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Breeding avifauna of mature forest stands in the Borki Forest and its dynamics at the turn of the 21st century

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Abstract. The composition and structure of the breeding bird community in the Borki Forest in north-eastern Poland were investigated during two separate periods: 1994–1996 and 2012–2014. Bird censuses were carried out in three plots located in mature oak-hornbeam, ash-alder and mixed coniferous forest stands. A standard combined mapping technique for estimating the number of breeding birds was applied. A total of 74 bird species bred at least once within any plot during 1994–1996 or 2012–2014. The structure of the bird assemblages on particular plots displayed a high degree of similarity, exceeding 75%, which means that they represent essentially the same bird community. However, the investigated assemblages have changed substantially over the 20 years. Both, the number of breeding bird species and the population densities on all plots, were much higher in 2012–2014 than in 1994–1996. The mean number of breeding species on all plots was over 50% higher in 2012–2014 than in 1994–1996, whereas the mean total density of breeding pairs increased by more than 60%. Total population densities on the plots increased as a result of an increase in population densities of individual bird species combined with an increase in the number of breeding species. Due to different rates of population growth for certain species, also the composition of dominating species group have changed. The observed changes in the avifauna of the Borki Forest were most probably due to an enrichment of the forest habitats structure, which was caused by natural factors, such as ageing of forest stands, forest succession and a change in water regime by beaver dams, as well as by forest management, including group felling within or in the vicinity of plots and uncovering of the forest edge.

Keywords: Borki Forest, bird assemblage structure, species richness, density changes, forest habitats

1. Introduction

The densities and species richness of bird assemblages result from two categories of factors: the carrying capacity of habitats and a degree of saturation of these habitats by individual bird species (Hilden 1965; Brown 1969; Fuller 2012). The carrying capacity of forest birds' habitats is primarily governed by the species, age and spatial structure of forests (James, Wamer 1982). The most important natural factors that influence the forest structure are site fertility, forest succession, tree stand ageing and death of the oldest trees as well as development of undergrowth. In managed forests, one of the most important factors shaping forest habitats and associated bird assemblages is forest management practice, including harvest cutting, thinning, forest regeneration activities and management of non-forest vegetation (Virkkala 1987; Avery, Leslie 1990; Edenius, Elmberg 1996; Brazaitis, Kurlavičius 2003; Scherzinger, Schumacher 2004; Zawadzka, Zawadzki 2005). At the same time, forest bird habitats can be affected by keystone species shaping forest ecosystems, such as beavers (*Castor fiber*) (Janiszewski et al. 2014).

The species composition and structure of bird community that inhabit a given forest complex are good indicators of its naturalness. The presence of a considerable number of bird species characteristic for mature forest stands, especially hole-nesting birds and those typical for forest interior, reflect a high

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degree of naturalness of a forest complex (Brotons et al. 2003; Zawadzka, Zawadzki 2006), in the same way as substantial bird species richness and relatively low density of breeding pairs (Tomiałojć et al. 1984; Tomiałojć, Wesołowski 2004). In the most of European countries, including Poland, natural or close to natural forests occur within the areas under strict legal protection that embrace fairly small acreages, that is, in strictly protected zones of national parks and nature reserves with no anthropogenic intervention allowed (Zawadzka, Zawadzki 2005). Forests outside strictly protected areas are characterised by different degrees of naturalness, depending on land topography, habitat types and forest management intensity. Amongst these, there are sustainably managed semi-natural forests with differentiated spatial, age and species structures as well as intensively exploited even-age forest monoculture plantations (Winter 2012).

The paper presents the results of a long-term ornithological study carried out in the Borki Forest (Masurian Lakeland, northern Poland) – an example of managed forest with a high degree of naturalness. First, during three subsequent years (1994–1996), an avifauna inventory was conducted on the three permanent research plots, which included the evaluation of bird species composition, breeding pair density and dominance of individual species. The research plots comprised mature tree stands that represented three types of forest communities occurring in the Borki Forest: oak-hornbeam forest, ash-alder forest and mixed coniferous forest. In the years 2012–2014, avifauna inventory on the same plots was carried out for the second time. The aim of the present study was to compare the results of the two censuses so as to examine over time changes in the Borki Forest avifauna and analyse reasons behind the changes.

2. Study area

2.1. Characteristics of the Borki Forest

The Borki Forest comprises the forest complex with an area of more than 22,000 ha that covers highly undulating terrain in the eastern part of the Masurian Lake District. At this point, the glacial relief of land is much diversified, and there occur numerous pushed moraine landforms, with kames, eskers and hollows filled with peat bogs or lake sub-glacial channels. Within the Borki Forest, the highest land elevation is the Góra Lipowa (223 m a.s.l.), and on the whole, nearly 90 m altitude differences within this area are some of the greatest in Poland's lowland forest complexes. The Borki Forest is located on the line that separates neighbouring drainage basins. There lack big rivers; however, forest streams form a quite dense hydrographic network. The biggest watercourse is the Łaźna Struga (the river Ełk upstream), which carries away waters from several large lakes situated in the south-eastern part of the Borki Forest. In soil cover, there prevail fertile luvisols (almost 40%) and rusty soils (almost 20%), and a share of peat soils is quite high (more than 10%). This area has relatively harsh climate, with features of the continental climate influenced by the Atlantic Ocean (next to mountain climate, climate in this region is one of the harshest in Poland) (Siuta 1994; BULiGL 2010).

The Borki Forest is one of the few Poland's large forest complexes with prevailing deciduous and mixed tree stands that grow on fertile sites. Attributable to diversified land relief, forest habitats form a mosaic. The main plant community forms oak-hornbeam forest (*Tilio-Carpinetum*), multispecies tree stands with a considerable share of Norway spruce (*Picea abies*). Quite large areas are covered by ash-alder riparian forest (*Fraxino-Alnetum*), sub-boreal mixed coniferous forest (*Serratulo-Pinetum*) and continental coniferous forest (*Peucedano-Pinetum*). Marshy, drainless hollows are covered with alder carrs (*Alnetea glutinosae*) and boggy mixed coniferous forest (*Sphagno girgensohnii-Piceetum*). Next to Norway spruce, the main forest-forming species are Scots pine (*Pinus sylvestris*), pedunculate oak (*Quercus robur*), black alder (*Alnus glutinosa*), silver birch (*Betula pendula*), common ash (*Fraxinus excelsior*), small-leaved lime (*Tilia cordata*) and common hornbeam (*Carpinus betulus*). In the Borki Forest, there dominate stands not older than 60 years, which cover approximately 60% of the forested area, whereas 100-year-old and older stands cover approximately 10% of the forested area. A high degree of naturalness of the Borki Forest is attributable to concordance between growing tree species and their site conditions, species richness in forest stands and low anthropogenic pressure (Sokołowski 2006; BULiGL 2010; Rąkowski 2015).

