SPRUCE- AND BEECH-DOMINATED PRIMARY FORESTS IN THE WESTERN CARPATHIANS DIFFER IN TERMS OF FOREST STRUCTURE AND BIRD ASSEMBLAGES, INDEPENDENTLY OF DISTURBANCE REGIMES

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ABSTRACT

Mountain spruce- and beech-dominated forests (SDPF and BDPF) are of major importance in temperate Europe. However, information on the differences between their historical disturbance regimes, structures, and biodiversity is still incomplete. To address this knowledge gap, we established 118 circular research plots across 18 primary forest stands. We analysed the disturbance history of the last 250 years by dendrochronological methods and calculated disturbance frequency, severity, and timing. We also measured forest structure (DBH, tree density, volume of deadwood, and other parameters). Breeding bird populations were examined by point count method during the spring seasons 2017–2018 (SDPF) and 2019–2020 (BDPF). Using direct ordination analysis, we compared the disturbance history, structure and bird assemblage in both forest types. While no differences were found regarding disturbance regimes between forest types, forest structure and bird assemblages were significantly different. SDPF had a significantly higher density of cavities and higher canopy openness, while higher tree species richness and more intense regeneration was found in BDPF. Bird assemblage showed higher species richness in BDPF, but lower total abundance. Most bird species which occurred in both forest types were more numerous in spruce-dominated forests, but more species occurred exclusively in BDPF. Further, some SDPF- preferring species were found in naturally disturbed patches in BDPF. We conclude that although natural disturbances are important drivers of primary forest structures, differences in the bird assemblages in the explored primary forest types were largely independent of disturbance regimes.

Keywords: beech; birds; Carpathian Mountains; disturbance history; forest structure; mountain temperate forests; spruce

Introduction

The Central European mountain landscape has been naturally covered mostly by forest since the last Ice Age (Vera 2000; Szabó et al. 2016). The species composition of these forests changes along an altitudinal gradient. In medium elevations (500–1,200 m a. s. l.), the forest was originally a mixture of many species, but mostly dominated by beech (*Fagus sylvatica*). At the highest altitudes, near the upper treeline (1,200–1,600 m a. s. l.), forests are naturally dominated by spruce (Mirek 2013; Čada et al. 2020). However, due to the long history of human settlement, most of the Central European forests have been subjected to more or less intensive use (Mikoláš et al. 2019). Therefore, only fragments of original forest remain in the most inaccessible and remote parts of the Western Carpathian mountains, which account for less than ~10,600 ha (0.5%) of Slovakian forests (Jasík and Polák 2011; Mikoláš et al. 2019).

In comparison with managed forests, primary forests are shaped exclusively by natural processes, mainly natural disturbances (Pickett and White 1985; FAO 2020; Vandekerkhove et al. 2022). In the Central European mountain primary forests, the main disturbance agents are windstorms, bark beetles (most importantly *Ips typographus* and to a smaller extent other insect species), amongst other factors including avalanches, ice storms and large herbivores (Nagel et al. 2013; Kulakowski et al. 2017; Synek et al. 2020). Disturbances predominantly affect forest ecosystems by creating patches of dead trees varying in spatial extent and severity (Pickett and White 1985; Čada et al. 2020). In contrast with managed forests, dead trees and their components remain in unmanaged forest as disturbance legacies (Seidl et al. 2014), contribute to the total carbon pool (Commarmot et al. 2005; Glatthorn et al. 2018), help facilitate regeneration after disturbance (Zielonka 2006; Michalová et al. 2017), whilst also providing important structural elements for biodiversity (Stokland et al. 2012; Thorn et al. 2017; Kozák et al. 2020).

The recent development of dendrochronological methods has allowed our scientific understanding of the long-term dynamics of Central European mountain primary forests to increase rapidly (e.g. Svoboda et al. 2014;

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Trotsiuk et al. 2014; Janda et al. 2017; Schurman et al. 2018; Čada et al. 2020; Frankovič et al. 2021). However, large knowledge gaps remain. Although BDPF and SDPF naturally occur next to each other and their disturbance regimes can both be described as mixed-severity/mixed-scale, the regimes differ to some extent (Nagel et al. 2013). Both forest types are shaped by wind, but in BDPF wind disturbances are mostly unsynchronised over large landscapes (Frankovič et al. 2021). This typically leads to structurally rich forests with patches of all developmental stages represented in small areas (Korpeľ 1989; Orman and Dobrowolska 2017). Conversely, SDPF are mainly shaped by medium-scale and medium-severity events (Čada et al. 2020). Synchronised severe disturbances, which are typically initiated by wind and secondarily enhanced by bark beetles, also occur regularly (Wermelinger 2004; Seidl et al. 2016). However, there is emerging evidence that medium- to high-severity and scale disturbances were also historically a part of BDPF disturbance regimes, although to a much lower extent than in SDPF (Frankovič et al. 2021). The diversity of disturbance regimes has differing effects on forest structure, which thereby has divergent effects on habitat availability for different taxonomic groups of species, thereby altering biological assemblages (Kozák et al. 2020; Langbehn et al. 2021; Ferenčík et al. 2022). Therefore, disentangling the impacts of disturbances across different forest types is crucial in these times of rapid biodiversity decline.

Birds (Aves) are an ecologically important taxonomic group (Sekercioglu et al. 2004; Whelan et al. 2015), which have various demands on forest structure for nesting, foraging and other activities (Brawn et al. 2001; Hanzelka and Reif 2016). They are also important from the nature conservation perspective as umbrella species (Mikoláš et al. 2017), flagship species (Kortmann et al. 2018) and indicator species (Braunisch et al. 2019). Bird assemblages of BDPF and SDPF differ to some extent, but only a minor number of species are strictly tied to one of them (Korňan 2004; Wesolowski et al. 2018; Kameniar et al. 2021). Generalist species such as chaffinch and European robin reach comparable abundances in both forest types (Saniga and Saniga 2004; Saniga 2009), but most species typically show a stronger or weaker preference to one of them (Wesołowski et al. 2003; Tomiałojć and Wesołowski 2004). Numerous studies on bird assemblages have been conducted in European mountain temperate beech- and spruce-dominated forests, but they largely focused on forests with a human-altered disturbance regime, structure and biodiversity (Moning and Müller 2008; Topercer et al. 2009; Baláž and Kocian 2015; Birčák and Reif 2015), or they explored only one or several primary forest fragments (Korňan 2004; Saniga and Saniga 2004; Saniga 2009). Moreover, most studies which focused on primary forests did not examine disturbance history and forest structure in detail. Although the study by Kameniar et al. (2021) explored the disturbance-structure-bird assemblage relationship in SDPF in the Western Carpathians, studies investigating BDPF remain absent.

