However, for a deeper understanding of how the
100 environmental variables affect bird communities, some groups of breeding birds were also
101 included in the analysis. As one of the main characteristics that determines the requirements
102 of bird species for their environment is the nesting site (e.g., Newton 1994), the species
103 richness and the abundance of two rough categories (cavity and non-cavity nesters) based on
104 this were examined. In addition, we expected that the needs of rare species could point out
105 some of the main limiting factors for birds in the region, thus, the species richness and the
106 abundance of two man-made groups (common and rare birds) were also analysed. Our study
107 was carried out in the temperate zone of Europe, in the highly forested Órség region in
108 Western Hungary. This region is especially suitable to examine the effects of the different
109 aspects of forest quality, as it hosts a great compositional and structural variation of forests,
110 under similar geological conditions (Tímár et al. 2002).

111

112 **Methods**

113

114 *Study area and plot selection*

115

116 The study was carried out in Órség, Western Hungary (Fig. 1, N 46° 51'-55' and W 16°
117 07'-23'). In the region the elevation is 250-300 m above sea level, with the topography

118 consisting of hills and small valleys. Annual precipitation is 700-800 mm, and mean annual
119 temperature is 9.0-9.5 °C (Dövényi 2010). The soil is acidic and nutrient-poor in this region.
120 Therefore, extensive forms of agriculture (such as mowing and grazing in meadows) and
121 forestry are prevalent. Forest cover of the region is approximately 60% (Gyöngyössy 2008).
122 The forests of the region are generally mixed, both tree species composition and stand
123 structure show large variations among the stands (Tímár et al. 2002). The main tree species
124 (*Quercus petraea* L. – sessile oak, *Quercus robur* L. – pedunculate oak, *Fagus sylvatica* L. –
125 beech, *Pinus sylvestris* L. – Scots pine) occur in different proportions in the stands, and the
126 number and the proportion of non-dominant tree species (*Carpinus betulus* L. – hornbeam,
127 *Picea abies* Karst. – Norway spruce, *Betula pendula* Roth – birch, *Populus tremula* L. –
128 aspen, *Castanea sativa* Mill. – chestnut, *Prunus avium* L. – wild cherry, *Acer* spp. – maple
129 species) is also high. The great variation of tree species, which makes this area so suitable for
130 the examination of the effects of forest composition, also has phylogeographic, geographic
131 and historical reasons. Besides the traditional selective cutting in private forests, state forests
132 have recently been managed in a more intensive shelterwood management system with a
133 rotation period of 70-110 years (Tímár et al. 2002). For a more detailed description of site
134 conditions and the history of this region, see Márialigeti et al. (2009) and Király et al. (2010).

135

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

142

143 *Environmental data collection*

144

145 In every selected stand, we designated a 40 m x 40 m plot that represented the average tree
146 species composition and the structure of the stand and was as far from the edges as possible,
147 in order to minimise side effects. Tree species composition and stand structure were measured
148 in these plots in 2006 and 2007. Species identity, height and diameter at breast height (DBH)
149 were measured for each tree with DBH thicker than 5 cm, including snags. Average diameter
150 and length of logs, thicker than 5 cm and longer than 0.5 m were recorded. Saplings and
151 shrubs (every individual thinner than 5 cm DBH, but taller than 0.5 m) were counted, in order
152 to estimate shrub layer density. The absolute cover of floor vegetation (herbs and seedlings
153 lower than 0.5 m), open soil and litter were visually estimated. To describe the area
154 surrounding each plot, the proportion of main forest types (beech, oak, pine and spruce, stand
155 age older than 20 yr), clear-cuts (stand age younger than 20 year) and non-forested areas
156 (settlements, meadows, arable lands) were estimated around the plots within a circle of 100,
157 200, 300, 400 and 500 m radius, using maps and the data of the Hungarian National Forest
158 Service (National Food Chain Safety Office 2015). Previous data analysis showed that the
159 larger surroundings have no significant effect on any of the examined bird variables, so we
160 used variables calculated from the smallest, 100 m radius, as it was the most effective for
161 predicting birds. Land use history data were generated based on the map of the Second
162 Military Survey of the Habsburg Empire from 1853 (Arcanum 2006). The presence of forests
163 in the plots was estimated (as a binary variable), and the proportion of forested areas in the
164 historical landscape (in a circle of 100 m radius) was calculated. All the included variables are
165 shown in Table 1. For the diversity of tree species and land cover types, the Shannon index
166 (Shannon and Weaver 1949) with natural logarithm was used, based on relative volume and
167 relative cover values, respectively. Volumes of tree individuals were calculated by species

