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Effects of forest management on bird assemblages in oak-dominated stands of the Western Carpathians – Refuges for rare species

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ABSTRACT

Forest management practices have varying impacts on biodiversity because the treatments and their outcomes do not always reflect the natural processes that maintain biodiversity. These management activities can be assessed using indicator species, among which birds are most frequently used. In 2018 we compared bird assemblages in oak (*Quercus* spp.)-dominated forests with admixtures of European beech (*Fagus sylvatica*), hereafter referred to as oak-beech forests, between managed and natural forest stands on opposite sides of the Carpathian range (south-facing in Slovakia and north-facing in Poland). The aim was to quantify and model the relationships between the quantitative parameters of bird assemblages and the main habitat parameters, as influenced by differing intensities of forest management. The point-count method with limited distance was applied to census birds (N = 100). Overall forest bird assemblages were found to be similar in respect to diversity indexes in managed and protected areas, as well as between southern and northern slopes of the Western Carpathian range, but all these types of forest differed in respect to bird species composition. However, both geographic location and management intensity, altogether with forest complexity contributed the mostly in explanation of bird diversity. The greatest differences were recorded for rare species, particularly those annexed in the Birds Directive of the European Union (mainly woodpeckers and flycatchers), as these birds were found either exclusively or in much greater numbers in nature reserves. Management intensity, forest complexity, and topography best explained the diversity of rare birds. Silvicultural systems applied in management of the Carpathian oak-beech forests, particularly the shelterwood system, seem to be sufficient for the preservation of overall bird diversity. However, decreased forest fragmentation and increased deadwood amounts are necessary measures to provide more close-to-nature stand structures, which will help support higher diversity of most bird species associated with mature forests. Because the oak-beech forests comprises only about 15% of the total forest area in the Western Carpathians, creating a network of natural or close-to-nature forest patches is recommended for the conservation of forest birds (and whole forest communities), including species annexed in the Birds Directive. Conservation priorities should be focused mainly in areas of harsh topography, where reduced wood production in these forests would have a less detrimental effect on the local forestry communities. These actions should also greatly improve the nature conservation system in the Carpathians and more generally throughout Central Europe.

1. Introduction

Forests are managed to meet societal demands for multiple ecosystem services and products, including wood production (Sotirov and Arts, 2018). To accommodate a balance between wood production and biodiversity conservation, among other societal demands, the integrative paradigm of 'sustainable forest management' has been the primary objective of international and national forest policies and laws (Šporšić, 2012, Forest Europe, 2015a, Sotirov and Arts, 2018). Because biodiversity quantification is very time-consuming and expensive, ecologists usually use bioindicators to detect changes in ecosystems (Landres et al., 1988; Kotwal et al., 2008). Birds are often used as surrogates for other elements of biodiversity because they are a well-studied group, not for their unique intrinsic value as environmental indicators (Gregory et al., 2008). Birds have been adopted by the European Union (EU) and many European countries as indicators of biodiversity and sustainable development. The occurrence of common breeding bird species related to forest ecosystems was also approved by

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the Forest Europe initiative as an indicator of sustainable forest management, in particular because it is an excellent means to report not only on general trends within wildlife populations, but also the state of the broader environment (Forest Europe, 2015b).

Forest-dependent birds have undergone slight but steady declines at the European and global levels (Gregory et al., 2007; Inger et al., 2015; Perry et al., 2018). Forest management is most frequently considered to be a major factor causing forest bird diversity declines (Virkkala, 1987; King and DeGraaf, 2000; Barlow et al., 2007). Forest management influences the composition and structure of forests; these changes alter the available animal habitats and promote changes in the composition and structure of local animal assemblages (Baker and Lacki, 1997, Perry et al., 2018). Depending on the silvicultural system applied, forest management often alters forest habitats primarily through forest fragmentation, the homogenization of stand structure, and an absence of deadwood (McComb and Lindenmayer, 1999; Fahring, 2003; Batáry et al., 2014; Hofmeister et al., 2017).

Changes in forest structure related to silvicultural treatments can negatively or positively affect forest bird species, depending on variable habitat preferences. While species associated with early successional habitats and forest edges usually benefit from harvesting and fragmentation, species associated with mature forest trees may decline or are extirpated after disturbance of mature forest structures (King and DeGraaf, 2000; Kellner et al., 2016; Perry et al., 2018). Many bird species associated with mature forests are facing population declines, thus managers should know how silvicultural practices affect bird species that rely on mature trees or forests for breeding, foraging, and other purposes (Perry et al., 2018). Understanding the habitat preferences of forest species and their response to habitat changes is essential for effective conservation and management strategies.

There are two primary methods to reveal changes in habitats caused by forest management or the abandonment of management. The first method considers bird responses immediately after harvest for long periods of time (Perry et al., 2018; Brown et al., 2019), while the second, more frequent method is a simultaneous comparison between sample plots (Hofmeister et al., 2017; Ameztegui et al., 2018; Lelli et al., 2019). We employed a comparative approach contrasting commercially logged forests managed using close-to-nature practices and natural forests located in nature reserves that have excluded human activity. We sampled oak (*Quercus* spp.)-dominated forests, with varying admixtures of European beech (*Fagus sylvatica*), hereafter referred to as oak-beech forests. In mountainous areas of Central Europe, the shelterwood system is the most common silvicultural system applied for long-term natural regeneration of forest stands (Peterken, 1993; Barna et al., 2010). The shelterwood system is a silvicultural method in which the forest regeneration is established under the shelter of the parent stand. The old stand is removed in a series of cuttings aimed to increase the light supply essential for developing regeneration. The size of regeneration elements is restricted (Saniga and Kucbel, 2013). Although this system meets the conditions of close-to-nature forest management, changes in microhabitat do occur but their influence on forest biodiversity is often difficult to detect and measure and thus overlooked by forest managers (Larsen, 2012; Schütz et al., 2016). Forest reserves often include important refugia for biodiversity conservation, and their study can contribute to a better understanding of anthropogenic changes as a result of forest management (Tomiałojć et al., 1984; Kropil, 1996a,b; Korňan and Adamík, 2014).

We sampled bird abundance, stand structural parameters, and site characteristics at census points across mature oak-beech forests located on the northern and southern slopes of the Western Carpathian range. We hypothesized that: (a) managed and protected mature oak-beech forests of the Western Carpathians sheltered similar bird assemblages, and (b) that forest management affects the occurrence of rare bird species, particularly those annexed in the European Union Birds Directive, through depleted critical structural elements of oak-beech forests, such as the number of old trees, amount of deadwood, or habitat complexity. Our objectives were (i) to assess abundance of forest birds using census points, (ii) to assess structural parameters of forest habitats hypothesized to influence local bird populations, and (iii) to quantify and model the relationship between important structural features and the abundance of birds at the species and guild levels, including rare taxa.

2. Materials and methods

2.1. Study area

Bird censuses were conducted at 100 randomly located census points in mature oak-beech forests, with 40 points located in natural forests and 60 points in managed forests (Table 1); additional details regarding census point locations are provided in Appendix A, organized according to Shapiro and Báldi (2012). All census points were located in the Western Carpathians, half in northern side (in Poland) and half in southern side (in Slovakia), within a geographic range 18°46.32′–21°30.18′E and 48°31.98′–49°57.84′N. Altitude ranged between 280 and 740 m a.s.l., with a mean annual temperature of 7.0–7.2 °C and mean annual precipitation of 675–700 mm (Michaeli, 2014). Census points were selected randomly within appropriate forest layer (mature woods with dominance of oaks and high share of beeches). Natural forests were situated in 10 nature reserves preserving the most valuable remnants of deciduous foothill forests of the Western Carpathians. The forests are classified as Querco-Fagetea with a mixture of deciduous associations dominated by oaks and beeches, particularly in the transition zones between oak-dominated associations, such as *Galio-Carpinetum betuli, Carici pilosae-Carpinetum, Melico uniflorae-Quercetum petraeae,* with minor inclusions of beech-dominated forest types, such as *Dentario bulbiferae-Fagetum, Dentario glandulosae-Fagetum*, and *Asperulo odoratae-Fagetum* (Matuszkiewicz, 2001; Jarolímek et al., 2008). The mean age of the stands was 100–200 years, with most being more than 150-years old. Oaks, most commonly *Quercus petraea*, and beech comprised much of the overstory, with oaks accounting for 20–100% (typically 50–80%) of the overstory tree volume. Other species with a minor presence in the overstory layer also included sycamore maple (*Acer pseudoplatanus*), scotch elm (*Ulmus glabra*), and lindens (*Tilia* spp.). Beech or common hornbeam (*Carpinus betulus*) were present in the understorey with a shrub layer that was moderately developed.

Managed forests were located in 10 areas representing submontane deciduous forests managed using the small-scale form of the shelterwood system, which entails the harvest of the overstory in a series of cuttings to promote the establishment of tree regeneration under the shade of the residual trees before the overstory is fully removed (Saniga and Kucbel, 2013). The mean age of the stands was 50–120 years (most frequently between 70 and 100 years). Oak and beech comprised the overstory, with oak typically making up 50–80% of oaks of the overstory tree volume. Other species present in the overstory also included sycamore maple, scotch elm, and lindens in very low numbers, with beech or common hornbeam in the understorey with a moderately developed shrub layer. The main differences between the protected and managed forests was the occurrence of fresh stumps, forest roads, and small clearings in the managed forests, and much higher amounts of deadwood and high numbers of tree cavities in protected forests. The detailed localization and description of all census points is given in Table 1.

2.2. Bird census

Censuses were conducted three times during the 2018 breeding season (April 1–15, May 1–15, May 16–31); we allowed at least a two-week break between consecutive visits at the same site. The point-count method with a limited distance up to 100 m was applied (Bibby et al., 2000). Census points were at least 300 m apart to minimize the

Table 1
Basic characteristics of localization and types of management of sampled plots.