Primary forest structure is directly created or influenced exclusively by natural disturbances (Rodrigo et al. 2022). Several structural features have been identified as important for bird assemblage diversity and abundance, including the amount of coarse woody debris (Rosenvald et al. 2011) and its subtypes, especially standing dead trees (a key habitat for woodpeckers (Pechacek and d'Oleire-Oltmanns 2004)), and uprooted trees, which are used by several species for nesting (Wojton and Pitucha 2020). Other important structural characteristics for forest birds have also been identified, such as large habitat trees (Kebrle et al. 2021), age of forest stand (Poulsen 2002), richness of vertical canopy structure (Goetz et al. 2007), canopy openness (Lewandowski et al. 2021), overall stand-level heterogeneity (Kebrle et al. 2022) and the presence of various microhabitats, especially cavities (Piechnik et al. 2022). These structural features change across several time and space scales, and their actual values depend on the given disturbance agent (or their combinations), disturbance severity, spatial extent, and timing (Mikoláš et al. 2017; Kameniar et al. 2021). However, it is still unclear how they differ in BDPF and SDPF in Central Europe.

In this study, our specific aims are: 1. to compare important structural variables for birds in BDPF and SDPF; 2. to compare bird assemblages between both forest types.

Material and Methods

Study area, stand selection and study plots establishment

Our study was conducted in the Western Carpathian Mountains (Slovakia), between 48.632749° and 49.523229° N and between 19.010233° and 20.118049° E, elevation of our research plots was between 769 and 1,534 m. Research plots were located inside primary forest remnants recognised by the national inventory of primary forests in Slovakia (Jasík and Polák 2011; Mikoláš et al. 2019). During inventory, all potential primary forest areas were visually surveyed for structural elements, typical for primary forests. Localities with signs of human alteration were excluded. Selected stands of potential primary forests were also checked on historical maps and aerial imagery, whether the selected area was covered with forest during that period. For details, see Mikoláš et al. (2019).

Eighteen study stands were distributed in seven mountain ranges with the largest areas of BDPF and SDPF – the Tatra Mts. (four spruce stands), the Low Tatra Mts. (two spruce stands), the Great Fatra Mts. (two spruce and four beech stands), Low Fatra Mts. (two beech stands), the Poľana Mts. (single spruce and single beech stand), Vepor Mts. (a single beech stand) and the Orava Beskids (a single spruce stand). Most of the SDPF stands are located on intrusive and metamorphic, acidic bedrock, and beech-dominated stands were very heterogeneous. Location of stands is displayed in Fig. 1.