168 specific equations from DBH and height variables (Sopp and Kolozs 2000). *Quercus petraea*,
169 *Q. robur* and *Q. cerris* were merged as oaks, because *Q. petraea* and *Q. robur* could not
170 clearly be distinguished in the region, and *Q. cerris* was very rare. Other rare tree species
171 were merged as non-dominant trees. Logs and snags were also merged as dead wood during
172 the analyses, because these two variables strongly and positively correlated with each other.

173

174 *Bird data collection*

175

176 Bird data collection was carried out in 2006, in the central areas of the 40 m x 40 m plots
177 by double-visit fixed radius point count technique (Moskát 1987, Gregory et al. 2004). The
178 first count took place between 15th April and 10th May, while the second was carried out
179 between 11th May and 10th June. In all cases, at least two weeks passed between the two
180 counts. In these periods, each survey was carried out for 10 minutes at dawn, between sunrise
181 and ten o'clock in the morning, if no strong wind was blowing (maximum 3 on the Beaufort-
182 scale), and there was no rain. During each count, we noted all the birds seen or heard within a
183 100 m radius circle. As the detectability is different for every species, the proportion of the
184 observed birds can differ among species, and our counts do not offer absolute abundances, but
185 rather indicator-like measurements that are comparable between sites (Gregory et al. 2004).
186 As birds of prey and corvids have larger territories than most of the forest bird species and the
187 size of our stands, these species were excluded from the analysis. After choosing our plots as
188 far from the edges as possible, and excluding the bird species whose territories do not fit with
189 the size of our stands, we assume that the side-effect is minimal in our data. We also excluded
190 cuckoo (*Cuculus canorus*) due to its special reproductive behaviour, so finally passerines,
191 woodpeckers and columbiformes were included in the analysis. For each species, we used the
192 maximum of the two counts for calculating our variables.

193

194 Species richness and the abundance of the whole assemblage and of the different
195 functional subsets based on nesting site and rarity were analysed (Table 2). For forest birds,
196 we calculated species richness and the abundance of cavity-nesters and non-cavity nesters. In
197 the group of cavity-nesters, primary cavity-nesters (woodpeckers) and secondary cavity-
198 nesters (tits, flycatchers, etc.) were merged, as these two groups are closely related to each
199 other. We also merged bird species nesting in the canopy or on the ground, as the species
200 richness and the abundance of these groups was too low for a separate analysis, and these two
201 categories are not obviously separable (e.g., robin – *Erithacus rubecula*, wren – *Troglodytes*
202 *troglodytes*). Grouping by rarity was based on the Hungarian population size of the species
203 (Birdlife Hungary 2012); species with a maximum of 100,000 breeding pairs in Hungary were
204 deemed rare. We found that this man-made criterion adequately separated the specialist,
205 vulnerable forest species from the generalist species in the region.

206

207 *Data analysis*

208

209 The breeding bird community composition was analysed by principal component analysis,
210 with detrended correspondence analysis as indirect and with redundancy analysis as direct
211 ordination methods (Podani 2000). Species with a frequency lower than three were excluded
212 from the analysis. Potential explanatory variables were standardized. Based on the principal
213 component analysis, we found that neither plot nor bird data shows aggregation, so the chosen
214 ordination methods were adequate to explore the main connections in our data structure.
215 Detrended correspondence analysis was used to reveal gradient length values along the axes.
216 As they were lower than 2.5 standard deviation units, redundancy analysis was used as direct
217 ordination method (ter Braak and Smilauer 2002, Lepš and Šmilauer 2003). Before the final

