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THE HABITAT SELECTION OF HOLE-NESTING BIRDS IN RIVERINE FORESTS ALONG THE DRAVA RIVER IN CROATIA

Izbor staništa ptica dupljašica u poplavnim nizinskim šumama uz rijeku Dravu u Hrvatskoj

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ABSTRACT

The influence of floristic and structural habitat characteristics on primary and secondary hole-nesting bird community characteristics was studied. Research was conducted at 66 points in riverine forest stands near the Drava River in Croatia. The standard point count method was used to study bird communities, and the circular plot method to study habitat characteristics. The average tree basal area was used as an indicator of age. The studied points were classified into four groups according to the dominant tree species. Forest habitat was found to be very heterogeneous. A total of 13 bird species were recorded (five primary and eight secondary hole-nesters). The results showed that the number of bird species, as well as their abundance, depend on both structural and floristic compositions of forest communities. Older forest stands had higher diversity of bird communities and higher abundance. Birds selected mixed and ash forest, and floristic characteristics had greater impact on the composition of secondary hole-nesters community. The number of species and the abundance of secondary hole-nesters were positively correlated with the number of species and the abundance of primary hole-nesters. The results may serve as a guideline for sustainable forest management.

Keywords: bird community, hole-nesters, forest habitat structure, forest age

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INTRODUCTION

The most important attributes of the forest habitat are structure, floristic composition, food, and dynamics of the habitat. They greatly affect the survival, reproduction, richness of bird species and their abundance (Karr 1990). It is often discussed whether it is floristic or structural habitat characteristics that show stronger influence on the composition of bird communities (MacArthur & MacArthur 1961, Blondel *et al.* 1973, Moscat 1988). Recent research on the relationship between forest birds and their habitat shows that both the structural and floristic components are very important for the explanation of the distribution of birds in different forest habitats (Hewson *et al.* 2011). Kirin *et al.* (2011) obtained similar results researching lowland oak and mountain forests in Croatia.

Hole-nesting birds were investigated in this research. Although they can nest in a variety of places (e.g. in the ground, rock crevices, buildings), most of them use trees. They are divided in two groups: primary hole-nesters such as woodpeckers, which can excavate a hole in the tree; and secondary hole-nesters, which cannot excavate a nesting hole, and therefore depend on the existing holes made by woodpeckers or by fungal decay (Newton 1994). Woodpeckers usually excavate in decaying or dead trees (Ćiković *et al.* 2014); thus the number and diversity of hole-nesting species increase with forest age (Camprodon *et al.* 2008, Haapanen 1965). Furthermore, due to the specific method of nesting site selection associated with it (see Matthysen & Adriaensen 1998, Mikusiński *et al.* 2001, Dolenec *et al.* 2008, Dolenec 2009, Kralj *et al.* 2009, Ćiković *et al.* 2014, Pakkalaa *et al.* 2018), the hole-nesting birds play a very important role in maintaining forest ecosystems. According to Passinelli (2007), nest trees of Middle and Great Spotted Woodpecker show characteristics of trees usually found in primeval forests, therefore are a good indicator of the preservation of natural forest habitats.

Bird habitat selection data can be a very significant modifier of forest management practices. Numerous studies show that the results of research on bird communities in riverine forests are important in recommendations for sustainable forest management (Fuller 1990, Garmendia *et al.* 2006, Wübbenhorst & Südbeck 2001). Hole-nesters like woodpeckers can be a very good indicator of habitat quality (Mikusiński *et al.* 2001, Wübbenhorst & Südbeck 2001, Kajtoch *et al.* 2015). Research conducted by Schulze *et al.* (2019) showed that changes in forest management significantly affect bird biodiversity, especially forest specialists. De Zan *et al.* (2017) showed that variables associated with the structure of beech forest fragments such as the number of large trees, the diversity of fallen large branches, and the number of dead trees positively affect the occurrence and the abundance of hole-nesting birds. Furthermore, the diversity of dead trees is a significant resource for food and nesting. It is important to understand how forest management affects natural processes such as habitat selection by birds, especially for large riverine forests affected by humans for centuries (Prpić & Milković 2005). The diversity of bird communities is therefore a good argument for the application of the sustainability principle in environmental management (Kubalikova *et al.* 2019).

Research on bird communities in forest habitats in Croatia has so far been mostly limited to pedunculate oak stands in the lowland area and mountain forests (Kirin *et al.* 2011, Kralj 2000). In lowland forest communities, in addition to the dominant pedunculate oak, ash, alder, poplar and willow forest stands are still preserved. They were included in the research of riverine forests of Baranja (Rucner & Rucner 1970). Riverine forests in Croatia belong to the sub-Pannonian and Pannonian vegetation zones (Trinajstić 1998). Since pedunculate oak forests predominate in these areas, soft deciduous species such as white willow, poplar, common alder, and narrow-leaved ash occupy smaller areas. In addition, the stands of these species are often very fragmented. Since the data on bird habitat selection in Croatia are incomplete, I investigated the characteristics of the hole-nesting bird communities in fragmented riverine forests along the Drava River.

The aim of this study was to determine the connection between primary and secondary hole-nesters community characteristics, and the structural and floristic characteristics of their habitat, as well as to compare the number of species and the abundance of primary and secondary hole-nesters. Since birds, especially woodpeckers, are a good indicator of the preservation of natural forest habitats, the results of this research contribute to the understanding of the general condition of forest habitats in Croatia. They may also reveal the advantages and the disadvantages of the current forest management model, and contribute to the creation of future, sustainable management models. In addition, the results combined with similar research in lowland pedunculate oak forests, and mountain forests offer a clearer picture of the state of forest bird communities in Croatia.

I propose the following hypotheses: the number of primary and secondary hole-nesting bird species, as well as their abundance, is correlated with structural and floristic habitat characteristics. Characteristics associated with forest age, such as higher number of large trees, greater basal area, and smaller number of trees are positively correlated with hole-nesters diversity and abundance. Forest stands with higher tree species diversity show greater hole-nesters diversity and abundance. The number of species and the abundance of secondary hole-nesting bird species is positively correlated with the number of species and the abundance of primary hole-nesting bird species.

MATERIALS AND METHODS

Study area

Fieldwork was carried out during breeding seasons of 2016 to 2019. The study area is located in riverine forests along the Drava River in North Croatia. Research was conducted on five study sites (Figure 1): riverine forests north of Varaždin in the Varaždin and the Međimurje Counties (16°19′ N 46°38′ E – 16°33′ N 46°34′ E, 23.9 km^2); the Pažut forest in the Međimurje County (16°82′ N 46 31′ E – 16 88′ N 46 30′ E, 4.6 km^2); the Repaš forest north of river Drava in the Koprivnica-Križevci County (17°06′ N 46°18′ E – 17°17′ N 46°13′ E, 35.2 km^2); the Gabajeva greda complex southwest of the Drava River in the Koprivnica-Križevci County (16°99′ N 46°15′ E – 17°04′ N 46°13′ E, 6.7 km^2); the Đurđevac lowland forest in the Koprivnica-Križevci County near the town of Đurđevac (17°11′ N 46°10′ E – 17°25′ N 46°00› E, 68.0 km^2).