No	Number	Country	Area	Site	N	E	Type of management	Side of the mountains
1	PL-res1	Poland	Wiśnicz Foothill	Bukowiec	49.839868°	20.591517°	Reserve	North-facing
2	PL-res2	Poland	Wiśnicz Foothill	Bukowiec	49.840027°	20.589031°	Reserve	North-facing
3	PL-res3	Poland	Beskid Wyspowy Mts.	Kostrza	49.771005°	20.304237°	Reserve	North-facing
4	PL-res4	Poland	Beskid Wyspowy Mts.	Kostrza	49.772019°	20.299881°	Reserve	North-facing
5	PL-res5	Poland	Wieliczka Foothill	Kozie Kąty	49.928634°	19.834549°	Reserve	North-facing
6	PL-res6	Poland	Wieliczka Foothill	Kozie Kąty	49.927536°	19.839201°	Reserve	North-facing
7	PL-res7	Poland	Wieliczka Foothill	Kozie Kąty	49.926355°	19.835888°	Reserve	North-facing
8	PL-res8	Poland	Wieliczka Foothill	Cieszynianka	49.949045°	19.875124°	Reserve	North-facing
9	PL-res9	Poland	Wieliczka Foothill	Cieszynianka	49.946239°	19.871712°	Reserve	North-facing
10	PL-res10	Poland	Wieliczka Foothill	Cieszynianka	49.945860°	19.874504°	Reserve	North-facing
11	PL-res11	Poland	Wiśnicz Foothill	Panieńska Góra	49.918945°	20.817314°	Reserve	North-facing
12	PL-res12	Poland	Wiśnicz Foothill	Panieńska Góra	49.921877°	20.819343°	Reserve	North-facing
13	PL-res13	Poland	Wiśnicz Foothill	Panieńska Góra	49.923425°	20.824530°	Reserve	North-facing
14	PL-res14	Poland	Wiśnicz Foothill	Panieńska Góra	49.926236°	20.824684°	Reserve	North-facing
15	PL-res15	Poland	Wiśnicz Foothill	Panieńska Góra	49.927059°	20.830155°	Reserve	North-facing
16	PL-res16	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.691651°	20.626582°	Reserve	North-facing
17	PL-res17	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.689829°	20.629785°	Reserve	North-facing
18	PL-res18	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.691792°	20.633416°	Reserve	North-facing
19	PL-res19	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.690241°	20.634783°	Reserve	North-facing
20	PL-res20	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.687976°	20.626054°	Reserve	North-facing
21	PL-man1	Poland	Wiśnicz Foothill	Bukowiec	49.840203°	20.597556°	Managed	North-facing
22	PL-man2	Poland	Wiśnicz Foothill	Bukowiec	49.839683°	20.594659°	Managed	North-facing
23	PL-man3	Poland	Beskid Wyspowy Mts.	Kostrza	49.767345°	20.294290°	Managed	North-facing
24	PL-man4	Poland	Beskid Wyspowy Mts.	Kostrza	49.766183°	20.288848°	Managed	North-facing
25	PL-man5	Poland	Wieliczka Foothill	Kozie Kąty	49.928114°	19.831616°	Managed	North-facing
26	PL-man6	Poland	Wieliczka Foothill	Kozie Kąty	49.925934°	19.831321°	Managed	North-facing
27	PL-man7	Poland	Wieliczka Foothill	Kozie Kąty	49.925660°	19.839669°	Managed	North-facing
28	PL-man8	Poland	Wieliczka Foothill	Cieszynianka	49.945526°	19.880130°	Managed	North-facing
29	PL-man9	Poland	Wieliczka Foothill	Cieszynianka	49.950064°	19.882158°	Managed	North-facing
30	PL-man10	Poland	Wieliczka Foothill	Cieszynianka	49.948246°	19.878705°	Managed	North-facing
31	PL-man11	Poland	Wiśnicz Foothill	Panieńska Góra	49.925254°	20.820731°	Managed	North-facing
32	PL-man12	Poland	Wiśnicz Foothill	Panieńska Góra	49.925042°	20.815176°	Managed	North-facing
33	PL-man13	Poland	Wiśnicz Foothill	Panieńska Góra	49.921756°	20.813877°	Managed	North-facing
34	PL-man14	Poland	Wiśnicz Foothill	Panieńska Góra	49.922503°	20.807704°	Managed	North-facing
35	PL-man15	Poland	Wiśnicz Foothill	Panieńska Góra	49.919115°	20.810534°	Managed	North-facing
36	PL-man16	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.690858°	20.637665°	Managed	North-facing
37	PL-man17	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.692079°	20.622714°	Managed	North-facing
38	PL-man18	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.680725°	20.618708°	Managed	North-facing
39	PL-man19	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.679632°	20.621731°	Managed	North-facing
40	PL-man20	Poland	Beskid Wyspowy Mts.	Białowodzka Góra	49.681869°	20.627116°	Managed	North-facing
41	PL-man21	Poland	Wiśnicz Foothill	Kopaliński Las	49.948525°	20.382008°	Managed	North-facing
42	PL-man22	Poland	Wiśnicz Foothill	Kopaliński Las	49.949375°	20.385274°	Managed	North-facing
43	PL-man23	Poland	Wiśnicz Foothill	Kopaliński Las	49.947390°	20.388575°	Managed	North-facing
44	PL-man24	Poland	Wiśnicz Foothill	Kopaliński Las	49.945917°	20.384349°	Managed	North-facing
45	PL-man25	Poland	Wiśnicz Foothill	Kopaliński Las	49.946653°	20.380763°	Managed	North-facing
46	PL-man26	Poland	Wieliczka Foothill	Wielki Las	49.959073°	20.100733°	Managed	North-facing
47	PL-man27	Poland	Wieliczka Foothill	Wielki Las	49.961566°	20.101168°	Managed	North-facing
48	PL-man28	Poland	Wieliczka Foothill	Wielki Las	49.964019°	20.104450°	Managed	North-facing
49	PL-man29	Poland	Wieliczka Foothill	Wielki Las	49.959835°	20.105259°	Managed	North-facing
50	PL-man30	Poland	Wieliczka Foothill	Wielki Las	49.958015°	20.103864°	Managed	North-facing
51	SK-res1	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.865844°	21.069834°	Reserve	South-facing
52	SK-res2	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.868493°	21.071209°	Reserve	South-facing
53	SK-res3	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.870483°	21.067857°	Reserve	South-facing
54	SK-res4	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.873223°	21.064157°	Reserve	South-facing
55	SK-res5	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.874861°	21.057698°	Reserve	South-facing
56	SK-res6	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.873392°	21.055477°	Reserve	South-facing
57	SK-res7	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.871083°	21.058393°	Reserve	South-facing
58	SK-res8	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.870230°	21.063333°	Reserve	South-facing
59	SK-res9	Slovakia	Čierna Hora Mts.	Bujanov NNR	48.866606°	21.063811°	Reserve	South-facing
60	SK-res10	Slovakia	Slanské vrchy Mts.	Malé Brdo NR	48.805012°	21.503672°	Reserve	South-facing
61	SK-res11	Slovakia	Slanské vrchy Mts.	Malé Brdo NR	48.807740°	21.502983°	Reserve	South-facing
62	SK-res12	Slovakia	Slanské vrchy Mts.	Malé Brdo NR	48.810686°	21.503476°	Reserve	South-facing
63	SK-res13	Slovakia	Slanské vrchy Mts.	Malé Brdo NR	48.809620°	21.499788°	Reserve	South-facing
64	SK-res14	Slovakia	Slanské vrchy Mts.	Malé Brdo NR	48.807503°	21.498899°	Reserve	South-facing
65	SK-res15	Slovakia	Štiavnické vrchy Mts.	Kašivárová NNR	48.463889°	18.773719°	Reserve	South-facing
66	SK-res16	Slovakia	Štiavnické vrchy Mts.	Kašivárová NNR	48.466632°	18.775655°	Reserve	South-facing
67	SK-res17	Slovakia	Štiavnické vrchy Mts.	Kašivárová NNR	48.467619°	18.772064°	Reserve	South-facing
68	SK-res18	Slovakia	Štiavnické vrchy Mts.	Kašivárová NNR	48.471164°	18.773613°	Reserve	South-facing
69	SK-res19	Slovakia	Slanské vrchy Mts.	Kokošovská dubina NNR	48.957253°	21.356119°	Reserve	South-facing
70	SK-res20	Slovakia	Slanské vrchy Mts.	Kokošovská dubina NNR	48.956633°	21.362089°	Reserve	South-facing
71	SK-man1	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.628710°	19.336705°	Managed	South-facing
72	SK-man2	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.627183°	19.334052°	Managed	South-facing
73	SK-man3	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.625372°	19.330942°	Managed	South-facing
74	SK-man4	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.623432°	19.326937°	Managed	South-facing

(*continued on next page*)

Table 1 (*continued*)