218 model selection, the significant explanatory variables were selected from among the potential
219 ones (Table 1) by manual forward selection. During the statistical selection, collinearity
220 between the explanatory variables was checked by pairwise correlations (Appendix 1), and
221 from strongly correlated variables ($r > 0.5$, Spearman-correlations), only one was used for
222 modelling. The effect of explanatory variables was tested by F-statistics via Monte-Carlo
223 simulation with 499 permutations. As the explained variance of the individual variables was
224 relatively low, the accepted significance level was 0.1 (ter Braak and Smilauer, 2002). The
225 significance of the canonical axes was tested in a similar way. The significances of the
226 canonical axes of redundancy analysis were also tested by Monte-Carlo simulations using F-
227 statistics. As the longitudinal EOV (Hungarian National Grid System) coordinate had a
228 significant effect on bird composition, it was included in the model as a covariate.

229

230 The relationships between the studied variables of bird assemblages (species richness and
231 abundance of the whole assemblage and the analysed groups) and explanatory variables were
232 revealed by general linear models (Faraway 2005, 2006), using Gaussian error structure and
233 identity link function. For species richness variables, Poisson models were also tested, but
234 both their diagnostics and their explanatory power were weaker, so all models presented here
235 supposed Gaussian error structure. If necessary, logarithmic transformation was used, both on
236 the bird and the explanatory variables, to achieve normality and for a better fit of the models.
237 Before modelling, preliminary selection and data exploration were performed. Pairwise
238 correlation analyses and graphical explorations were carried out between the dependent
239 variables and the potential explanatory variables (Appendix 2). Intercorrelations among
240 explanatory variables were also checked, to reduce collinearity (Appendix 1). Only the
241 explanatory variables which significantly correlated with the dependent variables, had
242 homogenous scatterplots, and low intercorrelations with other explanatory variables ($r < 0.5$,

243 Spearman-correlations) were included into the model selection process. After the
244 preliminary selection, 5-8 explanatory variables were chosen for the selection procedure of
245 the regression models. Models were built with backward elimination, by log likelihood tests,
246 using the Akaike Information Criterion (Faraway 2006). After that, deviance analysis with F-
247 test (ANOVA) was used to examine the relative importance of the variables in the models,
248 and the ones that did not significantly enhance the predictive power of the models were also
249 excluded, in order to find the minimal adequate models. After modelling, the normality and
250 variance homogeneity of residuals were checked. The spatial autocorrelation of the model
251 residuals were tested by Moran I correlation coefficient along the spatial range 1-7 km
252 (Moran 1950, Borcard et al. 2011). The residuals did not show spatial autocorrelation for any
253 of the models (the Moran I values did not differ significantly from zero and did not show any
254 trend along the studied spatial level).

255

256 For the multivariate analyses, Canoco for Windows 4.5 (ter Braak and Smilauer 2002) was
257 used. Linear regressions and descriptive statistics were carried out with R 3.0.2 (R Core Team
258 2013). For the spatial autocorrelation analysis, the “spdep” package was used (Bivand and
259 Piras 2015).

260

261 **Results**

262

263 In the 35 plots, 857 individuals and 37 bird species were recorded (Table 2). The mean
264 species richness of plots was 9.4 (range 5-19), and the mean abundance of birds was 12.8
265 (range 6-23). Species richness and abundance of each bird group correlated strongly ($r=0.90$
266 for forest birds, $r=0.94$ for cavity-nesters, $r=0.82$ for non-cavity nesters, $r=0.87$ for common
267 forest birds and $r=0.97$ for rare birds). As both the proportion of explained variance and the

268 relative importance of explanatory variables differed in species richness and abundance
269 models, here we present both models for forest birds and the analysed groups.

270

271 *Environmental drivers of bird species composition*

272

273 The first three axes of principal component analysis explained 45.1 % of species variance,
274 while the three canonical axes of redundancy analysis explained 15.8 % of it (Table 3, Fig. 2).

