



Tall, large-diameter trees and dense shrub layer as key determinants of the abundance and composition of bird communities in oak-dominated forests

Mariann Komlós¹ · Zoltán Botta-Dukát¹ ·
János Bölöni¹ · Réka Aszalós¹ · Katalin Veres¹ ·
Dániel Winkler² · Gábor Ónodi^{3,4}

Received: 29 September 2023 / Accepted: 4 December 2023
© The Author(s) 2024

Abstract Increasing human activity is altering the structure of forests, which affects the composition of communities, including birds. However, little is known about the key forest structure variables that determine the richness of bird communities in European temperate oak forests. We, therefore, aimed to identify key variables in these habitats that could contribute to the design of management strategies for forest conservation by surveying 11 oak-dominated forest sites throughout the mid-mountain range of Hungary at 86 survey points to reveal the role of different compositional and structural variables for forest stands that influence the breeding bird assemblages in the forests at the functional group and individual species levels. Based on decision tree modelling, our results showed that the density of trees larger

than 30 cm DBH was an overall important variable, indicating that large-diameter trees were essential to provide diverse bird communities. The total abundance of birds, the foliage-gleaners, primary and secondary cavity nesters, residents, and five specific bird species were related to the density of high trunk diameter trees. The abundance of shrub nesters was negatively influenced by a high density of trees over 10 cm DBH. The density of the shrub layer positively affected total bird abundance and the abundance of foliage gleaners, secondary cavity nesters and residents. Analysis of the co-dominant tree species showed that the presence of linden, beech, and hornbeam was important in influencing the abundance of various bird species, e.g., Eurasian Treecreeper (*Certhia familiaris*), Marsh Tit (*Poecile palustris*) and Wood Warbler (*Phylloscopus sibilatrix*). Our results indicated that large trees, high tree diversity, and dense shrub layer were essential for forest bird communities and are critical targets for protection to maintain diverse and abundant bird communities in oak-dominated forest habitats.

Project funding: This work was supported partly by LIFE4Oak Forests Project LIFE16NAT/IT/000245), the RRF 2.3.1 21 2022 00008 project, and the MERLiN project funded under the European Commission H2020 Programme (101036337 MERLiN H2020 LC GD 2020)

The online version is available at <http://www.springerlink.com>.

Corresponding editor: Tao Xu.

✉ Dániel Winkler
winkler.daniel@uni-sopron.hu

- ¹ Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány út 2–4, Vácrátót 2163, Hungary
- ² Institute of Wildlife Biology and Management, University of Sopron, Bajcsy-Zsilinszky Utca 4, Sopron 9400, Hungary
- ³ National Laboratory for Water Science and Water Security, HUN-REN Balaton Limnological Research Institute, Klebelsberg Kuno Utca 3, Tihany 8237, Hungary
- ⁴ HUN-REN Balaton Limnological Research Institute, Klebelsberg Kuno Utca 3, Tihany 8237, Hungary

Keywords Conservation ecology · Forest birds · Forest structure · Functional avian guilds · Hungary · Temperate oak forests

Introduction

Forests are the most biodiversity-rich terrestrial ecosystems on Earth (Clark and McLachlan 2003; Blicharska and Angelstam 2010). In temperate forests, stand structural diversity plays a key role in shaping forest-dwelling animal communities (James and Wamer 1982; Winkler 2005; Balestrieri et al. 2015; Hanzelka and Reif 2016). Natural oak forests are highly diverse habitats with various structural and compositional features, which can support highly

diverse bird communities (Proença et al. 2010; Lešo and Kropil 2015; Domokos and Domokos 2016; Ónodi et al. 2022). High structural and compositional diversity (tree species richness, canopy levels, shrub layer, standing and lying deadwood) offers important habitats for diverse avian communities (James and Wamer 1982; Roberge et al. 2008; Czeszczewik et al. 2013; Adrion 2016). Besides providing foraging and nesting habitats for ground- and shrub-nesting birds, dense understory also provides more feeding opportunities for birds that primarily forage in the canopy. Bird communities are explicitly sensitive to the quality of their habitat and to fine-scale structural variation and are able to respond immediately to habitat changes or loss and to the amount of deadwood (Walankiewicz et al. 2011; Czeszczewik et al. 2013, 2014; Ghadiri Khanaposhtani et al. 2013). However, classical clear-felling practices homogenize the forest by altering tree species richness, horizontal structure complexity, and the composition of the canopy, with fewer age classes of trees, the absence of large, old trees and dead trees, and fewer variant microhabitats (Frank and Szmorad 2014).

Diverse bird communities of large forest stands can include more sensitive forest specialists, indicating a healthy ecosystem, and vice versa: a decline in certain bird species is a sign of a decline in woody habitat (Fuller 1995). Because of these attributes and the fact that birds are easily detectable, birds can be highly effective indicators of habitat quality (Canterbury et al. 2000; Drever et al. 2008; Gregory and van Strien 2010) via qualitative and quantitative changes in the whole assemblages and in the guilds (Root 1967). As a result, studies on bird communities are widely used to examine the quality of numerous habitat types and monitor any changes (Hingston et al. 2014; Reif et al. 2022). However, most studies on bird responses to stand-level characteristics of forests have been done in the hemiboreal zone or in the Atlantic or Scandinavian region (Hinsley et al. 1996; Canterbury et al. 2000; Poulsen 2002; Proença et al. 2010; Bouvet et al. 2016) of Europe. Studies on oak forests, with a few exceptions (Székely and Moskát 1991; Lešo and Kropil 2015; Mag and Ódor 2015; Ónodi et al. 2022; Reif et al. 2022) are still scarce in the Central European region or in primeval forests (Walankiewicz et al. 2011; Czeszczewik et al. 2013). In particular, there is a lack of studies using a broad range of background vegetation variables to investigate the complex interconnections of forest ecosystems.

Our main goal was to reveal the role of different compositional and structural forest stand variables influencing the composition of breeding bird assemblages of Central European forests at the functional group and individual species levels. We hypothesized that more complex vegetation structure such as more diverse tree species composition, more large-diameter and taller trees, and the availability of various microhabitats (e.g., amount of deadwood) all

positively influence the total abundance and the abundance of individual guilds of breeding bird communities in oak forest stands. We also investigated the effects of the forest stand variables on each of the most frequent bird species.

Materials and methods

Study sites

We examined 11 oak-dominated forest sites located in mid-mountain areas (Bükk, Cserhát, Mátra, Börzsöny, and Pilis mountains, the Gödöllő hills, and the Balaton Uplands) in Hungary (Fig. 1). The stands are parts of the Natura 2000 network, with areas ranging between 42 and 376 ha (Fig. 1). At the study sites, the mean annual temperature is 8–10°C, and precipitation is 550–650 mm. The stand age ranges from 30 to 169 years, and the dominant forest types are mainly turkey oak (*Quercus cerris* L.)–sessile oak [*Quercus petraea* (Matt.) Liebl.] and sessile oak–hornbeam (*Carpinus betulus* L.) forests (see details in Table 1).

