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Breeding avifauna of the forest interior and forest edge in the Borki Forest

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Abstract. The composition and structure of breeding bird communities in the Borki Forest in North-Eastern Poland were investigated separately in the forest interior (years 2012–2014) and at the forest edge (years 2016–2018). In both areas, bird censuses were carried out on three plots located in mature oak-hornbeam, ash-alder and mixed coniferous forest stands. Plots were selected to cover similar forest types, encompass stands of similar age and to have similar acreage, both, in the forest interior and at the forest edge. A standard combined mapping technique for estimating the number of breeding birds was applied and a total of 97 bird species were found to have bred at least once within any plot. Regardless of the forest type, both the number of breeding bird species and the population densities were higher on plots situated at the forest edge than in the forest interior. The mean number of breeding species was over 20% higher and the mean total density of breeding pairs was higher by over 30%. Total population densities on the plots located at the forest edge were higher as a result of an increase in population densities of some individual bird species combined with an increase in the number of breeding species, including non-forest and non-typical forest interior species. The number of nesting species in the edge zone was higher than in the forest interior with common species and generalists clearly dominating. Specialist species typical of natural forests as well as rare and endangered species, such as three-toed woodpecker (*Picoides tridactylus*), white-backed woodpecker (*Dendrocopos leucotos*), collared flycatcher (*Ficedula albicollis*) and red-breasted flycatcher (*Ficedula parva*), for whom the Borki Forest is an important breeding site in Poland were less numerous. Despite the observed differences and a clear edge effect, bird assemblages inhabiting research plots in the forest interior and at the edge were not fundamentally different. We conclude that the edge zone is inhabited by a poorer-quality variant of bird assemblage typical of forest interior, enriched quantitatively by non-forest species associated with open and/or semi-open areas as well as by synanthropic species.

Keywords: Borki Forest, bird assemblage, edge effect, ecotonal zone, bird population densities, avifauna richness

1. Introduction

As natural habitats, the forest interior and its edge differ from each other in many respects, mainly because of their different local microclimatic parameters, such as temperature, humidity, wind, light conditions and others (Zięba et al. 2014). Forest habitats in the interior of a forest complex are more stable compared to its edge zone. The forest interior has higher moisture, much lower air movement and much less light reaches the forest floor. In the case of air and ground temperatures, the forest complex acts as a buffer. In its interior, spring and summer temperatures are usually lower than at the edge, and in the autumn and winter, the reverse occurs. These differences result in tree stands, even those representing the same type of forest community, with a slightly different form in the edge zone than in the interior of a forest complex, which was studied, amongst others, by Harper and Macdonald (2001), Zięba et al. (2014) and Ouini et al. (2015). According to these authors, stands in the edge zone were characterised by greater densities, higher volume and richer species composition, whereas the trees were lower and had larger crowns. In this zone, the understory and tree saplings were much better developed and had more microhabitats than the forest interior.

The differences in microclimatic conditions and the nature of the habitats translate into the differences in species compo-

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sition and the structure of the animal assemblages inhabiting the interior of the forest and its edge. The concept of 'edge effect' as a consequence of the impact of the ecotone zone on fauna was first introduced by Odum (1963), who defined it as a tendency towards increased population density and species richness at the point where two different habitats meet. The same author also suggested that this concept can be applied in particular to avifauna. The edge effect on bird communities in the ecotone zone between the forest and open areas has been analysed by many researchers (Johnston 1947; Strelke, Dickson 1980; Helle, Helle 1982; Kroodsma 1984; McCollin 1998; Kurosawa, Askins 1999; Flashpohler et al. 2001; Baker et al. 2002; Zurita et al. 2012; Terraube et al. 2016). Most of them pointed out that the forest edge zone is preferred by less-specialised species (generalists), which can use different habitats. Some pointed to additional factors, such as the pressure of humans and increased predation and parasitism, affecting the avifauna in the forest edge zone (Flashpohler et al. 2001; Terraube et al. 2016). In Poland, the edge effect on forest bird assemblages has been the subject of very few studies (Cieślak 1983, 1992; Cieślak, Dombrowski 1993; Kopij 2013). Information on this subject also appeared occasionally in several other publications (Gromadzki 1970; Tomiałojć et al. 1984; Markowski 1995; Kujawa 2009; Tryjanowski et al. 2009; Jakubiec, Wuczyński 2013).

This article presents a summary of the results of several years of ornithological research in the Borki Forest in the Masurian Lake District, which is a managed forest with a significant degree of naturalness (Rąkowski 2015; Rąkowski et al. 2016). During three seasons in 2016–2018, an inventory of the avifauna was conducted in three study plots at the forest edge along the western border of the Borki Forest. Species composition, density of breeding pairs and domination of particular species were assessed. The plots included mature tree stands representing the three types of forest communities most commonly found in this forest complex: oak-hornbeam, ash-alder and mixed coniferous forests. The results of these inventories were compared with those of similar surveys conducted in 2012–2014 in three permanent ornithological research sites located in the interior of the Borki Forest (at least 3 km from the forest edge) as part of a multi-year avifauna research program (Rąkowski et al. 2016). The study plots at the edge of the forest were chosen in such a way as to be as similar as possible to the permanent research plots in the forest interior, that is, they are comparable in size, include similar forest communities and include stands of a similar age. The purpose of this work is to compare the results of both inventories, determine the differences between the breeding bird assemblages inhabiting the forest interior and its edge and analyse the causes of these differences.

2. Research area and study plots

The geographic and natural characteristics of the Borki Forest are described in a publication presenting the results of many years of ornithological research in this forest complex (Rąkowski et al. 2016). The same study also describes the three study plots located deep inside the forest, consisting of three main forest types: G, oak-hornbeam (16.00 ha); Ł, ash-alder (6.00 ha); and BM, mixed coniferous (14.50 ha). For the purpose of this publication, the designations of these areas have been changed to G1, Ł1 and BM1, respectively, to distinguish them from the similar forest communities of G2, Ł2 and BM2, designated in the forest edge zone, whose characteristics are presented below (Fig 1). Except for the Ł1 plot (located in the Borki Nature Reserve), all the remaining ones were located within managed forests, where foresters harvest timber. Therefore, within the boundaries of some plots and/or in their immediate vicinity, the gap felling and individual tree felling were conducted.

Study plot G2 – The oak-hornbeam forest (18.43 ha) was located near the Diabla Góra forester's lodge and the Borki Forest Comprehensive Environmental Monitoring Station (KMŚ). It included parts of two forest units of the Diabla Góra Forest District within the Przerwanka branch of the Borki Forest Inspectorate. These were units 144 d, g and h and 145 g and h. Its boundaries were formed by forest roads and forest unit boundaries and by the edge of the forest on the southwest side. The terrain within the plot was strongly undulating; one of the highest elevations in the Borki Forest, Diabla Góra (199 m a.s.l.), is located here. The plot included the top and slopes of this hill cut from the west by dry erosional ravines and the deep valley of a small stream at the southern foot of the hill. The bottom of the valley on the southwestern edge of the area, at the border with meadows, was at an altitude of 140 m a.s.l. The dominant forest community was the *Tilio-Carpinetum* subcontinental oak-hornbeam forest. More than half of the plot consisted of a typical oak-hornbeam forest with many species of old trees aged about 130 years, with a low crown density dominated by common hornbeam (*Carpinus betulus* L.) Significant admixtures included pedunculate oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.) and Norway spruce (*Picea abies* [L.] H. Karst). Single trees of silver birch (*Betula pendula* Roth.), aspen (*Populus tremula* L.), Norway maple (*Acer platanoides* L.), field elm (*Ulmus minor* Mill.) and European larch (*Larix decidua* Mill.) were also present. The understory, made up of common hazel (*Corylus avellana* L.) as well as hornbeam and spruce saplings, was poorly developed, as was the groundcover. Part of the plot had slightly younger and more transformed hornbeam stands aged 80–100 years, in which spruce dominated, with a significant share of deciduous species, mainly hornbeam and oak, with admixture of limes, aspen and willow (*Salix caprea* L.). There was a very narrow belt of *Fraxino-Al-*

netum ash-alder riverine forest with the dominance of common alder (*Alnus glutinosa* Gaertn.) and an admixture of spruce in the valley of the stream. Several forest patches had been logged in the recent years within the plot (separating 144 h and 145 h), occupying a total area of about 2–3 ha. From the southwest, the plot bordered on open areas around the buildings of the KMŚ Borki Forest Station, 50 m from the forest edge. These were dry and moist meadows that were extensively mowed. There were numerous small clumps of trees and shrubs, as well as individual trees within the meadows. A vast marsh was found, partly covered by sedge tufts and reeds where a small stream flows out of the forest. The buildings of the forester's lodge were at a slightly greater distance (about 200 m) from the edge of the study plot.

Study plot Ł2 – The ash-alder riverine forest (6.40 ha) included units 78 a and b and part of the Knieja Łuczańska Forest District within the Borki Forest Inspectorate. The boundaries of the plot, located at an altitude of 151–164 m a.s.l., was bordered on the south and east by a narrow, rarely used forest road, from the west and south by a forest edge adjacent to open areas. The vast majority of the plot was covered by an ash-alder forest community of 70- to 110-year-old trees with a fairly high crown density, formed mainly by alder, with a small admixture of spruce and silver birch. The undergrowth consisted mainly of common hazel (*Frangula alnus* Mill.), rowan (*Sorbus aucuparia* L.), willow and alder saplings and was richly developed. The forest groundcover was also very well developed. The plot was intersected by the valley of a small, intermittent stream. From the west, the plot was bordered by a vast cultivated field with no trees or shrubs. From the north, the area was adjacent to an extensively used pasture located near two farms in Jeziorowskie village, surrounded by groups of trees and shrubs, about 100 and 150 m from the boundary of the study plot.