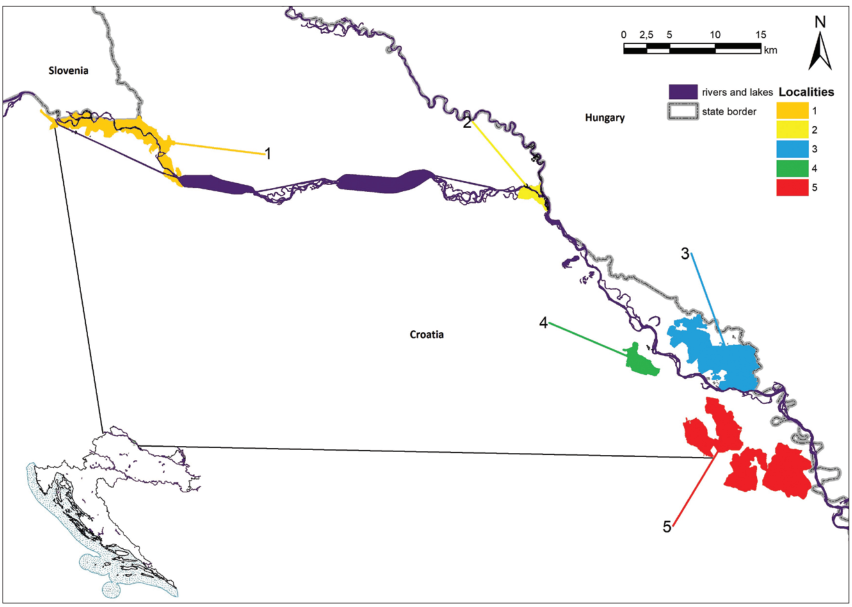

Figure 1. Position of the study sites: 1 - Varaždin lowland forests in the Varaždin and Međimurje County; 2 - Pažut forest in the Međimurje County; 3 - Repaš forest north of river Drava in the Koprivnica-Križevci County; 4 - Gabajeva greda complex southwest of river Drava in the Koprivnica-Križevci County; 5 - Đurđevac lowland forest in the Koprivnica-Križevci County

Slika 1. Položaj istraživanih područja: *1 - Varaždinske nizinske šume u Međimurskoj i Varaždinskoj županiji; 2 - Šuma Pažut u Međimurskoj županiji; 3 - Šuma Repaš sjeverno od Drave u Koprivničko-križevačkoj županiji, 4 - Kompleks Gabajeva greda jugozapadno od Drave, 5 - Đurđevačke nizinske šume u Koprivničko-križevačkoj županiji*

According to the Köppen distribution, the study area is characterized by the climate type “Cfwbx” (Seletković & Tikvić 2005). It is a moderately warm rainy climate with a uniform amount of precipitation throughout the year. The average annual rainfall is 869 mm, the average temperature is 10.3°C, and the maximum precipitation occurs in spring (May) and late summer (July or August), with a dry period in between (Seletković & Katušin 1992). According to Trinajstić (1998), the study area belongs to the Mid-European and Sub-panonian vegetation zones of the the Eurosiberian-North American region. As described in detail by Vukelić & Baričević (2005) and summarized in Slatki & Kralj (2020), the systematisation of floodplain forests is presented by eleven associations in three classes. In forest ecosystems, the decisive ecological factor is water, which appears as precipitation, flood, and groundwater. The height and duration of floodwaters in Croatian riverine forests are crucial for the survival of vegetation in spring, while rainwater and groundwater often play a crucial role in summer (Seletković & Tikvić 2005).

Bird community sampling

Standard point count method was used for bird community sampling (Bibby *et al.* 1992). The counting was carried out at 66 points from February to May in the period 2016 – 2019. The counting points were distributed evenly throughout poplar, alder and ash stands in the research area. The counting points were at least 300 m apart and placed at least 300 m from the edges of forests, roads, and water surfaces to avoid the edge effect. At each point, the count was conducted five times during the breeding season. Each counting visit started after sunrise and ended three hours later. The counting was not carried out in wind, rain, fog or during heavy clouds. Upon arrival at the counting point, two minutes of quiet spontaneous observation followed to allow the birds to adapt to the observer. After that, the counting protocol differs for primary and secondary hole-nesting species. During the first and the second count in February and March, the highest activity of primary hole-nesters was expected, so a vocal stimulation was used before the counting. The effectiveness of the playback has been proven for several species of woodpeckers that are very often hidden and cautious near humans (see Ćiković *et al.* 2015, Michalzuk & Michalzuk 2006). A two-minute recording sequence was used, containing a combination of territorial calls and drumming of all five expected species ranging from the smallest to the largest. The playback was reproduced using a digital mp3 player connected to a 25 W megaphone. The playback volume was previously calibrated, so that the human ear could hear it at a maximum distance of 100 meters to avoid attracting individuals from other counting points. The playback was followed by a period of 5 minutes, during which the activity of all birds was recorded. The time and number of counts in the season was determined according to the recommendations of Sorace *et al.*

(2000). No playback was used during the third, the fourth and the fifth count carried out from late March to May. After the arrival and two minutes of adjustment, a five-minute bird count started immediately. During all five counts, singing males were considered as representing breeding territories and used in the final analysis. Two counting bands were used, and birds were recorded separately for each band (the inner band with a diameter of 50 m from the observer, and the outer band outside the diameter of 50 m). Only birds recorded in the inner band were used for quantitative analysis. During the counting, a Zoom H5 digital recorder was used to create high-resolution audio tracks (WAV file format, sample rate 44 100 Hz, bit depth 24). Based on these recordings, the determination of species with similar song (e.g., tits and treecreepers) was performed. The determination was performed by hearing recordings, and by sonogram analysis in Raven Pro 1.6.1. (Center for Conservation Bioacoustics 2019). The following ornithological variables were used in the statistical analyses: the number of pairs for all individual hole-nesting species, the combined number of pairs for primary and secondary hole-nesting species, the number of primary hole-nesting species, the number of secondary hole-nesting species, the total number of pairs, the total number of species, the number of pairs for canopy feeding species, bark gleaning species, ground feeding species and aerial feeders. Only birds that feed in the canopy and bark gleaning species were included in the analysis regarding feeding layers, since birds that feed in the air and on the ground are represented by one species each (the Common Starling *Sturnus vulgaris* and the Collared Flycatcher *Ficedula albicollis*).

Habitat sampling

Habitat sampling was carried out during July at each counting point, separately from the bird censuses. The circular plot method was used (Bibby *et al.* 1992, Cyr & Oelke 1976, James & Shugart 1970). Plot diameter was 11.28 m, and it was measured precisely with a Bosch laser measuring tool (0.15–20 m, ± 3 mm). Tree species and tree diameter of all trees on the plot (DBH) were recorded. Tree diameter was measured with a calibrated ruler and assigned to one of the nine classes: S < 7.5 cm, A 7.5–15 cm, B 15–23 cm, C 23–38 cm, D 38–53 cm, E 53–68 cm, F 68–84 cm, G 84–101 cm, H > 101 cm. In each class basal area was calculated according to factors provided by Cyr & Oelke (1976). Trees from classes S, A and B were pooled together as "small", and C to G as "large" trees. The counting points were classified according to dominant tree species (poplar, alder, ash, or mixed stands) and according to absolute stand age obtained using the Croatian forestry inventory (< 40 years, 40 – 60 years, 60 – 80 years and ≥ 80 years). In addition, ground cover, canopy cover, shrub coverage, number and diameter of dead trees were recorded on each plot (methods described in Slatki & Kralj 2020). The following habitat variables were used in the statistical analyses: the relative tree number and relative basal area for ten most common tree species, the total number of trees, the total number of tree species, the absolute stand age, the number and percentage of small and large trees, the average tree basal area, the number of dead trees, shrub cover, ground cover and canopy cover for each plot (Table 1).