No	Number	Country	Area	Site	N	E	Type of management	Side of the mountains
75	SK-man5	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.626837°	19.319475°	Managed	South-facing
76	SK-man6	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.629380°	19.323045°	Managed	South-facing
77	SK-man7	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.632118°	19.326899°	Managed	South-facing
78	SK-man8	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.636663°	19.327679°	Managed	South-facing
79	SK-man9	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.639309°	19.330124°	Managed	South-facing
80	SK-man10	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.642092°	19.333367°	Managed	South-facing
81	SK-man11	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.645409°	19.335877°	Managed	South-facing
82	SK-man12	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.645951°	19.339887°	Managed	South-facing
83	SK-man13	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.645176°	19.332074°	Managed	South-facing
84	SK-man14	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.644298°	19.328423°	Managed	South-facing
85	SK-man15	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.642845°	19.324749°	Managed	South-facing
86	SK-man16	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.641119°	19.321686°	Managed	South-facing
87	SK-man17	Slovakia	Poľana Mts.	Kalinovec – Bugárovo	48.639183°	19.318808°	Managed	South-facing
88	SK-man18	Slovakia	Poľana Mts.	Kalinovec – Obchoditá	48.637919°	19.315763°	Managed	South-facing
89	SK-man19	Slovakia	Poľana Mts.	Kalinovec – Obchoditá	48.616918°	19.336900°	Managed	South-facing
90	SK-man20	Slovakia	Poľana Mts.	Kalinovec – Obchoditá	48.619683°	19.337202°	Managed	South-facing
91	SK-man21	Slovakia	Poľana Mts.	Kalinovec – Obchoditá	48.622360°	19.337864°	Managed	South-facing
92	SK-man22	Slovakia	Poľana Mts.	Kalinovec – Obchoditá	48.623083°	19.343206°	Managed	South-facing
93	SK-man23	Slovakia	Poľana Mts.	Kalinovec – Obchoditá	48.620765°	19.341028°	Managed	South-facing
94	SK-man24	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.534589°	19.095408°	Managed	South-facing
95	SK-man25	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.533345°	19.103194°	Managed	South-facing
96	SK-man26	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.533246°	19.107020°	Managed	South-facing
97	SK-man27	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.545409°	19.114777°	Managed	South-facing
98	SK-man28	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.547591°	19.117527°	Managed	South-facing
99	SK-man29	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.551771°	19.119681°	Managed	South-facing
100	SK-man30	Slovakia	Javorie Mts.	Zvolen – Desolate castle	48.553929°	19.116849°	Managed	South-facing

probability of double registrations of the same birds and to avoid spatial autocorrelation. All points were located at least 100 m from forest edges to avoid inclusion of species associated with the edge ecotone or open habitats (see Batáry et al., 2014). Surveys were conducted early in the morning, from sunrise to approximately 10 a.m., and in the absence of rain and strong wind. Upon each visit, after a few minutes of silence to reduce the effects of the observer traversing to the point, precisely five minutes were spent observing birds at each census point.

For the purposes of this study, only the relative abundance of birds was needed. Only birds exhibiting signs of territoriality, mating, or nesting behaviour were counted (majority of counts involved singing males). The number of territories/pairs for each species at each point was assigned the highest number detected during the three surveys. Species with large home-ranges, such as raptors (Falconidae and Accipitridae), owls (Strigidae), black storks (*Ciconia ciconia*), and crows (*Corvus*), were recorded, but they were not included in the analyses because the survey method used does not adequately estimate their abundance. The distance sampling method (Buckland et al., 2001) was not applied because the number of independent data units in each of examined group of forests was relatively low, what could led to estimation of too broad limits of values of bird densities. Moreover, the habitats in all examined forests have unified structure, what made comparison of collected data (among groups) straighforward. We are aware that such simplified estimation of bird numbers could led to some biases, however this should not affect the main conclusions of the study.

2.3. Habitat structural measurements

We attempted to include all the potentially important factors that influence the spatial distribution of birds. We measured 18 habitat variables at each census point (Table 2). Six variables, including type of management, stand age, forest area, exposure, altitude, and inclination, were evaluated using maps and forest management plans. Portion of clearings was assessed within a radius of 100 m around each census point. The length of roads was counted within a square area one hectare with the census point in the centre. The remaining variables, deadwood, stand and vegetation structures, were measured within a radius of 25 m around the census points. The deadwood amount at each point was estimated based on the number of logs (small end diameter of at least 10 cm) and the volume of standing dead trees, which was derived from estimates of diameter at breast height (DBH; cm) and height (m) of dead trees and the assumption of a cylindrical bole shape. Approximate coverage of tree layers, undergrowth, herbs and litter, and tree composition were estimated in the field following Khanaposhtani et al. (2012).

At each plot, habitat complexity was calculated following Khanaposhtani et al. (2012). The habitat complexity score was based on six variables describing vegetation structure (tree canopy cover, tall shrub cover, short shrub cover, ground herbaceous cover, proportion of logs/rocks, and ground litter cover; Table 2). Each variable was rated on a scale of 0–3, and the scores for each of the six features were summed.

2.4. Bird assignments

The bird census data was used in several ways. First, occurrence and abundance of particular species were used to calculate basic alpha diversity metrics (reverse Simpson diversity, 1/D – SIMPSON; and Pielou's evenness index, J – PIELOU). Bird species were assigned to trophic guilds (insectivores, herbivores [frugivores and granivores], and omnivores) and breeding guilds (hole-dwellers, branch-dwellers, and ground-dwellers) according to our knowledge of species biology and ecology examined under similar conditions (Lešo and Kropil, 2007; species guild assignments are listed in Appendix B). Finally, species were assigned to the groups based on assignment to Bird Directive of European Union (BD_BIRDS) [only species from Annex I (Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds) were considered], and also to the group of taxa characteristic of close-to-nature forests (for simplicity called RARE; details in Appendix B). To express differences in bird abundance between protected and managed forests, we compared occurrence and abundance of several bird species known to be associated with mature and close-to-nature forests (Tucker and Heath, 1994) and congeneric species considered to be common forest birds.

Table 2
Description of environmental variables used in analyses.

Variable	Unit	Description	Source
Design	Years	Years since designation of the nature reserve (for managed stands = 0)	Forestry data
Age	Years	Average age of trees (overstory)	Forestry data
Area	km2	Area of forest complex in which point was localized	Geoportal services
Exposure	Degree	Exposure of slope (0 – north)	Geoportal services
Altitude	m a.s.l.	Altitude	Geoportal services
Inclination	%	Inclination of slope	Geoportal services
Roads	m	Lenght of roads in 1 ha	Field survey
Clearings	%	Share of clearings within 100 m radius	Field survey
Veterans	N	Number of oldest tree (with DBH > 80 cm) within 25 m radius	Field survey
Stumps	N	Number of fresh stumps within 25 m radius	Field survey
Logs	N	Number of logs (of diameter > 10 cm) within 25 m radius	Field survey
Dead	m3	Approximate volume of dead wood within 25 radius	Field survey
Oak:Beech	Proportion	Proportion of oak trees to beech trees within 25 radius	Field survey
Complexity	HC score	Habitat Complexity score according to Khanaposhtani et al. (2012)	Field survey
Canopy	%	Closure of the canopy (dominating tree layer)	Field survey
Understory	%	Closure of trees and bushes (1–5 m tall)	Field survey
Undergrowth	%	Coverage by shrubs and herbs (< 1 m tall)	Field survey
Litter	%	Coverage by litter	Field survey

2.5. Data analysis

EstimateS 9.1 (Colwell, 2013) was used to plot species rarefaction curves for all forests and for each forest type (protected and managed) using the nonparametric method and augmenting the empirical sample set by a factor of two. Correlations between species' richness, abundance, and diversity were assessed using Spearman's rank correlation coefficient. Due to the significant and high correlation between these three measures (all $r_S > 0.8$), only the reverse Simpson index of diversity of birds was used in some of further analyses (e.g. general linear models). Statistical differences for bird diversity metrics and environmental variables between groups of points (reserves vs. managed and N-facing vs. S-facing) were assessed using the Mann-Whitney Z-test. Overall differences in bird diversity metrics and environmental variables among all groups of census points were tested using ANOVAs. The importance of environmental variables for bird diversity (reverse Simpson index) (separately for ALL_BIRDS and BD_BIRDS) was assessed using univariate models and Wald statistics, Akaike information criterion (AIC), and Nagelkerke pseudo R^2 values.

Principal component analysis (PCA) was used to evaluate collinearity among the studied environmental variables (Freckleton, 2011). Principal components were extracted for groups of correlated variables (rho > 0.6): 'Topography' (ALTITUDE and INCLINATION – PC1 = 73.3%), 'Layers' (CANOPY and LITTER – PC1 = 74.0%), 'Management' (DESIGN, AGE, VETERANS, LOGS, DEAD, ROADS, and STUMPS – PC1 = 55.6%). These components and the remaining independent environmental variables were used to build multivariate models using Generalized Linear Models (GLMs) and a Poisson error distribution. The resulting models were then ranked by increasing AIC values and Akaike weight (*w*) (Lebreton et al., 1992; Burnham and Anderson, 2004). Two sets of GLMs were built using the ALL_BIRDS and BD_BIRDS metrics as the response variables.

We used redundancy analysis (RDA) with four groupings (reserves vs managed and N-facing vs sS-facing) used as explanatory variables to indicate species-specific preferences toward these four plot categories. We also used RDA to visualize the relationship among the four categories of plots and environmental variables characterized in our study plots. Non-metric multidimensional scaling (NMDS) ordinations of species' abundance data at the surveyed forests were analysed using the Bray-Curtis dissimilarity index. Detrended correspondence analysis (DCA) was used to compare bird communities found in the four types of plots. The distribution of loadings of point-counts performed in protected and managed stands and in N-facing and S-facing forests differed along the first two DCA axes, and to address this, we used a permutation test with 999 permutations (ANOVA-like permutation test). Distribution of point-counts performed in the two types of groupings were visualised using kernel density estimation. Analyses were conducted using R 3.5.0 (R Core Team, 2018) and STATISTICA 12.0 software (StatSoft, 2012).

3. Results

3.1. Bird diversity

A total of 49 bird species were detected across all study plots (Appendix C). Slightly more species were detected in N-facing plots (46) compared to the S-facing plots (39; Appendix D, Fig. 1). The number of bird species was similar in reserves (48) and managed forests (47; Appendix E, Fig. 1). The same number of bird species (43) were detected in reserves and managed forests of N-facing Carpathians, whereas slightly more birds were present in reserves (38) compared to managed forests of S-facing Carpathians (37; Appendix F). A total of 2536 territorial birds were detected. Considering the overall abundance of birds, a very similar number of birds were detected in N-facing (25.7 territorial birds per plot) and S-facing (25.0 territorial birds per plot), and the values were also similar for reserves (27.0) and managed forests (24.3; Appendices D–F).

3.2. Guilds

Among the detected species, most were insectivores (24) and omnivores (21), whereas only four were herbivores. Insectivores were more abundant in protected stands (Z = 3.54, P < 0.001), while omnivores and herbivores were similarly common in both forest types (Z = 1.02, P = 0.311) (Appendix B, Fig. 2). Most species were cavity nesters (24), and bush dwellers (13), crown dwellers (12), and ground dwellers (9) were less common. Hole-dwellers were one-and-a-half times more abundant in reserves (Z = 4.20, P < 0.001), whereas birds that do not rely on cavities for breeding were similarly common in protected and managed forests (Z = 0.22, P = 0.216) (Appendix B, Fig. 2). There were no significant differences in abundance of birds from either foraging guilds or nesting guilds in respect to geographic location of sampling plots (on N- or S-facing slopes) (Z = 0.22, P = 0.832 for insectivores and Z = 0.94, P = 0.347 for herbivores & omnivores; Z = −0.51, P = 0.608 for cavity-dwellers and Z = 1.76, P = 0.079 for branch- & ground-dwellers).