Study plot BM2 – The mixed coniferous forest (15.28 ha) consisted of forest unit 33 of the Knieja Łuczańska Forest District within the Borki Forest Inspectorate. Its eastern border was a wide gravel forest road, the south and southwest border was a rarely used forest road, and the northwest border was the forest edge adjacent to a cultivated field. The plot has a terrain sculpted by a mosaic of moraines, located at an altitude of 151–163 m a.s.l. and varied in terms of the types of habitats and the character of its forest stand. Its largest part, consisting of low hills, was occupied by the *Serratulo-Pinetum* mixed coniferous forest community of the variety with spruce. Spruce with an admixture of common oak and alder decidedly dominated about 90-year-old forest stand of moderate crown density. Birch and pine (*Pinus sylvestris* L.) were also found individually. The undergrowth was moderate, mainly made up of hornbeam, common hazel, aspen and spruce saplings. Oak-hornbeam forest complex species occurred on the forest floor with an admixture of coniferous species. The depressions between the moraine hills, with a total area of about 3 ha, had an ash-alder forest community with tree stands of 50–90 years of age, mainly consisting of alder with an admixture of spruce, and single birches and aspens. Three marshy depressions of about 2.5 ha in total occurred in the study plot, occupied by young trees and shrub communities, with a predominance of alder, birch, willow and buckthorn. One of these marshes located at the northwestern edge of the plot is the source of a small watercourse flowing out of the forest. In 2017, several small areas of approximately 1.7 ha were logged in the northern part of the study plot. The northwest boundary of the study plot bordered a field that was cut by the channelled bed of the aforementioned watercourse. Two small clusters of trees and shrubs were found within the field, and a narrow belt of low shrubs grew along the watercourse. A single farmstead with trees was located at the edge of the field, about 200 m from the edge of the study plot.

Although the study plots at the edge of the Borki Forest were selected in such a way as to correspond as closely as possible in terms of size, type of forest community, age, species composition and stand structure to the plots within forest interior, the appropriate pairs of plots differed in some respects from each other. This was mainly due to the very varied relief and micro-relief of the terrain in the Borki Forest, with numerous hills, dry and swampy depressions, stream valleys and erosion gorges. The diversified terrain relief results in a mosaic of natural habitats, which means that within the phytocoenoses dominating in a given plot, there were enclaves of other forest types and, in some cases, also non-forest (wetland and water) communities. For these reasons, none of the study plots were uniform in phytosociological terms, and the mosaic of habitats in each of them differ from each other. Generally, the areas located in the edge zone had tree stands with a slightly greater crown density than in the forest interior, as well as a larger share of shrubs in the understory, especially in the immediate vicinity of the forest edge.

3. Methods

3.1. Methods of observing birds and their ecological groups

Bird observations in the study plots at the edge of the Borki Forest were conducted in the 2016–2017 spring season (April–June), in accordance with the standard combined variation of the cartographic method (Tomiałojć 1980) used in the study of the plots located within the forest and described by Rąkowski et al. (2016). The aforementioned study also specified the breeding criteria and criteria used to categorise the bird species into ecological groups, which were also used in this study. For each of these groups, we calculated the percentage share of the species composition of the nesting bird assemblages for each study plot in the forest interior and its edge (Fig. 4).

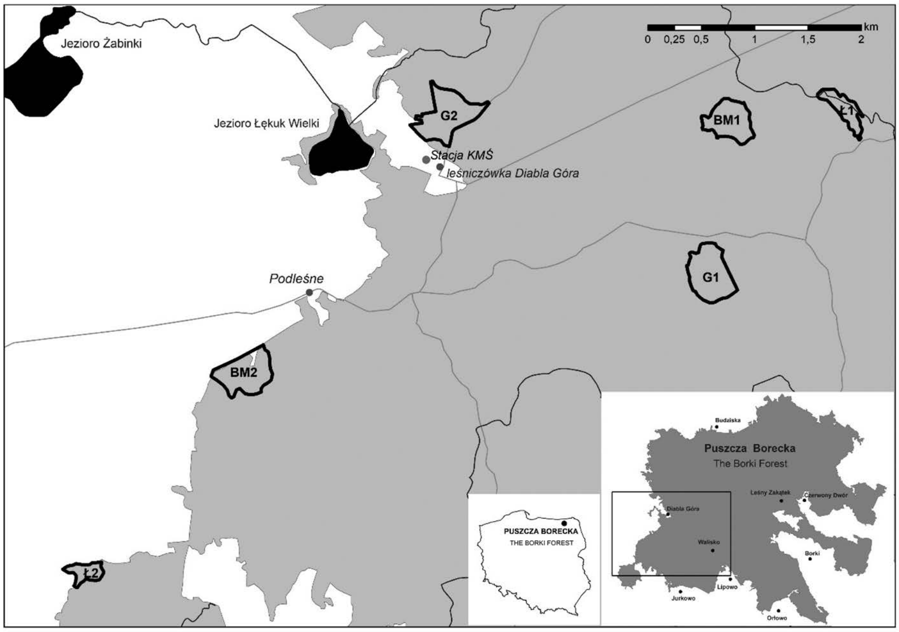

Figure 1. Distribution of study plots in the Borki Forest

3.2. Method of ornithological valorisation

For the purposes of this study, we performed an ornithological valorisation of nesting bird assemblages in individual study plots based on the following indicators proposed by Kot (2008):

- species rank index (*Rg*),
- avifauna richness index (*Wb*),
- equivalent index of avifauna richness (*RWB*).

The species rank index was determined for bird species listed in Annex I of the Birds Directive, which were confirmed as nesting (at least 0.5 of the breeding territory of one pair) in the study plots (Table 1). Species whose territories only bordered the study plots were not considered (+). Individual species were assigned numerical values from 1 to 20 in accordance with the scale proposed by Kot (2008). The rarest and most valuable species listed in the ‘Polish Red Book of Animals’ (Głowaciński 2001) received the highest values (from 10 to 20), depending on their category as a threatened species. The remaining species included in the ranking were given a coefficient value of 5 (relatively small in number, requiring specific habitats) or 1 (relatively numerous, not threatened).

The avifauna richness index *Wb* was calculated for each study plot to describe its ornithological value using the formula

$$\mathrm{Wb} = \sum \mathrm{p_n} \times \mathrm{Rg_n}$$

where

p_n is the number of breeding pairs of *n* species assigned a species rank index,

Rg_n is the value of the species rank index *Rg* assigned to this species.

The equivalent index of avifauna richness *RWb* was obtained by calculating the *WB* index for a study plot expressed in km^2.

3.3. Statistical analysis

The Sørensen *QS* coefficient (Sørensen 1948) was used to analyse the similarity of the species composition of nesting bird assemblages present in individual study plots:

$$QS = \frac{2c}{a+b} \times 100$$

where

a and *b* are the number of species present in the first and second assemblages, respectively,

c is the number of species present in both assemblages.

The Renkonen *DR* coefficient (Renkonen 1938) was used to analyse the similarity of the structure of the bird assemblages inhabiting individual study plots:

$$DR = \sum_{i=1}^{n} \min(p_i;\, q_i) \times 100$$

where

p_i, q_i are the relative frequency of *i* species in the studied assemblages.

Student’s t-test for independent samples was used for the statistical analysis of differences observed in the number of

Table 1. List of bird species from Annex I of the Birds Directive found to nest on controlled plots and taken into account when calculating the avifauna richness index (*Wb*)

No.	Species code	Species	PRDB/category of threat	Species rank index Rg
1.	A241	Three-toed woodpecker *(Picoides tridactylus)*	VU	20
2.	A239	White-backed woodpecker *(Dendrocopos leucotos)*	NT	15
3.	A217	Pygmy owl *(Glaucidium passerinum)*	LC	10
4.	A104	Hazel hen *(Tetrastes bonasia)*	-	5
5.	A127	Crane *(Grus grus)*	-	5
6.	A224	Nightjar *(Caprimulgus europaeus)*	-	5
7.	A238	Middle spotted woodpecker *(Dendrocopos medius)*	-	5
8.	A321	Collared flycatcher *(Ficedula albicollis)*	-	5
9.	A236	Black woodpecker *(Dryocopus martius)*	-	1
10.	A246	Wood lark *(Lullula arborea)*	-	1
11.	A320	Red-breasted flycatcher *(Ficedula parva)*	-	1
12.	A338	Red-backed shrike *(Lanius collurio)*	-	1

Explanations: PRDB – species from the Polish Red Data Book of Animals; kategorie zagrożenia / categories of threat: VU – vulnerable, NT – near threatened, LC – least concern

species and density of breeding pairs between the study plots located in the forest interior and at its edge. The calculations were performed using Statistica version 10 (StatSoft, Inc. 2011).

4. Results

A total of 97 species were confirmed in the study area, including 73 species in the forest interior and 87 at its edge (Tables 2–4). Ten species were found only in the study plots deep within the forest, whereas 24 species were only in plots at the forest edge; 63 species were recorded in both the habitats.