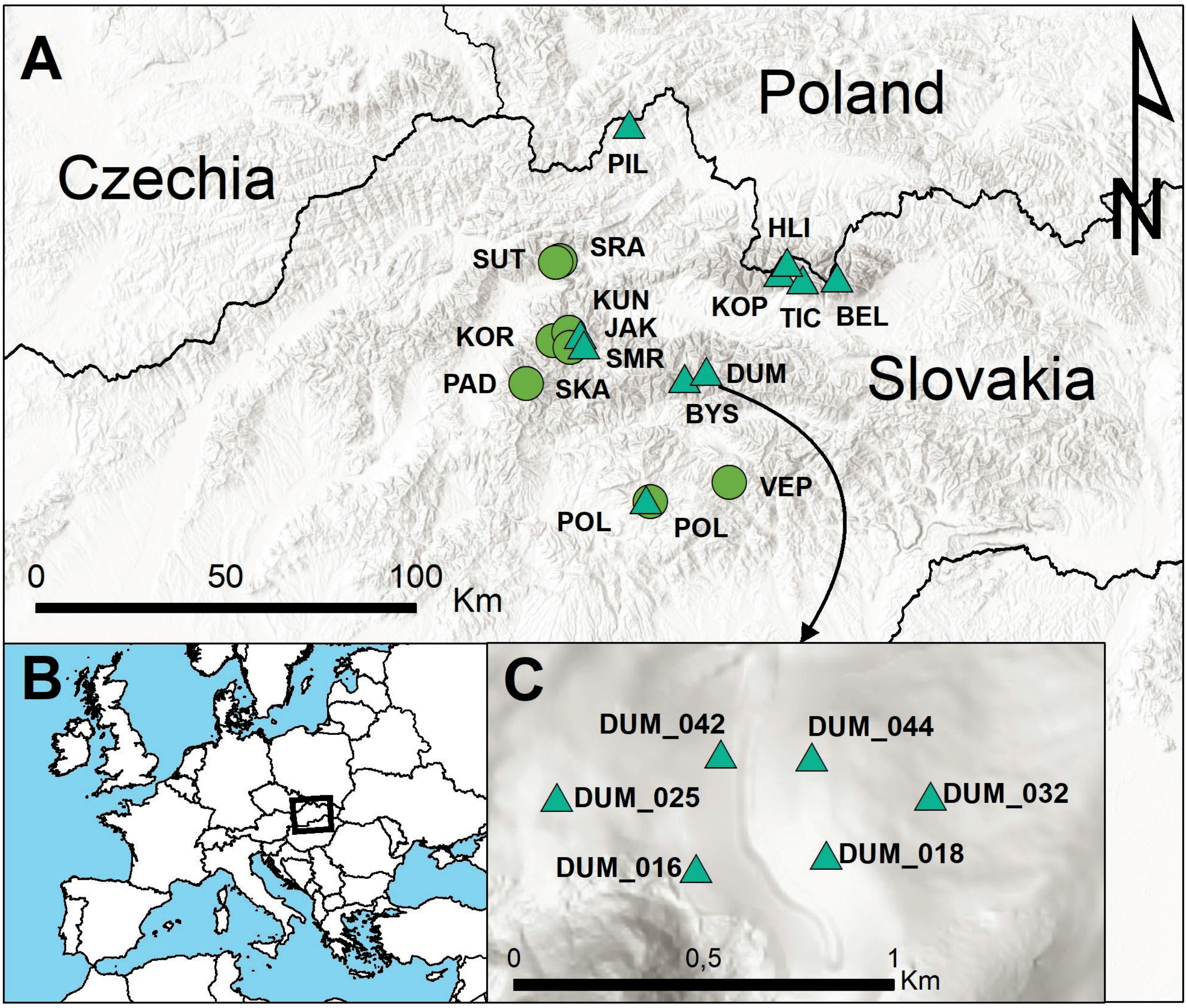

Fig. 1 a) research stands location in Western Carpathians – triangles represent spruce-dominated stands and circles beech-dominated research stands b) location of Western Carpathians in Europe, c) example of research stand with study plots. Spruce-dominated primary forest stands: BEL (Bielovodská valley, High Tatra Mts.), TIC (Tichá valley, High Tatra Mts.), HLI (Hlina, High Tatra Mts.), KOP (Kôprová valley, High Tatra Mts.), PIL (Piľsko, Orava Beskydy), JAK (Jánošíkova kolkáreň, Great Fatra Mts.), SMR (Smrekovica, Great Fatra Mts.), DUM (Ďumbier, Low Tatra Mts.), BYS (Bystrá valley, Low Tatra Mts.), POL (Mt. Poľana). Beech-dominated primary forest stands: POL (Mt. Poľana), VEP (Vepor, Vepor Mts.), SKA (Skalná alpa, Great Fatra Mts.), KUN (Kundráčka, Large Fatra Mts.), KOR (Kornietová, Great Fatra Mts.), PAD (Padva, Great Fatra Mts.), SUT (Šútovská valley, Low Fatra Mts.), SRA (Šrámková, Low Fatra Mts.).

Size of the sites studied (primary forest fragments) varied from 41 to 494 ha. In the case of the smallest fragments, several were treated as one stand. They were surrounded mostly by forests of differing naturalness: natural forests with or without recent management or intensively managed, less natural forests. Some parts are bordering with unnatural spruce plantations, salvage-logged areas, and alpine habitats. However, these environmental variables were not quantified in this study.

Tree species composition in the SDPF was strongly dominated by Norway spruce (over 90%). Other species, such as rowan (*Sorbus aucuparia* L.), fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.), larch (*Larix decidua* Mill.), pine (*Pinus* spp.) and birch (*Betula* spp.), were present only as an admixture (Janda et al. 2017). Except of beech, BDPF stands contained highly variable proportion of other tree species, mainly fir, spruce and maple, but also Norway maple (*Acer platanoides*), ash (*Fraxinus excelsior* L.), wych elm (*Ulmus glabra* Huds.), European hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.) and other species. Annual mean temperatures range from 1.6 to 3.4 °C in SDPF stands and from 5 to 5.5 in BDPF stands, annual precipitation varies from 1,205 to 1,365 mm in SDPF (Kozák et al. 2020) and around 1,067 mm in BDPF stands (Harris et al. 2020).

In the above mentioned 18 stands, 242 plots (97 in BDPF and 145 in SDPF) were established as part of an international primary forest research project (www.remoteforests.org). To position plot centres, a square grid was created using the ArcView 9.3 Environment (ESRI ArcGIS 2011) for each stand, and plot centres were placed using a stratified-random design (Svoboda et al. 2014; Frankovič et al. 2021). Within the inner part of each cell, three random points were generated. If the first point was unsuitable (e.g., rocks, water, steepness), then a second (or rarely a third) randomly generated point was used. In BDPF stands, a pair of circular plots (radius of 17.84 m) was positioned along the contour, one on each side of the identified random point. Paired plot centres were 40 m from the random point and 80 m from each other. Study plots in SDPF (radius of 12.62 or 17.84 m, depending on the stand density) were established directly on randomly generated points.

For bird assemblage and forest structure sampling, 58 plots were selected in SDPF stands (six plots per stand, except for one stand in the Tatra Mts. containing only four plots) and 60 plots in BDPF stands. In each stand, study plots were selected to cover the whole gradient of disturbance severities over the last 250 years. For this purpose, we split plots according to disturbance event timing into three equally large classes. We then selected two plots within each class on every stand, with differing severity if available. At the same time, we avoided locating any additional plots within 150 m around a given plot to minimise multiple counts of individual birds at different plots.

Forest structure data

Forest structural parameters were measured in 2017 in all spruce plots and in 2020–2021 in beech plots. For each plot, the GPS position was recorded. All live and dead trees with a diameter at breast height (DBH) ≥ 6 cm were numbered and DBH was measured using a measuring tape. The trees were also precisely mapped using laser rangefinders and customised software (Field-Map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic). Canopy position of each tree was assessed (suppressed: trees with crowns below the general canopy layer and receiving mostly diffuse light and released: trees with crowns forming part of the canopy layer and receiving at least 50% of full light). The diameter of horizontal crown projection was measured with an ultrasound device for a sample of trees to establish statistical relationships between crown area and DBH, which was later used to estimate the percentage disturbance of the canopy.

Species of trees and growth layer (upper, lower) were also recorded. Lying deadwood with a thickness greater than 10 cm was measured using above mentioned Field-Map technology. Both ends were mapped with a laser and the diameter measured using a sliding scale. Average stage of decay (1–5) and species was also recorded for every piece (Stokland et al. 2012). Height of standing deadwood with DBH over 6 cm was estimated as either 0–10 m, 10–20 m or 20–30 m. Subsequently, the volume of deadwood (standing and lying) was calculated. Mean canopy openness was calculated using hemispherical photographs taken at six locations in each plot. They were processed and analysed using image processing software (WinSCANOPY; Regent Instruments, Ste-Foy, Quebec, Canada). Individual pixels were classified as either sky- or leaf-dominated classes based on their spectral properties. Pixel classification results were aggregated to determine the overall mean fraction made up of sky. Number of regenerating trees was counted at the plot-level in three height categories: 0.5–1.3 m; 1.3–2.5 m and > 2.5 m, (at the same time, with DBH < 6 cm.

Age structure and disturbance history

For reconstructing the history of disturbance and estimating the age of the trees, increment cores were extracted from living trees at 1 m height from the base, perpendicular to the direction of the slope. In spruce plots, 15 or 25 (depending on the radius of the plot, 12.62 or 17.84 m) randomly selected trees with DBH ≥ 10 cm and canopy status classified as currently released were sampled. If there were not enough trees on a plot, the closest trees outside the plot were selected, and rotten trees were replaced by a nearby tree with a similar DBH in order to obtain the required sample size. An additional five randomly selected suppressed trees were cored to establish a growth-rate threshold for open canopy recruitment. In BDPF plots, a subplot with a radius of 7.99 m was established at the centre, where all trees (released and suppressed) with DBH ≥ 10 cm were sampled. In mixed beech-dominated plots, a subplot with a radius of 7.99 m was established at the centre, where all trees (released and suppressed) with DBH ≥ 10 cm were sampled. On the remaining part of the plot all released trees with DBH ≥ 10 cm and all suppressed trees with DBH ≥ 15 cm were cored, in addition to three randomly selected suppressed trees with DBHs between 10 and 15 cm. Further, 12 regularly distributed points were established outside the plot within a radius of 25.23 m from the centre of the plot and at each point the closest released tree with DBH ≥ 10 cm was sampled. The study plots were established as a part of the REMOTE Primary Forests network and the differences in sampling are due to the evolving needs of this long-term project.