The Borki Forest is a valuable fauna refuge. There reside one of Poland's five wild European bison (*Bison bonasus*) herds as well as the major (on the scale of the country) populations of rare mammal species, such as lynx (*Lynx lynx*) and wolf (*Canis lupus*). There also lives a thriving community of Eurasian beaver. Even though the total area of the Borki Forest is comparatively small, its avifauna is especially rich with almost 140 breeding and probably breeding bird species, amongst which numerous rare and endangered species occur. The current status of the Borki Forest's avifauna and the history of ornithological research in this area were described by Rąkowski (2015). Natural values of the Borki Forest constituted the basis for designation of this area as a Natura 2000 site (under both the Birds and the Habitats Directives) as well as the establishment of four forest natural reserves to protect habitats of multispecies deciduous and mixed forest (Rąkowski et al. 2012).

2.2. Research plots

All the research plots are situated in the central part of the Borki Forest, within the area of the Forest District Borki, on undulated moraine terrain with the absolute elevation ran-

ging from 178.5 to 215.5 m a.s.l. Except for a part of one of the research plots (BM, mixed coniferous forest), the plots are now situated within the area of the Borki nature reserve (440.22 ha) that was expanded in 2015 (during the observation period, only the research plot Ł, which was established in ash-alder forest, was situated in the nature reserve). The plot areas were designated in such a way that they comprised mature stands that represented different forest habitats. However, because of a mosaic of habitats as well as undulated relief in the Borki Forest, none of the plots represented homogeneous type of a given forest habitat.

The most uniform (in terms of forest habitat) plot G – oak -hornbeam (16 ha) – is situated on a flat top of a hill as well as on its northern and southern slopes above the valleys of the Borki Forest streams flowing in deep ravines. The western part of the plot connects with the narrow strip of a mid-forest meadow. Almost entire plot is covered by oak-hornbeam *Tilio-Carpinetum* old-growth forest. In 100–150 years old open canopy multispecies stand, there dominate ash, hornbeam and lime, whereas Norway maple (*Acer platanoides*), Norway spruce and silver birch are admixture species. Undergrowth is not well developed and consists mainly of common hazel (*Corylus avellana*) and young limes and hornbeams. Groundcover comprises species characteristic for deciduous forests. The north-western part of the plot borders on an open area of a small (0.5 ha) reforested clear-cut (tree felling was conducted in between the observation periods in this study). Two other newly reforested areas of a similar size are located in the neighbourhood.

The plot Ł – ash-alder (6.0 ha) – comprises a fragment of a forest stream valley. Most of the area is covered by ash -alder forest *Fraxino-Alnetum*. More than a decade ago (in between the observation periods), the stream was dammed by beavers, and the stream valley was partially filled with still waters all year through, thus nearly all of flooded trees died. Ash-alder forest (80–105 years old) endured in the north-western (not flooded) part of the plot as well as on stream valley slopes. In the tree layer, there dominates alder with admixtures of ash, lime. Norway spruce and birch. Undergrowth comprises mainly common hazel and young

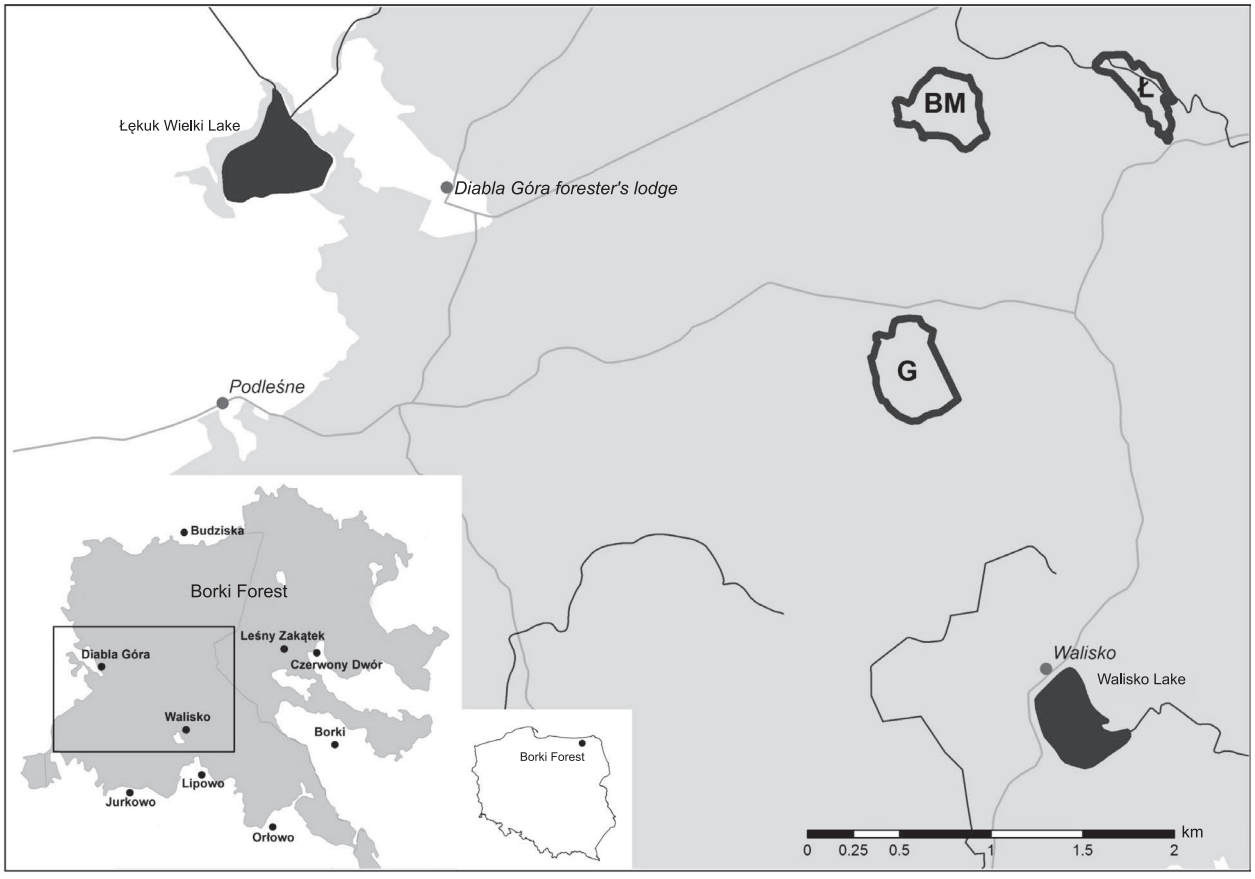

Figure 1. Distribution of study plots in the Borki Forest

Explanations: G – oak-hornbeam, Ł – ash-alder, BM – mixed coniferous

ash trees. On the borders of this study plot, there grows oak -hornbeam forest (*Tilio-Carpinetum*) old-growth stands that are 145–190 years old, formed mainly by lime and Norway spruce, Norway maple and hornbeam as admixtures.