On the basis of the data presented in Tables 2–4, we can distinguish species that prefer the edge of the forest or its interior and species that do not exhibit explicit preferences in this respect. Species with extensive territories, significantly larger than the study plots (i.e. all birds of prey and the black stork), were excluded from the following considerations because their relationship to the study area was very weak. The analysis also excluded all other species whose presence in the study area was limited only to its marginal areas, as well as the (very few) waterbirds and marsh birds, because their occurrence in the forest was dependent on the presence of non-forest habitats, that is, water bodies and wetlands, and was not related to the distance from the edge of the forest. As a result, 19 species were excluded from the total number of 97 found, which met one of the criteria listed above. The remaining 78 species can be divided into 3 groups: (1) those preferring the interior of the forest, (2) the much more numerous ones at its edge and (3) those showing no clear preferences in this respect.

The 12 species of birds occurring significantly more frequently in the forest interior than at its edge include: goldcrest (*Regulus regulus* L.), Eurasian wren (*Troglodytes troglodytes* L.), Eurasian treecreeper (*Certhia familiaris* L.), European pied flycatcher (*Ficedula hypoleuca* Pallas), red-breasted flycatcher (*Ficedula parva* Bechst.), collared flycatcher (*Ficedula albicollis* Temm.), willow tit (*Poecile montanus* Con.), white-backed woodpecker (*Dendrocopos leucotos* Bechst.), nutcracker (*Nucifraga carycatactes* L.), Eurasian three-toed woodpecker (*Picoides tridactylus* L.), European nightjar (*Caprimulgus europaeus* L.) and greenish warbler (*Phylloscopus trochiloides* Sund.), which did not occur at all in the edge zone.

Two groups can be distinguished amongst the 29 species that preferred the forest edge. The first includes forest species or those often breeding in forests but exhibiting relatively low habitat selectivity and those that can nest in various types of tree stands as well as outside of the forest. This includes the European starling *Sturnus vulgaris* L., which did not occur in the interior of the forest at all, and was in the group of dominants at the edge zone, reaching a very high average density of 13.5 pairs/10 ha in plot Ł2. The species that occurred in the forest interior but reached greater numbers at the edge also included: great tit (*Parus major* L.), Eurasian

Table 2. Breeding bird assemblage on oak-hornbeam forest stands situated in the forest interior (plot G1, 2012–2014) and on the forest edge (plot G2, 2016–2018)

No.	Species*	Ecological group	Forest interior, plot G1 (16.00 ha), 2012–2014					Forest edge, plot G2 (18.43 ha), 2016–2018				
			Number of pair			Mean		Number of pair			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
1.	*Fringilla coelebs*[ab]	L	26.0	24.0	24.0	15.4	19.2	24.0	25.0	25.0	13.4	15.2
2.	*Erithacus rubecula*[ab]	L	11.5	8.5	10.5	6.4	8.0	11.0	11.5	10.5	6.0	6.8
3.	*Coccothraustes coccothraustes*[ab]	L	10.0	10.0	9.0	6.0	7.5	9.0	10.0	9.0	5.1	5.7
4.	*Parus major*[ab]	L	8.0	7.5	7.5	4.8	6.0	11.0	10.5	11.0	5.9	6.6
5.	*Sylvia atricapilla*[a]	L	10.0	8.5	6.0	5.1	6.4	7.0	7.0	7.0	3.8	4.3
6.	*Turdus philomelos*[b]	L	6.0	6.0	5.5	3.7	4.6	8.0	8.5	8.0	4.4	5.0
7.	*Cyanistes caeruleus*	L	6.0	6.0	5.5	3.7	4.6	7.0	7.0	8.0	4.0	4.5
8.	*Turdus merula*	L	3.5	4.0	4.5	2.5	3.1	8.0	7.0	7.0	4.0	4.5
9.	*Troglodytes troglodytes*	L	4.5	6.5	5.5	3.4	4.2	5.0	5.0	4.5	2.6	3.0
10.	*Sitta europaea*	L	4.0	4.0	4.0	2.5	3.1	7.0	6.0	6.0	3.5	3.9
11.	*Ficedula hypoleuca*	L	3.0	4.5	4.5	2.5	3.1	4.0	3.0	2.0	1.6	1.8
12.	*Certhia familiaris*	L	3.0	4.5	4.0	2.4	3.0	3.0	3.5	4.0	1.9	2.1
13.	*Phylloscopus sibilatrix*	LN	3.5	3.0	1.0	1.6	2.0	4.0	5.0	9.0	3.3	3.7
14.	*Phylloscopus collybita*	L	2.0	3.5	1.5	1.5	1.9	6.0	7.0	6.0	3.5	3.9
15.	*Regulus regulus*	LN	4.0	3.0	3.0	2.1	2.6	3.0	2.5	2.0	1.4	1.5
16.	*Poecile palustris*	L	3.0	2.5	3.0	1.8	2.2	4.0	4.0	5.0	2.4	2.7
17.	*Dendrocopos major*	L	3.0	2.0	3.0	1.7	2.1	3.0	3.0	3.5	1.7	1.9
18.	***Ficedula parva***	LN	2.0	2.0	2.5	1.4	1.7	2.0	1.5	2.0	1.0	1.1
19.	*Columba palumbus*	L	2.0	1.0	1.5	0.9	1.1	3.0	3.0	3.0	1.6	1.8
20.	*Prunella modularis*	LN	1.0	1.0	2.0	0.8	1.0	2.0	1.0	2.0	0.9	1.0
21.	*Muscicapa striata*	L	2.0	2.0	2.0	1.3	1.6	4.0	5.0	4.0	2.4	2.7
22.	***Dendrocopos medius***	LN	1.5	1.5	1.0	0.8	1.0	2.0	2.0	1.0	0.9	1.0
23.	*Phylloscopus trochilus*	L	2.0	1.0	2.0	1.1	1.4	2.0	2.0	2.0	1.1	1.2
24.	*Regulus ignicapillus*	L	2.5	1.0	1.5	1.0	1.2	2.0	3.0	3.0	1.4	1.6

No.	Species*	Ecological group	Forest interior, plot G1 (16.00 ha), 2012–2014					Forest edge, plot G2 (18.43 ha), 2016–2018				
			Number of pair			Mean		Number of pair			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
25.	*Sylvia borin*	L	1.0	1.0	0.5	0.5	0.6	1.0	0.5	2.0	0.6	0.7
26.	*Garrulus glandarius*	L	0.5	0.5	0.5	0.3	0.4	1.0	1.0	1.0	0.5	0.6
27.	***Dryocopus martius***	LN	0.5	0.5	0.5	0.3	0.4	0.5	0.5	0.5	0.3	0.3
28.	*Strix aluco*	L	0.5	0.5	0.5	0.3	0.4	1.0	1.0	1.0	0.5	0.6
29.	*Anthus trivialis*	EN	1.0	0.5	-	0.3	0.4	1.0	-	+	0.2	0.2
30.	*Sylvia communis*	EN	-	-	0.5	0.1	0.1	1.0	1.0	1.0	0.5	0.6
31.	*Periparus ater*	LN	-	-	0.5	0.1	0.1	1.0	+	+	0.2	0.2
32.	***Ficedula albicollis***	LN	2.0	2.0	3.0	1.5	1.9	1.0	-	-	0.2	0.2
33.	***Grus grus***	L	+	+	0.5	0.1	0.1	0.5	0.5	0.5	0.3	0.3
34.	*Buteo buteo*	L	+	+	1.0	0.2	0.2	0.5	0.5	0.5	0.3	0.3
35.	*Columba oenas*	LN	-	0.5	0.5	0.2	0.2	0.5	0.5	0.5	0.3	0.3
36.	*Oriolus oriolus*	L	+	1.0	1.0	0.4	0.5	1.0	1.0	1.0	0.5	0.6
37.	*Turdus viscivorus*	L	-	1.0	+	0.2	0.2	1.0	1.0	1.0	0.5	0.6
38.	*Poecile montanus*	L	1.0	1.5	1.0	0.7	0.9	-	-	-		
39.	*Dendrocopos minor*	L	-	0.5	0.5	0.2	0.2	-	-	-		
40.	***Dendrocopos leucotos***	LN	1.0	0.5	0.5	0.4	0.5	-	-	-		
41.	*Tringa ochropus*	L	-	0.5	-	0.1	0.1	-	-	-		
42.	***Caprimulgus europaeus***	L	0.5	-	-	0.1	0.1	-	-	-		
43.	***Tetrastes bonasia***	LN	-	+	-			1.0	1.0	1.0	0.5	0.6
44.	*Corvus corax*	EN	+	+	+			0.5	0.5	0.5	0.3	0.3
45.	*Streptopelia turtur*	L	-	-	-			+	0.5	0.5	0.3	0.2
46.	*Cuculus canorus*	EN	+	+	+			0.5	0.5	0.5	0.3	0.3
47.	*Pyrrhula pyrrhula*	L	-	-	-			1.0	0.5	0.5	0.4	0.4
48.	*Scolopax rusticola*	LN	-	+	+			-	0.5	0.5	0.2	0.2
49.	*Hippolais icterina*	EN	-	+	-			2.0	1.0	1.0	0.7	0.8
50.	*Phoenicurus phoenicurus*	LN	-	-	+			1.0	1.0	1.0	0.5	0.6
51.	*Chloris chloris*	EN	-	-	-			1.0	1.0	1.0	0.5	0.6