3.3. Individual species

The rarest species observed were the white-backed woodpecker (*Dendrocopos leucotos*), middle spotted woodpecker (*Dendrocoptes*

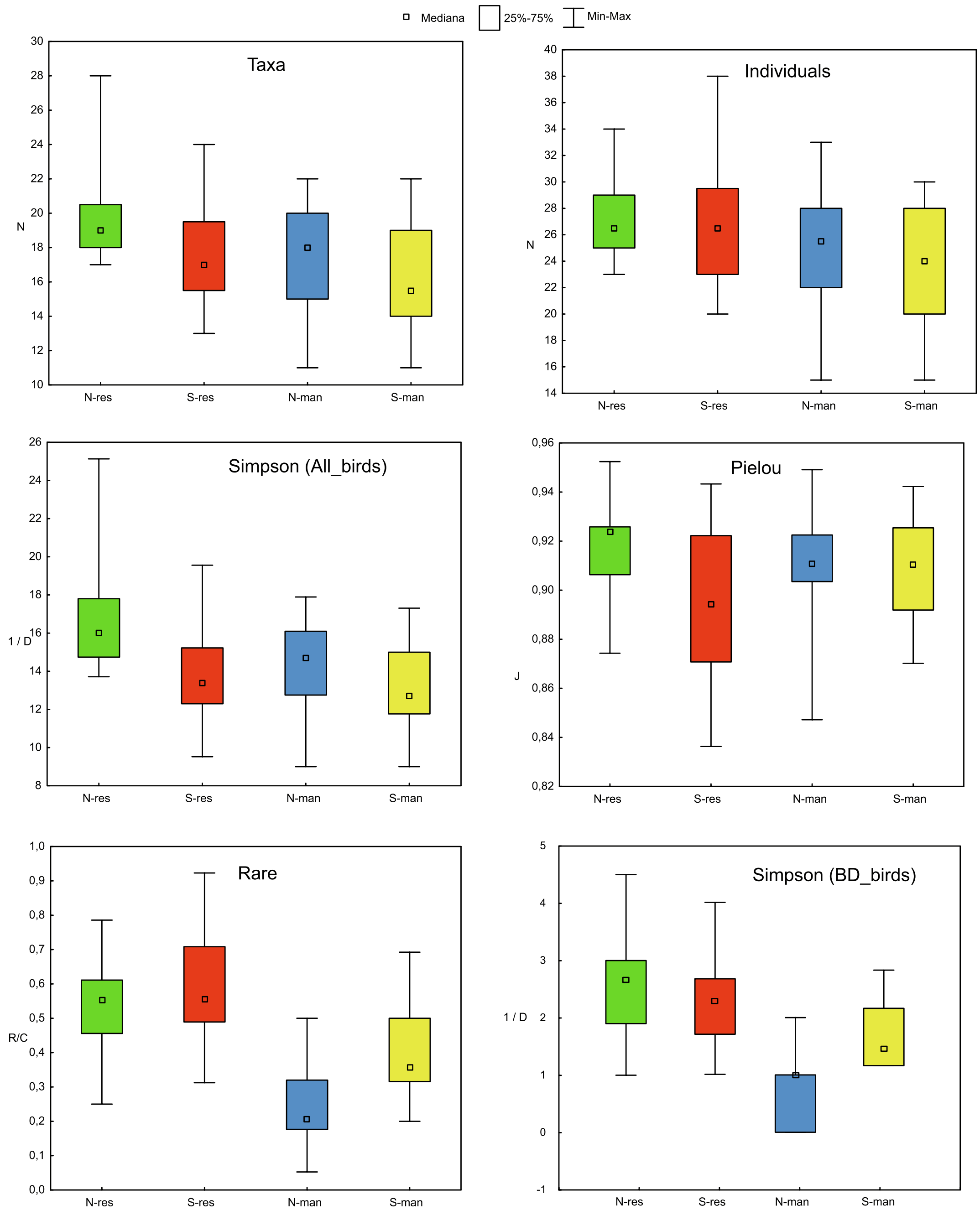

Fig. 1. Comparison of bird diversity indices calculated for four types of examined plots in oak-beech forests: N-res – nature reserves on N-facing slopes, S-res – nature reserves on S-facing slopes, N-man – managed forests on N-facing slopes, S-man - managed forests on S-facing slopes. N – number, 1/D – reverse Simpson index, J – evenness index, R/C – the number of rare species divided by a number of common species.

medius), Syrian woodpecker (*Dendrocopos syriacus*), black woodpecker (*Dryocopus martius*), grey-headed woodpecker (*Picus canus*), collared flycatcher (*Ficedula albicollis*), and red-breasted flycatcher (*Ficedula parva*) (Appendix B). There were also many more common birds associated with mature forests, including the stock dove (*Columba oenas*), common treecreeper (*Certhia familiaris*), golden oriole (*Oriolus oriolus*), marsh tit (*Poecile palustris*), redstart (*Phoenicurus phoenicurus*), wood warbler (*Phylloscopus sibilatrix*), garden warbler (*Sylvia borin*), and nuthatch (*Sitta europaea*). Common birds associated with younger stages of forest development, forest gaps, or ecotones were also present, including the yellowhammer (*Emberiza citrinella*), spotted flycatcher (*Muscicapa striata*), willow warbler (*Phylloscopus trochilus*), serin (*Serinus serinus*), lesser whitethroat (*Sylvia curruca*), or fieldfare (*Turdus pilaris*). Bird species characteristic of mature, close-to-nature, deciduous forests, such as stock dove, medium-spotted woodpecker, red-breasted flycatcher, or wood warbler, were two to four times more abundant in protected plots (Fig. 3). In contrast, we observed no differences in the occurrence of the common wood pigeon (*Columba palumbus*) between stand types, and the great spotted woodpecker (*Dendrocopos major*), spotted flycatcher, and willow warbler were one-and-a-half to three times more abundant in managed stands (Fig. 3). Considering all bird species, the RDA plot displayed a strong association of some taxa with management types or geographic location. Many species, including the white-backed woodpecker, medium spotted woodpecker, black woodpecker, grey-headed woodpecker, red-breasted flycatcher, stock dove, common treecreeper, wood warbler, and nuthatch, were associated with reserves (Fig. 4). Species associated with managed plots included the long-tailed tit (*Aegithalos caudatus*), common cuckoo (*Cuculus*

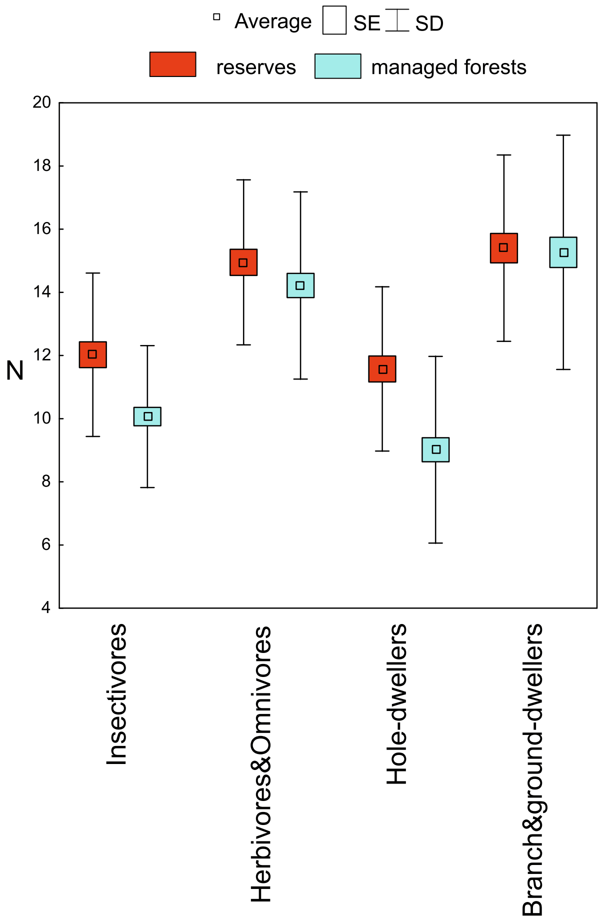

Fig. 2. Differences in the number of bird species from selected foraging and nesting guilds found in managed and protected plots. SD – standard deviation, SE – standard error.

canorus), tree pipit (*Anthus trivialis*), great spotted woodpecker, green woodpecker (*Picus viridis*), Eurasian jay (*Garrulus glandarius*), blackcap (*Sylvia atricapilla*), yellowhammer, and Chiffchaff (*Phylloscopus collybita*). Species such as the robin (*Erithacus rubecula*), European turtle dove (*Streptopelia turtur*), and collared flycatcher were associated with forests in N-facing Carpathians, while the icterine warbler (*Hippolais icterina*), pied flycatcher (*Ficedula hypoleuca*), lesser spotted woodpecker, wood pigeon, and lesser whitethroat were more strongly associated with forests in S-facing Carpathians.

3.4. Species annexed in Bird Directive

Overall bird diversity as expressed by the SIMPSON (ALL-BIRDS) and PIELOU indices was similar among examined plots, regardless of the geographic location (N- vs. S-facing) or forest management types (reserves vs. managed forests; Appendices D–F, and Fig. 1). However, the abundance of bird species associated with mature deciduous forests (RARE) was on average twice as common in plots within reserves compared to managed stands, but there were only slight differences between N-facing and S-facing forests (Appendices D–F, and Fig. 1). More pronounced differences were observed for species annexed in the Birds Directive (BD_BIRDS) because they were mostly observed in protected forests (3.5 times more likely in N-facing and 1.8 times more likely in S-facing), and they were more abundant in S-facing forests compared to N-facing forests (1.5 more likely in reserves and 2.9 times more likely in managed stands; Appendices D–F, and Fig. 1). Most differences in the bird diversity indices were determined to be significant when we compared the N-facing and S-facing data or data from protected and managed stands—the only exceptions were the evenness indices for both datasets and for individuals between countries (Table 3). Overall differences between defined groups of plots were found to be significant for all indices (Table 3).