Table 1. The PCA analysis using 28 different independent habitat variables; columns showing principal component scores (PC1–PC3). Note: the data for black and white poplar are merged as well as the data for white and field elm. The largest factor scores higher than [0.7] are given in **<u>bold and underlined</u>**, and large factor scores between [0.5] and [0.7] are given in **bold.**

Tablica 1. *Analiza glavnih komponenti s 28 nezavisnih varijabli staništa; stupci pokazuju faktorska opterećenja triju glavnih komponenti (PC1–PC3). Napomena: podaci za obje vrste topola (crna i bijela) te podaci za obje vrste brijesta (treperavi i poljski) su objedinjeni. Najznačajnija faktorska opterećenja iznad [0,7] otisnuta su* ***<u>masno i podcrtana</u>*** *a značajna faktorska opterećenja od [0,5] do [0,7]* ***masno.***

Habitat variables/*varijable staništa*	PC1	PC2	PC3
Populus sp. relative tree number/% *udio broja stabala topole*	0.248	**<u>-0.743</u>**	0.338
Salix alba relative tree number/% *udio broja stabala bijele vrbe*	-0.467	-0.313	0.480
Alnus glutinosa relative tree number/% *udio broja stabala crne johe*	-0.422	-0.025	**<u>-0.854</u>**
Quercus robur relative tree number/% *udio broja stabala hrasta lužnjaka*	0.385	0.090	0.274
Fraxinus angustifolia relative tree number/% *udio broja stabala poljskoga jasena*	0.167	**0.559**	-0.037
Carpinus betulus relative tree number/% *udio broja stabala običnoga graba*	0.313	**0.593**	0.314
Ulmus sp. relative tree number/% *udio broja stabala brijesta*	0.279	-0.363	0.106
Acer campestris relative tree number/% *udio broja stabala klena*	0.065	**0.575**	0.218
Total number of trees per point *ukupan broj stabala po točki*	**<u>-0.827</u>**	0.252	-0.038
Total number of species per point/ *ukupan broj vrsta po točki*	0.067	0.130	**0.694**
Absolute stand age/ *apsolutna starost šume*	**0.599**	0.494	0.006
Number of small trees (S-B)/ *broj malih stabala (S-B)*	**<u>-0.897</u>**	0.196	0.128
Share of small trees (S-B)/ *udio malih stabala (S-B)*	**<u>-0.864</u>**	0.174	0.329

Number of large trees (C-G)/ *broj velikih stabala (C-G)*	0.404	0.092	-0.467
Share of large trees (C-G)/ *udio velikih stabala*	**0.866**	-0.191	-0.315
Average tree basal area/ *prosječna temeljnica*	**0.821**	-0.332	0.039
Number of dead trees *Broj mrtvih stabala*	**-0.566**	-0.208	0.446
Shrub cover *Pokrovnost sloja grmlja*	0.142	**-0.618**	-0.151
Ground cover *Pokrovnost prizemnog sloja*	-0.275	0.189	-0.339
Canopy cover *Pokrovnost krošnji*	0.022	0.181	0.089
Populus sp. relative basal area/% *udio temeljnice topole*	0.134	**-0.794**	0.447
Salix alba relative basal area/% *udio temeljnice bijele vrbe*	-0.489	-0.250	0.409
Alnus glutinosa relative basal area/% *udio temeljnice crne johe*	-0.398	-0.020	**-0.863**
Quercus robur relative basal area /% *udio temeljnice hrasta lužnjaka*	0.364	0.204	0.274
Fraxinus angustifolia relative basal area /% *udio temeljnice poljskoga jasena*	0.157	**0.740**	0.098
Carpinus betulus relative basal area/% *udio temeljnice običnoga graba*	0.343	**0.618**	0.312
Ulmus sp. relative basal area/% *udio temeljnice brijesta*	0.202	-0.413	0.036
Acer campestris relative basal area/% *udio temeljnice klena*	0.151	0.557	0.204
Eigenvalue/ *svojstvena vrijednost*	6.168	4.975	3.916
Variance explained/ *varijanca*	0.220	0.178	0.140

According to the Shapiro-Wilks test, variables were not normally distributed; therefore, non-parametric correlation tests were used. The PCA analysis with 28 independent structural and floristic habitat variables was conducted. In this analysis, factor scores over [0.7] showed strong correlations and were marked as "largest". Factor scores between [0.5] and [0.7] were marked as "large". The Spearman rank correlation between the obtained primary components and ornithological variables was conducted.

The Shannon-Wiener index was used to express biodiversity. Regarding the main feeding layer, birds were divided into four groups: i) canopy feeding species, ii) bark gleaning species, iii) ground feeding species, iv) aerial feeders. This division has been used by many authors (e.g., Kirin *et al.* 2011, Tomiałojć *et al.* 1984). The selection indices analysis of individual bird species and bird groups (according to feeding layer and nesting site) for forest types and absolute age was performed (Krebs 1999). The significance of the selection was tested by the chi-square test. In this analysis, proportions of forest types according to the dominant tree species and the absolute age at study sites were determined as expected values. The standardized selection index was calculated according to Manly *et al.* (1993). Selection indices above 1/number of resources, or 0.25 in this case, indicate preference, while the lower ones indicate avoidance. 95% confidence limits with the Bonferroni correction were used to test the significance of the selection for each habitat type and age category. Confidence limits between values for two habitat types that did not overlap were considered to be selected differently; these differences were tested for the significance of the selection.

Statistical analyses were performed with Microsoft Excel for Office 365 MSO, Past v.3.14., STATISTICS v.8.0. (StatSoft 2007), and Ecological Methodology v.7.0 (Krebs 2009).

RESULTS

Only obligate hole-nesters were included in this study. In total, 13 hole-nesting species were recorded during the study five of which were primary and eight were secondary (Table 2): Grey-faced Woodpecker *Picus canus*, Black Woodpecker *Dryocopus martius*, Middle Spotted Woodpecker *Leiopicus medius*, Lesser Spotted Woodpecker *Dryobates minor*, Great Spotted Woodpecker *Dendrocopos major*, Marsh Tit *Poecile palustris*, Eurasian Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, Short-toed Treecreeper *Certhia brachydactyla*, Eurasian Treecreeper *Certhia familiaris*, Eurasian Nuthatch *Sitta europaea*, Common Starling *Sturnus vulgaris*, Collared Flycatcher *Ficedula albicollis*. The most frequently recorded species on all study sites were the Great Spotted Woodpecker (25.00%) and the Great Tit (23.33%), which together make up 48.33% of the recorded pairs. Table 3 shows the distribution of individual species on all five study sites. The highest number of pairs was recorded in Đurđevac lowland forests (132 pairs), and the lowest in Pažut (24 pairs). The Shannon-Wiener index of diversity was the highest in ash and mixed stands (Figure 2), and was increasing with stand absolute age (Figure 3). The secondary hole-nesters were positively correlated with the number of pairs (Spearman-rank correlation 0.492, $t = 4.520$, $p < 0.001$), as well as the number of species of primary hole-nesters (0.383, $t = 3.315$, $p < 0.005$).

Table 2. The distribution of the recorded species according to the share of the number of pairs in researched territory, nesting site and feeding layer, the average number of pairs per point and the average number of pairs in different forest types and age groups; feeding: c - canopy feeding species (on the leaves of bushes or trees), b - bark gleaning species, g - ground feeding species, a - aerial feeders; nesting: p - primary hole-nesters, s - secondary hole-nesters, N = number of counting points

Tablica 2. *Distribucija istraživanih vrsta prema udjelu parova zabilježenih na istraživanom teritoriju, supstratu hranjenja i mjestu gniježđenja, prosječnom broju parova na točki te prosječnom broju parova u različitim tipovima šume i starosnim skupinama; hranjenje: c - vrste koje se hrane u krošnji (na listovima grmlja ili drveća), b - vrste koje se hrane na kori, g - vrste koje se hrane na tlu, a - vrste koje hvataju hranu u zraku; gniježđenje: p - primarne dupljašice, s - sekundarne dupljašice, N = broj točaka prebrojavanja*