No.	Species*	Ecological group	Forest interior, plot G1 (16.00 ha), 2012–2014					Forest edge, plot G2 (18.43 ha), 2016–2018				
			Number of pair			Mean		Number of pair			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
52.	*Carduelis carduelis*	EN	-	-	-			0.5	0.5	0.5	0.3	0.3
53.	*Sturnus vulgaris*	EN	-	-	-			1.0	2.0	1.0	0.7	0.8
54.	*Certhia brachydactyla*	L	-	-	-			1.0	1.0	+	0.3	0.4
55.	*Emberiza citrinella*	EN	-	+	+			2.0	1.0	+	0.5	0.6
56.	*Lophophanes cristatus*	LN	-	-	-			-	0.5	+	0.1	0.1
57.	*Spinus spinus*	LN	+	-	-			-	1.0	-	0.2	0.2
58.	*Accipiter nisus*	L	-	-	-			+	+	+		
59.	*Ciconia nigra*	LN	-	+	+			+	+	+		
60.	*Turdus pilaris*	EN	-	-	-			-	+	+		
61.	*Gallinago gallinago*	EN	+	+	-			-	-	-		
62.	*Clanga pomarina*	LN	+	+	-			-	+	+		
63.	*Anas platyrhynchos*	EN	+	+	-			-	-	-		
64.	*Aegolius funereus*	LN	-	-	+			-	-	-		
65.	*Jynx torquilla*	L	-	-	-			+	+	+		
66.	*Picus canus*	EN	-	-	-			+	-	-		
67.	*Nucifraga caryocatactes*	LN	-	-	-			+	-	-		
68.	*Haliaeetus albicilla*	LN	-	-	-			-	+	+		
69.	*Pandion hailaetus*	EN	-	-	-			+	-	-		
	Number of pairs		132.0	128.0	125.5	80.3		163.5	163.0	161.5	88.23	
	Number of species		42.0	49.0	46.0			55.0	56.0	56.0		
	Mean number of species		47.5					55.67				
	Total number of species		55					61				

Explanations:
Z – density of breeding pairs; D – dominance; + – breeding species, less than 0.5 of a territory within the plot; - – species not found in a given year; LN – natural forest species; L – other forest species; EN – ecotone or non-forest species; [a] – dominant species in plots in the forest interior; [b] – dominant species in plots at the forest edge; * – bold indicates the valuable species taken into account when calculating the avifauna richness index.

Table 3. Breeding bird assemblage on oak-hornbeam forest stands situated in the forest interior (plot Ł1, 2012–2014) and on the forest edge (plot Ł2, 2016–2018)

No.	Species*	Ecological group	Forest interior, plot Ł1 (6.00 ha), 2012–2014					Forest edge, plot Ł2 (6.40 ha), 2016–2018				
			Number of pair			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
1.	*Fringilla coelebs*[ab]	L	13.0	12.0	12.5	20.8	16.5	12.0	10.5	11.0	17.5	10.3
2.	*Erithacus rubecula*[ab]	L	5.5	6.0	5	9.2	7.3	5.0	5.0	5.0	7.8	4.6
3.	*Sylvia atricapilla*[b]	L	3.5	4.0	3.5	6.1	4.8	9.0	9.0	8.0	13.6	8.0
4.	*Cyanistes caeruleus*[a]	L	4.0	4.0	4.0	6.7	5.3	4.0	4.0	4.0	6.3	3.7
5.	*Turdus philomelos*[a]	L	4.0	4.0	3.5	6.4	5.1	3.0	3.0	3.0	4.7	2.8
6.	*Parus major*	L	3.5	4.0	3.5	6.1	4.8	5.0	5.5	5.0	8.1	4.7
7.	*Ficedula hypoleuca*	L	2.5	3.0	3	4.7	3.7	2.0	2.0	1.0	2.6	1.5
8.	*Troglodytes troglodytes*	L	3.0	3.5	3.5	5.6	4.4	4.0	4.0	3.0	5.8	3.4
9.	*Certhia familiaris*	L	2.5	3.0	4.0	5.3	4.2	1.0	2	2.5	2.9	1.7
10.	*Turdus merula*	L	2.5	2.5	2.5	4.2	3.3	4.0	4.0	4.0	6.3	3.7
11.	*Phylloscopus collybita*	L	2.0	2.5	2.0	3.6	2.9	4.0	4.0	4.0	6.3	3.7
12.	*Regulus regulus*	LN	3.5	2.0	3.0	4.7	3.7	2.0	2.0	2.0	3.1	1.8
13.	*Sitta europaea*	L	3.5	3.0	3.0	5.2	4.2	1.0	1.0	1.0	1.6	0.9
14.	*Phylloscopus sibilatrix*	LN	2.5	0.5	+	1.7	1.3	1.0	2.0	1.0	2.1	1.2
15.	*Dendrocopos major*	L	1.0	1.5	2.0	2.5	2.0	2.0	2.0	2.0	3.1	1.8
16.	*Dendrocopos minor*	L	+	0.5	-	0.3	0.2	0.5	0.5	+	0.5	0.3
17.	*Prunella modularis*	LN	1.0	2.0	1.0	2.2	1.8	1.0	1.0	1.0	1.6	0.9
18.	*Poecile montanus*	L	1.0	1.0	0.5	1.4	1.1	-	+	-		
19.	***Ficedula albicollis***	LN	2.0	2.5	3.5	4.4	3.5	1.0	-	-	0.5	0.3
20.	***Dendrocopos medius***	LN	1.0	1.0	0.5	1.4	1.1	1.0	1.0	1.0	1.6	0.9
21.	*Columba palumbus*	L	1.0	1.0	1.0	1.7	1.3	1.0	1.0	1.5	1.8	1.1
22.	*Coccothraustes coccothraustes*	L	2.5	2.0	2.0	3.6	2.9	2.0	2.5	2.5	3.6	2.1
23.	*Tringa ochropus*	L	1.0	1.0	1.0	1.7	1.3	1.0	1.0	1.0	1.6	0.9
24.	*Strix aluco*	L	0.5	0.5	0.5	0.8	0.7	+	1.0	1.0	1.1	0.6
25.	*Muscicapa striata*	L	2.5	3.0	2.5	4.4	3.5	2.0	2.0	2.0	3.1	1.8

No.	Species*	Ecological group	Forest interior, plot Ł1 (6.00 ha), 2012–2014					Forest edge, plot Ł2 (6.40 ha), 2016–2018				
			Number of pairs			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
26.	*Phylloscopus trochilus*	L	1.5	2.0	1.0	2.5	2.0	4.0	3.0	3.0	5.2	3.1
27.	*Poecile palustris*	L	1.5	1.5	1.0	2.2	1.8	2.0	2.0	2.0	3.1	1.8
28.	*Regulus ignicapillus*	L	1.0	0.5	1.5	1.7	1.3	-	1.0	2.0	1.6	0.9
29.	*Phoenicurus phoenicurus*	LN	-	0.5	1.0	0.8	0.7	1.0	1.0	1.0	1.6	0.9
30.	*Aegithalos caudatus*	L	-	0.5	0.5	0.6	0.4	+	0.5	0.5	0.5	0.3
31.	*Garrulus glandarius*	L	+	0.5	+	0.3	0.2	1.0	+	1.0	1.1	0.6
32.	*Anas platyrhynchos*	EN	1.0	+	1.0	1.1	0.9	-	1.0	1.0	1.1	0.6
33.	***Dendrocopos leucotos***	LN	+	0.5	1.0	0.8	0.7	-	-	-		
34.	*Certhia brachydactyla*	L	-	-	0.5	0.3	0.2	1.0	1.0	-	1.1	0.6
35.	***Ficedula parva***	LN	0.5	+	+	0.3	0.2	-	-	-		
36.	*Periparus ater*	LN	0.5	+	+	0.3	0.2	-	+	-		
37.	*Columba oenas*	LN	+	+	0.5	0.3	0.2	-	-	-		
38.	*Bucephala clangula*	L	+	+	0.5	0.3	0.2	-	-	-		
39.	*Phylloscopus trochiloides*	L	-	-	0.5	0.3	0.2	-	-	-		
40.	*Sylvia borin*	L	-	+	+			2.0	1.0	2.0	2.6	1.5
41.	***Grus grus***	L	+	+	+			0.5	0.5	0.5	0.8	0.5
42.	*Buteo buteo*	L	+	-	-			0.5	0.5	0.5	0.8	0.5
43.	*Scolopax rusticola*	LN	+	+	+			0.5	0.5	0.5	0.8	0.5
44.	*Oriolus oriolus*	L	-	+	-			1.0	1.0	1.0	1.6	0.9
45.	*Sturnus vulgaris*[b]	EN	-	-	-			5.0	11.0	10.0	13.5	7.9
46.	*Emberiza citrinella*	EN	-	-	-			4.0	4.0	4.0	6.3	3.7
47.	*Hippolais icterina*	EN	-	-	-			3.0	3.0	2.0	4.2	2.5
48.	*Acrocephalus palustris*	EN	-	-	-			2.0	1.0	1.0	2.1	1.2
49.	*Chloris chloris*	EN	-	-	-			1.0	1.0	2.0	2.1	1.2
50.	*Anthus trivialis*	L	-	-	-			1.0	1.0	1.0	1.6	0.9
51.	*Turdus pilaris*	EN	-	-	-			1.0	1.0	1.0	1.6	0.9

