STRUCTURE OF THE BREEDING BIRD ASSEMBLAGE OF A NATURAL BEECH-SPRUCE FOREST IN THE ŠÚTOVSKÁ DOLINA NATIONAL NATURE RESERVE, THE MALÁ FATRA MTS

MARTIN KORŇAN[1,2,*] , PETER ADAMÍK[3]

[1] Centre for Ecological Studies, Ústredie 14, 013 62 Veľké Rovné, Slovak Republic; e-mail: martin.kornan@gmail.com

[2] Department of Forest Protection and Game Management, Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 20, 960 53 Zvolen, Slovak Republic; e-mail: martin.kornan@tuzvo.sk

[3] Department of Zoology, Palacký University, Tř. Svobody 26, 771 46 Olomouc, Czech Republic; e-mail: peter.adamik@upol.cz

*Author for correspondence

Abstract

Korňan M., Adamík P.: Structure of the breeding bird assemblage of a natural beech-spruce forest in the Šútovská dolina National Nature Reserve, the Malá Fatra Mts. Ekológia (Bratislava), Vol. 33, No. 2, p. 138–150, 2014.

The structure of a breeding bird assemblage of a natural beech-spruce forest in the Šútovská dolina National Nature Reserve, the Malá Fatra Mts was studied in the period 2000−2002. A 20-ha forest interior study plot was established for bird censusing. Population abundances were estimated by a combined version of the mapping method from April to the beginning of July. Altogether, 49 breeders were recorded and the total mean breeding bird assemblage density of the beech-spruce forest was 54.23±8.60 pairs/10 ha (CV = 15.85%). One species were characterised as eudominant (≥10%): *Fringilla coelebs*; and five species as dominant (≥5%): *Erithacus rubecula*, *Sylvia atricapilla*, *Parus ater*, *Regulus regulus* and *Certhia familiaris*. The Shannon diversity index (H') varied between 3.97 and 4.04 bites. The evenness index (J') reached values between 0.74 and 0.79. Expected species diversity in random sample of 100 pairs calculated by rarefaction [$E(S_{100\,pairs})$] was 21.02 ± 0.46 (SD) species derived as a mean value from the years 2000−2002. The mean rarefaction estimate on area [$E(S_{10\,ha})$] was 17.35 ± 1.31 species. Species richness compared to other studied mixed forest in Slovakia was one of the highest, yet the species diversity values belong among the lowest.

Key words: bird community, mixed forest, mapping method, population density, rarefaction, Western Carpathians, Slovakia.

Introduction

In 1990s descriptive studies on understanding patterns of species structure and richness, population densities, dominance, diversity and evenness in the remains of representative close to primeval or secondary natural forests in all altitudinal forest zones have started on the national scale in Slovakia (Kropil, 1993, 1996a, b; Bohuš, 1993; Bohuš et al., 1999; Korňan, 1996,

2004, 2009a, b, 2011, 2013; Fiala, 1997; Kocian, 1998; Lešo, 2001; Pochopová, Kropil, 2002; Ceľuch, Kropil, 2004; Baláž, Kocian, 2006; Baláž, Balážová, 2012). These studies are similar from methodological aspects that enable comparability of results on national and continental scale. Mapping method was accepted as a standard bird census technique to estimate breeding bird population densities. The vast majority of the study plots have been censused for 2–3 years.

The Šútovská dolina National Nature Reserve by its extend of 526.65 ha represents one of the largest tracks of natural Western Carpathian mixed forests in the Malá Fatra National Park (Krivánska Fatra Mts). The reserve was established in 1967 primarily for the protection of preserved complexes of typical Carpathian Mountain and high mountain forest for scientific, educational and cultural objectives. Šútovská Dolina NNR was subject of ornithological research of Saniga (1993a) and Topercer (1996) in the frame of doctoral dissertations that were later published (Saniga, 1993b, 1995; Topercer, 1997, 1998). Saniga (1993b) studied bird assemblages in the territory of the reserve in three seasonal aspects (spring, summer and winter) in 1990 by belt transect method. He analyzed species structure, density and dominance in three plots of distinct plant communities. Saniga (1995) studied the breeding bird assemblages from fir-beech vegetation belts to dwarfed pine vegetation belts in the Malá and Veľká Fatra Mts by the strip transect method during the period 1989–1991. In total, he set 20 bird count transects in four vegetation belts; out of them, one transect was placed in the Šútovská valley. The author did not analyze bird count data separately in each transect, he presented only pool data of species structure, density, dominance, Shannon species diversity and evenness for each vegetation belt. Topercer (1997, 1998) studied seasonal dominance patterns in bird assemblages of mountain valley gradients in selected valleys of high mountains in Slovakia including the Šútovská valley. Taking into consideration lack of more accurate census studies of breeding bird assemblage in this valuable forest reserve, we decide to apply combined version of mapping method, one of the most accurate bird census techniques, to analyse the breeding bird assemblage.