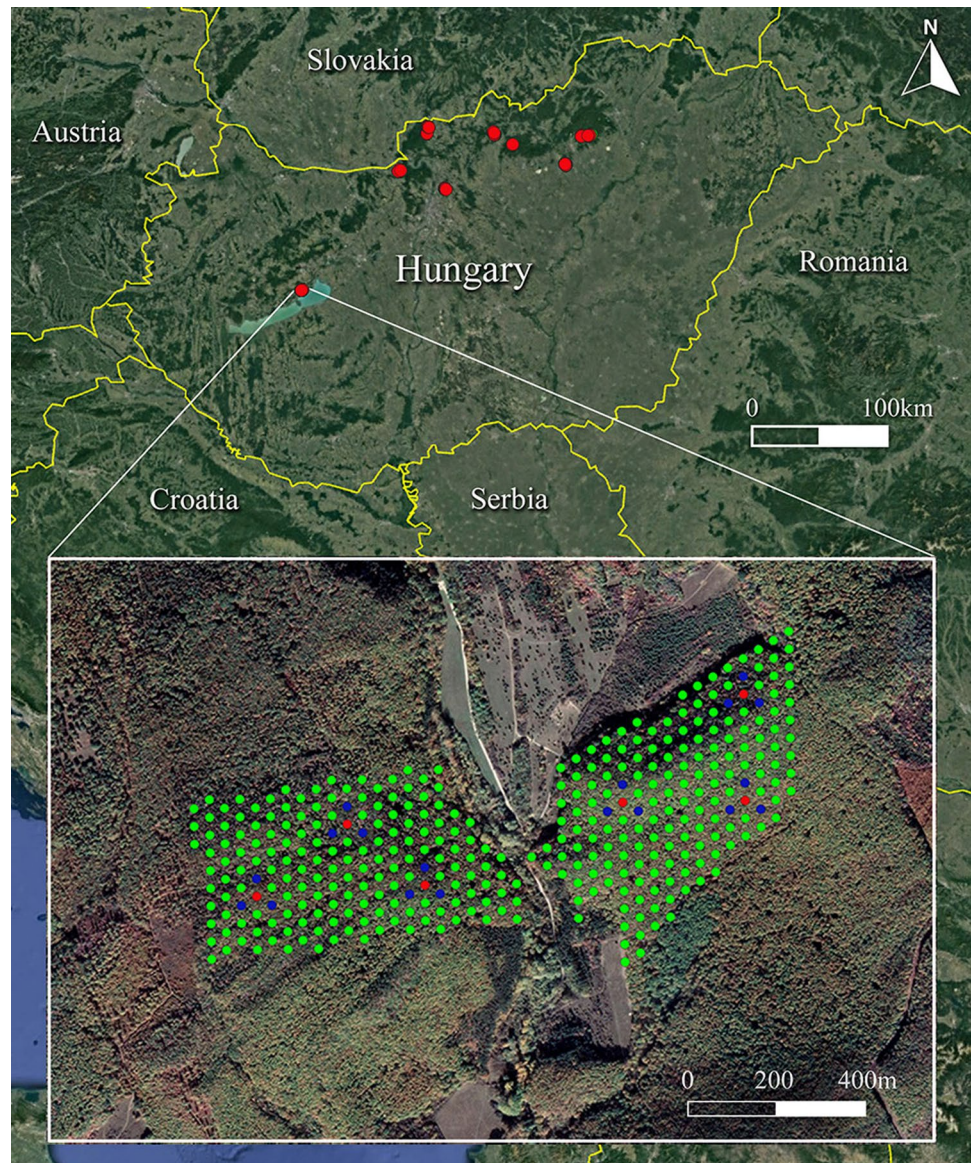
Study design

Forest stand survey

Our work is part of the baseline monitoring for the LIFE4Oak Forests Project (LIFE16NAT/IT/000245) on the effects of actions to enrich the structure of various forests on different taxonomic groups in oak-dominated hill forests in Hungary (Aszalós et al. 2019). In the framework of the LIFE project, we monitored forest stands in detail in an equilateral triangular grid pattern at 1430 stand survey points 40 m apart throughout the study sites. Plots were at least 40 m from the natural area boundary and main hiking trails and roads.

We established a circular plot with a 20 m radius (1256.6 m²) at each grid point (Fig. 2). To quantify species composition and stand structural characteristics, we recorded tree species and DBH of all woody species (DBH > 5 cm) within a circle with a radius (r) = 9 m if the stand was younger than 60 years or the mean DBH was lower than 20 cm. In other cases, the survey was done in a circle with r = 13 m. We also surveyed all the trees with DBH > 40 cm in a circle with r = 20 m. In each survey point, the height of 2–3 living dominant trees and all standing dead trees and snags were measured with a Haglöf (Långsele, Sweden) Vertex IV GS ultrasonic instrument and a T3 transponder. To estimate the abundance of the shrub layer in the forest stands, we sampled saplings (all woody species taller than 1.3 m, DBH < 5 cm) were sampled in a circle with r = 6 m and seedlings (all woody species 0.5 m < height < 1.3 m, DBH < 5 cm) in two nested plots of a circle with r = 2 m.

Fig. 1 Map of study sites and the 40-m equilateral triangle grid of forest stand survey points at one site. Red dots represent the central survey points of the point count stations; blue dots represent the three surrounding stand survey points



Hereafter, any mention of the shrub layer refers to the seedlings and saplings. The number of every woody species in each circle was recorded.

We estimated the amount of lying deadwood with the line intercept sampling method according to Ståhl et al. (2001). We established three transects (20 m long each) radiating from the center of the survey plot in the directions of 0° , 120° , and 240° . Each intersection of the transect and any lying deadwood (width ≥ 5 cm, longer than 0.5 m) was counted as a record, and the diameter of any lying deadwood crossing the lines was recorded. We recorded microhabitats on each measured tree based on Kraus et al. (2016); the simplified categories were exposed heartwood, dendrothelms and stump cavities, trunk cavities, bark pockets, bark loss, exposed sapwood, and stumps.

Bird censuses

Point count stations (in total 86) were appointed on the 40 equilateral triangle grids with 40 m side. Each point was at least 240 m from another and at least 80 m from the forest edge. A maximum of 10–11 points were placed in one study site based on the terrain. We used the average data of four stand survey points for every point count station: one in the center of each point count station and the three neighbouring stand survey points (Fig. 1). After a 3-min waiting period, to mitigate any disturbance caused by an approaching observer, the species of each bird seen or heard within 10 min was recorded. We excluded birds that flew over the sites. At every point, we recorded each bird that occurred in a circle of $r=50$ m. There were three visits from March to June 2019, with about a month between each visit per site. Visits

Table 1 Main characteristics of the examined forest areas

Study sites	Location	Area (ha)	Altitude (m a.s.l.)	No. survey points	No. bird points	Dominant forest type
Bükkzsérc	Bükk Mts	60.6	250–450	80	4	Pannonian-Balcanic turkey oak (<i>Quercus cerris</i>)–sessile oak (<i>Q. petraea</i>) (56%)
Cserépfalu	Bükk Mts	89.9	150–350	130	6	Pannonian-Balcanic turkey oak–sessile oak (56%)
Kerecsend	Bükk Mts	118	150–250	140	10	Euro-Siberian steppic woods with oak species (<i>Quercus</i> spp.) (58%)
Garáb	Cserhát Mts	42.4	350–550	60	7	Pannonic woods with sessile oak and hornbeam (<i>Carpinus betulus</i>) (42%)
Mátraszőlős	Cserhát Mts	72.9	300–400	100	8	Pannonian-Balkan turkey oak–sessile oak forests (49%), Pannonic woods with sessile oak and hornbeam (46%)
Mátraszentimre-Fallóskút	Mátra Mts	48.2	600–700	66	7	Pannonic woods with sessile oak and hornbeam (59%)
Diósjenő	Börzsöny Mts	55.1	250–350	70	6	Pannonic woods with sessile oak and hornbeam (52%)
Nagyoroszi	Börzsöny Mts	77.8	150–350	116	10	Pannonic woods with sessile oak and hornbeam (48%) and the Pannonian-Balcanic turkey oak–sessile oak (41%)
Esztergom	Pilis Mts	375.8	0–450	447	12	Pannonic woods with sessile oak and hornbeam (36%), Pannonian woods with downy oak (<i>Q. pubescens</i>) (33%)
Fót	Gödöllő Hills	93.4	150–250	125	10	Pannonian woods with downy oak (60%) and sub-pannonic steppic grassland (10%)
Balatonfüred-Koloska	Balaton Uplands	51.1	150–350	100	6	Pannonic woods with sessile oak and hornbeam (35%) and Pannonian woods with downy oak (35%)

were made in opposite directions to mitigate the effects of daily bird activity, and birds were counted from dawn until late morning when there was no heavy rain or wind. Among the data collected at each point, we only analysed the maximum abundance of each species.

Bird guilds

From all species recorded during the surveys, we created functional specialization guilds based on information from Wesolowski et al. (2015), Domokos and Domokos (2016), and Ónodi et al. (2022) (Table 2).

We classified the species into three main guild types (foraging, nesting, and migration guilds, respectively). Guilds based on foraging strategies included granivore species ($N=5$), ground insectivore species ($N=10$), bark insectivore species ($N=7$), foliage-gleaner species ($N=11$), flycatcher species ($N=2$), omnivores ($N=2$). We also distinguished species foraging outside of the forest ($N=8$). The nesting guilds comprised ground nester species ($n=9$), shrub nester species ($N=9$), canopy nester species ($N=9$), primary cavity nesters (cavity excavator species) ($N=6$), secondary cavity nesters ($N=12$), and nest parasite species ($N=1$). On the basis of migration strategies, we divided the bird species

into groups of residents ($N=23$), short and medium distance migrants ($N=10$), and long-distance migrants ($N=12$). The groups are exclusive for each characteristic; i.e., a species could be classified only into one group.

Statistical analyses

Most of our studied forest stand variables (Table 3) are averaged from the four-stand survey points. The maximum height and DBH were counted as the maximum value for survey points in the four stands. The structural heterogeneity index (SHI) was calculated as described by Sabatini et al. (2015). In this study, we considered birds living and foraging within the forest. Total bird abundance, species richness, individual guild, and species abundance were calculated as described by Czeszczewik et al. (2014). We only used the abundance of individual species present in at least 10% of all point count stations.

To avoid problems with multicollinearity of the explanatory variables, we calculated Spearman correlation coefficients. From the pairs of highly correlated ($r > 0.6$) (Hosmer and Lemeshow 1989) variables, we retained the ecologically more meaningful variables for further analyses.