No.	Species*	Ecological group	Forest interior, plot Ł1(6.00 ha), 2012–2014					Forest edge, plot Ł2 (6.40 ha), 2016–2018				
			Number of pairs			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
52.	*Sylvia communis*	EN	-	-	-			1.0	3.0	3.0	3.7	2.1
53.	*Linaria cannabina*	EN	-	-	-			-	0.5	+	0.3	0.2
54.	*Carduelis carduelis*	EN	-	-	-			-	1.0	0.5	0.8	0.5
55.	*Saxicola rubetra*	EN	-	-	-			-	0.5	-	0.3	0.2
56.	***Lullula arborea***	EN	-	-	-			-	1.0	1.0	1.1	0.6
57.	*Pyrrhula pyrrhula*	L	-	-	-			-	-	1.0	0.5	0.3
58.	***Tetrastes bonasia***	LN	+	-	-			1.0	-	+	0.5	0.3
59.	***Emberiza hortulana***	EN	-	-	-			1.0	+	-	0.5	0.3
60.	*Spinus spinus*	LN	+	-	-			-	1.0	-	0.5	0.3
61.	*Turdus viscivorus*	L	+	+	+			-	+	1.0	0.5	0.3
62.	*Upupa epops*	EN	-	-	-			1.0	-	-	0.5	0.3
63.	*Locustella fluviatilis*	EN	-	-	-			-	-	1.0	0.5	0.3
64.	*Streptopelia decaoto*	EN	-	-	-			0.5	-	-	0.3	0.2
65.	*Phoenicurus ochruros*	EN	-	-	-			0.5	-	+	0.3	0.2
66.	*Asio otus*	L	-	-	-			0.5	-	-	0.3	0.2
67.	*Accipiter nisus*	EN	-	-	+			+	+	+		
68.	*Lophophanes cristatus*	LN	-	-	-			-	-	+		
69.	*Lanius collurio*	EN	-	-	-			-	+	+		
70.	*Loxia curvirostra*	LN	-	-	-			-	+	-		
71.	*Ciconia nigra*	LN	-	-	-			+	+	+		
72.	*Clanga pomarina*	LN	+	+	-			-	-	-		
73.	*Cuculus canorus*	EN	+	+	+			+	+	+		
74.	*Corvus corax*	EN	+	+	+			+	+	+		
75.	*Nucifraga caryocatactes*	LN	-	+	+			-	-	-		
76.	*Dryocopus martius*	LN	+	+	+			+	+	+		
77.	*Picoides tridactylus*	LN	-	+	+			-	-	-		
78.	*Motacilla alba*	EN	-	+	-			+	-	-		

No.	Species*	Ecological group	Forest interior, plot Ł1 (6.00 ha), 2012–2014					Forest edge, plot Ł2 (6.40 ha), 2016–2018				
			Number of pairs			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
79.	*Gallinago gallinago*	EN	-	+	-			-	-	-		
80.	*Turdus iliacus*	L	-	+	-			-	-	-		
81.	*Haliaeetus albicilla*	LN	-	-	-			+	+	-		
82.	*Circus aeruginosus*	EN	-	-	-			+	+	+		
83.	*Milvus migrans*	EN	-	-	-			+	-	-		
84.	*Glaucidium passerinum*	LN	+	-	-			-	-	-		
85.	*Mergus merganser*	EN	+	-	-			-	-	-		
	Number of pairs		75.0	76.0	76.5	126.4		105.0	112.0	110.0	171.1	
	Number of species		47.0	51.0	48.0			58.0	62.0	59.0		
	Mean number of species			48.7						59.7		
	Total number of species			59.0						73.0		

See Table 2 for the explanations

blackcap (*Sylvia atricapilla* L.), wood warbler (*Phylloscopus sibilatrix* Bechst.), willow warbler (*Phylloscopus trochilus* L.), chiffchaff (*Phylloscopus collybita* Vieill.), tree pipit (*Anthus trivialis* L.), common whitethroat (*Sylvia communis* Lath.), blackbird (*Turdus merula* L.) and Eurasian golden oriole (*Oriolus oriolus* L. *heifolium*), whereas the fieldfare (*Turdus pilaris* L.), woodlark (*Lullula arborea* L.), long-eared owl (*Asio otus* L.) and wryneck (*Jynx torquilla* L.) were completely absent in the forest interior.

The second group of species that appeared at the edge of the forest and was completely absent in its interior are essentially non-forest birds associated with open and/or shrubby areas as well as synanthropic species: hoopoe (*Upupa epops* L.), ortolan bunting (*Emberiza hortulana* L.), European greenfinch (*Chloris chloris* L.), common linnet (*Linaria cannabina* L.), European goldfinch (*Carduelis carduelis* L.), whinchat (*Saxicola rubetra* L.), marsh warbler (*Acrocephalus palustris* Bechst.), river warbler (*Locustella fluviatilis* Wolf), thrush nightingale (*Luscinia luscinia* L.), Eurasian collared dove (*Streptopelia decaocto* Friv.), Northern wheatear (*Oenanthe oenanthe* L.), black redstart (*Phoenicurus ochruros* Gmel.). Added to these should be icterine warbler (*Hippolais icterina* Vieill), yellowhammer (*Emberiza citrinella* L.), white wagtail (*Motacilla alba* L.) and red-backed shrike (*Lanius collurio* L.), which were only occasionally observed in the forest interior.

The group of 37 species that in fact did not show a specific habitat preference is represented by those distinguished by a similar density in the forest interior and at its edge: common chaffinch (*Fringilla coelebs* L.), European robin (*Erithacus rubecula* L.), hawfinch (*Coccothraustes coccothraustes* L.), Eurasian blue tit (*Cyanistes caeruleus* L.), great spotted woodpecker (*Dendrocopos major* L.), middle spotted woodpecker (*Dendrocopos medius* L.) and tawny owl (*Strix aluco* L.). These are mainly forest-related generalists, and the only specialised forest species characteris-tic of natural forests is the middle spotted woodpecker. The remaining species from this group, because of fluctuations in their density or small numbers, cannot be clearly classified in terms of their preferences for the forest interior or its edge. They include four species from Annex I of the Birds Directive: Eurasian pygmy owl (*Glaucidium passerinum* L.), black woodpecker (*Dryocopus martius* L.), hazel grouse (*Tetrastes bonasia* L.) and common crane (*Grus grus* L.).

In addition to the differences in species composition, differences in the structure of the bird assemblages inhabit-

Table 4. Breeding bird assemblage on mixed forest stands situated in the forest interior (plot BM1, 2012–2014) and on the forest edge (plot BM2, 2016–2018)

No.	Species*	Ecological group	Forest interior, plot BM1 (14.50 ha), 2012–2014					Forest edge, plot BM2 (15.28 ha), 2016–2018				
			Number of pairs			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
1.	*Fringilla coelebs*[ab]	L	22.5	19.0	20.5	14.3	17.0	27.0	28.0	28.0	18.1	13.8
2.	*Erithacus rubecula*[ab]	L	11.0	10.5	9.5	7.1	8.5	13.0	13.0	12.0	8.3	6.3
3.	*Sylvia atricapilla*[ab]	L	8.5	7.0	7.5	5.3	6.3	13.0	12.0	11.0	7.9	6.0
4.	*Regulus regulus*[a]	LN	7.5	6.0	8.0	4.9	5.8	4.0	5.0	5.0	3.1	2.3
5.	*Phylloscopus sibilatrix*[b]	LN	4.5	4.5	4.0	3.0	3.6	20.0	8.0	8.0	7.8	5.9
6.	*Parus major*[a]	L	6.0	7.0	6.0	4.3	5.1	9.0	9.0	10.0	6.1	4.7
7.	*Turdus merula*[b]	L	3.5	3.5	4.0	2.5	3.0	11.0	11.0	10.0	7.0	5.3
8.	*Coccothraustes coccothraustes*	L	3.5	4.0	4.5	2.8	3.3	8.0	8.0	7.0	5.0	3.8
9.	*Cyanistes caeruleus*	L	4.5	4.5	5.0	3.2	3.8	6.0	6.0	6.0	3.9	3.0
10.	*Phylloscopus collybita*	L	2.5	2.5	3.5	2.0	1.8	9.0	8.0	8.0	5.4	4.2
11.	*Troglodytes troglodytes*	L	6.0	5.0	3.0	3.2	3.8	7.0	7.0	6.0	4.4	3.3
12.	*Turdus philomelos*	L	4.5	4.5	4.5	3.1	3.7	8.0	8.0	7.0	5.0	3.8
13.	*Certhia familiaris*	L	3.0	4.5	5.0	2.9	3.5	6.0	6.0	7.0	4.1	3.2
14.	*Sitta europaea*	L	3.5	3.0	3.0	2.2	2.6	5.0	5.0	5.0	3.3	2.5
15.	*Poecile palustris*	L	3.0	3.0	3.0	2.1	2.5	4.0	4.0	3.0	2.4	1.8
16.	*Phylloscopus trochilus*	L	3.0	3.0	2.0	1.8	2.1	3.0	3.0	4.0	2.2	1.7
17.	*Dendrocopos major*	L	2.0	2.5	3.0	1.7	2.0	4.0	4.5	4.0	2.7	2.1
18.	*Regulus ignicapillus*	L	2.5	2.0	2.0	1.5	1.8	3.0	4.0	3.0	2.2	1.6
19.	*Muscicapa striata*	L	2.0	2.0	2.0	1.4	1.7	3.0	3.0	4.0	2.2	1.7
20.	*Prunella modularis*	LN	1.5	2.0	1.5	1.1	1.3	3.0	3.0	3.0	2.0	1.5
21.	*Ficedula hypoleuca*	L	2.5	2.5	1.0	1.4	1.7	3.0	2.0	2.0	1.5	1.1
22.	*Poecile montanus*	L	2.0	2.0	2.0	1.4	1.7	2.0	1.0	-	0.7	0.5
23.	***Ficedula parva***	LN	1.0	1.0	1.0	0.7	0.8	1.0	2.0	2.0	1.1	0.8
24.	*Columba palumbus*	L	1.5	1.0	1.0	0.8	1.0	2.0	2.0	2.0	1.3	1.0
25.	*Periparus ater*	LN	1.0	1.0	1.0	0.7	0.8	1.0	1.0	0.5	0.6	0.4
26.	*Strix aluco*	L	0.5	1.0	1.0	0.6	0.7	1.0	1.0	1.0	0.7	0.5