3.5. Environmental variables

Many environmental features had very different values between protected and managed forests, although several factors, including EXPOSURE, ALTITUDE, OAK: BEECH, CANOPY, UNDERSTORY, UNDERGROWTH, and LITTER, were not significantly different between forest types (Table 3). Basic statistics describing these variables in the selected groupings of sample plots (geographic location and forest management type) are presented in Appendix F, and the raw data is available in Appendix G. In S-facing and Polis N-facing forests, we observed differences in: AGE, AREA, EXPOSURE, ALTITUDE, INCLINATION, OAK:BEECH, CANOPY, and LITTER. Overall, all features were found to be significantly different, with the exception of UNDERSTORY and UNDERGROWTH (Table 3). Some variables, such as DESIGN, AGE, VETERANS, LOGS, and DEAD, were more strongly associated with reserve plots, while variables such as CLEARINGS, STUMPS, and ROADS, were associated more with managed plots (Fig. 5). S-facing plots were associated with ALTITUDE, EXPOSURE, and OAK:BEECH, AND the N-facing plots were associated with UNDERGROWTH (Fig. 5).

3.6. Univariate modelling

Bird diversity of all species (SIMPSON – ALL_BIRDS) was best explained using univariate models including the variables N/S-FACING, ALTITUDE, VETERANS, COMPLEXITY, and CANOPY (Table 4). Among them, the model with the N/S-FACING and ALTITUDE variables had significant Wald statistics, lowest AIC, and highest R^2. In contrast, the diversity of BD_BIRDS could be explained through multiple models including some of the following: DESIGN, AGE, ALTITUDE, INCLINATION, ROADS, VETERANS, STUMPS, LOGS, DEAD, COMPLEXITY, CANOPY, and LITTER. Among these variables, the model with significant Wald statistics, the lowest AIC, and highest R^2 included DESIGN, AGE, INCLINATION, ROADS, VETERANS, LOGS, and DEAD (Table 4). Correlations among selected variables (VETERANS, STUMPS, COMPLEXITY) are visualized in Appendix H.

3.7. multivariate modelling

There were 15 GLMs that explained overall bird diversity (SIMPSON – ALL-BIRS) with ΔAIC of less than 2.0 (Appendix I). These models included the variables N/S-FACING, COMPLEXITY, CLEARINGS, and AREA, and the MANAGEMENT and TOPOGRAPHY components (Table 5). The highest sums of AIC weights were observed for N/S-FACING (0.72), COMPLEXITY (0.48), CLEARINGS (0.46), MANAGEMENT (0.36), AREA (0.32), and TOPOGRAPHY (0.30). The BD_BIRDS diversity was best explained by eight models with ΔAIC of less than 2.0 (Appendix I). These models included MANAGEMENT and TOPOGRAPHY components and COMPLEXITY and AREA variables (Table 5). The highest sums of AIC weights were observed for MANAGEMENT (0.98), TOPOGRAPHY (0.41), COMPLEXITY (0.39), and AREA (0.35).

THE RDA plot suggested that overall bird diversity indices (TAXA, INDIVIDUALS, SIMPSON – ALL-BIRDS, PIELOU) were linked mostly with COMPLEXITY (Fig. 5), whereas RARE and BD_BIRDS indices were linked with AGE and AREA, and slightly less with DESIGN, LOGS, and DEAD (Fig. 5). The DCA and NMDS plots displayed partial splits between bird assemblages associated with either plots in reserves or managed stands, or plots in N-facing or S-facing mountains (Fig. 6). Plot groupings based on geographic affinity displayed less overlap than plots grouped according to management types (Appendix J).

4. Discussion

In mature oak-beech forests of the Western Carpathians, we observed that overall species richness, abundance, and bird diversity did

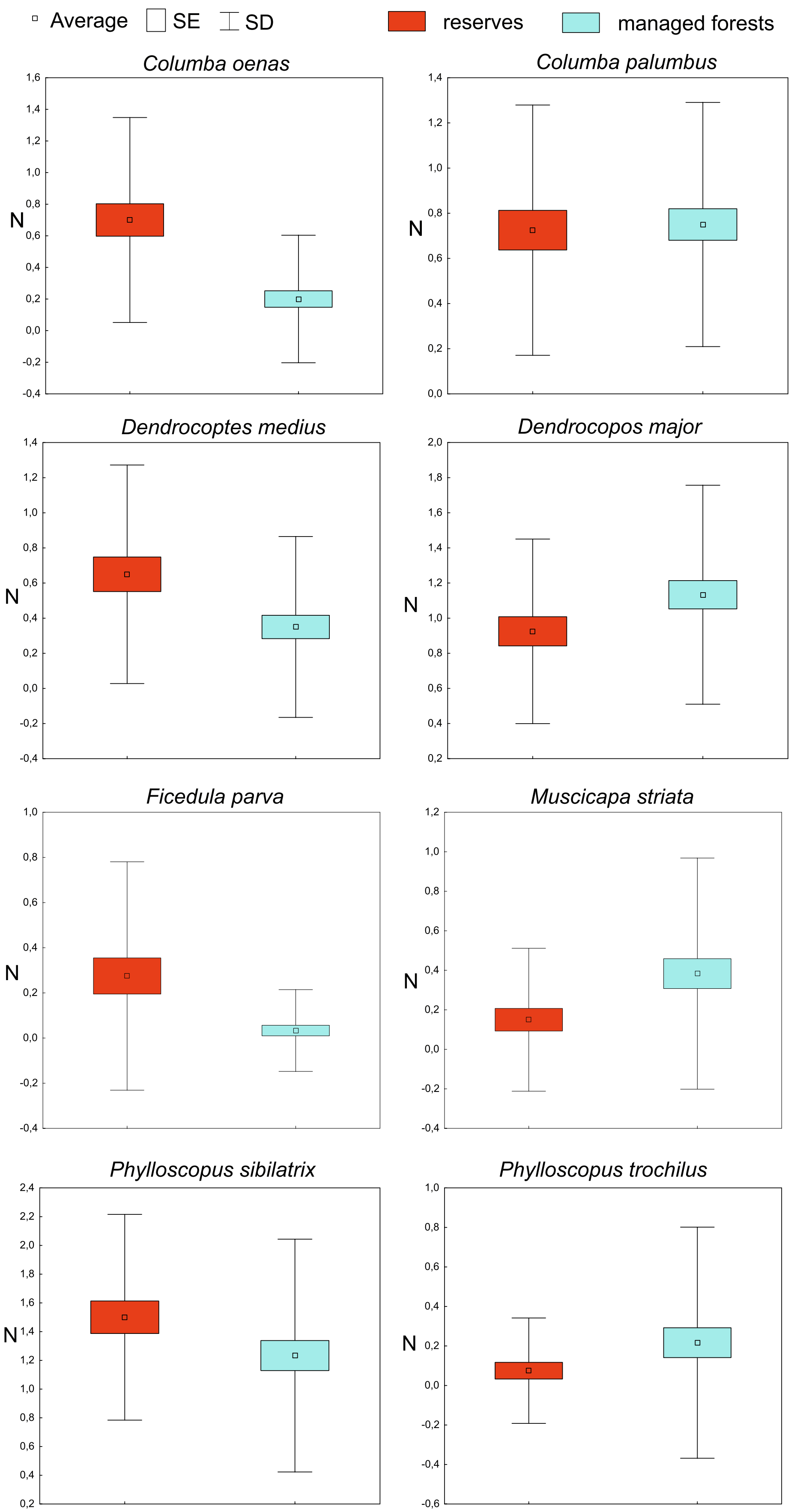

Fig. 3. Differences in the abundance of selected pairs of closely related bird species found in managed and protected plots. SD – standard deviation, SE – standard error.

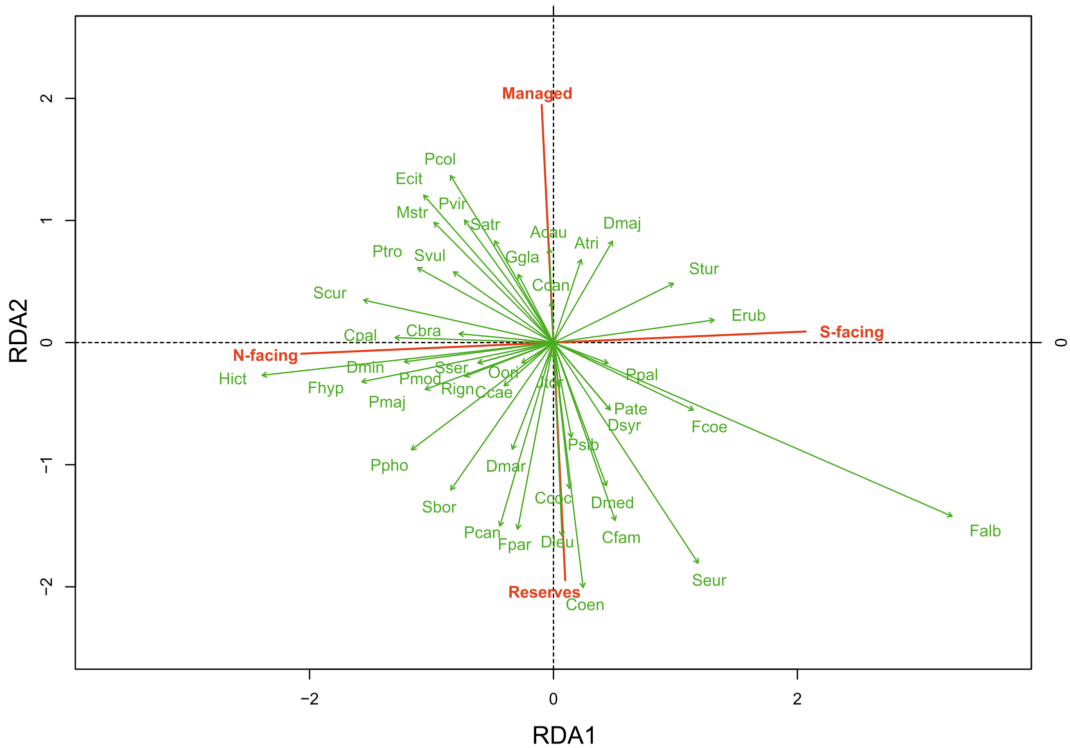

Fig. 4. Relationships between the occurrence of bird species and locality (N-facing slopes vs S-facing slopes) and management type of forests (managed vs reserves) revealed with use of Redundancy Analysis. Explanation of symbols of species names is provided in Appendix B.