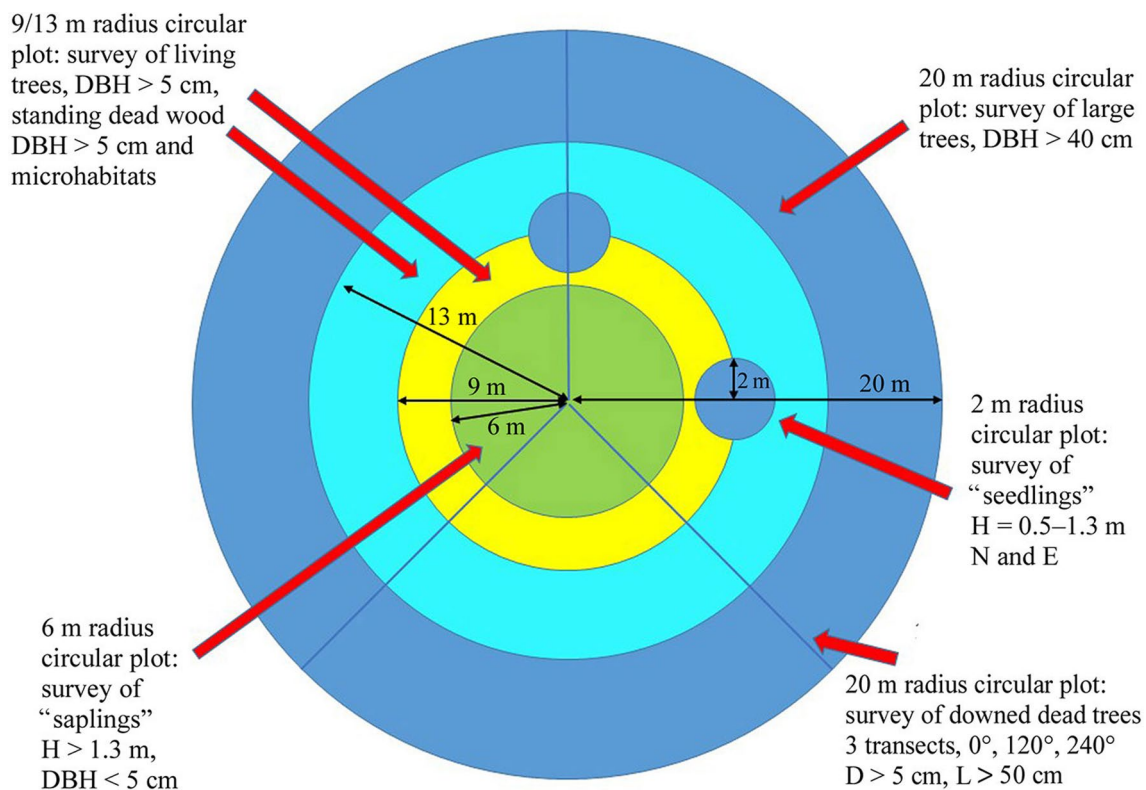


Fig. 2 Design for survey of forest stand characteristics at survey points used for point-count censuses of birds DBH = diameter at breast height; H = height; N = north; E = east; D = diameter; L = length

Decision tree modelling was used to explore relationships between the predictors (i.e., forest stand structure variables) and the occurrence and abundance of bird species. Decision trees are nonparametric statistical methods that treat the predictors individually and can handle nonlinear relationships and large sets of mixed-type predictors (De'ath and Fabricius 2000; Crawley 2007). The results are easy to interpret and indicate the variable that significantly distinguishes classes (Crawley 2007). The decision tree models were fitted in the R 4.1.2 environment (R Core Team 2020) using the party package (version 1.3–13, Hothorn et al. 2006). The tree function was used to generate a binary decision tree and apply simple permutation tests at each recursive step. A level of $P < 0.05$ was considered a significant difference.

Results

Bird survey results

In total, we detected 45 bird species at the 86 point count stations of the 11 study sites. The five most-abundant species were the Great Tit (*Parus major*, $N = 195$), the Common Chiffchaff (*Phylloscopus collybita*, $N = 146$), the Eurasian Nuthatch (*Sitta europaea*, $N = 111$), the European

Robin (*Erithacus rubecula*, $N = 107$), and the Great Spotted Woodpecker (*Dendrocopos major*, $N = 93$). Species richness ranged from 24 (at Diósjenő) to 34 species (at Cserépfalu).

Guild-specific relationships

Only significant results are presented here. For the total bird abundance, the density of trees over 30 cm DBH was the primary predictor variable (Fig. 3a); total abundance of birds was higher where the density of trees over 30 cm DBH was above 128 individuals per hectare. Where the amount of trees over 30 cm DBH was lower, the abundance of birds depended on the stem number in the shrub layer.

The foliage-gleaner guild was primarily affected by the same two variables: both higher DBH and a denser shrub layer increased their abundance (Fig. 3b).

The high density of trees with DBH over 10 cm lowered the abundance of shrub nesters (Fig. 3c). The abundance of primary cavity nesters depended on higher diameter trees (Fig. 3d), while for secondary cavity nesters, a dense shrub layer was also determinant (Fig. 3e).

The density of trees larger than 30 cm in diameter and of the shrub layer were significant explanatory variables, indicating an increase in the abundance of resident birds (Fig. 3f).

Table 2 List of observed bird species and their functional guild classifications

Common name	Scientific name	Foraging guild	Nesting guild	Migration guild
Common pheasant	<i>Phasianus colchicus</i>	Outside the forest	Ground nester	Resident
Common cuckoo	<i>Cuculus canorus</i>	Foliage gleaner	Nest parasite	Long distance
Stock dove	<i>Columba oenas</i>	Outside the forest	Secondary cavity nester	Short distance
Common wood pigeon	<i>Columba palumbus</i>	Outside the forest	Secondary cavity nester	Short distance
European turtle dove	<i>Streptopelia turtur</i>	Outside the forest	Shrub nester	Long distance
Eurasian collared dove	<i>Streptopelia decaocto</i>	Outside the forest	Canopy nester	Resident
Lesser spotted eagle	<i>Clanga pomarina</i>	Outside the forest	Canopy nester	Long distance
Common buzzard	<i>Buteo buteo</i>	Outside the forest	Canopy nester	Resident
Eurasian hoopoe	<i>Upupa epops</i>	Ground insectivore	Secondary cavity nester	Long distance
Great spotted woodpecker	<i>Dendrocopos major</i>	Bark insectivore	Primary cavity nester	Resident
Middle spotted woodpecker	<i>Leiopicus medius</i>	Bark insectivore	Primary cavity nester	Resident
Lesser spotted woodpecker	<i>Dryobates minor</i>	Bark insectivore	Primary cavity nester	Resident
Eurasian green woodpecker	<i>Picus viridis</i>	Ground insectivore	Primary cavity nester	Resident
Grey-faced woodpecker	<i>Picus canus</i>	Ground insectivore	Primary cavity nester	Resident
Black woodpecker	<i>Dryocopus martius</i>	Bark insectivore	Primary cavity nester	Resident
Eurasian golden oriole	<i>Oriolus oriolus</i>	Foliage gleaner	Canopy nester	Long distance
Common raven	<i>Corvus corax</i>	Omnivore	Canopy nester	Resident
Eurasian jay	<i>Garrulus glandarius</i>	Omnivore	Canopy nester	Resident
Marsh tit	<i>Poecile palustris</i>	Foliage gleaner	Secondary cavity nester	Resident
Blue tit	<i>Cyanistes caeruleus</i>	Foliage gleaner	Secondary cavity nester	Resident
Great tit	<i>Parus major</i>	Foliage gleaner	Secondary cavity nester	Resident
Woodlark	<i>Lullula arborea</i>	Ground insectivore	Ground nester	Short distance
Common chiffchaff	<i>Phylloscopus collybita</i>	Foliage gleaner	Ground nester	Short distance
Wood warbler	<i>Phylloscopus sibilatrix</i>	Foliage gleaner	Ground Nester	Long distance
Willow warbler	<i>Phylloscopus trochilus</i>	Foliage gleaner	Ground nester	Long distance
Long-tailed tit	<i>Aegithalos caudatus</i>	Foliage gleaner	Canopy nester	Resident
Eurasian blackcap	<i>Sylvia atricapilla</i>	Foliage gleaner	Shrub nester	Short distance
Garden warbler	<i>Sylvia borin</i>	Foliage gleaner	Shrub nester	Long distance
Eurasian nuthatch	<i>Sitta europaea</i>	Bark insectivore	Secondary cavity nester	Resident
Short-toed treecreeper	<i>Certhia brachydactyla</i>	Bark insectivore	Secondary cavity nester	Resident
Eurasian treecreeper	<i>Certhia familiaris</i>	Bark insectivore	Secondary cavity nester	Resident
Eurasian wren	<i>Troglodytes troglodytes</i>	Ground insectivore	Ground nester	Resident
Common blackbird	<i>Turdus merula</i>	Ground insectivore	Shrub nester	Resident
Song thrush	<i>Turdus philomelos</i>	Ground insectivore	Shrub nester	Short distance
Spotted flycatcher	<i>Muscicapa striata</i>	Flycatcher	Secondary cavity nester	Long distance
European robin	<i>Erithacus rubecula</i>	Ground insectivore	Ground nester	Short distance
Common nightingale	<i>Luscinia megarhynchos</i>	Ground insectivore	Shrub nester	Long distance
Collared flycatcher	<i>Ficedula albicollis</i>	Flycatcher	Secondary cavity nester	Long distance
Common starling	<i>Sturnus vulgaris</i>	Outside the forest	Secondary cavity nester	Short distance
Tree pipit	<i>Anthus trivialis</i>	Ground insectivore	Ground nester	Long distance
Common chaffinch	<i>Fringilla coelebs</i>	Granivore	Canopy nester	Short distance
Hawfinch	<i>Coccothraustes coccothraustes</i>	Granivore	Canopy nester	Short distance
European greenfinch	<i>Chloris chloris</i>	Granivore	Shrub nester	Resident
European goldfinch	<i>Carduelis carduelis</i>	Granivore	Shrub nester	Resident
Yellowhammer	<i>Emberiza citrinella</i>	Granivore	Ground nester	Resident