Species/*vrsta*	**Share**/ *udio* (%)	**Average number of pairs per point** / *prosječan br. parova na točki*	**Feeding layer**/ *supstrat hranjenja*	**Nesting site** /*gniježđenje*	**Forest type** / *tip šume*				**Age group** / *starosna skupina*			
					Mixed/ *mješoviti* N = 17	**Poplar**/ *topola* N = 15	**Ash**/ *jasen* N = 13	**Alder**/ *joha* N = 21	**< 40 yr.**/*g.*, N = 13	**40–59 yr.**/*g.*, N = 17	**60–79 yr.**/*g.*, N = 22	**≥ 80 yr.**/*g.*, N = 14
Grey-faced Woodpecker/*siva žuna* (*Picus canus*)	2.667	0.121	b	p	0.118	0.077	0.143	0.133	0.071	0.091	0.176	0.143
Black Woodpecker/ *crna žuna* (*Dryocopus martius*)	0.667	0.030	b	p	-	-	0.095	-	-	-	0.118	-
Middle Spotted Woodpecker/ *crvenoglavi djetlić* (*Leiopicus medius*)	3.000	0.136	b	p	0.176	0.231	0.048	0.133	0.071	0.045	0.118	0.357
Lesser Spotted Woodpecker/*mali djetlić* (*Dryobates minor*)	2.333	0.106	b	p	0.059	0.077	0.095	0.200	-	0.136	0.059	0.214

Great Spotted Woodpecker/*veliki djetlić* (*Dendrocopos major*)	25.000	1.136	b	p	1.412	1.154	0.810	1.133	0.643	1.182	0.941	1.571
Marsh Tit/*crnoglava sjenica* (*Poecile palustris*)	4.333	0.197	c	s	0.353	0.154	0.190	0.067	0.286	0.182	0.118	0.214
Eurasian Blue Tit/ *plavetna sjenica* (*Cyanistes caeruleus*)	8.333	0.379	c	s	0.412	0.538	0.286	0.333	-	0.409	0.471	0.571
Great Tit/*velika sjenica* (*Parus major*)	23.333	1.061	c	s	1.353	1.000	0.857	1.067	0.929	1.000	1.176	1.071
Short-toed Treecreeper/*dugokljuni puzavac* (*Certhia brachydactyla*)	2.667	0.121	b	s	0.118	0.077	0.190	0.067	0.071	0.045	0.294	0.071
Eurasian Treecreeper/ *kratkokljuni puzavac* (*Certhia familiaris*)	2.000	0.091	b	s	0.118	0.231	0.048	-	-	0.045	0.118	0.214
Eurasian Nuthatch/ *brgljez* (*Sitta europaea*)	9.667	0.439	b	s	0.529	0.462	0.238	0.600	0.286	0.364	0.412	0.714
Common Starling/ *čvorak* (*Sturnus vulgaris*)	9.667	0.439	g	s	0.706	0.692	0.143	0.333	0.214	0.318	0.588	0.643
Collared Flycatcher/ *bjelovrata muharica* (*Ficedula albicollis*)	6.333	0.288	a	s	0.412	0.615	0.190	-	0.071	0.045	0.412	0.714
All primary hole-nesters/*sve primarne dupljašice*	33.667	1.530	-	p	1.765	1.538	1.286	1.600	0.786	1.455	1.529	2.286
All secondary hole-nesters/*sve sekundarne dupljašice*	66.333	3.015	-	s	4.000	3.769	2.143	2.467	1.857	2.409	3.588	4.214

Table 3. The number of pairs of individual species on study sites (N = number of counting points, - indicates that the species was not recorded during the count)

Tablica 3. *Broj parova istraživanih vrsta na pojedinim lokacijama (N = broj točaka prebrojavanja, - označava da vrsta nije zabilježena tijekom prebrojavanja)*

Species/vrsta	Varaždin lowland forests/*Varaždinske nizinske šume* (N = 17)	Pažut/*Pažut* (N = 3)	Repaš/*Repaš* (N = 9)	Gabajeva greda/*Gabajeva greda* (N = 8)	Đurđevac lowland forest/*Đurđevačke nizinske šume* (N = 29)
Grey-faced Woodpecker/*siva žuna*	-	3	2	-	3
Black Woodpecker/*crna žuna*	-	-	-	-	2
Middle Spotted Woodpecker / *crvenoglavi djetlić*	2	-	3	-	4
Lesser Spotted Woodpecker/ *mali djetlić*	1	2	1	1	2
Great Spotted Woodpecker/ *veliki djetlić*	18	5	11	9	32
Marsh Tit/*crnoglava sjenica*	2	2	1	2	6
Eurasian Blue Tit/*plavetna sjenica*	5	1	5	2	12
Great Tit/*velika sjenica*	19	5	10	6	30
Short-toed Treecreeper/ *dugokljuni puzavac*	1	-	-	2	5
Eurasian Treecreeper/ *kratkokljuni puzavac*	-	-	3	-	3
Eurasian Nuthatch/*brgljez*	8	3	5	1	12
Common Starling/*čvorak*	5	3	6	5	10
Collared Flycatcher/*bjelovrata muharica*	-	-	5	3	11
Total/*ukupno*	61	24	52	31	132

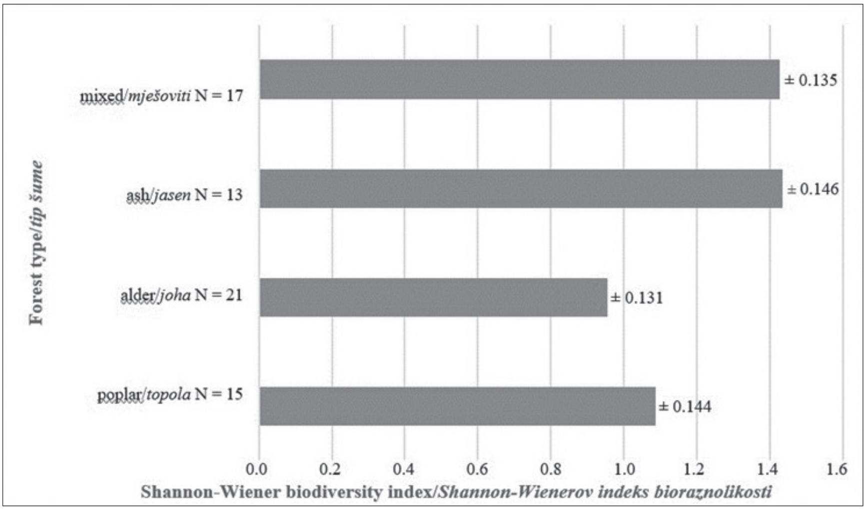

Figure 2. The Shannon-Wiener diversity index for hole-nesting species in different forest types (± standard error of the mean), N = number of counting points

Slika 2. *Shannon-Wienerov indeks bioraznolikosti dupljašica u različitim tipovima šuma (± standardna pogreška aritmetičke sredine), N = broj točaka prebrojavanja*

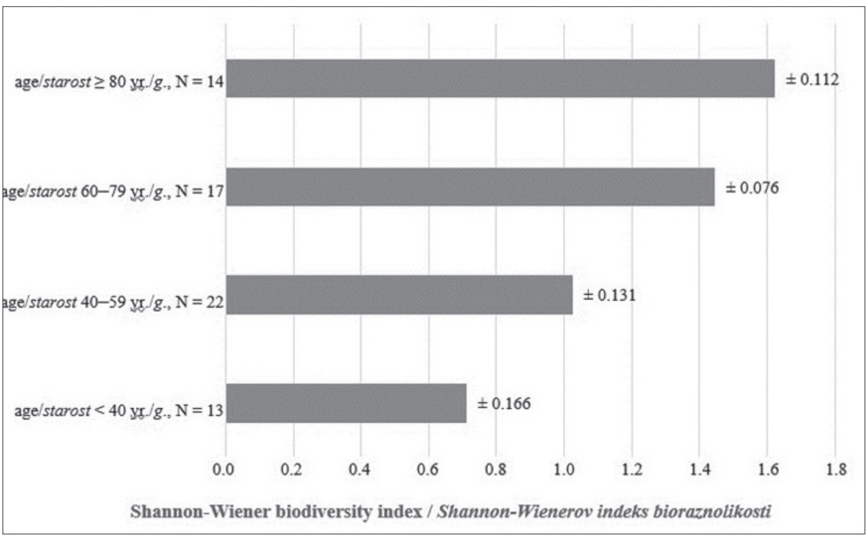

Figure 3. The Shannon-Wiener diversity index for hole-nesting species in different absolute age groups (± standard error of the mean), N = number of counting points.