275 The mean DBH of trees was the most influential variable for the community composition, but
276 the effect of floor vegetation cover and relative Scots pine volume was also considerable. The

277 first axis was determined mainly by mean DBH of trees, correlating negatively with it, while

278 the second axis correlated negatively with the cover of floor vegetation and positively with

279 relative Scots pine volume. Although our variables had a moderate power in explaining

280 canonical axis of redundancy analysis, the revealed effects could explain the position of many

281 species along these two axes. All of the primary (great spotted woodpecker – *Dendrocopos*

282 *major*, black woodpecker – *Dryocopus martius*) and secondary (treecreeper – *Certhia*

283 *familiaris*, stock dove – *Columba oenas*, collared flycatcher – *Ficedula albicollis*, coal tit –

284 *Parus ater*, great tit – *Parus major*, marsh tit – *Parus palustris*, blue tit – *Cyanistes caeruleus*,

285 nuthatch – *Sitta europaea*) cavity-nesters had negative scores on the first axis, as they need

286 large trees for nesting and feeding. On the contrary, many thrushes and warblers (chiffchaff –

287 *Phylloscopus collybita*, blackcap – *Sylvia atricapilla*, blackbird – *Turdus merula*, song thrush

288 – *Turdus viscivorus*) got negative values on the second axis, showing that they need forests

289 with denser floor vegetation. It should be noted that none of the species have high scores

290 either on the first or on the second axis. This could be related to the fact that Scots pine

291 volume had a negative effect on most of the bird species. In addition, nearly all of the forest

292 bird species had a positive relationship either with the mean DBH of trees or with the cover of
293 floor vegetation.

294

295 *Environmental drivers of bird species richness and abundance variables*

296

297 In each group, the same explanatory variables were significant in species richness and
298 abundance models, but the coefficients of determination values (R^2) were higher for
299 abundance than for species richness variables (the differences were approximately 15 %,
300 Table 4). Our models explained very different proportions of variation (from 20 % up to 60
301 %).

302

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

310

311 For cavity-nester species, the mean DBH of trees and dead wood volume seemed to have a
312 strong and positive effect, while floor vegetation cover did not seem to be important to them.

313 On the contrary, for non-cavity nesters this was the most important explanatory variable
314 beside soil cover. Both variables had a positive effect on none-cavity nesters.

315

316 Common forest birds were positively related to the mean DBH of trees and the cover of
317 floor vegetation, while the relative volume of oaks also had a positive, but much weaker
318 effect. On the other hand, the most important positive effect on rare forest birds was the
319 volume of dead wood. The mean DBH of trees positively influenced this group, but its effect
320 was much weaker on them than on the common forest birds. In addition, relative oak volume
321 had a marginally positive effect on rare forest bird abundance and species richness.

322

323 **Discussion**

324

325 *Effectiveness of our variables*

326

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

333

334 *Relative importance of different aspects of environment*

335

336 We found that the proportions of land cover types had no significant effect on forest
337 breeding bird communities. Although in many studies landscape variables were found to be at
338 least as important to birds as stand-level variables, in Órség this is not an unexpected result.
339 Here, the landscape is highly forested and, as other studies also showed (Hagan and Meehan
340 2002, Batáry et al. 2010), landscape-level variables can become important if the availability

341 of potential habitats in the landscape is low. However, if the landscape-level availability of
342 habitats is high, the quality of local stands is more determining. Besides, other attributions of
343 the landscape could have effects on bird community (e.g., patch size through side-effect,
344 Moskát and Báldi 1999), but in such a forested area we presume that these effects are not
345 determinant.

346

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

356

357 In accordance with most studies (e.g., MacArthur and MacArthur 1961, Muller et al.
358 2010), forest structural variables were found to be the major determinants of forest bird
359 communities, whereas compositional variables had only marginal effects. The studied stands
360 have a great variation in both groups of variables. Nevertheless, we have to notice that these
361 two aspects of forests conversely affect each other (Moskát et al. 1988, Hewson et al. 2011),
362 so at least indirect impacts of the composition are presumable.