The plot BM – mixed coniferous forest (14.5 ha) – encompasses the most diversified area with the mosaic relief. The largest part of the area is covered by sub-boreal coniferous mixed forest with a considerable share of Norway spruce. On moraine humps, there grow impoverished forms of oak-hornbeam forest (*Tilio-Carpinetum*). In stands that are 80–110 years old, there prevails Norway spruce, whereas ash, lime and pedunculate oak constitute considerable admixtures. Species such as hornbeam, birch and ash are less widespread here. Undergrowth is relatively well developed, with dominant common hazel and young Norway spruce, Norway maple, oak and ash trees. In groundcover, species characteristic for coniferous and deciduous forests occur. Small terrain hollows are overgrown by ash-alder forest, boggy mixed coniferous forest (*Sphagno girgensohnii-Piceetum*) and alder carr forest (*Ribeso nigri-Alnetum*). A few years ago, a forest path was cut through the research plot. At the same time, two small gaps (of joint area less than 1 ha) were formed due to group felling. These are now covered by dense natural forest regeneration.

2.3. Habitat changes

In the period of almost 20 years between the two avifauna inventories, in the habitats on the study plots and/or in their neighbourhood, several changes that could affect bird communities occurred. There took place ageing of forest stands, trees grew older and thicker, more deadwood was formed (standing dead trees and lying logs) as well as more hollow trees became available. In the sites with lower canopy density and those with natural stand gaps, undergrowth and groundcover were developed. The water regime changed on account of beaver activities, especially on the research plot Ł. Beavers also affected water flow in the streams adjacent to the research plots BM and G.

During avifauna inventories in 1994–1996 and 2012–2014, except for the research plot Ł (established in the nature reserve), the research plots were situated in managed forests, where foresters harvested trees, and therefore, several group felling gaps were formed within the area of BM plot and in the closest proximity of G plot. Some of the forest roads along the research plots were reconstructed and broadened at the beginning of the 21st century.

3. Methods

3.1. Methodology of bird observations

Bird censuses were carried out following the combined standard cartographic method by Tomiałojć (1980). In each observation season (from 15 April to 30 June), all the research plots were visited 10 times (8 morning and 2 evening observations). Morning observations were performed right after the sunrise and evening – at dusk. Each control started from different research plot edge. All records were documented on topographic maps. At least three records of the same species in the same research plot district constituted a basis to recognise a given species as the breeding species. In the cases when the major part of a given species territory comprised the area beyond the research plot or if the bird territory was considerably larger than the research plot area, a given species was recognised as the edge species (see + in Tables 1–3).

3.2. Bird ecological groups

For the purpose of this study, based on habitat preferences of individual bird species (Zawadzka, Zawadzki 2005, 2006; Sikora et al. 2007), three ecological groups were assigned: (1) birds of mature forests with natural character (from the list proposed by Zawadzka and Zawadzki (2006)), (2) other forest birds and (3) non-forest bird species as well as bird species not typical for forest interior. The latter comprised ecotone bird species, birds inhabiting open and semi-open areas, wetland birds and synanthropic birds. For each group, the percentage share in breeding bird community on a given research plot in 1994–1996 and 2012–2014 was determined (Fig. 4).

3.3. Statistical analysis

The similarity coefficient (Sørensen index QS, Sørensen 1948) was used in the analysis of similarities between the species composition of breeding birds occurring on the research plots:

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

where
a and b are the numbers of species in the first and the second sample, respectively,
c is the number of species that occur in both samples

The Renkonen similarity index (Renkonen 1938, DR) was used to test the similarities between the structures of bird communities on individual research plots

$$DR = \sum_{i=1}^{n} \min(p_i;q_i) \text{ x } 100\%$$

where
p_i and q_i are the relative frequencies of i-th species in the tested samples.

The Poisson distribution was assumed as an appropriate model for the analysis of data on the numbers of breeding

species examined (Fig. 2). The generalised linear model (GzLM) was used in the analysis of the changes in species numbers on individual research plots as well as those on all the research plots jointly. The Wald-type confidence intervals (95%) were determined. Significance of the changes in species numbers was tested based on the likelihood ratio chi-square statistic for type 3 analysis. The calculations were performed with the use of GENMOD procedure in SAS software (SAS Institute Inc. 2011).

T-Student test was used to compare the total densities of breeding pairs on the individual research plots (Fig. 3) in both the observation periods (1994–1996 and 2012–2014). In the case of unequal variances obtained for the periods studied, Welch's t-test was used. For sample numbers used in the analyses in the present study, the differences between the means in both periods studied were higher in all cases than the minimum difference between the real means that could be detected by *t* test or Welch's test of 95% power. The calculations were performed using StatSoft, Inc. 2011.

4. Results

On all the plots examined, the numbers of breeding bird species and population densities were much higher in 2012–2014 than those in 1994–1996 (Tables 1–3). In total, 74 breeding bird species were recorded on all the research plots. In 1994–1996, 54 breeding species were observed, and in 2012–2014, 73 breeding species were observed.

The European serin (*Serinus serinus*) was the breeding bird species recorded only in 1994–1996 (BM research plot) and not observed in 2012–2014 (Table 3). In the second observation period, on the research plots, altogether 20 new breeding species (not observed in 1994–1996), such as mallard (*Anas platyrhynchos*), common goldeneye (*Bucephala clangula*), goosander (*Mergus merganser*), black kite (*Milvus migrans*), Eurasian pygmy owl (*Glaucidium passerinum*), boreal owl (*Aegolius funereus*), three-toed woodpecker (*Picoides tridactylus*), common swift (*Apus apus*), spotted nutcracker (*Nucifraga caryocatactes*), red-backed shrike (*Lanius collurio*), short-toed treecreeper (*Certhia brachydactyla*), mistle thrush (*Turdus viscivorus*), common redstart (*Phoenicurus phoenicurus*), willow warbler (*Phylloscopus trochilus*), greenish warbler (*Phylloscopus trochiloides*), white wagtail (*Motacilla alba*), icterine warbler (*Hippolais icterina*), long-tailed tit (*Aegithalos caudatus*), common rosefinch (*Carpodacus erythrinus*) and common siskin (*Spinus spinus*), were recorded.