Table 3
Statistical differences between analyzed points in respect to selected environmental vaiables and bird diversity metrics. N – north-facing, S- south-facing, U – Mann-Whitney *U* test, ANOVA – Kruskal-Wallis ANOVA, p – significance (in bold – significant with $p < 0.05$). BD_birds – bird species annexed in Bird Directive (Annex I).

Compared groups	N vs S		Reserves vs managed		All points	
Test	U	p	U	p	ANOVA	p
Environmental variables						
Design	1127.0	0.34	**0.0**	**0.00**	**93.4**	**0.00**
Age	**728.0**	**0.00**	**158.0**	**0.00**	**66.9**	**0.00**
Area	**674.0**	**0.00**	**692.0**	**0.00**	**43.6**	**0.00**
Exposure	**517.5**	**0.00**	1041.5	0.26	**30.7**	**0.00**
Altitude	**415.5**	**0.00**	981.5	0.12	**35.5**	**0.00**
Inclination	**415.5**	**0.00**	**656.5**	**0.00**	**48.9**	**0.00**
Roads	1218.0	0.82	**260.0**	**0.00**	**48.0**	**0.00**
Clearings	1201.5	0.69	**842.5**	**0.00**	**9.3**	**0.03**
Veterans	1009.0	0.07	**246.0**	**0.00**	**56.2**	**0.00**
Stumps	1141.0	0.35	**620.0**	**0.00**	**27.4**	**0.00**
Logs	1227.0	0.87	**57.5**	**0.00**	**73.1**	**0.00**
Dead	1179.0	0.61	**112.0**	**0.00**	**63.6**	**0.00**
Oak:Beech	**559.0**	**0.00**	1036.5	0.25	**25.1**	**0.00**
Complexity	1040.0	0.14	**837.0**	**0.01**	**11.2**	**0.01**
Canopy	**552.0**	**0.00**	960.0	0.08	**27.5**	**0.00**
Understory	1079.5	0.24	1045.0	0.27	2.6	0.45
Undergrowth	1094.0	0.28	1026.5	0.22	3.4	0.34
Litter	**952.0**	**0.04**	971.0	0.10	**14.6**	**0.00**
Bird diversity metrics						
Taxa	**844.0**	**0.00**	**838.5**	**0.01**	**15.2**	**0.00**
Individuals	1103.0	0.31	**821.0**	**0.01**	**8.2**	**0.04**
Simpson (All_birds)	**793.0**	**0.00**	**889.0**	**0.03**	**16.4**	**0.00**
Pielou	984.5	0.07	1190.0	0.95	**8.5**	**0.04**
Rare	**804.0**	**0.00**	**310.0**	**0.00**	**52.3**	**0.00**
Simpson (BD_birds)	981.5	0.06	**345.0**	**0.00**	**31.1**	**0.00**

not differ much between sites in managed and reserve forest patches, and there were no pronounced differences between bird assemblages found among the southern (Slovak) and northern (Polish) slopes of the Western Carpathian arch. However, differences were evident for rare bird species, both: all taxa characteristic for forests close-to-nature (RARE), and particularly those protected under the Natura 2000 ecological network (BD_BIRDS). Threatened bird species were almost completely absent in managed forest stands due to a deficiency of natural features common to unmanaged forests, such as deadwood, the presence of veteran trees, or high structural heterogeneity.

4.1. Bird diversity

Forty-nine bird species were observed in our sampled oak-beech forests, which is consistent with the reported range of species richness (30–70 species) for deciduous forests within the mountainous areas of Central Europe (e.g., Domokos and Cristea, 2014; Lešo and Kropil, 2014). This high species richness reflect some very valuable bird assemblages, and our survey did not include birds with large territories in our analyses (an additional six species were observed).

Among the bird species detected in the oak-beech forests, the majority of taxa were forest generalists that occur in various forest types, including deciduous, mixed, and coniferous forests. The abundance of forest interior specialists (most woodpeckers and flycatchers, but also stock dove, marsh tit, and nuthatch) was generally higher in reserve forests. In managed forests, eurytopic species (or species associated with forest edges) were more abundant. There were few examples of species found only in forests of the southern side of the Western Carpathians (e.g., European turtle dove, coal tit [*Periparus ater*], or Syrian woodpecker) or only in forests on the northern side (e.g., redstart, icterine warbler, or pied flycatcher). These differences could be

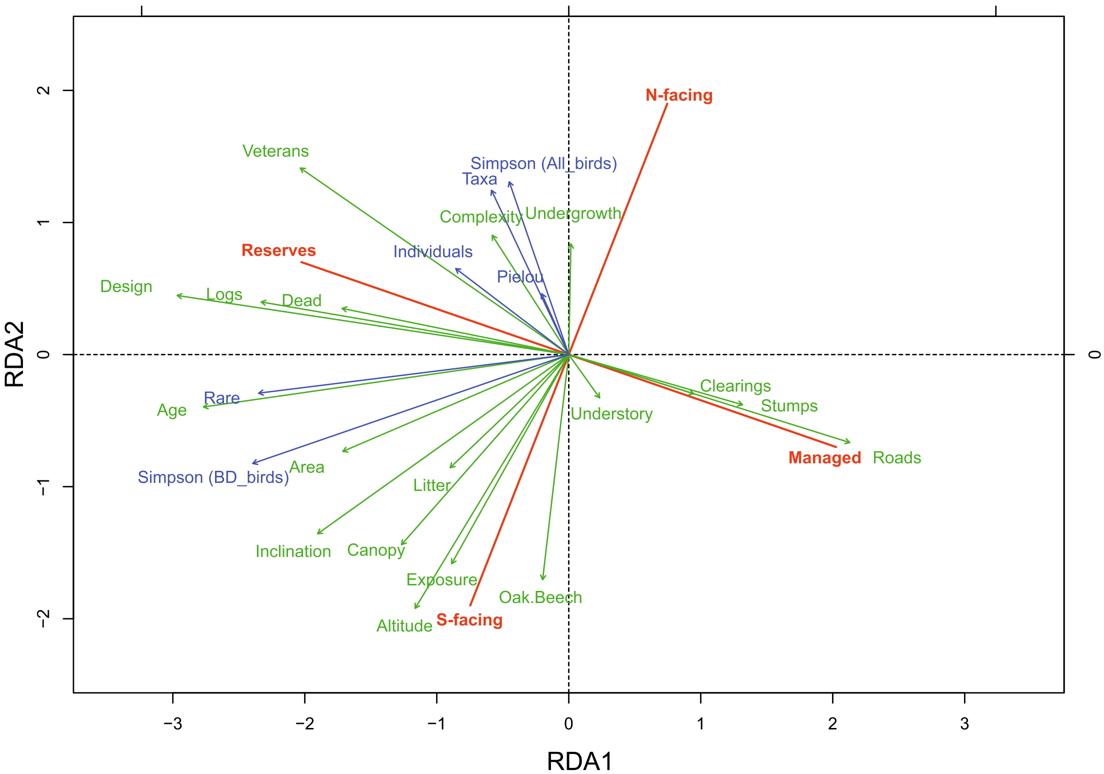

Fig. 5. Relationships between environmental characteristics of examined plots and bird diversity showed on the background of locality (N-facing slopes vs S-facing slopes) and management type of forests (managed vs reserves) revealed with the use of redundancy analysis. Explanation of symbols of environmental characteristics is provided in Table 2.

Table 4
Univariate models for examined predictors (environmental variables) calculated for two response variables: Simpson diversity [1/D] calculated for all species (All-birds) and for species annexed in Bird Directive (BD_birds). Wald – Wald statistics, p – value, AIC – Akaike Information Criterion, R2 – Nagelkerke pseudo R2.

Response variable	All_birds				BD_birds			
Predictors	Wald	p	AIC	R2	Wald	p	AIC	R2
N/S-facing	**4.4**	**0.04**	**244.8**	**0.09**	2.0	0.16	237.3	0.03
Design	0.7	0.41	248.5	0.01	**18.2**	**0.00**	**222.2**	**0.32**
Age	0.0	0.95	249.2	0.00	**15.8**	**0.00**	**224.4**	**0.28**
Area	0.0	0.99	249.2	0.00	2.4	0.12	237.1	0.04
Exposure	1.6	0.21	247.6	0.03	0.1	0.75	239.2	0.00
Altitude	**4.2**	**0.04**	**245.0**	**0.08**	**3.5**	**0.06**	235.7	0.06
Inclination	0.0	0.89	249.2	0.00	**10.2**	**0.00**	**229.2**	**0.18**
Roads	0.2	0.68	249.0	0.00	**12.0**	**0.00**	**226.2**	**0.21**
Clearings	1.6	0.21	247.7	0.03	1.1	0.28	238.1	0.02
Veterans	3.0	0.08	**246.2**	**0.06**	**17.1**	**0.00**	**223.4**	**0.30**
Stumps	0.0	1.00	249.2	0.00	**5.7**	**0.02**	232.4	0.10
Logs	0.1	0.73	249.1	0.00	**11.6**	**0.00**	**229.2**	**0.20**
Dead	0.8	0.37	248.4	0.02	**9.0**	**0.00**	**231.9**	**0.16**
Oak:Beech	1.3	0.26	247.9	0.03	0.4	0.52	238.9	0.01
Complexity	3.1	0.08	**246.1**	**0.06**	**4.3**	**0.04**	235.1	0.07
Canopy	3.7	0.05	**245.6**	**0.07**	**4.7**	**0.03**	234.2	0.08
Understory	1.0	0.33	248.2	0.02	0.7	0.42	238.6	0.01
Undergrowth	1.4	0.24	247.8	0.03	2.5	0.11	236.8	0.04
Litter	1.5	0.22	247.7	0.03	**3.1**	**0.08**	236.0	0.05
Intercept	**107.9**	**0.00**	247.2	–	**38.9**	**0.00**	237.3	–

related with different areal distribution of the species, as we observed slightly lower average altitudes for census points on the northern side, where perhaps more lowland species could access the Carpathian range (see Wilk et al., 2016).