Slika 3. *Shannon-Wienerov indeks bioraznolikosti dupljašica u sastojinama različitih apsolutnih starosti (± standardna pogreška aritmetičke sredine), N = broj točaka po kategoriji starosti.*

Of the 14 tree species that were recorded, the ten most common species were included in the analysis: common alder *Alnus glutinosa)*, narrow-leaved ash *Fraxinus angustifolia*, commnon hornbeam *Carpinus betulus*, field maple *Acer campestre*, white willow *Salix alba*, white poplar *Populus alba*, black poplar *Populus nigra*, pedunculate oak *Quercus robur*, white elm *Ulmus laevis*, field elm *Ulmus minor*. The data for black and white poplar were merged as well as were data for white and field elm. The black locust *Robinia pseudoacacia*, bird cherry *Prunus padus*, wild cherry *Prunus avium*, and common beech *Fagus sylvatica* were rare, and thus excluded from the analysis. The median absolute age of the researched forest territories is 54 (Q1-Q3 = 42.25-77.5) years.

All the studied areas showed heterogeneity in almost all the variables. Ash and mixed stands were on average older than alder and poplar stands. The most of the represented trees belong to the categories C and B; categories D, E, F and G were less represented; while the largest trees (group H) were completely absent (Table 4). The number of tree species was the lowest in alder type, and mixed forest type contained a similar number of species to poplar and ash forests. Mixed forests showed the highest values of the absolute age of a particular type of forest. All 14 types of trees were recorded only in the mixed forest type (Table 4). The common alder showed the greatest dominance in its plots; this was the only recorded tree species on a third of the plots categorized as alder type. The narrow-leaved ash showed great dominance in forests of its type too, but it was frequently combined with the common alder. Alder forests showed the greatest variety of age and representation of certain age groups of trees. On the other hand, mixed stands were the oldest and the most diverse in terms of vegetation. The pedunculate oak was very frequent and abundant in mixed stands (Table 4).

Table 4. Habitat structure for each forest type. N = number of counting points; MED = median, Q1–Q3 = interquartile range, ''-'' indicates complete absence of a particular species; tree diameter classes: S < 7.5 cm, A 7.5–15 cm, B 15–23 cm, C 23–38 cm, D 38–53 cm, E 53–68 cm, F 68–84 cm, G 84–101 cm; abbreviations: *Pop.nig = Populus nigra, Pop.alb = Populus alba, Sal.alb = Salix alba, Fag.syl = Fagus sylvatica, Aln.glu = Alnus glutinosa, Que.rob = Quercus robur, Fra.ang = Fraxinus angustifolia, Car.bet = Carpinus betulus, Ulm.lae = Ulmus laevis, Ulm.min = Ulmus minor, Rob.pse = Robinia pseudoacacia, Pru.avi = Prunus avium, Ace.cam = Acer campestre, Pru.pad = Prunus padus*

Tablica 4. *Vegetacijska struktura staništa po stanišnim tipovima (tip šume). N = broj točaka u pojedinom tipu šume; MED = medijan, Q1–Q3 = interkvartilni raspon, ''-'' označava potpuno odsustvo pojedine vrste; prsni promjer stabala: S < 7,5 cm, A 7,5–15 cm, B 15–23 cm, C 23–38 cm, D 38–53 cm, E 53–68 cm, F 68–84 cm, G 84–101 cm; kratice: Pop.nig = Populus nigra, Pop.alb = Populus alba, Sal.alb = Salix alba, Fag.syl = Fagus sylvatica, Aln.glu = Alnus glutinosa, Que.rob = Quercus robur, Fra.ang = Fraxinus angustifolia, Car.bet = Carpinus betulus, Ulm.lae = Ulmus laevis, Ulm.min = Ulmus minor, Rob.pse = Robinia pseudoacacia, Pru.avi = Prunus avium, Ace.cam = Acer campestre, Pru.pad = Prunus padus*

Forrest type/*tip šum*e		mixed/*mješoviti* N = 17	ash/*jasen* N = 13	alder/*joha* N = 21	poplar/*topola* N = 15
Variables/*varijable*		MED (Q1–Q3)	MED (Q1–Q3)	MED (Q1–Q3)	MED (Q1–Q3)
Number of trees by tree diameter classes/*broj stabala po kategorijama prsnog promjera*	S	0.00 (0.00–0.00)	1.00 (0.00–2.00)	0.00 (0.00–1.00)	0.00 (0.00–0.50)
	A	3.00 (1.00–5.00)	2.00 (1.00–10.00)	3.00 (1.00–7.00)	1.00 (0.50–3.50)
	B	4.00 (2.00–6.00)	3.00 (2.00–5.00)	5.00 (2.00–15.00)	1.00 (1.00–3.50)
	C	6.00 (5.00–7.00)	7.00 (2.00–9.00)	7.00 (6.00–13.00)	3.00 (2.00–4.00)
	D	3.00 (1.00–4.00)	3.00 (1.00–4.00)	2.00 (0.00–4.00)	2.00 (1.00–4.00)
	E	1.00 (0.00–2.00)	1.00 (0.00–2.00)	0.00 (0.00–0.00)	1.00 (0.50–2.50)
	F	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–1.00)
	G	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.00)
	Σ	19.00 (13.00–21.00)	19.00 (16.00–23.00)	22.00 (18.00–37.00)	13.00 (9.50–17.00)

Number of small trees/*broj malih stabala* (S–B)	7.00 (3.00–11.00)	5.00 (3.00–16.00)	7.00 (2.00–29.00)	4.00 (3.00–7.50)
Share of small trees/*udio malih stabala* (S–B)/%	40.00 (25.00–67.86)	37.50 (21.05–65.52)	38.46 (11.11–75.61)	40.00 (15.48–58.55)
Number of large trees/*broj velikih stabala* (C–G)	10.00 (9.00–12.00)	9.00 (7.00–14.00)	11.00 (8.00–16.00)	8.00 (6.00–9.50)
Share of large trees/udio velikih stabala (C–G)/%	60.00 (52.63–75.00)	62.50 (34.48–78.95)	61.54 (24.39–88.89)	60.00 (41.45–84.52)
Number of species/*broj vrsta*	4.00 (3.00–4.00)	3.00 (3.00–4.00)	2.00 (1.00–3.00)	4.00 (2.00–4.00)
Number of dead trees/*broj mrtvih stabala*	1.00 (0.00–2.00)	1.00 (0.00–2.00)	1.00 (0.00–2.00)	0.00 (0.00–3.00)
Ground cover/*pokrovnost prizemnog sloja*/%	50.00 (35.00–60.00)	70.00 (65.00–80.00)	65.00 (50.00–75.00)	55.00 (30.00–57.50)
Canopy cover/*pokrovnost krošnje*/%	75.00 (65.00–80.00)	65.00 (60.00–70.00)	75.00 (70.00–80.00)	70.00 (52.50–80.00)
Absolute age/*apsolutna starost odsjeka*/yrs./*god.*	80.00 (50.00–86.00)	74.00 (61.00–76.00)	50.00 (36.00–70.00)	47.00 (42.50–51.00)
Total basal area/*ukupna bazalna površina*	1.42 (1.14–1.72)	1.51 (1.18–1.81)	1.43 (1.23–1.62)	1.50 (1.15–1.92)
Average basal area/*prosječna bazalna površina*	0.09 (0.06–0.10)	0.09 (0.05–0.12)	0.06 (0.04–0.10)	0.11 (0.09–0.13)