In the period between the two observation series, none of the species with abundant populations (more than 2 pairs/10

Table 1. The breeding bird assemblage on plot G (oak-hornbeam forest stand. 16.0 ha) in 1994–1996 and 2012–2014

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Fringilla coelebs[a,b]	23	23.5	27.5	15.4	31.2	26	24	24	15.4	19.2
Erithacus rubecula[a,b]	8.5	7	9	5.1	10.3	11.5	8.5	10.5	6.4	8
Cyanistes caeruleus[a]	6	6.5	8	4.3	8.6	6	6	5.5	3.7	4.6
Troglodytes troglodytes[a]	6	5	6	3.6	7.3	4.5	6.5	5.5	3.4	4.2
Parus major[a,b]	5	5	4	2.9	5.9	8	7.5	7.5	4.8	6
Ficedula hypoleuca[a]	4	4	4	2.5	5.1	3	4.5	4.5	2.5	3.1
Phylloscopus sibilatrix	4	7	0.5	2.4	4.9	3.5	3	1	1.6	2
Sitta europaea	3	3	4	2.1	4.2	4	4	4	2.5	3.1
Certhia familiaris	2	2	3	1.4	2.8	3	4.5	4	2.4	3
Sylvia atricapilla[b]	1	1.5	2.5	1	2.1	10	8.5	6	5.1	6.4
Regulus regulus	1	2	2	1	2.1	4	3	3	2.1	2.6
Turdus philomelos	1	2	1.5	0.9	1.9	6	6	5.5	3.7	4.6
Turdus merula	1	1	2	0.8	1.7	3.5	4	4.5	2.5	3.1
Poecile palustris	1	1	2	0.8	1.7	3	2.5	3	1.8	2.2
Dendrocopos major	1	1	1.5	0.7	1.5	3	2	3	1.7	2.1

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Coccothraustes coccothraustes[b]	1	1	1.5	0.7	1.5	10	10	9	6	7.5
Poecile montanus	1	1	1	0.6	1.3	1	1.5	1	0.7	0.9
Ficedula parva	1	1	1	0.6	1.3	2	2	2.5	1.4	1.7
Strix aluco	0.5	1	1	0.5	1.1	0.5	0.5	0.5	0.3	0.4
Phylloscopus collybita	0.5	0.5	0.5	0.3	0.6	2	3.5	1.5	1.5	1.9
Columba palumbus	0.5	0.5	0.5	0.3	0.6	2	1	1.5	0.9	1.1
Prunella modularis	+	1	-	0.2	0.4	1	1	2	0.8	1
Muscicapa striata	-	1	-	0.2	0.4	2	2	2	1.3	1.6
Anthus trivialis	0.5	0.5	-	0.2	0.4	1	0.5	-	0.3	0.4
Dendrocopos minor	-	-	1	0.2	0.4	-	0.5	0.5	0.2	0.2
Dendrocopos medius	-	-	1	0.2	0.4	1.5	1.5	1	0.8	1
Sylvia communis	-	-	0.5	0.1	0.2	-	-	0.5	0.1	0.1
Periparus ater	-	-	0.5	0.1	0.2	-	-	0.5	0.1	0.1
Ficedula albicollis	-	-	-			2	2	3	1.5	1.9
Phylloscopus trochilus	-	-	-			2	1	2	1.1	1.4
Regulus ignicapillus	-	-	-			2.5	1	1.5	1	1.2
Sylvia borin	-	-	-			1	1	0.5	0.5	0.6
Garrulus glandarius	+	+	+			0.5	0.5	0.5	0.3	0.4
Grus grus	-	+	+			+	+	0.5	0.1	0.1
Buteo buteo	+	+	-			+	+	1	0.2	0.2
Dendrocopos leucotos	+	-	-			1	0.5	0.5	0.4	0.5
Dryocopus martius	+	-	+			0.5	0.5	0.5	0.3	0.4
Columba oenas	-	-	+			-	0.5	0.5	0.2	0.2
Tringa ochropus	-	-	-			-	0.5	-	0.1	0.1
Oriolus oriolus	-	-	+			+	1	1	0.4	0.5
Caprimulgus europaeus	-	-	-			0.5	-	-	0.1	0.1
Turdus viscivorus	-	-	-			-	1	+	0.2	0.2
Tetrastes bonasia	+	+	-			-	+	-		
Corvus corax	+	+	+			+	+	+		
Streptopelia turtur	+	-	-			-	-	-		
Cuculus canorus	-	-	+			+	+	+		
Pyrrhula pyrrhula	-	-	+			-	-	-		
Accipiter nisus	-	-	+			-	-	-		
Ciconia nigra	-	-	+			-	+	+		

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Turdus iliacus	-	-	+			-	-	-		
Emberiza citrinella	-	+	-			-	+	+		
Scolopax rusticola	-	-	-			-	+	+		
Gallinago gallinago	-	-	-			+	+	-		
Clanga pomarina	-	-	-			+	+	-		
Anas platyrhynchos	-	-	-			+	+	-		
Spinus spinus	-	-	-			+	-	-		
Hippolais icterina	-	-	-			-	+	-		
Phoenicurus phoenicurus	-	-	-			-	-	+		
Aegolius funereus	-	-	-			-	-	+		
Number of pairs	72.5	79	86	49.5		132	128	125.5	80.3	
Number of species	30	30	36			42	49	46		
Mean number of species	32					47.5				
Total number of species	44					55				

Explanations: Z – density of breeding pairs; D – dominance; + – breeding species. less than 0.5 territory within the plot; - – species non breeding in a given year; *bold marks dominant species (dominance >5%); [a]dominant species in 1994–96; [b]dominant species in 2012–14.

Table 2. The breeding bird assemblage on Ł plot (ash-alder forest stand. 6.0 ha) in 1994–1996 and in 2012–2014

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Fringilla coelebs[a.b]	11	10	13	18.9	25.2	13	12	12.5	20.8	16.5
Cyanistes caeruleus[a.b]	4	3	3.5	5.8	7.7	4	4	4	6.7	5.3
Parus major[a]	3.5	3	3.5	5.6	7.5	3.5	4	3.5	6.1	4.8
Ficedula hypoleuca[a]	3	2.5	4	5.3	7.1	2.5	3	3	4.7	3.7
Erithacus rubecula[a.b]	2	3	4.5	5.3	7.1	5.5	6	5	9.2	7.3
Troglodytes troglodytes[a.b]	3	2	2	3.9	5.2	3	3.5	3.5	5.6	4.4
Phylloscopus collybita	2	2	1.5	3.1	4.1	2	2.5	2	3.6	2.9
Turdus philomelos[b]	1	2.5	2	3.1	4.1	4	4	3.5	6.4	5.1
Regulus regulus	1.5	1.5	2.5	3.1	4.1	3.5	2	3	4.7	3.7
Sitta europaea	1.5	1.5	2.5	3.1	4.1	3.5	3	3	5.2	4.2
Phylloscopus sibilatrix	1	2	1	2.2	2.9	2.5	0.5	+	1.7	1.3
Certhia familiaris	1	1	2	2.2	2.9	2.5	3	4	5.3	4.2
Turdus merula	1	1	1.5	1.9	2.5	2.5	2.5	2.5	4.2	3.3