No.	Species*	Ecolo-gical group	Forest interior, plot BM1 (14.50 ha), 2012–2014					Forest edge, plot BM2 (15.28 ha), 2016–2018				
			Number of pairs			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
27.	***Dendrocopos medius***	LN	1.5	1.5	1.0	0.9	1.1	2	2.0	1.0	1.1	0.8
28.	***Ficedula albicollis***	LN	2.5	3.0	2.0	1.7	2.0	1.0	-	-	0.2	0.2
29.	*Garrulus glandarius*	L	0.5	0.5	0.5	0.3	0.4	1.0	1.0	1.0	0.7	0.5
30.	***Dryocopus martius***	LN	1.0	1.0	0.5	0.6	0.7	+	0.5	0.5	0.2	0.2
31.	***Grus grus***	L	0.5	0.5	0.5	0.3	0.4	0.5	0.5	0.5	0.3	0.3
32.	*Tringa ochropus*	L	1.0	1.0	1.0	0.7	0.8	1.0	1.0	1.0	0.7	0.5
33.	*Sylvia borin*	L	1.5	1.5	0.5	0.8	0.8	1.0	-	1.0	0.5	0.3
34.	*Turdus viscivorus*	L	0.5	1.0	0.5	0.5	0.6	1.0	2.0	1.5	1.0	0.8
35.	***Tetrastes bonasia***	LN	1.0	+	1.0	0.5	0.6	1.0	1.0	1.0	0.7	0.5
36.	*Scolopax rusticola*	LN	0.5	+	0.5	0.2	0.2	0.5	0.5	0.5	0.3	0.3
37.	*Oriolus oriolus*	L	-	0.5	0.5	0.2	0.2	2.0	2.0	2.0	1.3	1.0
38.	*Columba oenas*	LN	-	0.5	0.5	0.2	0.2	0.5	+	0.5	0.2	0.2
39.	*Sylvia communis*	EN	0.5	+	0.5	0.2	0.2	1.0	2.0	1.0	0.9	0.7
40.	*Lophophanes cristatus*	LN	1.0	-	-	0.2	0.2	1.0	-	1.0	0.5	0.3
41.	*Anthus trivialis*	L	0.5	+	+	0.1	0.1	1.0	0.5	1.0	0.6	0.4
42.	*Dendrocopos minor*	L	-	+	1.0	0.2	0.2	1.0	+	1.0	0.5	0.3
43.	*Spinus spinus*	EN	0.5	-	+	0.1	0.1	1.0	1.0	1.0	0.7	0.5
44.	*Pyrrhula pyrrhula*	L	0.5	-	+	0.1	0.1	0.5	+	1.0	0.3	0.2
45.	*Nucifraga caryocatactes*	LN	-	-	0.5	0.1	0.1	-	-	-		
46.	***Picoides tridactylus***	LN	-	0.5	+	0.1	0.1	-	-	-		
47.	*Streptopelia turtur*	L	+	-	-			1.0	1.0	1.0	0.7	0.5
48.	*Aegithalos caudatus*	L	+	+	+			0.5	0.5	0.5	0.3	0.3
49.	*Emberiza citrinella*	EN	-	+	+			1.0	2.0	3.0	1.3	1.0
50.	*Hippolais icterina*	EN	-	-	+			4.0	2.0	2.0	1.7	1.3
51.	*Anas platyrhynchos*	EN	-	-	+			2.0	1.0	1.0	0.9	0.7
52.	*Phoenicurus phoenicurus*	LN	-	-	-			1.0	2.0	2.0	1.1	0.8
53.	*Sturnus vulgaris*	EN	-	-	-			4.0	3.0	3.0	2.2	1.6
54.	*Certhia brachydactyla*	L	-	-	-			2.0	1.0	+	0.7	0.5
55.	*Motacilla alba*	EN	-	-	-			-	0.5	0.5	0.2	0.2

No.	Species*	Ecolo-gical group	Forest interior, plot BM1 (14.50 ha), 2012–2014					Forest edge, plot BM2 (15.28 ha), 2016–2018				
			Number of pairs			Mean		Number of pairs			Mean	
			2012	2013	2014	Z (p/10 ha)	D (%)	2016	2017	2018	Z (p/10 ha)	D (%)
56.	***Lullula arborea***	EN	-	-	-			-	1.0	1.0	0.5	0.3
57.	*Acrocephalus palustris*	EN	-	-	-			-	1.0	1.0	0.5	0.3
58.	*Chloris chloris*	EN	-	-	-			-	1.0	1.0	0.5	0.3
59.	*Carduelis carduelis*	EN	-	-	-			-	0.5	0.5	0.2	0.2
60.	*Oenanthe oenanthe*	EN	-	-	-			-	0.5	0.5	0.2	0.2
61.	*Jynx torquilla*	L	-	-	-			-	1.0	-	0.2	0.2
62.	*Falco subbuteo*	EN	-	-	-			-	-	1.0	0.2	0.2
63.	***Lanius collurio***	EN	-	+	-			-	-	1.0	0.2	0.2
64.	*Turdus pilaris*	EN	-	-	-			1.0	-	-	0.2	0.2
65.	***Glaucidium passerinum***	LN	-	-	-			0.5	-	-	0.1	0.1
66.	*Luscinia luscinia*	EN	-	-	-			-	-	0.5	0.1	0.1
67.	*Clanga pomarina*	LN	+	+	+			+	+	+		
68.	*Ciconia nigra*	LN	-	-	-			+	-	+		
69.	*Buteo buteo*	L	+	+	+			+	+	+		
70.	*Corvus corax*	EN	+	+	+			+	+	+		
71.	*Cuculus canorus*	EN	+	+	+			+	+	+		
72.	*Gallinago gallinago*	EN	+	+	+			-	-	-		
73.	*Loxia curvirostra*	LN	-	-	-			-	+	+		
74.	*Dendrocopos leucoctos*	LN	-	+	+			+	-	-		
75.	*Picus viridis*	EN	-	-	-			-	+	+		
76.	*Erythrina erythrina*	EN	-	+	-			-	-	-		
77.	*Apus apus*	EN	-	+	+			-	-	-		
78.	*Milvus migrans*	EN	-	+	-			+	-	-		
79.	*Bucephala clangula*	EN	-	+	-			-	-	-		
	Number of pairs		127.0	120.0	119.5.0	84.2		210.0	197.0	195.0	131.1	
	Number of species		48.0	55.0	56.0			62.0	62.0	66.0		
	Mean number of species			53.0						63.33		
	Total number of species			62.0						73.0		

See Table 2 for the explanations

Table 5. Ornithological evaluation of plots located in the forest interior and at the forest edge

Plot / Index		Forest interior	Forest edge
Oak-hornbeam	*Wb*	32.01	17.83
	RWb	200.06	96.74
Ash-alder	*Wb*	23.50	11.84
	RWb	391.67	184.00
Mixed coniferous	*Wb*	30.16	22.17
	RWb	208.00	145.09
All plots	*Wb*	85.67	51.85
	RWb	234.71	129.27

Explanations: *Wb* – avifauna richness index; *RWb* – equivalent index of avifauna richness.

ing the forest interior and its edge were also observed. The chaffinch was the dominant species in all the study areas. Species in the dominant group, constituting at least 5% of the breeding population in the majority of the study plots, also included the European robin (with the exception of plot Ł2) and the Eurasian blackcap (except for plots G2 and Ł1). Aside from the species already mentioned, dominant species in the oak-hornbeam forest also included great tit and hawfinch (study plots G1 and G2), song thrush (*Turdus philomelos* Brehm) and starling (only in plot G2); blue tit (only in plot Ł1) and song thrush (only in plot Ł1) in the ash-alder habitat; and goldcrest (only in plot BM1), wood warbler and blackbird (only in plot BM2) in the mixed coniferous forest.