363

364 *Stand structural variables affecting breeding bird communities*

365

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

375

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

388

389 Besides the mean size of trees, the cover of floor vegetation seemed to be the other
390 determinant of forest breeding bird assemblages. The importance of understory layers for

391 forest birds is well known. Many studies showed the significance of the shrub layer on birds
392 (e.g., Moskát and Fuisz 1992, Hagan and Meehan 2002, Melles et al. 2003, Fernandez-Juricic
393 2004, Wilson et al. 2006), but fewer underlined the importance of floor vegetation as ours did
394 (e.g., Donald et al. 1998, Hewson et al. 2011). As many of the common forest birds nest
395 and/or feed on the ground or close to it (e.g., thrushes, warblers, wren, robin, blackcap,
396 blackbird), this result is not unexpected. We additionally noted that the cover of floor
397 vegetation had the greatest predictive power for non-cavity nesters, the group containing most
398 of the above species. Conversely, the fact that the shrub layer was not a relevant factor for any
399 of the studied bird groups is a little bit surprising, although many of the discussed species feed
400 and some of them even nest in this layer. The effectiveness of floor cover in predicting the
401 abundance and species richness of birds related to understory layers may be partly caused by
402 an indirect effect. In this project, some light measurement methods were used to estimate
403 direct and indirect light conditions in the understory (Tinya et al. 2009), but we did not use
404 these variables during the analyses of bird data, as they are expected to have only indirect
405 effect on them at the most. Bird species related to understory layers are presumed to be
406 sensitive to the heterogeneity and density of foliage in the understory which primarily depend
407 on light conditions and canopy openness. The reason for the importance of floor cover for
408 birds may be that ground vegetation is a good indicator of foliage density in the understory
409 (besides, it is important for many birds in itself). This concept was partly confirmed by the
410 fact that the cover of floor vegetation correlated significantly with the mean relative diffuse
411 light at 1.3 m height ($r=0.52$, $p=0.001$, Spearman-correlation), but the cover of shrub layer
412 did not ($r=0.19$, $p=0.283$, Spearman-correlation, Tinya et al. 2009). The shrub layer could be
413 strongly affected by management (Tímár et al. 2002), but the foliage density (partly caused by
414 nearby trees) can sensitively respond to the light conditions, similarly to floor vegetation.

415 Further research is needed for the verification of this theory, but in this way, the floor
416 vegetation could be a useful indicator of habitat quality for forest birds.

417

418 The third component of forest structure, which has a smaller, but also significant effect on
419 breeding bird community, was the volume of dead wood. The importance of dead wood for
420 woodpeckers and some other forest bird species is well known (Angelstam and Mikusinski
421 1994, Fuller 1995, Rosenvald et al. 2011). However, it is notable that the effect of dead wood
422 was marginal for the total bird community, while this was the most important effect for rare
423 birds. Although this variable had the smallest effect from among the three discussed above,
424 this fact underlines that dead wood can be one of the key factors in the conservation of
425 vulnerable forest birds. Conversely, the fact that many birds related to dead wood are rare
426 shows that this can be one of the major limits of their presence in Hungary (e.g., many of the
427 woodpeckers that need dead trees for predation and/or nesting: grey-headed woodpecker –
428 *Picus canus*, green-woodpecker – *Picus viridis*, black woodpecker – *Dryocopus martius*,
429 lesser spotted woodpecker – *Dendrocopos minor*, or middle spotted woodpecker –
430 *Dendrocopos medius*, which is so rare that it does not even exist in our plots). There is
431 relatively little information available on the dead wood volumes of forests in Hungary, but in
432 most of the studied stands, its amount reaches only 20-40% of the supposed natural reference
433 of this forest type (Hanski and Walsh 2004, Christensen et al. 2005).

434

435 We would like to note that from this work it cannot be diagnosed whether the abundance or
436 the species richness of a bird group is more affected by the explanatory variables, as these
437 characteristics are highly correlated to each other. However, the higher variance explanation
438 of abundance models shows that our relatively simple structural variables may primarily
439 determine the abundance of breeding birds by controlling the amount of available food for

440 them (Holmes and Schultz 1988, Bereczki et al. 2014). In this case, the reason for the lower
441 variance explanation of the species richness models could be that the specific needs of forest
442 specialists are not so easily examined by our variables. Moreover, these specialists with their
443 different needs were pooled in our bird groups, as here our aim was to analyse the whole bird
444 community.

445

446 Our study also showed that different groups of forest birds can be sensitive to completely
447 different aspects of the environment. Thus, it is strongly recommended to examine at least a
448 few functional groups of forest birds in ecological researches, as the only use of total species
449 richness and abundance may hide the needs of some specific groups (see also Mag et al.
450 2012).