Cores were processed using standard dendrochronological techniques and ring-width series were measured using a stereomicroscope and a LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany, http://www.rinntech.com). Cross dating was done using the marker years approach (Yamaguchi 1991) and verified with PAST4 (www.sciem.com), CDendro (Holmes 1983; Larsson 2003), and COFECHA (Holmes 1983) software. For core samples that missed the pith, the number of missing rings was estimated using the method of Duncan (1989). The total number of cores processed was 5,740 (2,284 from BDPF, 3,456 from SDPF); cores that could not be properly cross dated (rotten, damaged) were not included in the analysis, resulting in 5,092 valid samples (1,803 from BDPF and 3,289 from SDPF).

In the next step, radial growth patterns were analysed in order to identify two types of tree canopy accession events: (1) release – abrupt, sustained increase in tree growth, indicating the death of a former canopy tree, and (2) open canopy recruitment – rapid juvenile growth indicating recruitment in a former canopy gap (Lorimer and Frelich 1989). Releases from suppression were identified using the absolute increase method (Fraver and White 2005) as pulses in which the difference between average growth rates of adjacent 10-year running intervals (absolute increase) was greater than or equal to 1.25 standard deviations of all the calculated absolute increase values. To avoid false detection, when mean growth rates are largely influenced by several extreme years, increases had to be sustained for at least seven years to be considered a release event (Fraver et al. 2009). Variables characterising the age structure and disturbance history covering the last 250 years of individual plots were used to describe the disturbance histories. The reconstructed disturbance chronologies were limited to 250 years (1750–2000) to avoid potential bias due to the small number of trees sampled that were older than 250 years. Estimates of disturbance recorded after the year 2000 were not included, as the sample size was too small, which resulted in the exclusion of more recent tree recruitment.

Bird assemblages

Data on species composition of breeding bird assemblages were collected for plots from the end of April until the end of June, i.e., during the peak breeding season. Each plot was visited three times per season on average, SDPF plots in 2017 and 2018 and BDPF plots in 2019 and 2020. Some plots were visited less often due to bad weather. Point counts were used as a field technique with a census point located in the centre of each plot (Verner 1985). During each visit to the plots, all birds within an estimated distance of 60 m from the observer were counted and recorded for 10 minutes. All birds were recorded regardless of age and sex, but most records were based on bird song, particularly that of males defending their territory. After arrival at a given plot, one minute was spent silently before counting started to minimise the observer's influence on bird activity (Sutherland 2006). Counts were done early in the morning (5:00 – 10:00 AM), and only during optimal weather conditions without heavy rain and strong wind (Moning and Müller 2008). Birds recorded during all counts were summarised per plot and then standardised to account for unequal number of counts (Table 3). In the analysis we used species presence/absence data. Species numbers in BDPF and SDPF were not corrected for different sampling intensity as it was very high and almost identical (324 plot counts in BDPF vs. 329 plot counts in SDPF). At the same time, the number of species (53) was relatively low compared to the number of counts and recorded bird individuals (4,745).

Statistical analysis

An ordination analysis was used to target the aims. Redundancy analysis, RDA (Rao 1964), of the correlation matrix of structural characteristics was used to compare structural variables important for birds and disturbance characteristics in BDPF and SDPF (Fig. 2). Finally, distance-based redundancy analysis, db-RDA (Legendre and Anderson 1999), was used to test for differences in the composition of bird assemblages in the two types of forest (Fig. 3). Rarely observed species of birds (frequency of occurrence < 3 plots) were excluded from the datasets to improve the signal-to-noise ratio. Species presence/absence data were converted to Sørensen dissimilarities (1-Sørensen similarity), which disregards double absences and gives higher weight to shared occurrences (Sørensen 1948). The dissimilarity matrix was submitted to db-RDA and the differences between SDPF and BDPF were tested using randomization tests. Since the data were collected in a hierarchical design (plots nested within stands), we performed a spatially restricted randomization scheme (Anderson and ter Braak 2003) where no randomization was performed at the plot level, but the whole stands were freely reshuffled 10,000 times. The ordination analyses were performed in R v. 4.1.2 (R Core Team 2021) and the library vegan (Oksanen et al. 2019).

Table 1 All analysed structural variables with their description.

structural variable	description	units
missing_bark	number of trees with bare wood patches with bark loss and wood in a decay stage of less than 2	number
n_trees_dead_500	density of the large dead trees (DBH ≥ 500 mm, height > 1.3 m) per hectare	number of stems per hectare
volume_dead_total	amount of lying and standing deadwood	m^3/ha
openness_mean	mean openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY	% of canopy area
volume_dead_lying	volume of lying deadwood with thickness on thinner end ≥ 100 mm	m^3/ha
n_trees_live_500	density of the large living trees (DBH ≥ 500 mm) per hectare	number of stems per hectare
n_trees_ha	density of the living trees (DBH ≥ 60 mm) per hectare	number of stems per hectare
dbh_mean_live_60	mean diameter of the living trees (DBH ≥ 60 mm)	mm
age_5oldest	age of 5 oldest living trees (DBH ≥ 60 mm)	years

structural variable	description	units
age_median	median age of living trees (DBH ≥ 60 mm)	years
age_mean	mean age of living trees (DBH ≥ 60 mm)	years
regeneration_250_100	density of the regeneration (height > 250 cm, DBH < 100 mm) per hectare based on the data of the plot	number of stems per hectare
regeneration_130_250	density of the regeneration (130–250 cm height) per hectare based on the data of the plot	number of stems per hectare
regeneration_50_130	density of the regeneration (50–130 cm height) per hectare based on the data of the plot	number of stems per hectare

Results

Structure in beech- and spruce-dominated primary forests

The redundancy analysis revealed that the structure of BDPF is significantly different from that of SDPF (*pseudo-F* = 15.1, *p* < 0.0001, Fig. 2). SDPF have a significantly higher density of cavities and higher canopy openness, whereas in BDPF there is a higher tree species richness and more regeneration (Fig. 2). Tree density and age characteristics were comparable in the two types of forest. The research plots were selected to cover the whole disturbance gradient to filter out the differences in disturbance regimes and redundancy analysis showed that there are no significant differences in disturbance characteristics between our plot selection in BDPF and SDPF (*pseudo-F* = 1.8, *p* = 0.127, Fig. 2).