4.2. Guilds

High numbers of cavity dwellers are a typical feature of bird assemblages in oak mature forests (Tomialojc et al., 1984; Glowacinski, 1990; Lešo and Kropil, 2014). The presence of woodpeckers, primary cavity excavators, is crucial for the presence and diversity of other hole dwellers (Mikusiński et al., 2001), and we observed 9 of 11 European woodpecker species were observed in our sampled forests. There was also a large number of secondary cavity nesters (24 species, including all species of flycatchers native to Central Europe). Ground dwellers were represented by nine species, which may be partially explained by a general avoidance of pure deciduous forests by some species (e.g., grouse species need coniferous trees; Matysek et al., 2018) and by limited suitable nesting sites on the ground (low coverage in the undergrowth layer). Low numbers of bush dwellers is also characteristic of oak-beech forests, which reflects high canopy cover that inhibits suitable conditions for adequate bush layer development (Lešo and Kropil, 2014).

Approximately half of the observed breeding birds were insectivores foraging on various invertebrates from different microhabitats (on live or dead trees, bushes, herbs, litter, etc.). Insectivores are usually the dominant guild of birds in forests, however, in highly transformed wooded stands, this guild is comprised of a relatively few species in high abundance and they forage on only some types of invertebrates (mostly caterpillars, which are often considered to be pests; Heinrich and Collins, 1983); species that depend on cambioxylophagous insects are mostly absent in these forests due to a deficiency of deadwood resources. Birds are known to be highly adaptive and they can adopt wider foraging strategies (Lešo and Kropil, 2007), thus differences in bird foraging guilds between two types of forest are simply not distinguishable.

Table 5
Generalized Linear Models constructed on examined environmental variables (and components for correlated ones, see Methods) for two response variables: Simpson diversity [1/D] calculated for all species (All-birds) and for species annexed in Bird Directive (BD_birds). Only models with ΔAIC < 2.0 are presented.

No.	variables				df	AIC	ΔAIC	*w*
All-birds								
1	N/S-facing				1	244.8	0.00	0.06
2	Complexity	N/S-facing			2	244.8	0.03	0.06
3	Management	Clearings	N/S-facing		3	244.8	0.04	0.06
4	Clearings	N/S-facing			2	245.3	0.56	0.04
5	Management	N/S-facing			2	245.4	0.64	0.04
6	Complexity	Clearings	N/S-facing		3	245.6	0.86	0.04
7	Complexity				1	246.1	1.27	0.03
8	Area	N/S-facing			2	246.1	1.30	0.03
9	Management	Complexity	Clearings	N/S-facing	4	246.2	1.41	0.03
10	Management	Complexity	N/S-facing		3	246.2	1.45	0.03
11	Complexity	Area	N/S-facing		3	246.3	1.52	0.03
12	Area	Clearings	N/S-facing		3	246.3	1.53	0.03
13	Topography	N/S-facing			2	246.6	1.80	0.02
14	Topography	Complexity	N/S-facing		3	246.7	1.90	0.02
15	Management	Area	Clearings	N/S-facing	4	246.7	1.93	0.02
	INTERCEPT					250.0	5.24	0.00
BD-birds								
1	Management				1	217.3	0.0	0.12
2	Topography	Management			2	218.2	0.9	0.08
3	Management	Complexity			2	218.4	1.1	0.07
4	Management	Area			2	218.5	1.2	0.06
5	Topography	Management	Complexity		3	218.6	1.3	0.06
6	Management	N/S-facing			2	219.0	1.7	0.05
7	Management	Clearings			2	219.2	1.9	0.04
8	Topography	Management	Area		3	219.2	1.9	0.04
	INTERCEPT					240.3	23.0	0.00

4.3. Species annexed in the EU Birds Directive

Overall number of breeding bird species, a major component of bird diversity, is a good estimator for the importance of particular site or habitat for birds (Spellerberg, 1992), however, from a different perspective, the presence of rare species may offer greater insight (Lelli et al., 2019). The greatest differences in between protected and managed forests, and between forests along the northern and southern slopes of the Western Carpathians, would be more apparent if only rare species were considered. Rarer species were observed mainly in nature reserves, where they were found in much higher numbers, which is consistent with their narrow habitat requirements (e.g., Roberge and Angelstam, 2006; Pakkala et al., 2014). Interesting is that overall number of rare birds (both taxa and individuals) was higher in S-facing than in N-facing plots, both in reserves and managed forests, but if we consider only BD_BIRDS, we find similar levels of diversity of birds in reserves on the northern and southern sides of the Western Carpathian arch, but these species were almost absent in managed stands on N-facing slopes. In the studied forests, five woodpecker and two flycatcher species annexed in the Birds Directive were found. Our finding that white-backed woodpecker is a species not only typical for mountain beech stands, but it is also commonly found in oak-dominated forests located in much lower altitudes of the Carpathians is consistent with previous studies (e.g., Pavlík, 1999; Lešo and Kropil, 2014; Kajtoch

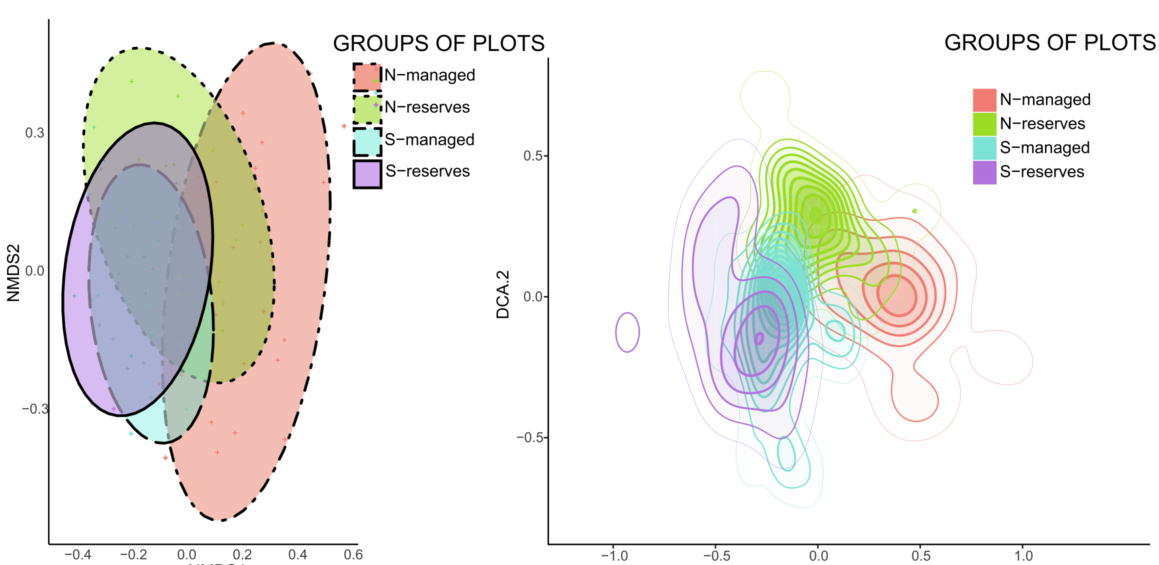

Fig. 6. Expression of coverage between bird communities found in four types of examined plots revealed with use of non-metric multidimensional scaling plots (NMDS) and detrended correspondence analysis (DCA).

et al., 2016). The white-backed woodpecker is considered to be a good umbrella species for conservation of biodiversity associated with forests with an abundance of deciduous trees and they are strictly associated with large amounts of deadwood (Roberge et al., 2008), thus its more frequent presence in natural forests, as we observed in nature reserves, emphasizes the importance of unmanaged forest patches in protected areas. Mikusiński et al. (2001) found higher species richness of forest birds in landscapes where the white-backed woodpecker occurred.

The middle spotted woodpecker breeds mostly in old-growth deciduous forests in the lowlands (Pasinelli, 2000) and this study provides evidence that it is also abundant in similar forests of the lower mountain slopes. We found a significantly higher abundance of the middle spotted woodpecker in reserves. It is considered to be an umbrella species for the entire assemblage of animals associated with mature broadleaved trees, especially oak (Müller et al., 2009).

The third rare woodpecker species we observed, the Syrian woodpecker, is known to be synantropic in Europe, where it breeds only in rural and urban woodlands (Gorman, 2004). Therefore, the presence of this species in the interior of oak-beech forests is unusual, but only for Europe, as there are reports of similar behaviour Syrian woodpeckers from deciduous mountain forests of Iran, where the species is a regular breeder (Khanaposhtani et al., 2012).

Red-breasted flycatcher is a typical species for forest interiors with high complexity (Brazaitis and Angelstam, 2004), and it has been considered to be the best bird indicator of forest biodiversity (Pakkala et al., 2014). Our results support this assumption because it was approximately six times more abundant in reserves compared to managed forests. Another flycatcher annexed in the Birds Directive, the Collared flycatcher, is mostly known from mature deciduous forests with high abundance of tree cavities and semi-cavities (Tomiałojć et al., 1984; Wesołowski, 2007b; Kralj et al., 2009). Similar abundance of this species in all mature oak-beech forests may indicate good quality habitat for cavity dwellers not only in protected forests, but also in managed forests of the Carpathians.