451

452 *Implications for forest conservation and management*

453

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

464 structural elements simultaneously at fine spatial level and maintaining diverse forest bird
465 communities, thus healthier forest ecosystems.

466

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

Explanatory variables	Unit	Mean (Min.-Max.)
<i>Tree species composition</i>		
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)
<i>Stand structure</i>		
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)
<i>Proportion of land cover types</i>		
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)
<i>Land use history</i>		
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	-

637 **Table 2** Common and scientific names, group membership, Freq.=frequency (number of plots
638 where a species is observed) and Abu.=abundance (sum of the detected maximum number of
639 a species) of the detected bird species. Grouping was carried out by nesting site (CN=cavity-
640 nester and NCN=Non-cavity nester) and rarity (R=Rare and C=Common). Bird species are
641 presented in taxonomical order.

Common name	Latin Name	Nesting Site	Rarity	Freq.	Abu.
stock dove	<i>Columba oenas</i>	CN	R	4	5
wood pigeon	<i>Columba palumbus</i>	NCN	C	12	12
turtle dove	<i>Streptopelia turtur</i>	NCN	C	3	3
wryneck	<i>Jynx torquilla</i>	CN	R	1	1
grey-headed woodpecker	<i>Picus canus</i>	CN	R	1	1
green woodpecker	<i>Picus viridis</i>	CN	R	2	2
black woodpecker	<i>Dryocopus martius</i>	CN	R	9	9
great spotted woodpecker	<i>Dendrocopos major</i>	CN	C	18	18
lesser spotted woodpecker	<i>Dendrocopos minor</i>	CN	R	2	2
wren	<i>Troglodytes troglodytes</i>	NCN	R	7	8
robin	<i>Erithacus rubecula</i>	NCN	C	30	52
blackbird	<i>Turdus merula</i>	NCN	C	13	15
song thrush	<i>Turdus philomelos</i>	NCN	C	30	46
mistle thrush	<i>Turdus viscivorus</i>	NCN	R	8	11
blackcap	<i>Sylvia atricapilla</i>	NCN	C	14	20
chiffchaff	<i>Phylloscopus collybita</i>	NCN	C	17	20
willow warbler	<i>Phylloscopus trochilus</i>	NCN	R	2	2
goldcrest	<i>Regulus regulus</i>	NCN	R	2	2
firecrest	<i>Regulus ignicapillus</i>	NCN	R	1	1
collared flycatcher	<i>Ficedula albicollis</i>	CN	R	4	5
long-tailed tit	<i>Aegithalos caudatus</i>	NCN	C	1	1
blue tit	<i>Cyanistes caeruleus</i>	CN	C	20	26
marsh tit	<i>Parus palustris</i>	CN	R	13	14
crested tit	<i>Parus cristatus</i>	CN	R	1	1
coal tit	<i>Parus ater</i>	CN	R	5	6
great tit	<i>Parus major</i>	CN	C	26	39
nuthatch	<i>Sitta europaea</i>	CN	C	14	14
treecreeper	<i>Certhia familiaris</i>	CN	R	16	18
short-toed treecreeper	<i>Certhia brachydactyla</i>	CN	C	3	4
golden oriole	<i>Oriolus oriolus</i>	NCN	C	6	6
starling	<i>Sturnus vulgaris</i>	CN	C	2	2
chaffinch	<i>Fringilla coelebs</i>	NCN	C	33	73
hawfinch	<i>Coccothraustes coccothraustes</i>	NCN	C	10	10

642

643 **Table 3** Explanatory variables of the redundancy analysis. The canonical axes explained
644 15.8% of variance (redundancy analysis is significant, $F=1.877$, $p=0.001$). For the included
645 variables, explained variance (Variance %) and F-statistics (F-value and p) are shown.