The values of the avifauna richness index (*Wb*) and the equivalent index of avifauna richness (*RWb*) (Table 5) were the result of the number of breeding birds in individual study plots and the rank assigned to particular species (Table 1). Regardless of the type of forest community, these values were always much higher for plots located in the forest interior. This was especially evident in the case of oak-hornbeam and ash-alder forests, where the value of the referenced indices for the forest interior was about twice as high as at the edge. The value of the *RWb* index for the ash-alder forest, regardless of its location, was significantly higher than that for the plots in the other two types of forest.

The number of species occurring at the forest edge was in each case higher than that in the plots of the forest interior. On an average, nearly 50 species of birds nested in each plot in the Borki Forest and nearly 60 at its edge – over 20% more (Fig. 2). The number of breeding species, both inside the forest and at its edge, was the highest in the mixed coniferous forest and amounted to an average of 53 species in plot BM1 and 63.3 species in plot BM2.

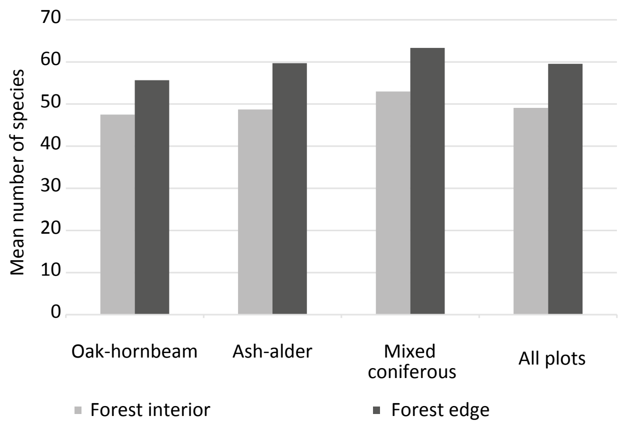

Figure 2. Species richness of breeding bird assemblages of the Borki Forest in the forest interior and at the forest edge

In all the habitats the mean number of species at the forest edge was significantly higher than that in the forest interior (Student's t test, $p \leq 0.05$).

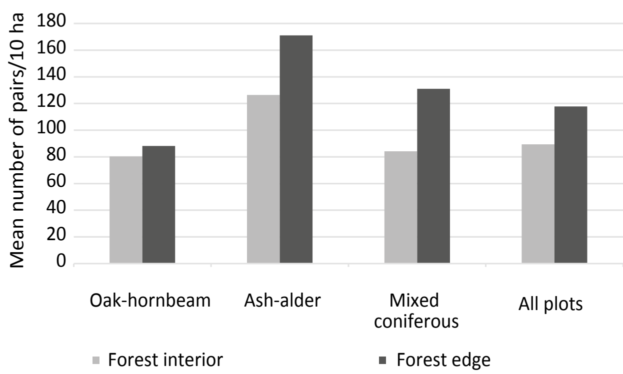

Figure 3. Total density of breeding bird assemblages of the Borki Forest in the forest interior and at the forest edge

In all the habitats the mean density of breeding pairs at the forest edge was significantly higher than that in the forest interior (Student's t test, $p \leq 0.05$).

Also, the density of breeding pairs in all plots at the forest edge was higher than that in its interior. It was, on an average, nearly 90 pairs/10 ha in each plot in the forest interior and nearly 118 pairs/10 ha at the forest edge, that is, more than 30% higher (Fig. 3). The average density of breeding pairs, both at the forest edge and in its interior, was the highest in the ash-alder forest and amounted to more than 126 pairs/10 ha and more than 171 pairs/10 ha, respectively. This means that at the Borki Forest edge, the density of avifauna in the ash-alder forest was 35% higher than that in its interior, and this was the highest difference recorded in the density of avifauna between the two habitats of the studied forest community types. In turn, the density of breeding pairs in the oak-hornbeam forest was only 10% higher at its edge than that in its interior.

Typical forest species dominated in each of the study plots (Fig. 4). At the forest edge, the share of untypical species for the forest interior, ecotone and non-forest species (associated with shrubs, open and semi-open terrain, water and marshes as well as synanthropic areas), was significantly higher (on an average, twice high – increasing from 16.4% to 33.3%), whereas the share of species typical of natural forests was lower than that in the plots in the interior of the Borki Forest (a decrease of 28.8–24.2%). These differences were most marked in the ash-alder forest, where the share of untypical species for the forest interior was three times higher in edge plots (rising from 11.9% to 32.9%) and the share of species characteristic for natural forests decreased by one-third (from 30.5% to 20.5%).

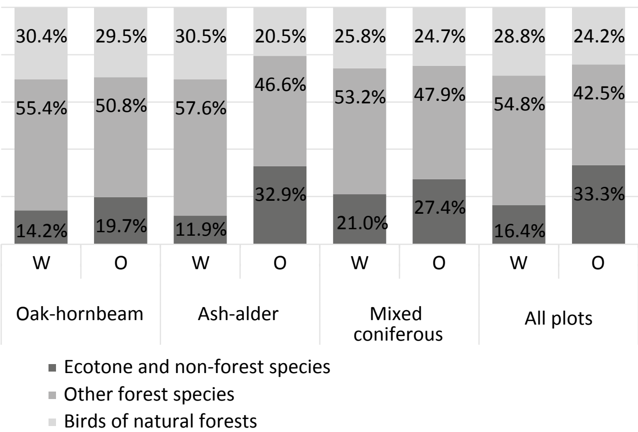

Figure 4. Share of ecological groups in species composition of nesting bird assemblages on research plots in the Borki Forest located in the forest interior and at the forest edge

Explanations: W – forest interior; O – forest edge.

A comparative analysis of the similarity of breeding bird assemblages in the study plots in the forest interior and its edge (Table 6) showed that in almost all cases, both the Sørensen QS index reflecting the similarity of the species composition and the Renkonen DR index reflecting the similarity of the percentage share (dominance) of individual species reached values above 70, regardless of the type of forest community and location of the study plot. According to the scale proposed by Tomiałojć (1970), this indicates a very significant similarity of bird assemblages inhabiting both these habitats. Only in the case of the ash-alder forest, the value of the Renkonen DR index was slightly lower in each case, both in the comparison of its edge to its interior in the Borki Forest as well as in comparison to other forest types. These values ranged from 64.0 to 65.9 but still, however, indicate a high degree of similarity. The analysis of bird assemblages inhabiting individual study plots in the forest interior (Table 7) and its edge (Table 8) also showed a very significant degree of similarity between them, regardless of the forest type.

5. Discussion

The most important differences between breeding bird assemblages inhabiting the interior and edge of the Borki Forest is the fact that at the edge, regardless of the type of forest, both the number of nesting species and the density of breeding pairs were higher than that in the forest interior. A similar relationship, referred to as the edge effect, in various types of forest ecosystems and different geographic regions, has been demonstrated by numerous researchers in the country (amongst others, Tomiałojć et al. 1984; Cieślak 1992, Kopij 2013) and abroad (Johnston 1947; Hogstad 1967; Helle, Helle 1982; Kroodsma 1984; Kurosawa, Askins 1999; Flashponder et al. 2001; Zurita et al. 2012; Terraube et al. 2016).

Table 6. Similarities of bird assemblages from different habitats in the forest interior and at the forest edge

Study plot		Forest interior							
		Oak-hornbeam G1		Ash-alder Ł1		Mixed coniferous BM1		All plots G1, Ł1, BM1	
		QS	DR	QS	DR	QS	DR	QS	DR
Forest edge	Oak-hornbeam G2	82.1	81.4	75.0	77.9	79.7	79.3	-	-
	Ash-alder Ł2	73.4	64.0	71.2	64.9	75.6	65.9	-	-
	Mixed coniferous BM2	81.3	76.2	77.3	75.6	83.0	80.2	-	-
	All plots G2, Ł2, BM2	-	-	-	-	-	-	78.8	80.6

Explanations: QS – Sørensen index: similarity of species composition; DR – Renkonen index: similarity of percentage composition (dominance).

Table 7. Similarities of bird assemblages from different plots within the forest interior

Study plot	G1		Ł1		BM1	
	QS	DR	QS	DR	QS	DR
G1	-	-				
Ł1	83.0	80.5	-	-		
BM1	89.3	78.2	79.2	77.5	-	-

See Table 6 for the explanations

Table 8. Similarities of bird assemblages from different plots at the forest edge

Study plot	G2		Ł2		BM2	
	QS	DR	QS	DR	QS	DR
G2	-	-				
Ł2	75.0	69.6	-	-		
BM2	83.6	83.7	86.3	74.9	-	-

See Table 6 for the explanations

The higher density of breeding pairs at the forest edge found in the Borki Forest is mainly the result of the 20% increase in the number of nesting species there than in the forest interior. These were primarily a group of species that were absent from the forest interior who foraged outside of the forest and used the edge zone as a convenient nesting site (Sikora et al. 2007; Kuczyński, Chylarecki 2012). An additional factor strengthening the edge effect was the increase in the number of breeding pairs amongst the generalists preferring this habitat, although at the same time, some species associated with the forest interior had smaller numbers at the edge plots. A specialised forest species whose increased presence in the edge zone is somewhat surprising was the wood warbler.