The objectives of this paper were as follows:
1. To analyse quantitative structure of the interior bird assemblage from the aspects of species richness, abundance, population densities, dominance, diversity and evenness;
2. To compare the analysed beech-spruce forest with similar mixed forests studied by the same census method in Slovakia (Kropil, 1996a, b; Pochopová, Kropil, 2002; Ceľuch, Kropil, 2004; Korňan, 2004, 2013; Baláž, Kocian, 2006).

Material and methods

Study area

The study was conducted in the Šútovská dolina NNR (526.65 ha), Malá Fatra Mts, NW Slovakia (Fig. 1). The approximate geographic coordinates in the system WGS84 corresponding to the 20 ha census plot (500×400 m) corners (see Fig. 1) are (1) 49°11′16.70″N, 19°05′45.88″E; (2) 49°11′29.08″N, 19°05′30.08″E; (3) 49°11′08.38″N, 19°05′31.10″E; (4) 49°11′20.71″N, 19°05′15.07″E. The study plot represents a climax stage of Western Carpathian temperate mixed forest. The plot was approximately situated in the elevation 925–1177 m a.s.l. Two mountain streams run in the plot and create deep channels surrounded by vegetation. In summer, both streams usually dry out. The reserve belongs to a cold mountainous climatic zone with the mean July air temperatures of 10–12 °C. The total mean annual precipitation varies between 1200–1600 mm (Miklós et al., 2002).

The census plot vegetation structure was estimated from the forestry database of the National Forest Centre in Zvolen (state to 1 January 2002). The plot is situated in the forest segments 19 (overlap 0.09%), 20A (24.20%), 20B
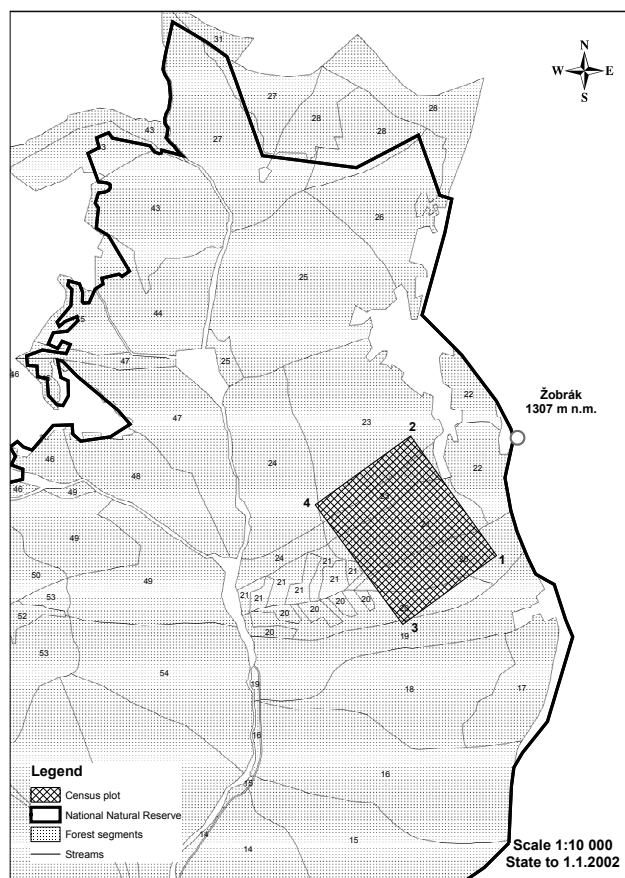
Fig. 1. Map of the 20 ha (500×400 m) census plot in the Šútovská dolina NNR, the Malá Fatra Mts., Slovakia. The exact geographic coordinates of the plot corners in WGS 84 are indicated in the section Study area. The digital layers for the map construction were given by the National Forest Centre in Zvolen.