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Sylvia atricapilla	1	1	1.5	1.9	2.5	3.5	4	3.5	6.1	4.8
Dendrocopos major	1	1	1	1.7	2.3	1	1.5	2	2.5	2
Dendrocopos minor	1	0.5	1	1.4	1.9	+	0.5	-	0.3	0.2
Prunella modularis	1	1	-	1.1	1.5	1	2	1	2.2	1.8
Poecile montanus	1	-	1	1.1	1.5	1	1	0.5	1.4	1.1
Ficedula albicollis	1	-	1	1.1	1.5	2	2.5	3.5	4.4	3.5
Dendrocopos medius	+	0.5	1	0.8	1.1	1	1	0.5	1.4	1.1
Columba palumbus	+	0.5	0.5	0.6	0.8	1	1	1	1.7	1.3
Coccothraustes coccothraustes	+	+	1	0.6	0.8	2.5	2	2	3.6	2.9
Sylvia borin	1	-	+	0.5	0.7	-	+	+		
Tringa ochropus	-	0.5	+	0.3	0.4	1	1	1	1.7	1.3
Strix aluco	0.5	+	+	0.3	0.4	0.5	0.5	0.5	0.8	0.7
Garrulus glandarius	+	+	+			+	0.5	+	0.3	0.2
Muscicapa striata	-	-	-			2.5	3	2.5	4.4	3.5
Phylloscopus trochilus	-	-	-			1.5	2	1	2.5	2
Poecile palustris	-	-	+			1.5	1.5	1	2.2	1.8
Columba oeans	-	-	+			+	+	0.5	0.3	0.2
Phoenicurus phoenicurus	-	-	-			-	0.5	1	0.8	0.7
Regulus ignicapillus	-	-	-			1	0.5	1.5	1.7	1.3
Dendrocopos leucotos	-	-	-			+	0.5	1	0.8	0.7
Aegithalos caudatus	-	-	-			-	0.5	0.5	0.6	0.4
Ficedula parva	-	+	-			0.5	+	+	0.3	0.2
Periparus ater	-	-	-			0.5	+	+	0.3	0.2
Anas platyrhynchos	-	-	-			1	+	1	1.1	0.9
Bucephala clangula	-	-	-			+	+	0.5	0.3	0.2
Phylloscopus trochiloides	-	-	-			-	-	0.5	0.3	0.2
Certhia brachydactyla	-	-	-			-	-	0.5	0.3	0.2
Grus grus	+	+	+			+	+	+		
Tetrastes bonasia	+	+	-			+	-	-		
Ciconia nigra	+	-	+			-	-	-		
Clanga pomarina	-	+	-			+	+	-		
Cuculus canorus	-	+	-			+	+	+		

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Corvus corax	+	-	-			+	+	+		
Buteo buteo	-	-	+			+	-	-		
Dryocopus martius	-	-	-			+	+	+		
Scolopax rusticola	-	-	-			+	+	+		
Gallinago gallinago	-	-	-			-	+	-		
Turdus iliacus	-	-	-			-	+	-		
Turdus viscivorus	-	-	-			+	+	+		
Nucifraga caryocatactes	-	-	-			-	+	+		
Picoides tridactylus	-	-	-			-	+	+		
Motacilla alba	-	-	-			-	+	-		
Oriolus oriolus	-	-	-			-	+	-		
Mergus merganser	-	-	-			+	-	-		
Spinus spinus	-	-	-			+	-	-		
Glaucidium passerinum	-	-	-			+	-	-		
Accipiter nisus	-	-	-			-	-	+		
Number of pairs	43	40	51.5	74.7		75	76	76.5	126.4	
Number of species	29	28	30			47	51	48		
Mean number of species		29					48.7			
Total number of species		37					61			

For explanations see Table 1.

Table 3. The breeding bird assemblage on plot BM (mixed coniferous forest stand. 14.5 ha) in 1994–1996 and in 2012–2014

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Fringilla coelebs[a,b]	22	19	24	14.9	27.2	22.5	19	20.5	14.3	17
Regulus regulus[a,b]	8.5	7.5	7	5.3	9.7	7.5	6	8	4.9	5.8
Phylloscopus sibilatrix[a]	8	8.5	5	4.9	9.0	4.5	4.5	4	3	3.6
Erithacus rubecula[a,b]	5.5	4.5	6.5	3.8	6.9	11	10.5	9.5	7.1	8.5
Cyanistes caeruleus[a]	4	4	5	3	5.5	4.5	4.5	5	3.2	3.8
Parus major[b]	3	4	4.5	2.6	4.8	6	7	6	4.3	5.1
Troglodytes troglodytes	4.5	2.5	4.5	2.6	4.8	6	5	3	3.2	3.8

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Sylvia atricapilla[b]	2	2	3	1.6	2.9	8.5	7	7.5	5.3	6.3
Certhia familiaris	3	2	2	1.6	2.9	3	4.5	5	2.9	3.5
Ficedula hypoleuca	1.5	2	3	1.5	2.7	2.5	2.5	1	1.4	1.7
Poecile montanus	2	2	2	1.4	2.6	2	2	2	1.4	1.7
Turdus philomelos	1.5	2	2.5	1.4	2.6	4.5	4.5	4.5	3.1	3.7
Dendrocopos major	1.5	1	3	1.3	2.4	2	2.5	3	1.7	2
Phylloscopus collybita	1	1.5	2	1	1.8	2.5	2.5	3.5	2	1.8
Turdus merula	1	1	2	0.9	1.6	3.5	3.5	4	2.5	3
Ficedula parva	1	1	2	0.9	1.6	1	1	1	0.7	0.8
Sitta europaea	1	1	2	0.9	1.6	3.5	3	3	2.2	2.6
Coccothraustes coccothraustes	1	+	2	0.7	1.3	3.5	4	4.5	2.8	3.3
Muscicapa striata	1	-	2	0.7	1.3	2	2	2	1.4	1.7
Prunella modularis	1	-	2	0.7	1.3	1.5	2	1.5	1.1	1.3
Grus grus	0.5	0.5	1.5	0.6	1.1	0.5	0.5	0.5	0.3	0.4
Columba palumbus	+	1	1	0.5	0.9	1.5	1	1	0.8	1
Periparus ater	+	1	1	0.5	0.9	1	1	1	0.7	0.8
Lophophanes cristatus	1	-	1	0.5	0.9	1	-	-	0.2	0.2
Strix aluco	0.5	0.5	0.5	0.3	0.5	0.5	1	1	0.6	0.7
Dendrocopos medius	+	-	1	0.2	0.4	1.5	1.5	1	0.9	1.1
Regulus ignicapillus	+	-	1	0.2	0.4	2.5	2	2	1.5	1.8
Poecile palustris	+	-	1	0.2	0.4	3	3	3	2.1	2.5
Phylloscopus trochilus	-	-	-			3	3	2	1.8	2.1
Ficedula albicollis	-	-	-			2.5	3	2	1.7	2
Garrulus glandarius	+	+	+			0.5	0.5	0.5	0.3	0.4
Pyrrhula pyrrhula	+	+	+			0.5	-	+	0.1	0.1
Tetrastes bonasia	+	+	+			1	+	1	0.5	0.6
Dryocopus martius	+	-	+			1	1	0.5	0.6	0.7
Tringa ochropus	+	-	+			1	1	1	0.7	0.8
Scolopax rusticola	-	-	+			0.5	+	0.5	0.2	0.2
Sylvia borin	-	-	-			1.5	1.5	0.5	0.8	0.8
Turdus viscivorus	-	-	-			0.5	1	0.5	0.5	0.6
Picoides tridactylus	-	-	-			-	0.5	+	0.1	0.1