Table 3 Studied variables and their minimum (Min) and maximum (Max) values

Factor		Min	Max
Project	Stand age	30.00	169.00
	Maximum height (m)	12.00	39.40
	Density, DBH > 0 cm (stems/ha)	535.71	8821.27
	Density, DBH > 10 cm (stems/ha)	147.33	1778.21
	Density, DBH > 20 cm (stems/ha)	0.00	559.99
	Density, DBH > 30 cm (stems/ha)	0.00	296.58
	Density, DBH > 40 cm (stems/ha)	0.00	141.25
	Density, DBH > 50 cm (stems/ha)	0.00	63.66
	Mean DBH (cm)	13.21	42.18
	Max DBH (cm)	19.00	105.00
	No. of DBH classes	4.00	16.00
	DBH < 5 cm (shrub layer) (stems/ha)	9.82	6145.15
	Standard deviation DBH 0 – 10 cm	50.08	3764.15
	Standard deviation DBH > 10 cm	9.81	993.84
	Basal area of standing dead wood, trees (m ² /ha)	0.00	3.48
	Basal area of standing dead wood, snags (m ² /ha)	0.00	4.34
	No. of large standing dead wood DBH > 30 cm (stems/ha)	0.00	23.54
	Lying dead wood volume (m ³ /ha)	1.81	66.45
	SHI	0.14	0.58
	Number of tree species DBH > 10 cm (stems/ha)	1.00	10.00
Tree species	Oak species (m ² /ha)	0.00	37.61
	Not oak species (m ² /ha)	0.00	100.00
	Pine species (m ² /ha)	0.00	26.52
	Linden species (m ² /ha)	0.00	25.42
	Ash species (m ² /ha)	0.00	22.01
	Maple species (m ² /ha)	0.00	9.63
	Beech + Hornbeam (m ² /ha)	0.00	19.75
	Beech (m ² /ha)	0.00	13.67
	Hornbeam (m ² /ha)	0.00	16.11
	Willow and Poplar species (m ² /ha)	0.00	11.43
	Fruits (m ² /ha)	0.00	8.16
	Shrub species (m ² /ha)	0.00	10.18
	Microhabitats	Wet stumps cavities (no./ha)	0.00
Dry stump cavities (no./ha)		0.00	157.19
Trunk cavities (no./ha)		0.00	84.87
Bark pockets (no./ha)		0.00	88.42
Bark loss and exposed sapwood (no./ha)		0.00	255.43
Old stumps (no./ha)		0.00	195.40
New stumps (no./ha)		0.00	18.83

SHI structural heterogeneity index

Species-specific relationships

The stand variables had the following effects on bird species: the Blue Tit (*Cyanistes caeruleus*) was more abundant where the density of trees over 30 cm DBH was remarkably high (Fig. 4a). The Middle Spotted Woodpecker (*Leiopicus medius*) or Collared Flycatcher (*Ficedula albicollis*) only appeared where the density of trees over 30 cm DBH was above 106 (Fig. 4b) and 134

(Fig. 4c) individuals per hectare, respectively. When the density of large DBH trees was lower than 154 individuals per hectare, Marsh Tit's (*Poecile palustris*) occurrence depended on the presence of hornbeam (*C. betulus*) (Fig. 4d). Besides the diameter of trees, the presence of beech (*Fagus sylvatica*) and hornbeam trees was also a significant factor for Wood Warblers (Fig. 4e). The high density of trees larger than 10 cm DBH lowered the abundance of the Common Blackbird (*Turdus merula*) (Fig. 4f). The

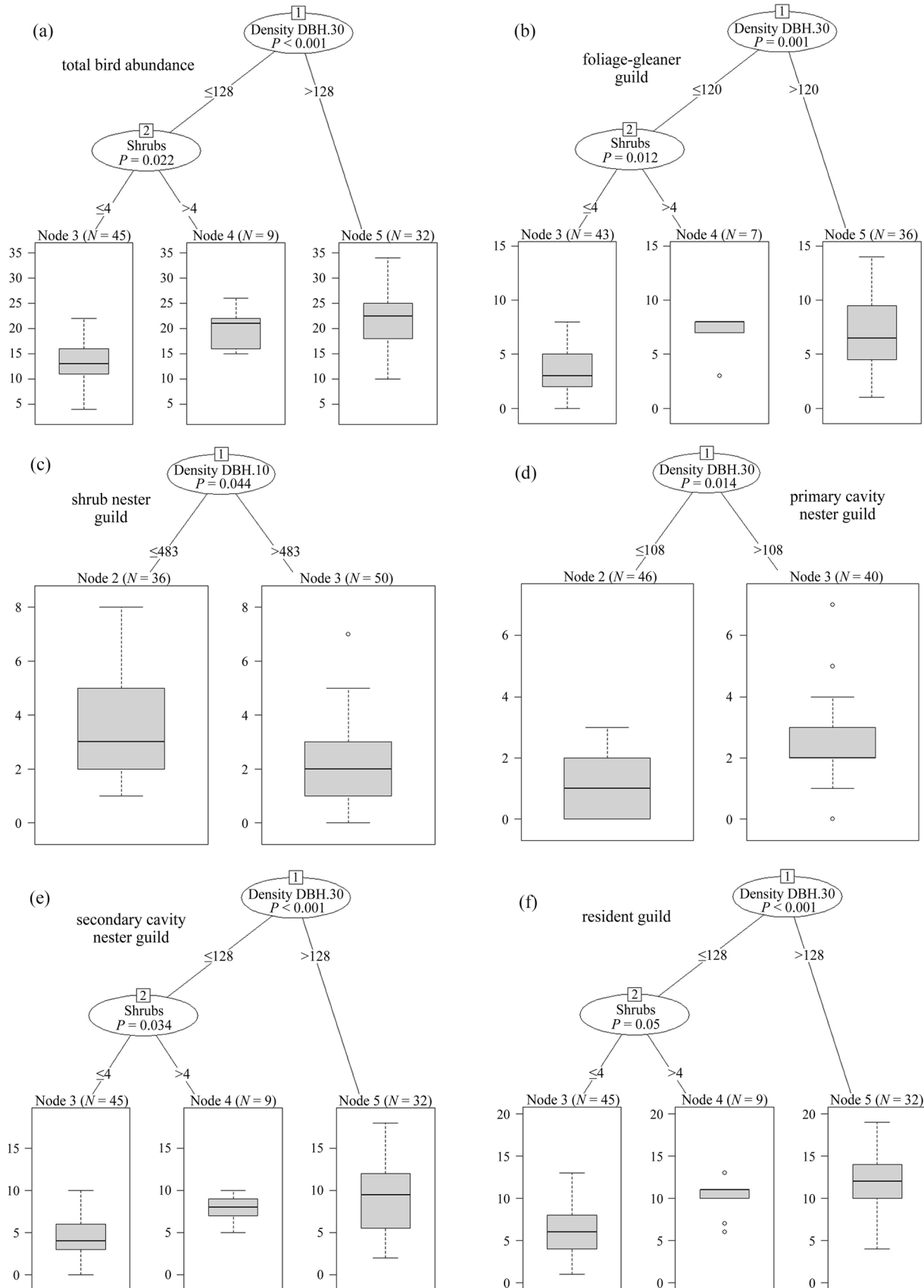


Fig. 3 Classification tree models of forest structure and composition variables influencing the abundance of forest bird guilds. Each split is described with the predictor used, the Bonferroni-corrected Type I error rate (P -value) of the split and the values at which the separation occurs. At each node, the number of observations (N) is given with the values of the response variables (= abundance) below. Total abundance of **a** All birds, **b** Foliage gleaners, **c** Shrub nesters, **d** Primary cavity nesters, **e** Secondary cavity nesters, **f** Residents. In the box plots (analysed for differences using Tukey's test), the horizontal line represents the median, the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively, the whiskers represent the lowest and highest values, and circles represent outliers. DBH.10, DBH.30: diameter at breast height over 10 cm and over 30 cm, respectively

abundance of the Common Chiffchaff was significantly higher where the shrub layer was substantial (Fig. 4g). Where the maximum height of trees in the forest stand was above 31 or 26 m, respectively, the abundance of Common Chaffinch (*Fringilla coelebs*) (Fig. 4h) and Eurasian Nuthatch (Fig. 4i) increased. The presence of linden tree species (*Tilia* spp.) was essential for the occurrence of the Eurasian Treecreeper (*Certhia familiaris*) (Fig. 4j).