There were higher amounts of deadwood in SDPF (293.8 m^3 ha^{-1} on average, stand level averages 144.8–628.3 m^3 ha^{-1}), plot-level values varied between 71–978 m^3 ha^{-1}. In BDPF it was 169.3 m^3 ha^{-1} on average (stand level averages 92.2–254.4 m^3 ha^{-1}, plot-level volumes between 12–628 m^3 ha^{-1}). Average stand-level canopy openness was 4.4% in BDPF (stand averages between 2.4–6.2%, plot level values between 1.0–24.9%) and 14.4% in SDPF (stand level averages 9.6–21.0%, plot level values between 2.9–50.5%). Number of trees per hectare was higher in BDPF, with an average at stand level of 480, compared to 385 in SDPF (for details, see Table 2).

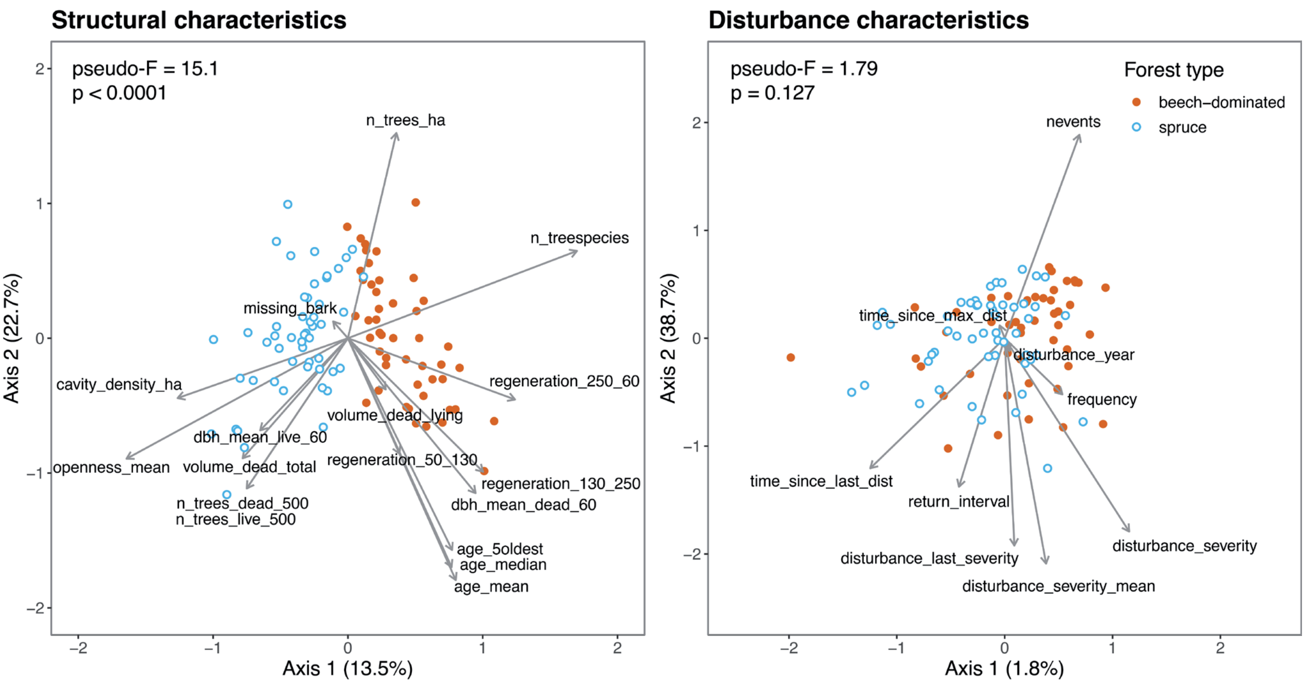

Fig. 2 Results of RDAs testing for differences between BDPF and SDPF in structural and disturbance characteristics. Ordination diagrams show scores of sampling plots (empty circles – spruce plots, full circles – beech plots) and vectors of environmental variables (arrows). The proportion of variance explained by the ordination axes is given in parentheses. The ordination plots are scaled symmetrically. Description of variables is in Table 1.

Table 2 Selected structural parameters averaged at stand level.

Stand	Forest type	Elevation (m a.s.l.)	Age mean (years)	Mean canopy openness (% of canopy cover)	Total volume of deadwood [m³/ha]	Number of dead trees with DBH over 500 mm per ha	Number of trees per ha	Number of tree species
BEL	spruce	1361	162.0	17.6	628.3	63.3	293	1.5
BYS	spruce	1416	168.3	21.0	326.5	30.0	315	1.8
DUM	spruce	1497	158.3	11.7	144.8	13.3	383	1.8
HLI	spruce	1421	129.5	13.8	285.0	40.0	460	1.3
JAK	spruce	1307	128.4	15.9	150.8	4.0	312	1.6
KOP	spruce	1409	107.2	10.9	404.0	23.3	938	2.7
KOR	beech	1117	192.9	3.6	177.3	11.6	524	3.7
KUN	beech	1091	231.0	5.7	207.0	12.4	295	3.9
PAD	beech	1161	178.2	6.2	138.3	4.5	430	3.7
PIL	spruce	1330	186.2	12.5	200.3	15.0	263	1.0
POL	beech	1144	139.8	2.4	206.6	9.4	559	4.2
POL	spruce	1377	127.5	9.6	260.3	15.0	333	2.5
SKA	beech	1165	191.9	4.7	254.4	18.4	388	2.6
SMR	spruce	1383	135.0	14.0	233.5	20.0	210	1.8
SRA	beech	1050	104.7	5.6	161.9	7.7	751	3.7
SUT	beech	1054	153.7	3.8	92.2	10.0	565	3.0
TIC	spruce	1420	112.0	17.2	304.0	38.3	338	1.5
VEP	beech	1197	149.4	3.5	116.9	7.7	323	4.1

Bird assemblage in beech- and spruce-dominated forests

In total, 4,745 birds belonging to 53 species, were recorded, 45 species in BDPF (beech-) and 37 in SDPF (spruce-dominated primary forests). When accounting for differences in sampling effort, 17.3% fewer individuals were recorded in BDPF. 29 (53.7% of all species) occurred in both types of forest, but 17 of them were more numerous in SDPF. 24 species were recorded only in one of the two types of forest, with 16 in BDPF and 8 in SDPF. Species with dominance over 5% accounted for 60% of the total number of individuals in BDPF (6 species) and 74% in SDPF (8 species).