Forrest type/tip šume		mixed/mješoviti N = 17	ash/jasen N = 13	alder/joha N = 21	poplar/topola N = 15
Variables/*varijable*		MED (Q1-Q3)	MED (Q1-Q3)	MED (Q1-Q3)	MED (Q1-Q3)
Relative basal area for each tree species/*udio temeljnice pojedine vrste*/%	*Pop.nig*	0.00 (0.00–0.00)	-	-	43.69 (0.00–71.82)
	Pop.alb	0.00 (0.00–0.00)	-	-	37.86 (1.00–86.92)
	Sal.alb	0.00 (0.00–0.00)	-	-	0.00 (0.00–8.70)
	Fag.syl	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.00)
	Aln.glu	0.00 (0.00–7.07)	0.00 (0.00–4.64)	85.57 (71.05–100.00)	0.00 (0.00–0.00)
	Que.rob	0.00 (0.00–35.71)	0.00 (0.00–1.28)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
	Fra.ang	24.32 (0.00–52.04)	66.43 (63.39–81.36)	0.69 (0.00–22.06)	0.00 (0.00–0.00)
	Car.bet	18.02 (0.00–23.03)	3.54 (0.00–13.82)	0.00 (0.00–0.00)	-
	Ulm.lae	0.00 (0.00–0.00)	0.00 (0.00–0.00)	-	1.33 (0.00–11.17)
	Ulm.min	0.00 (0.00–0.00)	0.00 (0.00–0.65)	0.00 (0.00–0.00)	-
	Rob.pse	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.00)
	Pru.avi	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.67)
	Ace.cam	0.00 (0.00–11.63)	7.83 (1.47–8.85)	0.00 (0.00–0.00)	-
	Pru.pad	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.24)

Relative tree number for each tree species/*udio broja stabala pojedine vrste*/%	*Pop.nig*	0.00 (0.00–0.00)	-	-	11.11 (0.00–28.37)
	Pop.alb	0.00 (0.00–0.00)	-	-	37.50 (1.25–60.56)
	Sal.alb	0.00 (0.00–0.00)	-	-	0.00 (0.00–23.08)
	Fag.syl	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.00)
	Aln.glu	0.00 (0.00–6.25)	0.00 (0.00–4.55)	90.91 (73.91–100.00)	0.00 (0.00–0.00)
	Que.rob	0.00 (0.00–20.00)	0.00 (0.00–4.35)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
	Fra.ang	9.52 (0.00–14.29)	44.83 (31.25–61.11)	2.17 (0.00–16.67)	0.00 (0.00–0.00)
	Car.bet	19.05 (0.00–53.33)	4.35 (0.00–22.73)	0.00 (0.00–0.00)	-
	Ulm.lae	0.00 (0.00–0.00)	0.00 (0.00–0.00)	-	5.00 (0.00–22.22)
	Ulm.min	0.00 (0.00–0.00)	0.00 (0.00–2.27)	0.00 (0.00–0.00)	-
	Rob.pse	0.00 (0.00–0.00)	-	-	0.00 (0.00–0.00)
	Pru.avi	0.00 (0.00–0.00)	-	-	0.00 (0.00–2.50)
	Ace.cam	0.00 (0.00–13.33)	18.18 (6.90–25.00)	0.00 (0.00–0.00	-
	Pru.pad	0.00 (0.00–0.00)	-	-	0.00 (0.00–11.11)

The PCA analysis resulted in three principal components that accounted for 53.8% of the total variance (Table 1). PC1 accounted for 22.0% of the variance and described the forest age (positive correlation with share of large trees, average tree basal area, absolute stand age, negative correlation with the total number of trees, the percentage of small trees, the number of small trees, and the number of dead trees). PC2 accounted for 17.8% of the variance. It showed negative correlation with the relative number of black and white poplar trees, the relative black and white poplar basal area and shrub cover, as well as a positive correlation with the narrow-leaved ash relative basal area, with the narrow-leaved ash, the common hornbeam and the field maple relative tree number, and the common hornbeam relative basal area. PC3 accounted for 14.0% of the variance and showed negative correlation with the common alder relative tree number and common alder relative basal area, and a positive correlation with the total number of species.

The Spearman-rank correlation between principal components and ornithological variables showed differences between primary and secondary hole-nesters (Table 5). The number of primary hole-nesting pairs showed positive correlation with PC1, which means that they prefer older forest stands. The variables of secondary hole-nesting species (number of pairs and number of species) showed positive correlation with all three axes, indicating preference for older stands with a smaller relative percentage of the black and white poplar and the common alder, a higher percentage of the narrow-leaved ash, the common hornbeam and the maple, and a larger number of tree species. This means that floristic characteristics have an impact on secondary hole-nesters' habitat selection. The abundance of bark gleaning species was positively correlated with PC1 and PC3 (Table 6), showing a preference for older forests without the common alder and with a greater number of tree species. The correlation between the abundance of birds feeding in the canopy and the absolute age of the forest was close to the threshold of significance (0.233, $p = 0.060$).

Table 5. The Spearman-rank correlation between the principal components and the number of pairs and number of species of hole-nesting birds; the principal component scores (PC1—PC3) extracted using the PCA analysis with 28 different independent habitat variables as the principal components (N = 66). Significant values are given in **bold**.

Tablica 5. *Spearman-rank korelacija između glavnih komponenti i broja parova te broja vrsta dupljašica; glavne komponente (PC1–PC3) dobivene su analizom glavnih komponenti s 28 nezavisnih varijabli staništa (N = 66). Značajne vrijednosti otisnute su* ***masno****.*

		Spearman	**t (N - 2)**	**p value/ *p vrijednost***
Primary hole-nesters/*primarne dupljašice*	Number of pairs & PC1/ *broj parova i PC1*	**0.246**	**2.034**	**< 0.050**
	Number of pairs & PC2/ *broj parova i PC2*	0.058	0.464	0.644
	Number of pairs & PC3/ *broj parova i PC3*	0.134	1.084	0.282
	Number of species & PC1/*broj vrsta i PC1*	0.206	1.682	0.097
	Number of species & PC2/*broj vrsta i PC2*	0.052	0.413	0.680
	Number of species & PC3/*broj vrsta i PC3*	0.191	1.559	0.124
Secondary hole-nesters/ *sekundarne dupljašice*	Number of pairs & PC1/ *broj parova i PC1*	**0.297**	**2.486**	**< 0.050**
	Number of pairs & PC2/ *broj parova i PC2*	**0.355**	**3.040**	**< 0.005**
	Number of pairs & PC3/ *broj parova i PC3*	**0.337**	**2.861**	**< 0.010**
	Number of species & PC1/*broj vrsta i PC1*	**0.324**	**2.739**	**< 0.010**
	Number of species & PC2/*broj vrsta i PC2*	**0.409**	**3.583**	**< 0.001**
	Number of species & PC3 *broj vrsta i PC3*	**0.307**	**2.580**	**< 0.050**
Primary and secondary hole-nesters/*primarne i sekundarne dupljašice*	Number of pairs & PC1/ *broj parova i PC1*	**0.319**	**2.690**	**< 0.010**
	Number of pairs & PC2/ *broj parova i PC2*	**0.277**	**2.309**	**< 0.050**
	Number of pairs & PC3/ *broj parova i PC3*	**0.307**	**2.584**	**< 0.050**
	Number of species & PC1/*broj vrsta i PC1*	**0.321**	**2.714**	**< 0.010**
	Number of species & PC2/*broj vrsta i PC2*	**0.329**	**2.785**	**< 0.010**
	Number of species & PC3/*broj vrsta i PC3*	**0.310**	**2.606**	**< 0.050**