Discussion

In this study of the effects of forest stand characteristics on bird assemblages, functional guilds and species, we assumed that birds are primarily affected by stand structural components (Laiolo et al. 2004). Birds generally are less abundant at increasing tree density, but their abundance is higher when the density of large-diameter trees is higher (Bereczki et al. 2014; Czeszczewik et al. 2014; Balestrieri et al. 2015; Bouvet et al. 2016). Regarding the overall tree density, we also found negative trends in the density of all trees over 10 cm trunk diameter in relation to the abundance of shrub nesters and the Common Blackbird. For woody stems above 10 cm as trees, with higher tree density, less light reaches the undergrowth, and the shrub layer is less developed; thus, shrub nesters such as the Common Blackbird, are present in lower abundance (Ghadiri Khanaposhtani et al. 2012). The density of the shrub layer affected the abundance of all birds, the foliage gleaners, the secondary cavity nesters and the resident guild. This background variable also influenced the Common Chiffchaff, which is a foliage-gleaner that prefers thick understory (Haraszthy 2019).

The abundance of all birds, foliage gleaners, primary and secondary cavity nesters, residents, and five species were connected to the density of relatively larger trunk diameter trees (> 30 cm). Mature large trees are known for supporting diverse bird communities (Roberge et al. 2008; Ghadiri Khanaposhtani et al. 2013). Mag and Ódor (2015) also demonstrated that the diameter of their studied trees was the most important explanatory variable for breeding

bird communities in similar Hungarian deciduous forests, supporting our results. Older, thicker trees develop rougher bark surfaces, crevices, cracks, and more extensive canopies with dead and dying parts, thus harboring a higher diversity of arthropods (Jackson 1979; Czeszczewik et al. 2014; Balestrieri et al. 2015; Stański et al. 2020). The abundant invertebrates in such trees can support a wide variety of insectivorous birds (Czeszczewik et al. 2014). However, in other studies (Poulsen 2002; Rosenvald et al. 2011; Bereczki et al. 2014), tree size heterogeneity rather than larger diameter was the most important explanatory variable for insectivorous birds.

For cavity nesters, the diameter of potential nest trees was significant; both primary and secondary cavity nesters were associated with the number of older, thicker tree individuals, as underlined by our results (Hardersen 2004; Cockle et al. 2011; Hebda et al. 2017). Larger diameter trees can be important for nesting or roosting; hence, cavity excavators can benefit from sufficient wall thickness and cavity volume even in younger stands with sporadic presence of trees of greater diameter (Remm et al. 2006). In Romanian deciduous forests, Great Spotted Woodpeckers preferred oak trees above 30 cm as nesting trees (Domokos and Cristea 2014). In our study, Middle Spotted and Black Woodpeckers chose thicker trees for nesting, above 40 and 60 cm, respectively. In the meta-analysis of Gutzat and Dormann (2018) of 51 European and North American studies on habitat utilization of cavity-nesting birds, the minimal DBH of cavity trees was 20 cm (mean 35.6 cm), but their results suggested that relatively larger trees would be selected for nesting only if the mean diameter in the forest is low, which might explain why some studies on overall older forests did not confirm this association (Milne and Hejl 1989). Seavy et al. (2012) also suggested that the importance of DBH of selected cavity trees decreases with the increasing diameter of available trees. Komlós et al. (2021) found an association of the frequency of woodpecker-foraging signs with increasing diameter and height, and Stański et al. (2020) showed that Great Spotted Woodpeckers also prefer taller trees with larger diameter. Cavity-nesting species respond positively to the increased density of thicker trees (Delahaye et al. 2010; Hebda et al. 2016), as we also found for the cavity-nesting Middle Spotted Woodpecker, Blue Tit, Marsh Tit and Col-lared Flycatcher.

Winkler (2005) stated that the proportion of resident bird species tended to increase with the age of the forest stand. This phenomenon can be related to our result on resident birds, which mainly consisted of cavity-nesting species that were associated with the density of thicker trees, indicating that the stands are older and more developed. Ónodi et al. (2022) also found a higher abundance of resident birds in oak stands with larger stem diameters in a study comparing

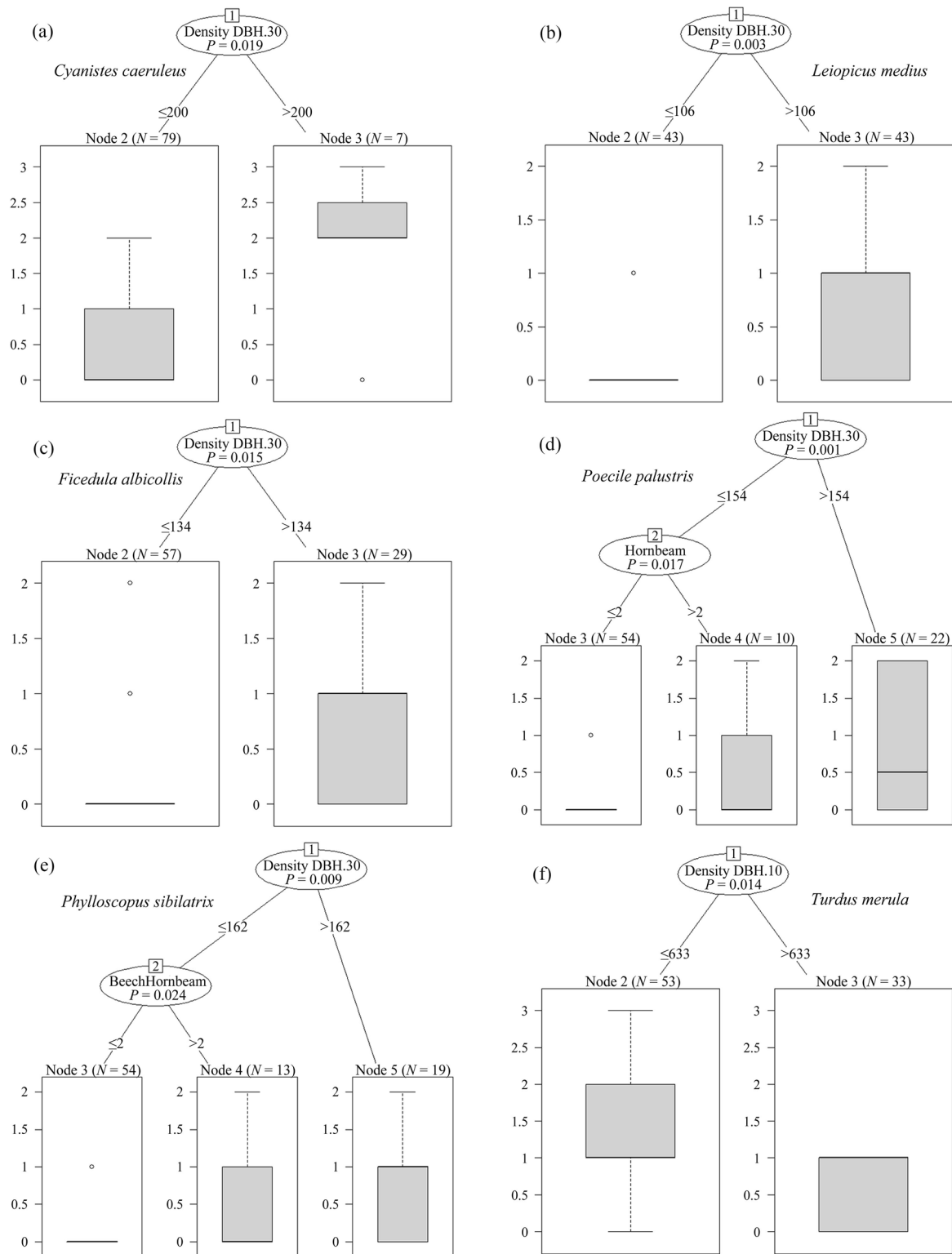


Fig. 4 Classification tree models of forest structure and composition variables influencing the abundance of forest bird species. Each split is described with the predictor used, the Bonferroni-corrected Type I error rate (P -value) of the split, and the values at which the separation occurs. At each node, the number of observations (N) is given with the values of the response variables (=abundance) below. Abundance of **a** Blue tit, **b** Middle spotted woodpecker, **c** Collared flycatcher, **d** Marsh tit, **e** Wood

warbler, **f** Common blackbird, **g** Common chiffchaff, **h** Common chaffinch, **i** Eurasian nuthatch, **j** Eurasian treecreeper. In the box plots (analysed using Tukey's test), the horizontal line represents the median value, the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively, the whiskers represent the lowest and highest values, and circles represent outliers. DBH.10, DBH.30: diameter at breast height over 10 cm and over 30 cm, respectively; MaxH, maximum tree height