Species*	Years 1994–1996					Years 2012–2014				
	Number of pairs			Mean		Number of pairs			Mean	
	1994	1995	1996	Z (p/10 ha)	D (%)	2012	2013	2014	Z (p/10 ha)	D (%)
Oriolus oriolus	-	-	-			-	0.5	0.5	0.2	0.2
Columba oenas	-	-	-			-	0.5	0.5	0.2	0.2
Sylvia communis	-	-	-			0.5	+	0.5	0.2	0.2
Dendrocopos minor	-	-	-			-	+	1	0.2	0.2
Anthus trivialis	-	-	-			0.5	+	+	0.1	0.1
Spinus spinus	-	-	-			0.5	-	+	0.1	0.1
Nucifraga caryocatactes	-	-	-			-	-	0.5	0.1	0.1
Clanga pomarina	+	+	-			+	+	+		
Ciconia nigra	-	+	+			-	-	-		
Buteo buteo	+	+	-			+	+	+		
Corvus corax	+	+	-			+	+	+		
Cuculus canorus	-	+	-			+	+	+		
Streptopelia turtur	-	-	+			+	-	-		
Gallinago gallinago	-	-	+			+	+	+		
Caprimulgus europaeus	-	-	+			-	-	-		
Serinus serinus	-	-	+			-	-	-		
Dendrocopos leucoctos	-	-	-			-	+	+		
Aegithalos caudatus	-	-	-			+	+	+		
Apus apus	-	-	-			-	+	+		
Emberiza citrinella	-	-	-			-	+	+		
Lanius collurio	-	-	-			-	+	-		
Carpodacus erythrinus	-	-	-			-	+	-		
Hippolais icterina	-	-	-			-	-	+		
Milvus migrans	-	-	-			-	+	-		
Bucephala clangula	-	-	-			-	+	-		
Anas platyrhynchos	-	-	-			-	-	+		
Number of pairs	76	68.5	93.5	54.7		127	120	119.5	84.2	
Number of species	36	30	39			48	55	56		
Mean number of species		35					53			
Total number of species		43					63			

For explanations see Table 1

ha) showed decreased population numbers on any of the research plots (Tables 1–3). Populations of a few species remained stable, that is, those of common chaffinch (*Fringilla coelebs*), Eurasian blue tit (*Cyanistes caeruleus*), Eurasian wren (*Troglodytes troglodytes*) and European pied flycatcher (*Ficedula hypoleuca*), whereas the population numbers of wood warbler (*Phylloscopus sibilatrix*) considerably fluctuated. All other most abundant species increased their population numbers on the research plots, especially Eurasian blackcap (*Sylvia atricapilla*), hawfinch (*Coccothraustes coccothraustes*), common blackbird (*Turdus merula*), song thrush (*Turdus philomelos*) and collared flycatcher (*Ficedula albicollis*).

As a result of the changes in population numbers, changes in the species structure of dominant (at least 5% of breeding population) bird species on individual research plots were observed (Tables 1–3). Within all the plots examined, the share of chaffinch (super-dominant species) considerably decreased, given that it was one of the few species whose numbers did not increase during the observation period. Next to the chaffinch, the European robin (*Erithacus rubecula*) remained the dominant species on all the plots during the entire observation period. Other dominant species (although not on all the plots) were great tit (*Parus major*), Eurasian blue tit and goldcrest (*Regulus regulus*). The following bird species fell out of the group of dominant species: Eurasian wren, European pied flycatcher and wood warbler. New dominant species observed in 2012–2014 were Eurasian blackcap, hawfinch and song thrush – bird species with considerably increased populations.

In the period between the observation series, the mean number of breeding species within the area of all the research plots increased from 32 to almost 49, which is equal to species richness increase by more than 50% (Fig. 2). During both observation periods (1994–1996 and 2012–2014), the numbers of breeding species on BM plot were higher when compared to Ł and G plots and amounted to 35 and 53 species, respectively. On the other hand, the comparatively greatest increase of breeding species numbers within a given research plot was observed on Ł plot: from, on an average, 29 to almost 49 species (nearly 69% increase).

In the period between the two observation series, the density of breeding pairs on all the plots examined increased considerably (Fig. 3). The total increase in all the plots was, on an average, more than 60% (from 65 pairs/10 ha to 105 pairs/10 ha). When compared to BM and G research plots, the highest mean pair density was observed on Ł plot in both the periods of observation (nearly 74 pairs/10 ha and over 126 pairs/10 ha, respectively).

On each research plot, bird species typical for forests definitely dominated. However, in between the observations, on all the plots, the share of bird species not typical for forest interior, such as ecotone bird species and those living outside of forests (in bushes, open and semi-open areas, wetlands) as well as synanthropic species, increased twofold (on an average, from 7.3% to 14.56%). In the group of typical forest species, several percent increase (on an average, from 23.6% to 28.1%) of the share of bird species associated with mature forest stands with a high degree of naturalness was observed. The number of such species increased by over

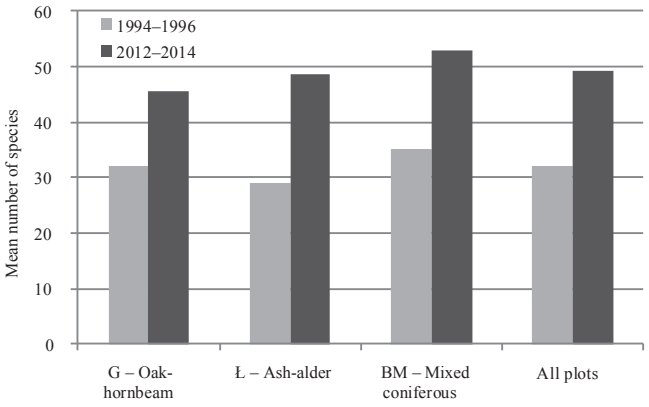

Figure 2. Species richness of breeding bird assemblages of Borki Forest stands in 1994–1996 and 2012–2014

In all stands the mean number of species in 2012–2014 was significantly higher than in 1994–1996 (likelihood ratio test according to type 3 analysis, $p \leq 0.05$).

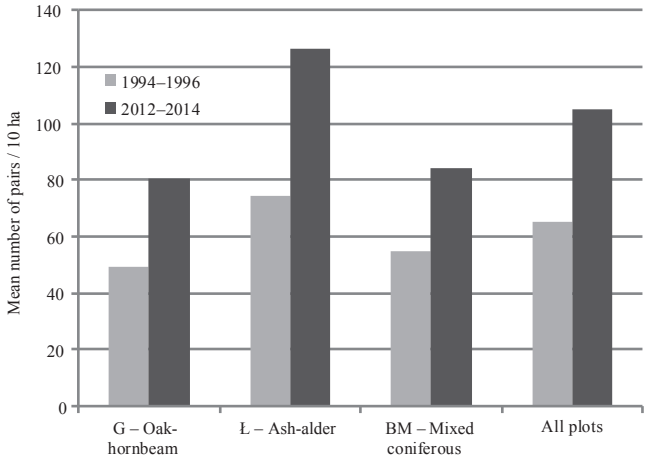

Figure 3. Total density of breeding bird assemblages of Borki Forest stands in 1994–1996 and 2012–2014.