Table 6. The Spearman-rank correlation between the principal components and number of bark gleaning and canopy feeding pairs; the principal component scores (PC1—PC3) extracted using the PCA analysis with 28 different independent habitat variables as the principal components (N = 66). Significant values are given **in bold.**

Tablica 6. *Spearman-rank korelacija između glavnih komponenti i broja parova koji se hrane na kori i u krošnji; glavne komponente (PC1–PC3) dobivene su analizom glavnih komponenti s 28 nezavisnih varijabli staništa (N = 66). Značajne vrijednosti otisnute su* ***masno****.*

		Spearman	**t (N - 2)**	**p value/ *p vrijednost***
Number of bark gleaning pairs/*broj parova vrsta koje se hrane na kori*	PC1	**0.262**	**2.172**	**< 0.050**
	PC2	0.124	0.999	0.321
	PC3	**0.259**	**2.143**	**< 0.050**
Number of canopy feeding pairs/*broj parova vrsta koje se hrane u krošnji*	PC1	0.233	1.916	0.060
	PC2	0.117	0.941	0.350
	PC3	0.186	1.518	0.134

The selection indices showed preference of almost all bird species for the ash and mixed forest types and for older forests. The preference for forest type is significant only in the Common Starling and the Collared Flycatcher, and for age only in Collared Flycatcher. The Common Starling showed significant selectivity towards the mixed type compared to the poplar and the alder ($\chi2 = 3.987$, $p < 0.05$, df = 1, $\chi2 = 11.686$, $p < 0.05$, df = 1, respectively), and to ash compared to alder ($\chi2 = 6.798$, $p < 0.05$, df = 1). The Collared Flycatcher showed significant selectivity towards the mixed type compared to the poplar and the alder ($\chi2 = 11.454$, $p < 0.05$, df = 1, $\boldsymbol{\chi}$**2** = 3.726, $p < 0.05$, df = 1, respectively), and towards the ash compared to the poplar and the alder ($\chi2 = 11.455$, $p < 0.05$, df = 1, $\boldsymbol{\chi}$**2** = 5.775, $p < 0.05$, df = 1, respectively). All hole-nesting species combined showed no clear preference for either forest type or age. The selection indices of all feeding groups showed preference for the mixed type and older forest stands. However, the selectivity was significant only for the Common Starling and the Collared Flycatcher, which were the only species representing groups that forage on the ground and in the air.

DISCUSSION

The key findings of this study confirm that both primary and secondary hole-nesting species in riverine forests in Croatia select their habitat relying on structural habitat characteristics. This is a valuable addition to the studies conducted so far in Croatia. It shows that structural habitat characteristics associated with stand age and maturity (e.g. stand age, the percentage of large trees, and average tree basal area) have a pronounced positive effect on hole-nesters' habitat selection. Additionally, floristic habitat characteristics are important for secondary hole-nesters. They are positively affected by a more diverse floristic structure of the habitat. It is not exactly clear which floristic elements have the greatest impact; thus further studies should be conducted. Furthermore, the diversity and the abundance of secondary hole-nesting bird species was positively correlated with the number of species and the abundance of the primary hole-nesting bird species. This might be important for identifying keystone and/or umbrella species associated with habitat preservation. These species should be taken into consideration in forestry management, because they can be good indicators of habitat quality.

The structure of hole-nesting bird communities recorded in this study is in accordance with the research conducted so far in deciduous and mixed forests in Croatia and Europe (Rucner & Rucner 1970, Herrera 1981, Kralj 2000, Diaz 2005, Sakhvon 2009, Kirin *et al.* 2011). The species recorded in this study can inhabit many different types of forest habitats. As expected, the Great Spotted Woodpecker and the Great Tit were the most abundant. The Great Spotted Woodpecker is opportunistic when it comes to choosing its habitat and diet; it therefore inhabits almost all types of habitats with trees (Cramp 1985). In this study it was recorded on all locations, in all forest types with the highest number of pairs in older forests and a slightly higher number of pairs in the mixed type, which is consistent with woodpecker research in different habitats (e.g. Rucner & Rucner 1970, Božič 2002, Walankiewicz *et al.* 2011, Ćiković *et al.* 2015). In some studies, the preference for oak was found (Kosiński & Kempa 2007), which might be indicated by its highest abundance in mixed forests in this study. Relatively small number of the Grey-faced Woodpecker pairs with the largest number of pairs recorded in older stands corresponds to other results from riverine forests (Tomiałojć & Wesołowski 1995), where it occurs with a low population density. According to Bauer *et al.* (2005), this species maintains large territories (> 50 ha and up to 1 km^2) resulting in sparse occurrence with low densities. A study covering the same species of primary hole-nesters in Poland (Kosiński & Kempa 2007) concluded that all species prefer older stands for nesting. The Black Woodpecker almost always chooses old forests with an average DBH greater than 45 cm for nesting, while in slightly younger stands it can show territorial behavior, because it uses them for feeding (Majewski & Rolstad 1993, Garmendia *et al.* 2006). With a small number of plots dominated by the largest trees (categories E–G), the study area is not suitable for nesting of this species. The Middle Spotted Woodpecker and the Lesser Spotted Woodpecker were also rarely recorded in this study. They prefer older habitats with a larger number of standing dead trees and avoid mixed stands of coniferous and deciduous trees (Olsson *et al.* 1992, Pasinelli & Hegelbach 1997, Pasinelli 2007). The Great Tit is very abundant throughout Croatia (Kralj 1997); and it regularly stands out as one of the most numerous species in all forest habitats (Božič 2002, Sakhvon 2009, Kirin *et al.* 2011). The Eurasian Blue Tit, although recorded on all locations and in all forest types except in the youngest stands in this study, is always less abundant than the Great Tit. Dhondt & Eyckerman (1980) found that the abundance of the Eurasian Blue Tit and its nesting parameters are greatly influenced by competition with the dominant Great Tit for food and nesting space. Sakhvon (2009) recorded the Great Tit domination in oak forests and black alder forests, which is in accordance with this study. The Short-toed Treecreeper and the Eurasian Treecreeper were both recorded in this study. Out of these two species, the Short-toed Treecreeper is the dominant species, and it regularly constrains Eurasian Treecreeper to higher altitudes (Gil 1997, Schepers & Török 1997). Furthermore, in studies covering riverine oak forests in Croatia, the Eurasian Treecreeper is almost never recorded (Kralj 2000). Suorsa *et al.* (2005) concluded that the Eurasian Treecreeper prefers forest patches with a higher amount of old forest cover and trunks with a large circumference. According to Southwood (1961), oak trees have the highest number of insect species. This could be very important for bark feeding species such as treecreepers. Therefore, riverine forests in our research represent a habitat of lower quality with less feeding opportunities, so it can breed here alone or in sympatry with the Short-toed Treecreeper. This is also in line with research conducted by Sakhvon (2009). The Eurasian Nuthatch is also a very common species recorded on all locations and in all forest types with the lowest number of pairs in the alder type, and increasing abundance with forest age. The Eurasian Nuthatch prefers mature forest areas with a larger volume of live wood, and shows a preference for areas with a higher proportion of oak trees (Hardersen 2004). The Common Starling was recorded on all locations, in all types of forest, with a greater abundance in the ash type and mixed type, and increasing number of pairs with forest age. The preference for the mixed type is significant compared to the poplar and the alder, and for the ash compared to the alder. This may be a result of the difference in the average age and structure of these forest types. Due to its specific feeding preferences, the Common Starling prefers habitats covered with grass (Williamson & Gray 1975). Forests in this study very often have ground well covered with grass, which makes them a good habitat for this species. Also, the fragmentation of forests in the research area and the presence of arable land and pastures near the forest are likely reasons for the abundance of the Common Starling. According to Smith & Bruun (2002), the breeding density of this species is positively related to the availability of pasture near colonies and the reduction of pasture in modern agricultural landscape could be one of the reasons for a declined population size. The Collared Flycatcher was not recorded only in the poplar forest type, and the largest number of pairs was recorded in the ash type and in the oldest forests. According to the studies done so far, it prefers oak and beech over coniferous stands, forests with a smaller number of trees with larger average basal area, and lower shrub cover due to its specific way of feeding (Kralj *et al.* 2009). The results of this research have partially confirmed this; significant selectivity towards older mixed type forests (with a large proportion of oak) and ash in comparison compared to poplar were shown.