The composition of the bird assemblages in BDPF was significantly different from that in SDPF (*pseudo-F* = 17.6, p < 0.0001). Crested tit (*Lophophanes cristatus* (Linnaeus, 1758)), three-toed woodpecker (*Picoides tridactylus* (Linnaeus, 1758)), dunnock *Prunella modularis* (Linnaeus, 1758)), Eurasian bullfinch (*Pyrrhula pyrrhula* (Linnaeus, 1758)), ring ouzel (*Turdus torquatus* (Linnaeus, 1758)) and Eurasian siskin (*Carduelis spinus* (Linnaeus, 1758)) were indicative for SDPF. Collared flycatcher (*Ficedula albicollis* (Temminck, 1815)), white-backed woodpecker (*Dendrocopos leucotos* (Bechstein 1802)), wood warbler (*Phylloscopus sibilatrix* (Bechstein, 1793)) and great tit (*Parus major* (Linnaeus, 1758)) and mistle thrush (*Turdus viscivorus* (Linnaeus, 1758)) were typical for BDPF (Fig. 3). The chaffinch (*Fringilla coelebs* Linnaeus, 1758) and European robin (*Erithacus rubecula* (Linnaeus, 1758)) were the most abundant species in both types of forest, other abundant common species were coal tit (*Periparus ater* (Linnaeus, 1758)), Eurasian blackcap (*Sylvia atricapilla* (Linnaeus, 1758)) and Eurasian wren (*Troglodytes troglodytes* (Linnaeus, 1758). For a complete list of the species recorded in BDPF and SDPF with dominances see Table 3.

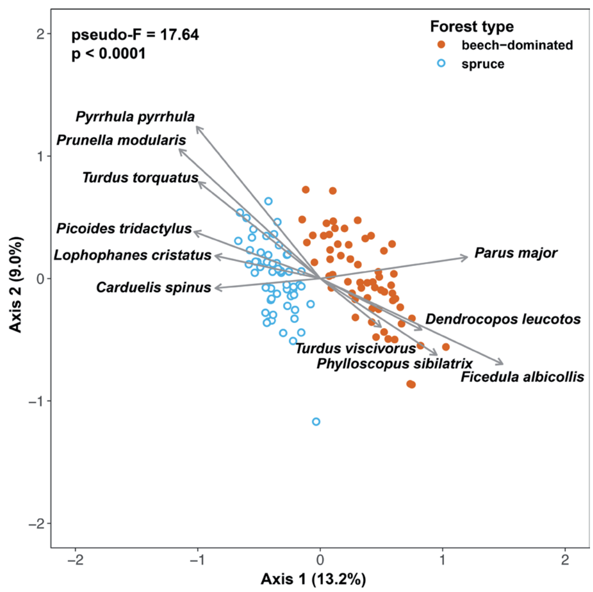

Fig. 3 Results of db-RDAs testing for differences in the composition of species of birds in BDPF and SDPF. Ordination diagrams show scores for the plots sampled (dots) and species vectors (arrows). Only species with a good fit to the ordination (|r| > 0.4) are displayed. The percentage of variance explained by the ordination axes is given in parentheses. The ordination plots are scaled symmetrically.

Several less numerous birds were recorded, which are of conservation concern in the Carpathians. In SPDF it was the three-toed woodpecker, capercaillie (*Tetrao urogallus* Linnaeus, 1758), Eurasian pygmy owl (*Glaucidium passerinum* (Linnaeus 1758)), boreal owl (*Aegolius funereus* (Linnaeus 1758)), golden eagle (*Aquila chrysaetos* (Linnaeus 1758)) and black woodpecker (*Dryocopus martius* (Linnaeus 1758)). In BDPF it was the Ural owl (*Strix uralensis*), peregrine falcon (*Falco peregrinus* Tunstall, 1771) and red-breasted flycatcher (*Ficedula parva* (Bechstein, 1792)).

Table 3 Differences in recorded bird assemblage species. Number of individuals in SDPF and BDPF were adjusted to account for different sampling efforts.

	Total abundance		Dominance	
species	beech	spruce	beech	spruce
Accipiter nisus	1	0	0.0	0.0
Aegithalos caudatus	2	0	0.1	0.0
Aegolius funereus	0	2	0.0	0.1
Anthus trivialis	2	6	0.1	0.2
Aquila chrysaetos	0	1	0.0	0.0
Bonasa bonasia	3	14	0.1	0.5
Buteo buteo	0	4	0.0	0.2
Carduelis spinus	1	27	0.0	1.0
Certhia familiaris	96	108	4.6	4.1
Coccothraustes coccothraustes	13	1	0.6	0.0
Columba oenas	14	0	0.7	0.0
Columba palumbus	23	15	1.1	0.6
Corvus corax	1	1	0.0	0.0
Cuculus canorus	2	18	0.1	0.7
Cyanistes caeruleus	3	0	0.1	0.0
Dendrocopos leucotos	26	0	1.2	0.0
Dendrocopos major	18	1	0.9	0.0
Dryocopus martius	4	3	0.2	0.1
Erithacus rubecula	215	257	10.3	9.8
Falco peregrinus	2	0	0.1	0.0
Ficedula albicollis	84	0	4.0	0.0
Ficedula parva	1	0	0.0	0.0
Fringilla coelebs	539	670	25.7	25.6
Garrulus glandarius	9	4	0.4	0.2
Glaucidium passerinum	0	5	0.0	0.2
Lophophanes cristatus	2	32	0.1	1.2
Loxia curvirostra	1	52	0.0	2.0
Muscicapa striata	12	0	0.6	0.0
Nucifraga caryocatactes	0	29	0.0	1.1
Parus major	38	0	1.8	0.0
Periparus ater	131	232	6.2	8.9
Phoenicurus phoenicurus	0	1	0.0	0.0
Phylloscopus collybita	172	155	8.2	5.9
Phylloscopus sibilatrix	42	0	2.0	0.0
Phylloscopus trochilus	43	31	2.1	1.2
Picoides tridactylus	2	43	0.1	1.7
Picus canus	2	0	0.1	0.0
Poecile palustris	3	0	0.1	0.0
Prunella modularis	54	180	2.6	6.9
Pyrrhula pyrrhula	23	71	1.1	2.7
Regulus ignicapilla	46	43	2.2	1.7
Regulus regulus	83	123	4.0	4.7
Scolopax rusticola	0	6	0.0	0.2
Sitta europaea	42	13	2.0	0.5
Strix aluco	1	0	0.0	0.0
Strix uralensis	1	0	0.0	0.0
Sylvia atricapilla	127	116	6.1	4.4
Tetrao urogallus	0	6	0.0	0.2
Troglodytes troglodytes	102	158	4.9	6.0
Turdus merula	68	32	3.2	1.2
Turdus philomelos	65	53	3.1	2.0
Turdus torquatus	8	65	0.4	2.5
Turdus viscivorus	13	0	0.6	0.0

Discussion

In our study, we made the first attempt to compare bird assemblages, forest structure and disturbance regimes across the largest beech- and spruce-dominated primary forest (BDPF and SDPF) remnants in the Western Carpathians in Slovakia. We showed that forest structure and bird assemblages differ significantly, despite similar disturbance regimes.