In all stands the mean density of breeding pairs in 2012–2014 was significantly higher than in 1994–1996 (t test or Welch test, $p \leq 0.05$).

20% on the research plots G and Ł, whereas on the plot BM, the number of forest interior bird species basically did not change in 20 years (1994–2014).

The analysis of similarities between species composition in bird assemblages on the research plots examined (Table 4) showed that both the Sørensen index QS (which reflected similarities between species compositions) as well as the Renkonen index DR (which reflected the similarities between percentage shares of individual bird species) reached the values over 75% in both periods of observations (1994–1996 and 2012–2014). In line with the scale proposed by Tomiałojć (1970), this shows a quite high degree of similarity between bird assemblages that inhabit the research plots examined. At the same time, the patterns of changes in bird species composition on each plot were similar.

5. Discussion

No statistically significant differences found between species composition of bird assemblages observed in different forest types of the Borki Forest (Table 4) allow for the conclusion that mature deciduous and mixed stands in this forest complex are inhabited by basically one bird assemblage, notwithstanding habitat examined. Analogous results were obtained in the Białowieża Primeval Forest by Tomiałojć et al. (1984) as well as Tomiałojć and Wesołowski (1996). This is attributable to mosaic forest habitats associated with diversified terrain relief within the area of the Borki Forest, in addition to considerable diversity of tree species growing in this forest complex. In general, there lack large forest fragments, uniform in terms of forest habitats and stand age. Within relatively small areas, different types of

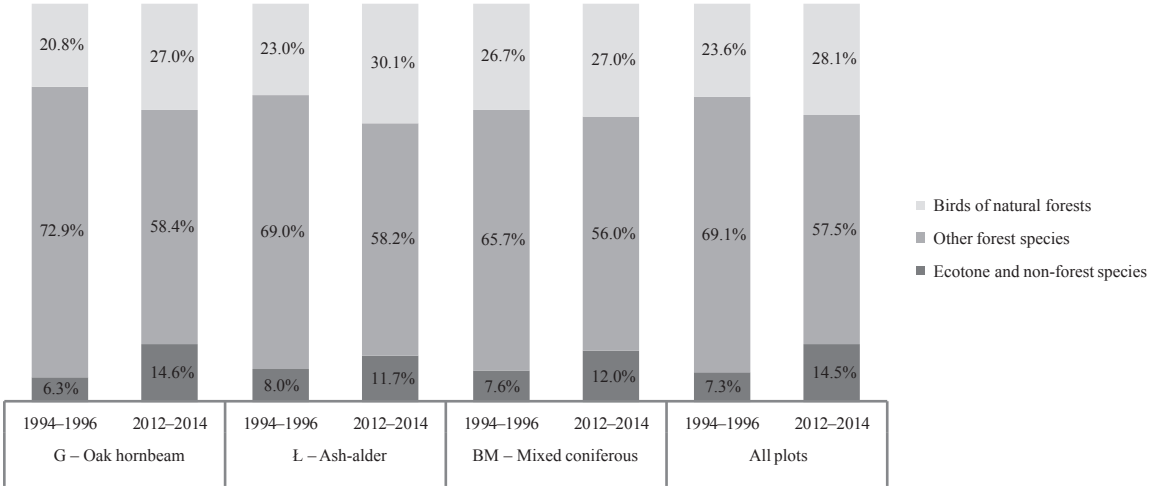

Figure 4. Share of ecological groups in species composition of bird assemblages on different plots in 1994–1996 and 2012–2014

Table 4. Similarities of bird assemblages from different plots in 1994–1996 and 2012–2014

Years 1994–1996						Study plot	Years 2012–2014					
Oak-hornbeam G		Ash-alder Ł		Mixed coniferous BM			Mixed coniferous BM		Ash-alder Ł		Oak-hornbeam G	
QS	DR	QS	DR	QS	DR		QS	DR	QS	DR	QS	DR
-	-	83.0	80.5	89.3	78.2	oak-hornbeam	88.6	86.0	81.5	83.6	-	-
		-	-	79.2	77.5	ash-alder	75.3	83.4	-	-		
				-	-	mixed coniferous	-	-				

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

forest plant communities often neighbour each other. Homogeny of avifauna in the Borki Forest is the effect of the above described characteristics.

Amongst bird species breeding within the research plots, bird species characteristic for interior forest parts definitely dominated, including those from the group of species typical for mature forests with a high degree of naturalness, determined by Zawadzka and Zawadzki (2006). There were observed a few rare and endangered species, who found refuge in the Borki Forest as one of their most important breeding grounds on the country's scale: middle spotted woodpecker (*Dendrocopos medius*), common goldeneye, green sandpiper (*Tringa ochropus*), hazel grouse (*Tetrastes bonasia*) and collared flycatcher (Rąkowski 2015).

Over 20 years, both the number of species and breeding pair density within the research plot areas examined in the present study considerably increased. The observed increase in the density of breeding pairs was a result of increased numbers of nesting species as well as increased population numbers of a lot of these species.

When comparing the obtained results with the records of the Program of Common Breeding Birds Monitoring in Poland (Monitoring Ptaków 2016), it should be noted that the stability of populations of blue tit, wren and pied flycatcher as well as an increase of the numbers of blackcap, blackbird, song thrush and willow warbler are generally in accordance with trends observed at a country level. On the other hand, in the Borki Forest, blackcap, blackbird, song thrush and willow warbler population numbers increased more when compared to those observed at a country level. Increased blackcap population numbers in the Borki Forest can be associated with the increasing abundance of natural gaps in mature stands (as a result of falling apart old or windblown trees), which are readily colonised by this species, as it was also observed in the Białowieża Primeval Forest (Fuller 2000; Wesołowski et al. 2015). The stability of chaffinch population in the Borki Forest as well as fluctuations of wood warbler population also reflect the trends observed in the country. On the scale of Poland, chaffinch population numbers slightly decrease, and those of wood warbler tend to increase; the latter fluctuate over years. A great increase in the population of hawfinch in the Borki Forest is difficult to explain, because the numbers of this species in Poland are relatively stable, regardless of seasonal fluctuations.

Noteworthy is the fact that despite a general increase in the number of breeding species and their density in the Borki Forest, within all the research plots examined, the percentage share of non-forest bird species and those untypical for forest interior areas increased. At the same time, a fairly increasing number of species characteristic for old forest stands with diversified structure characteristic for semi-natural or natural forests was observed. Amongst 20 breeding bird species newly observed in the second period of observations (2012–2014), 10 species are associated with ecotone habitats, semi-open and overgrown by bushes areas, wetlands or synanthropic terrains, whereas 6 bird species represent those characteristic for old tree stands.