Riverine forests in this study are represented by smaller forest fragments with very heterogeneous structural and floristic characteristics. Several aspects of habitat selection for hole-nesting birds are thus not entirely clear. Although some of them demonstrate preference for a certain type of habitat (Diaz 2005, Kralj *et al.* 2009, Kirin *et al.* 2011), this study has not confirmed strong preference. The hole-nesting birds generally show preference for older forest stands and structural characteristics related to age have the greatest influence on the population density of different ecological groups of birds (Kirin *et al.* 2011). This has been confirmed by studies showing that the size of trees and the number of dead trees are very important habitat factors for hole-nesters (Berg 1997, Suorsa *et al.* 2005, De Zan *et al.* 2017). This study has moreover confirmed the importance of tree size. The biodiversity index for investigated species increases with stand age. Since this study covers only hole-nesting birds and the biodiversity indices refer only to them, they cannot be compared with the research including all the species in an area. Furthermore, the Spearman-rank correlation between the principal components obtained by the PCA analysis and the ornithological variables shows that both primary and secondary hole-nesters prefer older forests as habitat. This is in line with previous research by Blondel *et al.* (1973) and MacArthur & MacArthur (1961). However, the increase in the abundance of primary hole-nesting species is not completely consistent with the increase in the absolute forest age: the number of pairs in forests 60-79 years old is lower than in forests 40-59 years old. In the category of 60-79 year-old forests, the alder and ash-type forests, which are clearly not suitable high-quality habitats, predominate. In the same age category, there are no poplar forests at all, while the pedunculate oak appears with a smaller percentage at only two points. Moreover, almost none of the bird species show positive selection towards alder and poplar forests. This is probably a result of preferring forests with a higher diversity of tree species and a higher proportion of oak, rather than avoiding the common alder, in which woodpecker holes were often located (Ćiković *et al.* 2014). The reasons for choosing older forest habitats are foraging and the availability of nesting sites for the hole-nesting species. Numerous studies of herbivorous insects confirm that the density and the richness of forest entomofauna increases with forest age (Økland

1994, Irmler *et al*. 1996, Jeffries *et al*. 2006). The hole-nesting species mainly rely on insect larvae during the nesting season (Moeed 1980, Török 1986, Wilkin *et al.* 2009). In addition, older forests abound in trees with a larger DBH, which are very important for the availability of the nesting cavities (Remm *et al*. 2006, Aitken & Martin 2007, Ćiković *et al*. 2014). In this study, the floristic composition of the forest had an impact on secondary hole-nesters. They preferred certain types of trees and a more diverse floristic structure of the habitat. Moskat (1988) proved the importance of floristic composition in the beech forest bird communities in Hungary too. Several studies show that plant species richness and plant functional group richness have a significant positive effect on the overall insect species richness (Haddad *et al.* 2001). Among the secondary hole-nesters, there are species with different feeding habits; thus more different tree species mean more feeding opportunities. The influence of floristic structure on the communities of hole-nesters should be further investigated on samples of approximately equal forest age in order to determine which floristic components have the greatest influence. The existing cavities are very important for secondary hole-nesters. They often use natural holes, which were not made by primary hole-nesters but created by tree decay in the place of broken branches or fungal decay. However, most holes available for nesting in forests are excavated by primary hole-nesters (Aitken & Martin 2007), making them more available for secondary hole-nesters in the upcoming breeding seasons. That is why this research has established positive correlation between the number of pairs and the number of species of primary and secondary hole-nesters. This is in accordance with the research by Mikusiński *et al*. (2001), who showed a strong connection between the number of forest bird species and woodpeckers, and established that the number of forest specialists is positively correlated with the number of woodpecker species.

When designing sustainable forestry management, the impact on all faunal components cannot easily be considered. Therefore, the results of research on smaller groups, such as bird communities, can be used as a guideline when applying the principles of sustainable management (Fuller 1990, Kubalikova *et al.* 2019). Since woodpeckers stand out as good indicators of the state of forest ecosystems (Mikusiński *et al.* 2001, Wübbenhorst & Südbeck 2001, Kajtoch *et al.* 2015), the study of their communities is very important. Fuller (1990) revealed special importance of the share of old trees, canopy coverage and the density of the shrub layer, and suggests forest management with a combination of cutting and preserving older trees to preserve species positively correlated with shrub density and hole-nesters dependent on old trees. Based on their research of hole-nesters, Camprodon *et al.* (2008) propose a management model in which 20 to 30 large trees (55-75 cm DBH) are preserved per hectare of forest, out of which at least several are dead trees. These trees should be kept in a homogeneous arrangement to avoid competition. Økland (1994) emphasizes the importance of maintaining the remaining forest areas with continuity in succession, and suggests the practice of cutting down trees in previously logged forests instead of natural, less managed habitats. Forest management in Croatia shows a certain flexibility and compliance with relevant scientific knowledge, but it is still quite intensive and invasive. Management methods include intensive cutting and thinning, transport and utilization of wood mass, especially old wood, and adaptation of natural forest habitats to human exploitation (Krpan 1992, Matić & Skenderović 1992). Furthermore, it is common to remove species that are economically less important and represented in smaller share. This research confirmed the necessity of preserving older forest stands, more suitable for hole-nesters, to preserve their populations; however, it is at the same time important to nurture a more diverse floristic structure of the forest habitat suitable for secondary hole-nesters.

It may be concluded that the main hypotheses of this study have been confirmed. In the Croatian riverine forests, the number of primary and secondary hole-nesting bird species, as well as their abundance, is significantly correlated with structural habitat characteristics. In addition, the importance of floristic characteristics for secondary hole-nesters was also observed, especially in the preference for forests with a larger number of tree species. As expected, older forest stands show greater bird biodiversity and abundance, whereas the number and the abundance of secondary hole-nesting bird species is positively correlated with the number of species and the abundance of primary hole-nesting bird species. Further studies of the effects of floristic and structural characteristics on bird communities might provide more valuable data for establishing sustainability principles in forestry management.

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SAŽETAK

U ovom radu istražen je utjecaj florističkih i strukturnih karakteristika šumskog staništa na karakteristike zajednica primarnih i sekundarnih ptica dupljašica. Istraživanje je provedeno na ukupno 66 točaka u nizinskim poplavnim šumama uz rijeku Dravu u Hrvatskoj. Standardna metoda prebrojavanja u točki korištena je za istraživanje zajednica ptica, a metoda kružnih ploha za istraživanje karakteristika staništa. Prosječna bazalna površina stabala korištena je kao indikator starosti, a istraživane točke klasificirane su u četiri skupine prema dominantnoj vrsti stabla. Uočena je velika heterogenost staništa. Zabilježeno je ukupno 13 vrsta dupljašica (pet vrsta primarnih i osam vrsta sekundarnih). Ustanovljeno je da broj vrsta ptica i brojnost ptica dupljašica ovise i o strukturnom i florističkom sastavu šumskih zajednica. Starije šumske sastojine imale su veću raznolikost zajednica ptica i veću brojnost. Ptice su preferirale miješane šume i šume tipa jasena, a florističke karakteristike su imale veći utjecaj na sastav zajednica sekundarnih

dupljašica. Broj vrsta i brojnost sekundarnih dupljašica bili su pozitivno korelirani s brojem vrsta i brojnošću primarnih dupljašica. Rezultati istraživanja mogu biti korišteni kao smjernice za održivo gospodarenje šumama.