4.4. Environmental variables

Although bird assemblages associated with oak-beech mature forests of the Carpathians have been rather well studied (for a review of the studies, see Lešo and Kropil, 2014 as an example), this is the first study that focused on bird diversity in consideration of various types of management and geographic location. The advantage of this study over most other similar research is that it includes data not only from one particular area. Data obtained from some geographic area is generally easier to analyse and it does not need to be corrected, if the examined habitat is constant over space. However, in contrast to lowland forests, mountain forests could differ substantially depending on local topography and climatic conditions related to altitude, inclination, and exposure. These local conditions could cause differences in bird occurrence. In this study, sites located on the northern slopes of the Western Carpathian arch, which are typically colder and wetter, differed from the warmer and drier southern slopes in terms of local habitats (see below) and bird assemblages (Sections 4.1 and 4.2); however, these differences were not pronounced.

Protection of forest areas does not ensure the presence of higher bird diversity (Rayner et al., 2014). However, in the case of oak-dominated mature forests, the higher bird diversity in protected areas was noticeable, particularly when compared to primeval woods in lowland forests in Europe, such as Białowieża Forest (Tomiałojć et al., 1984; Wesołowski, 2007a) and in mountain forests, such as the Carpathians (e.g., Baláž and Balážová, 2012). Contrary to expectations, this study showed that overall bird diversity in protected and managed oak-beech forests from opposite slopes of the Western Carpathians did not differ so much. Overall diversity of birds (Simpson index) was found to be significantly different only in respect to following variables: N/S-facing, altitude, number of veterans, forest complexity, clearings, and canopy coverage. N/S-facing, which reflects geographic location of sampling sites, was present in all models with the lowest AICs, which suggests that geographic locations should also be considered in bird studies with large geographic ranges. Overall bird diversity was best explained by the intensity of forest management, as interpreted by age, abundance of old trees, deadwood amounts, and the number of roads and stumps. This finding agrees with numerous other studies on bird assemblages from protected/unmanaged and managed sites (Lohmus, 2004; Honkanen et al., 2010). The proportion of clearings was a good indicator of overall bird diversity because even in mature forests, any gaps in the forest structure have an effect on bird communities. Similar patterns have been observed in studies on other bird taxa, even strict forest-dwellers (e.g., Matysek et al., 2018). Such gaps, even of very small area, such as individual treefalls, create additional microhabitats that can be used by birds for foraging or nesting. Larger forests would be expected to sustain more local habitats and be less affected by forest fragmentation, as well as by inner fragmentation caused by logging (e.g., see Mazgajski et al., 2010).

Occurrence of BD_BIRDS was best explained by models that included: forest age, altitude, inclination, number of roads and stumps, number of veteran trees, amount of deadwood, forest complexity, and coverage of canopy and litter layers. Similar to bird diversity, our models demonstrated that intensity of forest management was a significant factor that influenced the diversity of BD_BIRDS. This is rather obvious if one considers the habitat requirements of these birds, which are known to be highly dependent on the presence of old-growth forests with high amounts of deadwood and not affected by recent harvesting or silviculture practices (e.g., Roberge and Angelstam, 2006; Pakkala et al., 2014). Other factors that best explained the diversity of birds annexed in Bird Directive were topography, forest complexity, and forest area. Explanation of the role of forest area in increasing of bird diversity is already described above. Topography can be an especially important factor in mountainous areas, as numerous microhabitats are formed by valleys, gorges, rocks, and springs. These abiotic features are accompanied by biotic features, including multilayer structure of forests, uprooted trees, snags, logs, and lianas, among other features (Kraus et al., 2016). Many of these features increase the number of potential breeding sites, act as shelters, and they can be important foraging sites for numerous bird species (Urban and Smith, 1989).

Redundancy analyses clearly showed that in mature oak-beech forests of the Western Carpathians, the management practices, as expressed predominantly by the area of gaps and the high number of roads and stumps, reduce or eliminate critical environmental variables characteristic of close-to-natural forests, such as the number of old trees, the overall average age of forest stands, number and amount of deadwood, and the complexity of forest structure. These findings are not novel, as forest management associated with wood production inevitably changes stand age, forest structure, and the presence of microhabitats. However, in contrast to most managed forests, particularly monoculture tree plantations, oak-beech forests of the Western Carpathians seem to offer several advantages for bird diversity and habitats when the shelterwood system is employed to foster the long-term natural regeneration of forest stands (Peterken, 1993; Barna et al., 2010). The small-scale form of the shelterwood system (also referred to as the polycyclic harvesting method) appears to be particularly effective because it creates different regeneration units (e.g., gaps or strips) that offer more complex forest structure; it is considered to be the most effective silvicultural method to perpetuate long-term regeneration in oak-beech forest stands and it is consistent with the principles of sustainable forest management (Schütz et al., 2016). Mature oak-beech stands managed using shelterwood systems have some features similar to natural forests, such as a multilayer structure, structural heterogeneity, the presence of many microhabitats, including deadwood and cavities, and uneven age of forests at large spatial scales (Saniga and Kucbel, 2013). In fact, some of these stands in the Western Carpathians have remained intact for dozens of years and have been designated as nature reserves and considered equivalent to close-to-nature forests (Korpeľ, 1995).

4.5. Implications for conservation management

The shelterwood system applied in oak-beech mature forests of the Carpathians seems to be effective for preserving bird assemblages, as overall bird diversity observed in reserve and managed stands were similar. However, without targeted additional measures, the shelterwood system is likely not adequate to conserve some rare and stenotopic taxa, including BD_BIRDS. For these rarer species, forest management, particularly in Special Protected Areas (SPA), needs to seek a more balanced approach between wood production and the habitat requirements of protected species. When comparing reserves and managed forests, considering bird assemblages at the guild level seems to be a good tool to reveal differences in habitat structure. The most conspicuous differences in bird assemblages from reserves and managed forests was the abundance of cavity dwellers and ecotone species. The significantly higher percentage of hole dwellers in reserves reflects the considerably higher volume of deadwood typically associated with these stands. We found an average of approximately 62–76 $m^3 ha^{-1}$ of standing deadwood in reserves (slightly higher value was from forests on S-facing slopes) and only approximately 4–11 $m^3 ha^{-1}$ (higher value was from forests on S-facing slopes) in managed forests. The difference was expected because deadwood is typically present in low volumes in managed forests in comparison to natural ones (Vítková et al., 2018). In Europe, the average volume of total deadwood (standing and lying) is around 11.5 $m^3 ha^{-1}$ (Forest Europe, 2015a). High concentrations of plots with more than 50 $m^3 ha^{-1}$ of deadwood have been recorded in the Alpine regions, including the Carpathians (Puletti et al., 2018). Slovakia and Poland are among the countries with the highest documented deadwood volumes in European natural forests (Saniga and Schütz, 2001; Bobiec, 2002). The recognition of the importance of deadwood to biodiversity has led to the development of quantitative parameters for the necessary abundances of deadwood to support biodiversity monitoring programmes; for example, the European Environmental Agency includes deadwood as one of its 15 core biodiversity indicators (Merganičová et al., 2012), and Forest Europe includes it as one of 45 pan-European indicators for sustainable forest management (Forest Europe, 2015b). For deadwood to be an effective indicator, reference values representative of "natural" states are needed (Merganičová et al., 2012). Based on the analysis of a substantial published and unpublished dataset, Müller and Bütler (2010) estimated a threshold volume of 30–50 $m^3 ha^{-1}$ of deadwood (standing and lying) was required to effectively impact biodiversity conservation in lowland oak-beech forest conditions. These values seem to be high if regarding average total wood stock in the managed forests of the Western Carpathians (around 220–270 $m^3 ha^{-1}$; https://www.bdl.lasy.gov.pl/). Simple calculations suggest that for the most demanding species, the white-backed woodpecker (Müller and Bütler, 2010), it should be left approx. 20% of total wood to natural dead in managed stands, which likely would not be acceptable to forest managers whose primary focus is wood production. Reaching these thresholds should not be impossible for SPAs because lost timber profits can be compensated (only private owners) with state or EU funds. However, current forest and environmental policy of countries of the Western Carpathians does not sufficiently motivate owners to join in forest and environmental projects with low payment rates (ca. 50€ ha^{-1} annually) for adherence to close-to-nature forest management focused on target bird species.

The Carpathians mountain range contains an exceptional number of well-preserved natural forests (Bublinec et al., 2003). However, there are only a few oak-beech forests in central Europe classified as natural or close-to-natural; it's estimated that less than 5% of the total area of natural forests in this region are oak-beech forests (Korpeľ, 1995; Šebeň, 2017). This was a result of extensive human impacts and forest management in easily accessible foothills and low mountains of the Carpathians and other mountain ranges in Central Europe (Kozak, 2009; Saniga et al., 2014). The area of oak-beech forests in the Carpathians comprises only about 15% of the total forest area in the Western Carpathians (Šebeň, 2017). Thus, a network of natural or close-to-nature patches in those forest associations is necessary for conservation of birds (and whole communities) related to broadleaved forests, including BD_BIRDS and several other rare species (Köck et al., 2014). Applying measures mentioned above, the quality of managed oak-beech forests for biodiversity conservation can be substantially improved in accordance with the Carpathian Convention. To reduce financial losses, forests in inaccessible locations should certainly be assigned and supported for biodiversity conservation. Because of the harsh topography of the mountains, forest districts in those areas often operate with annual deficits and must be subsidized, particularly in the mountain forest districts in Poland (Marszałek, 2011). Aside from nature reserves, protected forests also play an important role in biodiversity conservation in oak-beech forests because they preserve soils from erosion on steep rocky slopes, ridges, and screes, and typically no silvicultural treatments are applied there. Relative to nature reserves, protected forests cover a relatively large total area (2–3 times more) and they have a similar structures, thus they represent critical habitats for bird assemblages related to mature oak stands (Pavlík, 2017). Because birds are good indicators of the overall quality of habitats and biodiversity (Gregory et al., 2008), the protection of valuable oak-beech forests in the Carpathians can help to greatly improve nature conservation systems throughout Central Europe.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117620. These data include Google maps of the most important areas described in this article.

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