The increase in the bird species numbers and breeding pair density on the research plots in the Borki Forest presumably results from two major factors. The first factor is forest succession and natural ageing of tree stands, which cause the progress of spatial and qualitative diversity of bird habitats, followed by an increase in the habitat's carrying capacity. As described by Głowaciński and Järvinen (1975), the rates of forest succession processes and related succession of forest bird assemblages slow down with tree stand age. In Białowieża National Park (BNP), which comprises strictly protected old forest stands that represent almost climax forest community, breeding bird assemblages have hardly ever changed during the past 40 years (Wesołowski et al. 2015). The research plots established in the Borki Forest comprised mature stands, however, younger than those in the BNP; therefore, the succession rate was comparatively faster and this was probably the reason for the increase in species number and breeding pair density within all the research plots over 20 years. The increase in the population numbers as well as increased percentage shares of birds associated with natural forests, such as those nesting in tree hollows, that is, black woodpecker (*Dryocopus martius*), white-backed woodpecker (*Dendrocopos leucotos*), collared flycatcher and stock dove (*Columba oenas*), and at the same time, the occurrence of rare and valuable species such as three-toed woodpecker and owls (Eurasian pygmy owl, boreal owl) can be certainly linked to ageing forest stands and deadwood abundance. The occurrence of wetland bird species (mallard, common goldeneye, goosander) deep in the forest is attributable to the beavers activities who built dames that caused the formation of one small water reservoir within the area Ł and several of these in the neighbourhood of other research plots. Furthermore, beaver activities added to the deadwood formation (dead tree trunks, standing dead trees in flooded forest areas), which resulted in increase in the population numbers of bird species associated with deadwood, above all – woodpeckers. Similar effects of beaver activity were recorded in other countries (Janiszewski et al. 2014).

The second major factor that influenced the increase in the number of species of breeding birds as well as their population numbers in the Borki Forest was forest management, particularly group felling performed within the research plot BM and on the border of G research plot. Timber harvesting resulted in opening forest edges and formation of open areas

with natural regeneration. This encouraged the occurrence of willow warblers (*Phylloscopus trochilus*) who avoid mature stands with closed canopy, which is a species absent in old-growth stands in the BNP (Wesołowski et al. 2015). Owing to the forest management practices, the occurrence or increased population numbers of bird species atypical for inside forest areas, such as yellowhammer (*Emberiza citrinella*), tree pipit (*Anthus trivialis*), common whitethroat (*Sylvia communis*), garden warbler (*Sylvia borin*), common rosefinch, red-backed shrike, common swift, icterine warbler and white wagtail, who represent the species associated with open and semi-open ecotone, shrub and synanthropic habitats, was also observed. Similar effects of forest management activities on avifauna were described by Brazaitis and Kurlavičius (2003) as well as Pepłowska-Marczak (2009, 2011). It seems that enlargement of forest roads in the Borki Forest could also affect bird populations, as the roads constituted specific corridors enabling non-typical forest species penetration of interior forest parts. Another factor that could possibly add to the increase in breeding pairs density was the so-called edge effect, that is, when compared to the forest interior parts, higher breeding pair density is observed in the forest edge zone – approximately 200-m-wide strip bordering with the forest edge (Cieślak 1992). In the Borki Forest, group felling led to the formation of the edge zones inside forest complex .

The results of the present study can be compared with those of similar long-term ornithological research conducted in forests situated in other Poland's regions. The longest lasting over 40 years and still continued investigation of breeding birds community dynamics have been conducted in the Białowieża Primeval Forest (BNP). The so far results have proved substantial stability of forest avifauna. Regardless of the forest community type, during 40 years, both the species composition and the number of breeding species have remained unchanged. Also, the density of breeding pairs has changed only slightly, even though some fluctuations have been noted (Wesołowski et al. 2015). The observed stability of avifauna reflects the stability of habitats in the BPN that represent nearly climax forest communities, isolated from anthropogenic impact (strict protection).

The study carried out by Jermaczek (2010) in old alder-ash forest in the Kręcki Łęg nature reserve located in Lubusz Land (western Poland) showed that over 28 years, the number of breeding species was not changed, whereas avifauna species composition changed and breeding pair density decreased by 20–40%. These changes were interpreted as a response of avifauna to transformation of the forest structure because of succession. In the urban nature reserve Las Bielański (Warsaw), Luniak (1991) and Mazgajski et al. (2001) showed that over more than a dozen years, the number of bird species did not change; however, the density of breeding pairs significantly increased.

All the aforesaid studies were carried out in protected forests. The results of long-term studies in managed forests such as the Borki Forest have been hardly available. There exist some publications on the impact of forest management (e.g. tree felling) on forest bird populations. The effect of group cutting on birds was analysed by Brazaitis and Kurlavičius (2003) as well as Pepłowska-Marczak (2009, 2011). These authors showed that in general, within forest areas with artificial gaps because of group felling, there increased the number of breeding bird species. After tree felling, next to bird species characteristic for forest interior parts, there start to occur bird species that avoid tree stands with high canopy density (associated with ecotone zones and semi-open wooded areas). This mechanism resembles the influence of natural treefall gaps in mature forest stands on the distributions of breeding birds (Fuller 2000).

6. Conclusions

Notwithstanding the forest plant community type, mature deciduous and mixed stands situated in the central part of the Borki Forest are inhabited generally by one bird assemblage, which is a result of mosaic patterns of forest habitats connected with diversified terrain relief as well as species diversity in tree stands of this forest complex.

Over 20 years, considerable changes in avifauna of old tree stands in the Borki Forest occurred as a consequence of transformation of forest habitats. The major reasons behind the transformation were the ongoing natural processes in tree stands associated with tree ageing and forest succession as well as forest management activities. Both these factors caused an enhancement of spatial and qualitative diversification of bird habitats within the research plots and their neighbourhood, followed by the development of the carrying capacity of these habitats. Consequently, a considerable increase in the number of breeding species as well as the density of breeding pairs was observed.

Owing to stand ageing, the number of bird species and number of populations of birds associated with natural forests and deadwood (especially birds nesting in tree hollows) were increased. Forest management activities carried out deep inside the forest caused occurrence or increased populations of bird species atypical for forest interior areas, that is, species associated with open or semi-open areas, ecotone habitats and synanthropic birds, for example, yellowhammer, red-backed shrike, common rosefinch, garden warbler, common whitethroat, common swift and white wagtail. Beaver activities caused the occurrence of wetland species (e.g. goldeneye, goosander and mallard) in the interior parts of the Borki Forest.

The increase in the total density of breeding pairs in the Borki Forest was the effect of the increased number of nesting bird species as well as increased populations of the majority of these species. Population numbers of blackcap, hawfinch, song thrush, common blackbird and collared flycather increased comparatively the most. An additional factor that increased bird population density was probably the so-called edge effect, which in all probability caused the increase in the breeding pairs density in the forest edge zone created by group felling within the investigated plots or in their vicinity.

Conflict of interest

The authors declare no conflict of interest

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Source materials

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Authors' contribution

G.R. – study conception, designation of research plots, preparation of study results, paper writing and editing; K.C. – field observations, preparation of the results; J.U. – statistical analyses, text editing.

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