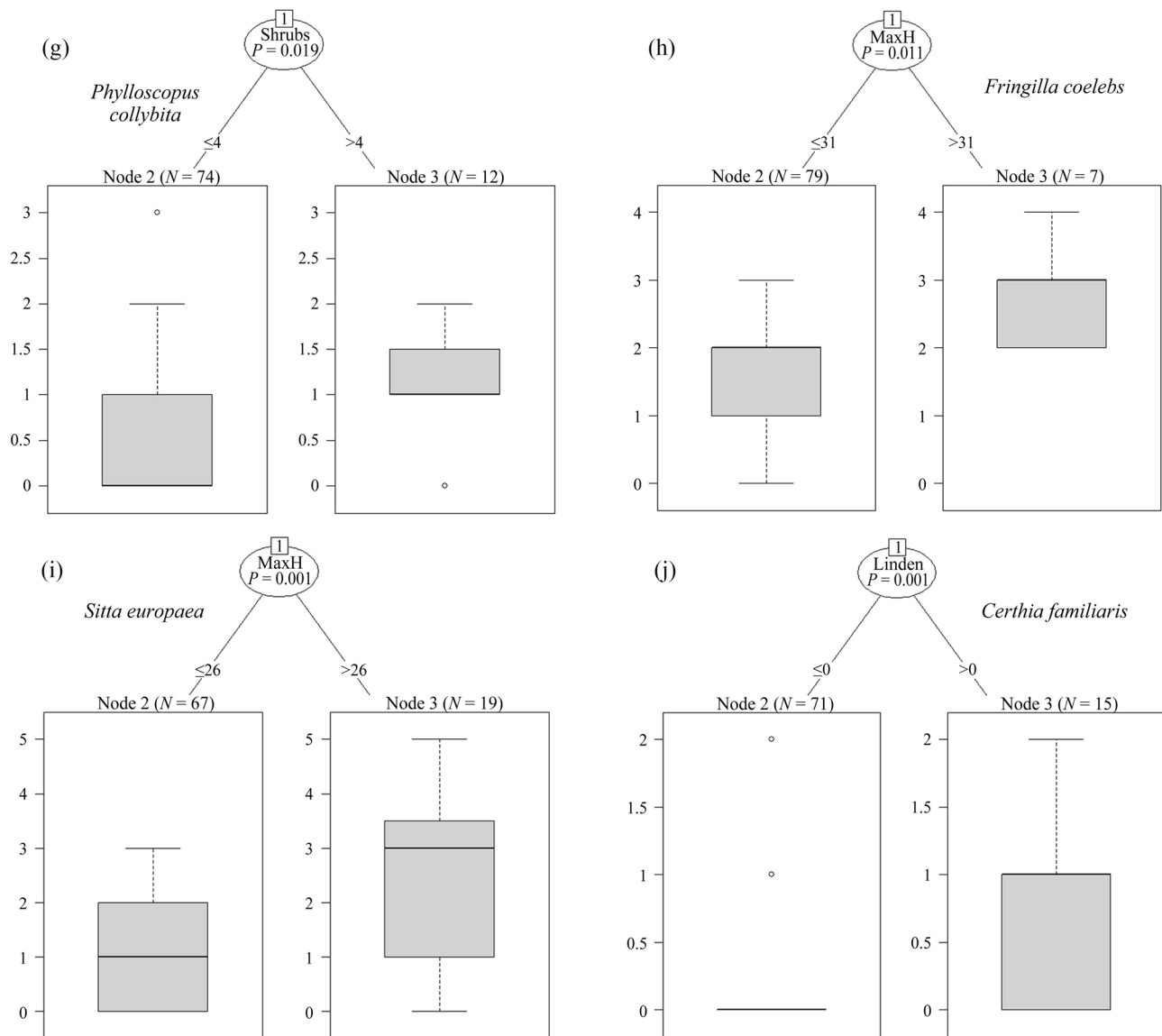


Fig. 4 (continued)

middle-aged managed oak stands with remnants of old oak forest steppes.

In our study, maximum tree height was an important factor for two species, Eurasian Nuthatch and Chaffinch. Trees taller than 26 m influenced the abundance of Eurasian Nuthatch. In our study, oak species dominated the upper canopy layer. Oak trees have a complex bark structure, providing suitable habitats for birds feeding on and from under the bark (Proença et al. 2010; Robles et al. 2011; Domokos and Cristea 2014; Porro et al. 2020; Komlós et al. 2021; Ónodi et al. 2021; Stański et al. 2021). In a study on the Hyrcanian deciduous forests of Iran, Khosroshahi et al. (2011) found that the density of tall trees was a significant predictor and had a positive effect on the abundance of the Eurasian Nuthatch. We found that a higher abundance of Chaffinches was

also associated with tree height, as we found significantly more individuals where the maximum tree height was over 31 m. According to Krams (2001), Chaffinches prefer taller trees in mature forests to sing from just under the canopy, lowering predation risk.

Tree species richness is also crucial for avifauna (Ellison et al. 2005; da Silva et al. 2021; Kaushik et al. 2022). In habitats dominated by oak species, the presence of secondary tree species can be essential for increasing biodiversity. Such tree species are foraging sources for numerous defoliating caterpillars, which are essential for the foliage-gleaning guild consisting of numerous pest-controlling species (Bereczki et al. 2014; Czeszczewik et al. 2014; Eötvös et al. 2021). In this regard, we have found that the presence of

secondary tree species, such as linden, beech, and hornbeam, was important for various bird species.

We also found an association between the presence of linden trees and the abundance of Eurasian Treecreepers. In a mixed deciduous temperate forest, Schönfeld (1983) investigated the breeding success and nesting tree selection of the two European species of treecreepers. He found that after the sessile oak, linden was the second most preferred tree species by the Eurasian Treecreeper in terms of both probable and proven nesting.

Besides the density of large-diameter trees, beech, and hornbeam was also important for the Wood Warbler. Wood Warblers are known to prefer beech forests (Glutz von Blotzheim and Bauer 1991) and other tall, well-developed mesophilic deciduous or even mixed coniferous stands with a closed canopy and less-dense shrub and herb layers (Broughton et al. 2020). Nevertheless, Wesolowski et al. (2009) stated that the availability of food sources or the low predator risk seems more important for Wood Warblers choosing their nest sites than the fine structure or composition of their immediate surroundings.

We have found a positive relationship between the abundance of Marsh Tits and incidence of hornbeam. On the other hand, Broughton et al. (2012) stated that tree species composition is less important than structural variables to Marsh Tits, but Hinsley et al. (2007) found that understory characteristics were more significant than canopy characteristics. Nevertheless, we found no particular relationships with structural variables.

Our study revealed that deadwood did not significantly impact bird abundance. However, various manifestations of deadwood are clearly essential for woodpeckers, hole-nesting birds (Cockle et al. 2011; Czeszczewik et al. 2013; Kilgo and Vokovich 2014; Aszalós et al. 2020) and other bird species (Mag and Ódor 2015). In our investigation, the stands are relatively poor in standing and lying deadwood compared to more natural stands or old-growth forests, so their impact on the abundance of the breeding community is not substantial.

Conclusion

According to our results, to maintain a diverse forest bird community, a key structural characteristic to conserve is a high density of trees above 30 cm in diameter, a key determinant for the total abundance of birds, the abundance of foliage-gleaners, primary and secondary cavity nesters, residents, and some single species. Tall trees and a dense shrub layer were also determinants for the total bird abundance and abundance of shrub nesters, foliage gleaners, secondary cavity nesters, and residents. We found that the presence of

secondary tree species creates unique biodiversity hotspots, particularly for foliage-gleaner species. Protecting these forest elements with appropriate management practices is crucial to maintain diverse, abundant bird communities in oak-dominated forest habitats.

Acknowledgements This study was part of and funded by a detailed, conservation-oriented management project (LIFE4Oak Forests Project, LIFE16NAT/IT/000245), which is focused on the structural enrichment of certain oak-dominated woodlands in the Hungarian mountains through various management techniques. We express our gratitude for the essential supporting work of the colleagues of the Bükk, Balaton-felvidék, and Duna-Ipoly National Parks, and the fieldwork support of László Albert. The research for this article was carried out within the framework of the Széchenyi Plan Plus program with the support of the RRF 2.3.1 21 2022 00008 project, and the MERLiN project funded under the European Commission H2020 Programme (101036337-MERLiN-H2020-LC-GD-2020). The publication is also a part of the bilateral Austrian-Hungarian Joint Research Project RIMECO co-funded by the Austrian Science Fund (FWF) (I 5006) and the ANNOTKA (141884) grant.