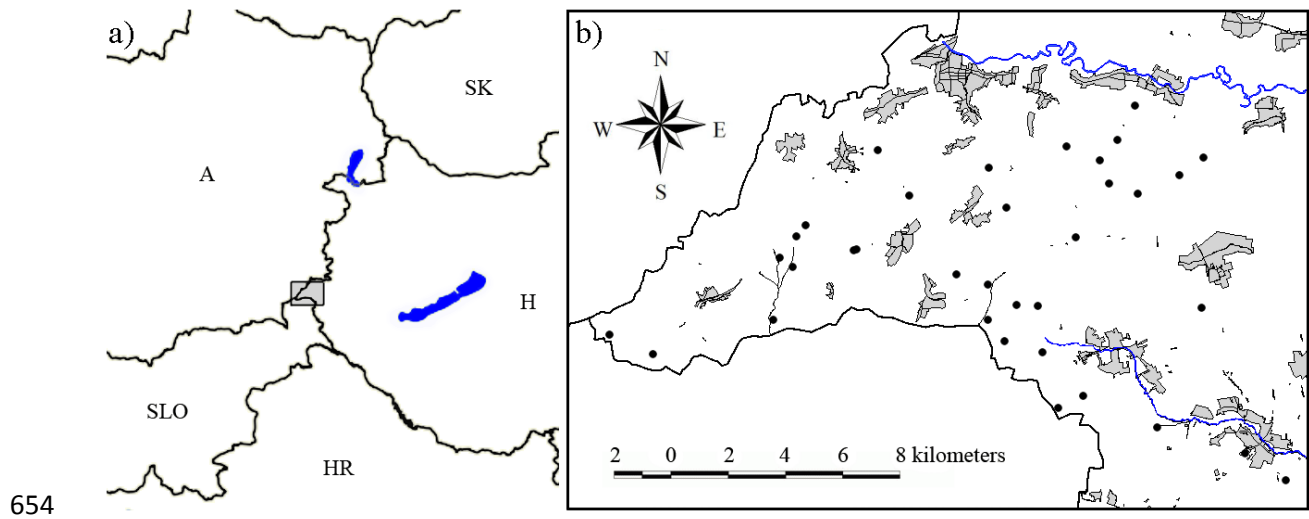
	Variance (%)	F-value	p
Mean DBH of trees	6.3	2.30	0.008
Cover of floor vegetation	4.7	1.74	0.043
Relative Scots pine volume	3.9	1.47	0.098