Forest structure in beech- and spruce-dominated primary forests

Natural disturbances are the main drivers of Carpathian primary forest structure (Mitchell 2013; Kameniar et al. 2021; Rodrigo et al. 2022, Kameniar et al. 2023). Their impact on forest is shaped by climatic conditions, which varies along altitudinal gradients, and by tree species composition. With increasing elevation, exposure to windstorms generally increases (Senf and Seidl 2017), whilst the risk of drought is less probable (Marchand et al. 2023). On the other hand, changes in tree species composition affects the abiotic factors and largely shapes the response to biotic factors. In lower altitudes, forests are generally more resilient to disturbance because they are more diverse in terms of species of trees and forest structures (Walker et al. 2004; Pardos et al. 2021).

Our results indicate that the important bird habitat structures of BDPF and SDPF differ significantly (Fig. 2), even though the design of the study aimed to equally represent the plot level disturbance history categories (see Methods: Study area, stand selection and study plots establishment and Fig. 2). Level of canopy openness is the main structural variable differentiating between BDPF and SDPF (Fig. 2), together with the number of tree species, which shows an opposing trend. Average stand-level canopy openness varied between 9.6–21.0% in SDPF and 2.4–6.2% in BDPF stands. Other studies also report low gap proportions, a variable more frequently used to represent canopy openness in BDPF; 1.2% at a Slovenian locality (Borčina 2000), 2.7 and 4.2% at two primary forest localities in Poland (Orman and Dobrowolska 2017) and 7–8% (or 15–16%, depending on gap characterisation) at two localities in the Slovakian part of the Eastern Carpathians (Drössler and von Lüpke 2005). We are not aware that comparable numbers have been published from SDPF. However, the study by Čada et al. (2020), which analysed the historical disturbance regimes in central European spruce primary forests, indicates that the proportion of stand disturbed varied between 25% and 75% in 69% of the researched area. Janda et al. (2017) found that 89.1% of the studied stands in the Western Carpathians SDPF experienced disturbance (35.6% loss of canopy) between 1840s–1860s. These results imply that canopy openness in this forest type is, on average, considerably higher than in beech forests. Spruce forests generally have a lower tree species diversity than mixed forests, which plays a role in canopy openness, as lower species diversity reduces productivity (Pretzsch et al. 2012).

The age variables did not differ considerably between forest types; BDPF stands were only slightly older (Fig. 2). In general, beech has been proven to be the tree with the longest lifespan among four most common tree species in temperate forests. Fir and maple also reach higher lifespans than spruce (Pavlin et al. 2021).

We found higher amounts of deadwood in SDPF (293.8 m^3 ha^{-1} on average, stand level averages 144.8–628.3 m^3 ha^{-1}) than in BDPF (average 169.3 m^3 ha^{-1}, stand level averages 92.2–254.4 m^3 ha^{-1}). This difference probably results of a higher incidence of disturbance events in SDPF (Synek et al. 2020; Frankovič et al. 2021). Other factors which likely play a role is the significantly longer decomposition time of spruce deadwood in comparison with beech, and colder climate in higher altitudes, which also slows wood decomposition (Weedon et al. 2009). In the primary forests of the Făgăraș Mts. (Southern Carpathians, Romania) the differences in the amounts of deadwood in BDPF and SDPF were smaller; on average it was 145.2 m^3 ha^{-1} (stand-level averages 83–245) in BDPF, and 151 m^3 ha^{-1} (stand-level averages 87–224 m^3 ha^{-1}) in SDPF (Kameniar et al. 2023). The lower total amounts of deadwood recorded in this study can be partly explained by the different methods used to measure lying deadwood. In our study it was measured with greater precision, which yields higher total volumes (see Methods: Forest structure data). The different ratios between BDPF and SDPF in both studies are also probably caused by higher recent mortality of trees in SDPF in the Western Carpathians (Synek et al. 2020).

The results indicate that the incidence of regeneration in BDPF is higher than in SDPF. This is attributed to the different regeneration strategies of the dominant tree species; specifically, spruce regenerate predominantly on downed deadwood (Korpeľ 1989). For example, a study in the Western Carpathians (Zielonka 2006) report that large pieces of deadwood covered only 4% of the forest floor, but it was a substrate for 43% of all seedlings and there is a 20 times higher density of seedlings on deadwood than the mineral soil. In contrast, beech and fir regenerate predominantly on mineral soil, which allow them to use more space. It is also a possible explanation for the slightly higher number of trees per hectare in BDPF. Our results also indicate a significant difference in the density of tree cavities in the two types of forest, with higher densities in spruce than beech forests. The higher cavity density in SDPF can be attributed to the higher number of large dead trees (Fig. 2), which are more likely to have cavities in addition to other microsites (Kozák et al. 2023). The population density of woodpeckers (another cause of tree cavities) is unlikely to play a significant role, as their numbers were similar in both types of forest (48 in SDPF and 50 in BDPF, for details see Table 3).

Bird assemblages in beech and spruce-dominated primary forests

In total, 53 bird species were recorded (Table 3). In SDPF we recorded 37 species, whilst 45 were identified in BDPF stands. These results are comparable to those found in other studies which also explored beech- (Korňan 2004; Saniga and Saniga 2004) and spruce-dominated mountain forests (Ślizowski 1991; Kocian et al. 2005; Saniga 2009; Baláž and Kocian 2015) in the Western Carpathians. Our work adds further evidence that naturally shaped unmanaged spruce forest supports more diverse assemblages than spruce monocultures (Kocian et al. 2005; Bashta 2007; Baláž and Kocian 2015), including rare and threatened species (see Results: Bird assemblage in beech- and spruce-dominated forests).