Similar results were obtained by Hogstad (1967) who showed an increased number of species in the edge zone by 14–21%, whereas Tomiałojć et al. (1984) found about a 30% higher number of nesting species in the edge zone than in the forest interior and Cieślak (1992) found about a 35% increase in their numbers. It is worth noting that although the number of breeding species in the edge zone of the Borki Forest was only 20% higher than that in its interior, the actual difference in the species composition of the bird assemblages inhabiting each of these habitats was much higher, because about 35% of all species nested in only one habitat, and only about 65% in both. At the edge plots compared to the forest interior, the number of non-forest species was twice as high, whereas the number of specialised forest species associated with natural forests was smaller only by just under 5%.

As was also noted by Hogstad (1967), Helle and Helle (1982), Helle (1983) and Cieślak (1992), the observed increase of about 30% in the population density of birds at the edge of the Borki Forest compared to its interior – an expression of the edge effect – was higher than the increase in the number of species. Tomiałojć et al. (1984) also obtained similar results in the Białowieża Forest, showing a corresponding increase in densities of 25–33%. Hansson (1983) stated that two times more breeding pairs nested in the edge zone than in the forest interior, Frochot (1979) noted that the increase in densities in the edge zone was 7–35% depending on the methodology used and season, whereas Cieślak (1983) and Zurita et al. (2012) stated that the size of this parameter depends on the type of habitat at the forest's edge. Cieślak (1992) assumed that the increase in breeding pair density may be a consequence of the reduction by some species of the size of their territories in the edge zone. This same author, as well as Strelke and Dickson (1980) and McCollin (1998), suggested that the increased number of some generalists at the forest edge is due to the possibility of accessing two different habitats and to obtain additional food. In the Borki Forest, the increase in breeding pair densities in the edge zone was primarily the result of the increase in the number of nesting species, as demonstrated by Tomiałojć et al. (1984) and Cieślak (1992), and, to a lesser extent, the result of the increase in the number of some generalists, which Kroodsma (1982) found in his research. As was found in the Białowieża Forest (Tomiałojć et al. 1984), the number and population of specialised forest species was also similar in both the forest interior and the edge in the Borki Forest.

The presence of a larger number of species and a greater breeding pair density at the forest edge is, as may be expected, the result of several factors. The first of these is the greater diversity of microhabitats in the forest edge zone compared to its interior, as shown by Zięba et al. (2014) and Ouin et al. (2015), which is a consequence of the lower stability of the microclimatic parameters. These factors increase the spatial and qualitative diversity of forest bird habitats (amongst others, slightly denser tree stand crown and a greater share of shrubs in the undergrowth), which in turn increases the capacity of these habitats and provides greater nesting possibilities, which was pointed out by Helle (1983) and Cieślak (1992). A second factor is the proximity to non-forest areas, which results in the expansion into the edge zone of species associated with such habitats, which are absent in the forest interior.

Although the number of nesting species in the studied edge zones was greater than that in the forest interior, common and non-specialised species predominated. Much fewer species and less individuals of valuable, rare and threatened species were found there. On the other hand, almost all birds from the group preferring the forest interior are specialised forest species, half of whom are typical for natural forests (Zawadzka, Zawadzki 2006). All of them are not very abundant in Poland, and they include two threatened species listed in the 'Polish Red Book of Animals' (three-toed woodpecker and white-backed woodpecker) as well as five species included in the Natura 2000 program (apart from the woodpeckers mentioned above, also the collared flycatcher, red-breasted flycatcher, and nightjar) listed in Annex I of the Birds Directive. Aside from the nightjar, which is occasional and unusual for the forest interior, the other four species are the object of protection in the Borki Forest PLB280006 Natura 2000 area, whereas the collared flycatcher and white-backed woodpecker have one of their numerous national refuges here (Rąkowski et al. 2016; Sikora et al. 2016). The three-toed woodpecker (not present in the Borki Forest edge) and the red-breasted flycatcher are considered to be excellent indicators of forest bird species richness (Pakkala 2012). The Borki Forest interior has a greater avifaunal value than its edge, which is reflected in the much higher values of the avifauna richness index (Table 5). Regardless of the influence of other factors, this may be related to the lower resistance of threatened species to human pressure, which is great at the edge of the forest. Similar results were obtained by Kurosawa and Askins (1999) in Japan, who showed that rare bird species are more often found in the forest interior than at its edge.

Some researchers stated that different bird assemblages inhabit the forest edge than its interior, which was allegedly evidenced by a characteristic set of species typical of the ecotone (Johnston 1947; Cieślak 1992). The results obtained from the study in the Borki Forest, however, lead to a conclusion that, similar to Baker et al. (2002) and Imbeau et al. (2003), the bird assemblage inhabiting the forest edge does not consist of species specifically associated with its edge zone, which are relatively few – they include, amongst others, the nightjar and the tree pipit (Harris, Harris 1991, Terraube et al. 2016) but is rather composed of two main groups – not very selective forest species and decidedly non-forest species associated with the open areas adjacent to the forest (meadows and fields), shrubs and synanthropic areas. Apart from these, although less frequently, specialised forest species, including those characteristic for the forest interior, also occur on the studied edge plots. Their presence was most probably partly due to the fact that fragments of these plots farther away from the edge of the forest were already basically located outside the zone in which the edge effect is noted. The width of this zone is assessed by researchers in different ways. From Cieślak (1992), one can assume that the edge effect, in relation to the bird population, is noticeable in a strip of 200 m from the edge of the forest. Almost all of the area of plot Ł2, about half of plot BM2 and only about one-third of plot G2 were within this strip. As can be surmised, this is the reason why the edge effect in plot Ł2 was the strongest, and the value of the Renkonen similarity index (DR) of the bird assemblage in this plot compared with plot Ł1 and the other plots was the lowest.

In general, despite the observed differences and a clear edge effect, the QR and DR indices of similarity between forest bird assemblages and those at the edge, regardless of forest type, reached high values, which indicate that these assemblages do not fundamentally differ. These similarity indices are also high when comparing the bird assemblages in the different types of forest communities, both within the edge zone as well as in the forest interior. Therefore, one can conclude that regardless of the type of forest community, all of the Borki Forest is inhabited by one bird assemblage, which was previously suggested by Rąkowski et al. (2016), whereas its edge has a poorer-quality variant of the assemblage typical for the forest interior, which is quantitatively enriched by non-forest species associated with open and/or semi-open and synanthropic areas. Similar conclusions were drawn by Tomiałojć et al. (1984) when summarising their research in the Białowieża National Park, who stated that regardless of the type of habitat, it had basically one assemblage of birds.

The very diversified relief of the terrain in the Borki Forest and the mosaic of habitats could have had an impact on the reduction of the differences between the forest interior and its edge. For this reason, none of the study plots was uniform in terms of the type of forest community, and different enclaves of other forest as well as non-forest habitats were found within the dominant communities. Tomiałojć et al. (1984) also observed the possible influence of such factors on reducing the differences in the avifauna of different study plots in the same forest complex of the Białowieża Forest, although the relief there is much less varied than that in the Borki Forest.

The edge effect in the bird assemblage in the Borki Forest could have been weakened as a result of forest management. This particularly applies to the gap logging used on a large scale in this forest complex, both within as well as in neighbouring areas to the study plots. Edge zones are formed around these small, often rather densely distributed logged patches, even in the interior of the forest, with the edge effect appearing to a greater or lesser degree. This phenomenon was analysed by Strelke and Dickson (1980), Hansson (1983), Avery and Leslie (1990), Brazaitis and Kurlavičius (2003), Sławski (2008), Pepłowska-Marczak (2009, 2011) and Rąkowski et al. (2016). The result of the emergence of a large number of logged patches in the Borki Forest could have been the increased presence in the study plots of species not typically found in the forest interior, which reduced the differences between the compared bird assemblages. Another result of this forest management method is the systematic increase of the edge zone at the expense of the forest interior, which forms around each logged patch. One could expect that in the long-term, this will be a serious threat to the valuable bird species mentioned above, which have an important refuge in the Borki Forest and which clearly avoid the forest edge. This is especially true of the two rarest species of woodpeckers, the white-backed and the three-toed, whose threat from forest management practices was also noted, amongst others, by

Tomiałojć and Wesołowski (2004), Czeszczewik and Walankiewicz (2006) and Kajtoch and Figarski (2014).

6. Summary

In the comparison to the breeding bird assemblages inhabiting the mature tree stands of the interior and edge of the Borki Forest, a distinct edge effect was observed regardless of the type of forest community. Both the number of species and the density of breeding pairs in the study plots located in the edge zone were higher than those in the forest interior (by ~20% and ~30%, respectively).

The increase in the number of nesting species at the forest edge was mainly the result of the appearance of many non-forest species and those not typically found in the forest interior. The increased density of breeding pairs was a consequence of both the increased number of nesting species as well as the increased population of some non-specialised forest species. The number of nesting species at the forest edge was greater than that in the forest interior; however, common and generalist species dominated amongst them. There were, however, significantly fewer and lower numbers of specialised species typical of natural forests as well as rare and threatened species.

Despite the observed differences and the clear edge effect, the bird assemblages inhabiting the study plots in the Borki Forest and its edge do not fundamentally differ, and it can be concluded that the edge zone is inhabited by a poorer-quality variant of the bird assemblage typical of the forest interior, quantitatively enriched by non-forest species associated with open and/or semi-open as well as by synanthropic areas.

Conflict of interest

The authors declare the lack of potential conflicts of interest.

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Authors' contribution

G.R. – concept of the research study, determination of the study plots, development of the research results, writing the article, corrections; K.C. – performance of field observations, development of the research results.

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