646

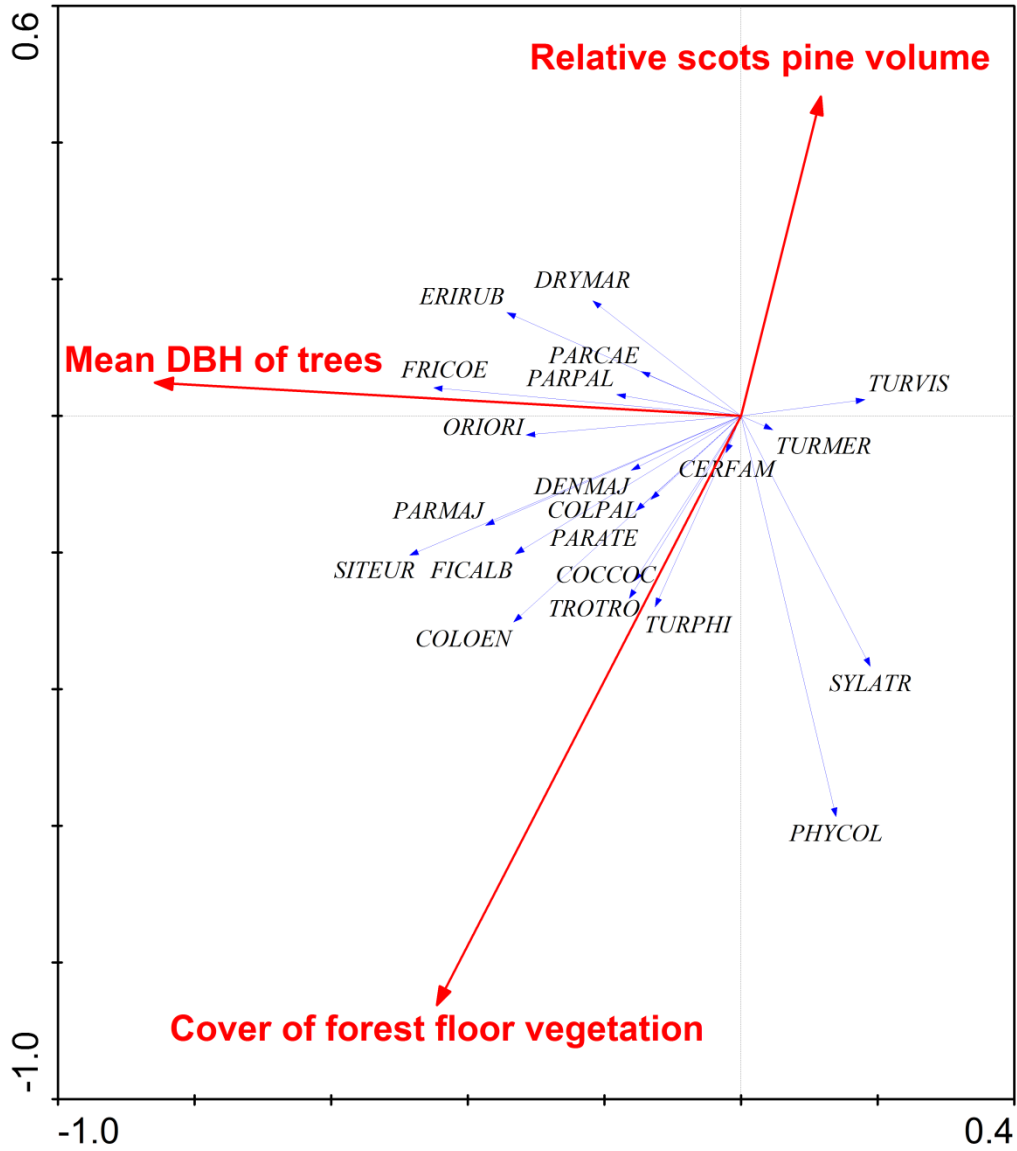
647 **Table 4** Explanatory variables of the general linear models. For the presented models,
 648 adjusted coefficient of determination (R^2) or direction of the parameters of the variables
 649 (Sign), explained variances (Var) and significance (F-statistics, $n=35$, $p<0.1$, * $p<0.05$, **
 650 $p<0.01$, *** $p<0.001$) are shown.

Explanatory variables	Sign	Var (%)	Explanatory variables	Sign	Var (%)
<i>Abundance of forest birds; $R^2=0.590$</i>			<i>Species richness of forest birds; $R^2=0.397$</i>		
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
<i>Abundance of cavity-nesters; $R^2=0.530$</i>			<i>Species richness of cavity-nesters; $R^2=0.429$</i>		
Mean DBH of trees	+	35.5***	Mean DBH of trees	+	26.5***
Volume of dead wood	+	17.5***	Volume of dead wood	+	16.3**
<i>Abundance of non-cavity nesters; $R^2=0.364$</i>			<i>Species richness of non-cavity nesters; $R^2=0.189$</i>		
Cover of floor vegetation	+	28.2***	Cover of floor vegetation	+	18.9**
Cover of soil	+	8.1			
<i>Abundance of common forest birds; $R^2=0.501$</i>			<i>Species richness of common forest birds; $R^2=0.288$</i>		
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			
<i>Abundance of rare forest birds; $R^2=0.294$</i>			<i>Species richness of rare forest birds; $R^2=0.298$</i>		
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

651 **Fig. 1** Geographical position of a) the study area in the region and b) the 35 plots (black dots)
652 included in the analysis. With blue, the main rivers and lakes of the region are shown for an
653 easier orientation. A: Austria, H: Hungary, HR: Croatia, SK: Slovakia, SLO: Slovenia.



655 **Fig. 2** Ordination plot of the first and second axes of redundancy analysis, bird species and
 656 significant explanatory variables are shown. Codes of bird species are derived from the first
 657 three letters of their genus and their species names (see Table 1).



658

659 **Electronic supplementary material**

660

661 **Appendix 1** Correlation coefficients among environmental variables. Significant values

662 ($p < 0.1$, $df = 34$) are bold.

663

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

665 Significant values ($p < 0.1$, $df = 34$) are bold.