As the disturbance histories of BDPF and SDPF plots were not significantly different (Fig. 2) whilst the forest structure and bird assemblages' composition differed (Fig. 2 and Fig. 3), it is obvious that other factors than disturbance history are responsible for these differences. In our previous study from SDPF, where we used part of the data presented here (Kameniar et al. 2021) we also found that bird assemblage abundance, species richness and Shannon diversity remained unchanged under variable disturbance histories. However, in a study relating disturbance histories with the data on occurrence of one species, Capercaillie (*Tetrao urogallus*), a significant relationship was found (Mikoláš et al. 2017). The relationships between disturbance history variables and organism assemblages were found in other taxonomic groups such as fungi (Ferenčík et al. 2022), lichens (Langbehn et al. 2021) and saproxylic beetles (Kozák et al. 2020). In our case this relationship was probably distorted by the high mobility of birds and by the impact of recent disturbances which occurred in approximately the last 20 years, which are not detectable by our methods. Recent disturbances (including single tree mortality) are most likely the decisive processes shaping forest structure and therefore indirectly also bird assemblages' composition (Kameniar et al. 2021).

Our results showed that bird assemblages differ in BDPF and SDPF in terms of assemblage composition and diversity; species which constituted the most significant parts of the bird assemblage occurred predominantly in BDPF or SDPF. This difference in bird assemblages between forest types can likely be attributed mainly to the differences in tree species composition: higher tree diversity in broadleaved/mixed forests offer more niches, because of various food sources, nesting and mating opportunities (Willson and Comet 1996; Reif et al. 2008). Part of the difference is also caused by more harsh environmental conditions which are tied to higher elevations – especially lower temperatures, which influence all components and processes of the local ecosystem (Micu et al. 2015).

We also found that in SDPF, although there is higher diversity of birds in lower elevations, their absolute abundance is higher. In addition, a larger part of the species shared between both forest types were more abundant in SDPF. We attribute this pattern to the fact that these species are at least to some extent specialised to spruce and therefore, they reach highest abundances in almost pure spruce forest. It partly matches with the results of Baláž and Balážová (2012). In our case, also additional species were more abundant in spruce-dominated primary forest.

Regarding BDPF and SDPF specialists and their strict avoidance of the second forest type, we also found a difference in assemblage composition between forest types. Specifically, in BDPF, species that shaped the ordination most were collared flycatcher, white-backed woodpecker, wood warbler, mistle thrush and great tit (Fig. 3), which were not recorded in SDPF. This might indicate that structural parameters other than the species composition of the trees, coincide with their habitat requirements. Other studies on SDPF or natural spruce forests also report these species as very rare or absent in this type of forest (Ślizowski 1991; Baláž and Kocian 2015). On the other hand, species typical of SDPF were not specific to this type of forest, as a few individuals also occurred in BDPF. These species are also considered as spruce or coniferous specialists in other studies: the crested tit, dunnock, ring ouzel, Eurasian bullfinch, Eurasian siskin, and three-toed woodpecker (Fuller 1995; Pechacek and d'Oleire-Oltmanns 2004; Braunisch et al. 2014).

This difference in the degree of avoidance of SDPF and BDPF by specialists can be explained by the fact that whereas beech is generally rare in SDPF (Čada et al. 2020; Synek et al. 2020), an admixture of spruce is common in BDPF (Orman and Dobrowolska 2017; Parobeková et al. 2018; Frankovič et al. 2021). In some of the beech plots spruce made up a significant part of the canopy cover (several tens of percent). Such mixed forest is suitable for spruce specialists. For example, the only two individuals of the three-toed woodpecker recorded were in two research plots in the stand Skalná Alpa, Great Fatra Mts., which are located close to a 2.5 ha patch of forest with a large proportion of recently dead large spruce trees. A high density of standing dead spruce trees, which are used by three-toed woodpeckers for foraging and nesting, is mentioned in the literature as a crucial structural element for this species (Pechacek and d'Oleire-Oltmanns 2004). The presence of spruce specialists in BDPF is also documented in other studies (Korňan 2004; Saniga and Saniga 2004; Korňan and Adamík 2014).

Along with the BDPF and SDPF specialists, several other species were recorded that occurred in both types of forest, but not at the same density. In the case of several of these species, presence or absence is probably influenced by forest structure, independently of the species composition of the trees. For example, dunnock is recorded as a species characteristic of SDPF in the ordination analysis (Fig. 3). It is considered to be a species that mainly occurs in spruce-dominated forests (Tuomenpuro 1989). However, they were also recorded frequently in BDPF. They were typically present in recently disturbed plots with low canopy cover, large amounts of deadwood and dense regeneration, as is reported in other studies (e.g., Moning and Müller 2008). This kind of structure is more common in SDPF, which likely causes this forest type to be preferred by the dunnocks and several other species (i.e., Eurasian wren). Naturally disturbed patches in BDPF are used by these predominantly SDPF species because they found suitable forest structure there, which is otherwise lacking in closed canopy BDPF.

The described patterns of bird species occurrence in BDPF and SDPF are likely to change soon due to climate change. Even currently, we are witnessing the retreat of spruce in BDPF localities in Slovakia (Parobeková et al. 2018) and in other European countries (Diaci et al. 2011; Janík et al. 2014; Jaloviar et al. 2017; Keren et al. 2017). Spruce mortality will probably temporarily create suitable habitats for spruce-related bird species (especially the three-toed woodpecker and other open-forest species), but in the long term, they are likely decrease in abundance. Thus, SDPF species will become more restricted to SDPF, which could negatively affect their populations (Braunisch et al. 2014). At the same time, the abundance of beech is reported to be increasing at high altitudes and thus transforming the species composition of trees in SDPF (Saltré et al. 2015). As a result, it is likely that the specialist birds of BDPF are likely to colonize SDPF.

Conclusions

In our study, we presented the analysis of an exceptional dataset which describes forest structure and bird assemblages in two forest types of major importance in Central

Europe in their primary state. Our results from best preserved temperate primary forests can serve as an important benchmark reference for forest management and conservation strategies focused on biodiversity conservation. We showed that bird assemblages and forest structure differ in beech- and spruce-dominated forests, independently of the disturbance regime. Both forest types with their high tree age, high standing and downed deadwood volumes and multiple tree related microhabitats provide important habitat opportunities for numerous rare bird species, which highlights the important role of primary forests in the conservation of biodiversity. Thus, protecting existing primary forests, allowing managed forests to attain older ages, and increasing the heterogeneity and availability of primary forest structures in the landscapes will maintain diverse beech and spruce forest assemblages in times of accelerating environmental change.

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