Funding Open access funding provided by University of Sopron.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Adrian L (2016) Effects of structural heterogeneity of floodplain forests and hydrological dynamic on bird assemblages: a case study from the Donau-Auen National Park (Eastern Austria) Master of Science Thesis University of Vienna
- Aszalós R, Bölöni J, Frank T (eds.) (2019) Life 4 Oak Forests (LIFE16NAT/IT/000245)-Monitoring protocol-Deliverable of A2 Action. Centre for Ecological Research of the Hungarian Academy of Sciences, Vácrátót, Hungary, Available at: <http://www.life4oakforests.eu/project-outputs/>
- Aszalós R, Szigeti V, Harnos K, Csernák S, Frank T, Ónodi G (2020) Foraging activity of woodpeckers on various forms of artificially created deadwood. *Acta Ornithol* 55(1):63–76. <https://doi.org/10.3161/00016454AO2020.55.1.007>
- Balestrieri R, Basile M, Posillico M, Altea T, De Cinti B, Matteucci G (2015) A guild-based approach to assessing the influence of beech forest structure on bird communities. *Forest Ecol Manag* 356:216–223. <https://doi.org/10.1016/j.foreco.2015.07.011>
- Bereczki K, Ódor P, Csóka G, Mag Z, Báldi A (2014) Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. *Forest Ecol Manag* 327:96–105. <https://doi.org/10.1016/j.foreco.2014.05.001>

- Blicharska M, Angelstam P (2010) Conservation at risk: conflict analysis in the Białowieża Forest, a European biodiversity hotspot. *Int J Biodivers Sci Ecosyst Serv Manag* 6:68–74. <https://doi.org/10.1080/21513732.2010.520028>
- Bouvet A, Paillet Y, Archaux F, Tillon L, Denis P, Gilg O, Gosselin F (2016) Effects of forest structure, management and landscape on bird and bat communities. *Environ Conserv* 43(2):148–160. <https://doi.org/10.1017/S0376892915000363>
- Broughton RK, Hill RA, Freeman SN, Bellamy PE, Hinsley SA (2012) Describing habitat occupation by woodland birds with territory mapping and remotely sensed data: an example using the Marsh Tit (*Poecile palustris*). *Condor* 114(4):812–822. <https://doi.org/10.1525/cond.2012.110171>
- Broughton RK, Bubnicki JW, Maziarz M (2020) Multi-scale settlement patterns of a migratory songbird in a European primeval forest. *Behav Ecol Sociobiol* 74:128. <https://doi.org/10.1007/s00265-020-02906-0>
- Canterbury GE, Martin TE, Petit DR, Petit LJ, Bradford DF (2000) Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conserv Biol* 14(2):544–558. <https://doi.org/10.1046/j.1523-1739.2000.98235.x>
- Clark JS, McLachlan JS (2003) Stability of forest biodiversity. *Nature* 423(6940):635–638. <https://doi.org/10.1038/nature01632>
- Cockle KL, Martin K, Wesolowski T (2011) Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Front Ecol Environ* 9(7):377–382. <https://doi.org/10.1890/110013>
- Crawley MJ (2007) *The R Book*. John Wiley, Chichester, p 942. <https://doi.org/10.1002/9780470515075>
- Czeczczewik D, Walankiewicz W, Mitrus C, Tumiel T, Stański T, Sahel M, Bednarczyk G (2013) Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. *Bird Conserv Int* 23(4):414–425. <https://doi.org/10.1017/S0959270912000354>
- Czeczczewik D, Zub K, Stanski T, Sahel M, Kapusta A, Walankiewicz W (2014) Effects of forest management on bird assemblages in the Białowieża Forest. *Poland Iforest* 8(3):377–385. <https://doi.org/10.3832/ifor1212-007>
- da Silva BF, Pena JC, Viana-Junior AB, Vergne M, Pizo MA (2021) Noise and tree species richness modulate the bird community inhabiting small public urban green spaces of a Neotropical city. *Urban Ecosys* 24(1):71–81. <https://doi.org/10.1007/s11252-020-01021-2>
- De'athFabricius GKE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192. [https://doi.org/10.1890/0012-9658\(2000\)081\[3178:CARTAP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2)
- Delahaye L, Monticelli D, Lehaire F, Rondeux J, Claessens H (2010) Fine-scale habitat selection by two specialist woodpeckers occurring in beech and oak-dominated forests in southern Belgium. *Ardeola* 57:339–352. <https://doi.org/10.3161/000164510X551363>
- Domokos E, Cristea V (2014) Effects of managed forests structure on woodpeckers (Picidae) in the Niraj valley (Romania): woodpecker populations in managed forests. *North-West J Zool* 10(1):110–117
- Domokos E, Domokos J (2016) Bird communities of different woody vegetation types from the Niraj Valley, Romania. *Turk J Zool* 40:1–9. <https://doi.org/10.3906/zoo-1510-64>
- Drever MC, Aitken KEH, Norris AR, Martin K (2008) Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biol Conserv* 141:624–634. <https://doi.org/10.1016/j.biocon.2007.12.004>
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloepfel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3(9):479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Eötvös CB, Hirka A, Gimesi L, Lövei GL, Gáspár C, Csóka G (2021) No long-term decrease in caterpillar availability for invertivorous birds in deciduous forests in Hungary. *Forests* 12(8):1070. <https://doi.org/10.3390/f12081070>
- Frank T, Szomorad F (2014) *Védett erdők természetességi állapotának fenntartása és fejlesztése*. Rosalia kézikönyvek 2. Duna–Ipoly Nemzeti Park Igazgatóság, Budapest, p 160 (in Hungarian)
- Fuller RJ (1995) *Bird Life of Woodland and Forest*. Cambridge University Press, Cambridge, p 260
- Ghadiri Khanaposhtani M, Kaboli M, Karami M, Etemad V, Baniasadi S (2012) Effect of habitat complexity on richness, abundance and distributional pattern of forest birds. *Environ Manage* 50:296–303. <https://doi.org/10.1007/s00267-012-9877-7>
- Ghadiri Khanaposhtani M, Kaboli M, Karami M, Etemad V, Baniasadi S (2013) Effects of logged and unlogged forest patches on avifaunal diversity. *Environ Manage* 51:750–758. <https://doi.org/10.1007/s00267-012-9979-2>
- Glutz von Blotzheim UN, Bauer KM (Eds) (1991) *Handbuch der Vögel Mitteleuropas 12./I. Passeriformes (3. Teil) Sylviidae*. Aula-Verlag, Wiesbaden
- Gregory RD, van Strien A (2010) Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithol Sci* 9(1):3–22. <https://doi.org/10.2326/OSJ.9.3>
- Gutzat F, Dormann CF (2018) Decaying trees improve nesting opportunities for cavity-nesting birds in temperate and boreal forests: a meta-analysis and implications for retention forestry. *Ecol Evol* 8(16):8616–8626. <https://doi.org/10.1002/ece3.4245>
- Hanzelka J, Reif J (2016) Effects of vegetation structure on the diversity of breeding bird communities in forest stands of non-native black pine (*Pinus nigra* A.) and black locust (*Robinia pseudoacacia* L.) in the Czech Republic. *Forest Ecol Manag* 379(1):102–113. <https://doi.org/10.1016/j.foreco.2016.08.017>
- Haraszthy L (2019) Magyarország fészkelő madarainak költésbiológiája. 2. kötet. Sárgarigóféltől a sármányfélékig (Passeriformes). Pro Vértes Nonprofit Zrt., Csákvár, p 827 (in Hungarian)
- Hardersen S (2004) Habitat usage of woodpeckers and nuthatch. In: Cerretti P, Hardersen S, Mason F, Nardi G, Tisato M, Zapparoli M (eds) *Ricerche naturalistiche a Bosco della Fontana. Quaderni Conservazione Habitat 3*. Cierre Grafica Editore, Verona, pp 49–59
- Hebda G, Wesolowski T, Rowiński P (2016) Nest sites of middle spotted woodpeckers *Leucopicus medius* in a primeval forest. *Ardea* 104:119–128. <https://doi.org/10.5253/arde.v104i2.a5>
- Hebda G, Wesolowski T, Rowiński P (2017) Nest sites of a strong excavator, the great spotted woodpecker *Dendrocopos major*, in a primeval forest. *Ardea* 105:61–71. <https://doi.org/10.5253/arde.v105i1.a8>
- Hingston AB, Jordan GJ, Wardlaw TJ, Baker SC (2014) Bird assemblages in Tasmanian clearcuts are influenced by the age of eucalypt regeneration but not by distance from mature forest. *Glob Ecol Conserv* 2:138–147. <https://doi.org/10.1016/j.gecco.2014.09.003>
- Hinsley SA, Bellamy PE, Newton I, Sparks TH (1996) Influences of population size and woodland area on bird species distributions in small woods. *Oecol* 105:100–106. <https://doi.org/10.1007/BF00328797>
- Hinsley SA, Carpenter JE, Broughton RK, Bellamy PE, Rothery P, Amar A, Hewson CM, Gosler AG (2007) Habitat selection by Marsh Tits *Poecile palustris* in the UK. *Ibis* 149:224–233. <https://doi.org/10.1111/j.1474-919X.2007.00691.x>
- Hosmer DW, Lemeshow S (1989) *Applied logistic regression*. Wiley, New York

- Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: a conditional inference framework. *J Comput Graph Stat* 15:651–674. <https://doi.org/10.1198/106186006X133933>
- Jackson JA (1979) Tree surfaces as foraging substrates for insectivorous birds. In: Dickson JG, Connor RN, Fleet RR, Jackson JA, Kroll JC (eds) *The role of insectivorous birds in forest ecosystems*. Academic Press, Nacogdoches, pp 69–93
- James FC, Wamer NO (1982) Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63(1):159–171. <https://doi.org/10.2307/1937041>
- Kaushik M, Tiwari S, Manisha K (2022) Habitat patch size and tree species richness shape the bird community in urban green spaces of rapidly urbanizing Himalayan foothill region of India. *Urban Ecosyst* 25(2):423–436. <https://doi.org/10.1007/s11252-021-01165-9>
- Khosroshahi FB, Shabani AA, Kaboli M, Karami M, Najafabadi MS, Ahmadi-Mamaqani Y (2011) A probabilistic model for presence of Eurasian Nuthatch (*Sitta europaea*) in the Alborz Mountains. *Northern Iran Wilson J Ornithol* 123(4):741–747. <https://doi.org/10.1676/10-101.1>
- Kilgo JC, Vukovich MA (2014) Can snag creation benefit a primary cavity nester: response to an experimental pulse in snag abundance. *Biol Conserv* 171:21–28. <https://doi.org/10.1016/j.biocon.2014.01.003>
- Komlós M, Botta-Dukát Z, Winkler D, Ónodi G, Aszalós R (2021) Woodpecker foraging activity in oak-dominated hill forests in Hungary. *Ornis Hung* 29(1):82–97. <https://doi.org/10.2478/orhu-2021-0006>
- Krams I (2001) Perch selection by singing chaffinches: a better view of surroundings and the risk of predation. *Behav Ecol* 12(3):295–300. <https://doi.org/10.1093/beheco/12.3.295>
- Kraus D, Büttler R, Krumm F, Lachat T, Larrieu L, Mergner U, Paillet Y, Rydkvist T, Schuck A, Winter S (2016) Catalogue of tree microhabitats—Reference field list Integrate Technical p 16. <https://doi.org/10.13140/RG.2.1.1500.6483>
- Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J Appl Ecol* 41:294–304. <https://doi.org/10.1111/j.0021-8901.2004.00893.x>
- Lešo P, Kropil R (2015) Breeding bird assemblages of three West Carpathian oak-beech natural forests (eastern Slovakia). *Sylvia* 50:66–85
- Mag Z, Ódor P (2015) The effect of stand-level habitat characteristics on breeding bird assemblages in Hungarian temperate mixed forests. *Community Ecol* 16:156–166. <https://doi.org/10.1556/168.2015.16.2.3>
- Milne KA, Hejl SJ (1989) Nest-site characteristics of white-headed woodpeckers. *J Wildlife Manage* 53(1):50–55. <https://doi.org/10.2307/3801305>
- Ónodi G, Botta-Dukát Z, Winkler D, Rédei T (2022) Endangered lowland oak forest steppe remnants keep unique bird species richness in Central Hungary. *J Forestry Res* 33(1):343–355. <https://doi.org/10.1007/s11676-021-01317-9>
- Ónodi G, Csiszár A, Botta-Dukát Z, Csörgo T, Winkler D (2021) Intersexual segregation in winter foraging of great spotted woodpecker *Dendrocopos major* in riparian forests infested with invasive tree species. *Scand J Res* 36(5):354–363. <https://doi.org/10.1080/02827581.2021.1943516>
- Porro Z, Chiatante G, Bogliani G (2020) Associations between forest specialist birds and composition of woodland habitats in a highly modified landscape. *For Ecol Manage* 458:117732. <https://doi.org/10.1016/j.foreco.2019.117732>
- Poulsen BO (2002) Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. *Biodivers Conserv* 11:1551–1566. <https://doi.org/10.1023/A:1016839518172>
- Proença VM, Pereira HM, Guilherme J, Vicente L (2010) Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. *Acta Oecol* 36(2):219–226. <https://doi.org/10.1016/j.actao.2010.01.002>
- R Core Team (2020) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <http://www.R-project.org/>
- Reif J, Skálová AJ, Vermouzek Z, Voříšek P (2022) Long-term trends in forest bird populations reflect management changes in Central European forests. *Ecol Indic* 121:109137. <https://doi.org/10.1016/j.ecolind.2022.109137>
- Remm J, Lohmus A, Remm K (2006) Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? *Forest Ecol Manag* 221(1–3):267–277. <https://doi.org/10.1016/j.foreco.2005.10.015>
- Roberge JM, Mikusiński G, Svensson S (2008) The white-backed woodpecker: umbrella species for forest conservation planning? *Biodivers Conserv* 17:2479–2494. <https://doi.org/10.1007/s10531-008-9394-4>
- Robles H, Ciudad C, Matthyssen E (2011) Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: the role of traditional management practices. *Forest Ecol Manag* 261(8):1428–1435. <https://doi.org/10.1016/j.foreco.2011.01.029>
- Root RB (1967) The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol Monogr* 37:317–350. <https://doi.org/10.2307/1942327>
- Rosenvald R, Lohmus A, Kraut A, Remm L (2011) Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. *Forest Ecol Manag* 262(8):1541–1550. <https://doi.org/10.1016/j.foreco.2011.07.002>
- Sabatini F, Burrascano S, Lombardi F, Chirici G, Blasi C (2015) An index of structural complexity for Apennine beech forests. *iFOR-EST* 8:314–323. <https://doi.org/10.3832/ifor1160-008>
- Schönfeld M (1983) Beiträge zur Ökologie und zum intraspezifischen Verhalten der Baumläufer *Certhia familiaris* und *C. brachydactyla* in Eichen Hainbuchen-Lindenwäldern unter dem Aspekt der erhöhten Siedlungsdichte durch eingebrachte Nisthöhlen. *Hercynia* 20:290–311
- Seavy NE, Burnett RD, Taille PJ (2012) Black-backed woodpecker nest-tree preference in burned forests of the Sierra Nevada. *California Wildlife Soc B* 36(4):722–728. <https://doi.org/10.1002/wsb.210>
- Ståhl G, Ringvall A, Fridman J (2001) Assessment of coarse woody debris: a methodological overview. *Ecol Bull* 49:57–70
- Stański T, Czeszczewik D, Stańska M, Walankiewicz W (2020) Foraging behaviour of the great spotted woodpecker *Dendrocopos major* in relation to sex in primeval stands of the Białowieża national park. *Acta Ornithol* 55(1):120–128. <https://doi.org/10.3161/00016454AO2020.55.1.012>
- Stański T, Czeszczewik D, Stanska M, Walankiewicz W (2021) Anvils of the great spotted woodpecker (*Dendrocopos major*) in primeval oak-lime-hornbeam stands of the Białowieża (z) over dota national park. *Eur Zool J* 88(1):1–8. <https://doi.org/10.1080/24750263.2020.1844324>
- Székely T, Moskát C (1991) Guild structure and seasonal changes in foraging behaviour of birds in a Central-European oak forest. *Ornis Hung* 1:10–28
- Walankiewicz W, Czeszczewik D, Tumiel T, Stański T (2011) Woodpeckers abundance in the Białowieża Forest – a comparison between deciduous, strictly protected and managed stands. *Ornis Pol* 52:161–168
- Wesolowski T, Rowiński P, Maziarz M (2009) Wood Warbler *Phylloscopus sibilatrix*: a nomadic insectivore in search of safe breeding grounds? *Bird Study* 56(1):26–33. <https://doi.org/10.1080/00063650802681540>

- Wesolowski T, Czeszczewik D, Hebda G, Maziarz M, Mitrus C, Rowiński P (2015) 40 years of breeding bird community dynamics in a primeval temperate forest (Białowieża National Park, Poland). *Acta Ornithol* 50:95–120. <https://doi.org/10.3161/00016454AO2015.50.1.010>
- Winkler D (2005) Ecological succession of breeding bird communities in deciduous and coniferous forests in the Sopron Mountains,

Hungary. *Acta Silv Lign Hung* 1:49–58. <https://doi.org/10.37045/aslh-2005-0004>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.