(7.86%), 21A (0.001%), 21B (37.97%), 23 (14.52%) and 23 (15.29%) and 24 (0.06%). The age of forest stand in the segment 19 was estimated at 150 years, in the segment 20A at 160 years, in the segment 20B at 160 years, in the 21A at 130 years, in the 21B at 135 years, in the both segments 23 at 160 years and in the 24 at 160 years.

The study plot is dominated by beech *Fagus sylvatica* (69.0%, mean height 19.7 m), Norway spruce *Picea abies* (21.8%, mean height 27.5 m), silver fir *Abies alba* (6.1%, mean height 26.7 m) and sycamore *Acer pseudoplatanus* (3.1%, mean height 19.0 m). The mean canopy height in the census plot was estimated on 22.8 m. The shrub layer is relatively poorly developed and mainly consists of hazel *Corylus avellana* and saplings of the dominant tree species. The herb layer is mainly composed *Dryopteris filix-mas*, *Athyrium filix-femina*, *Rubus* spp., *Impatiens glandulifera*, *Senecio nemorensis*, *Oxalis acetosella*, *Galium odoratum*, *Dentaria bulbifera*, *Lunaria rediviva*, *Homogyne alpina*, *Luzula nemorosa*, *Calamagrostis arundinacea* and small shrubs *Vaccinium myrtillus*.

Bird censusing

Population densities were estimated by the combined version of the mapping method (Tomiałojć, 1980; Korňan, 1996). In order to construct an effective orientation system within the study plot, a 50×50 m grid system based on a colour plastic tape marking on tree trunks was established in the 20 ha (500×400 m) rectangular study plot. Breeding bird censuses were carried out in the years 2000–2002 from April to mid-July. Totally, 10 (2000: PA observer and analyst; 2001: PA observer and partly analyst, MK partly analyst; 2002: PA partly observer, MK partly observer and analyst) valid census visits per breeding season were performed in the time period beginning at 04:30 and ending usually by 9:00 CET (sometimes by 10:00 CET) for morning visits, from 16:00 to 19:30 CET for evening visits and from 19:00 to 22:00 CET for night visits. Proportion of evening visits was always two out of the total number of visits. In the beginning of April, one night visit focused on owl registrations was carried out. The study design controlled effects of weather and season on density estimates.

Each visit involved walking and mapping 100 m alternate grid lines beginning at the one plot edge and ending on the opposite. The starting point and direction of observer movement were regularly switched so that census timing during season between different parts of the plot was similar. While censusing, all acoustic and visual registrations,

found nests or other important data related to bird occurrence and dispersal patterns were recorded onto the visit maps of the scale 1:1667. A special attention during census visits was paid to contemporary contacts of territorial singing males so that the neighbouring territories could have been correctly distinguished. Some bird species, e.g. *Turdus philomelos*, *Muscicapa striata*, *Certhia familiaris*, *Columba* ssp., *Pyrrhula pyrrhula* and *Coccothraustes coccothraustes* caused considerable problems during census and interpretational procedure. Censusing and the identification of territories on the species maps was based on recommendations of Nilsson (1977), Svensson (1978, 1980), Tomiałojć (1980, 2004), Tomiałojć and Lontkowski (1989), Morozov (1994), Korňan (1996) and Walankiewicz et al. (1997). In order to correctly identify the proportions of edge territories in the study plots, bird registrations were recorded to 100 m distance behind the plot edge lines. Overlap of edge territories to the study plot was estimated on ¼, ⅓, ½, however, only species with abundance even or higher than 0.5 pair per study plot were included in the total count of breeding pairs (territories). Any further details regarding the mapping procedure and the principles of species map analyses are given in the Korňan's (1996) thesis.

Registrations of individual species from visit maps were transferred to species maps using number order beginning from the first species record in the plot. The criteria for territory interpretation were principally based on the IBCC (1969) recommendations. However, in the case of some secretive species or species with not well-evolved territorial behaviour (mentioned above), species specific minimum number of registration (acceptance level of territory) and other criteria required to accept a cluster as a territory may have been modified (Svensson, 1978). Especially useful information on dispersal patterns of these species in the plot were gained during independent plot visits when foraging bird observations were recorded that was a part of another study (Korňan, 2000; Adamík et al. 2003; Korňan, Adamík, 2007). In the case of species with abundance <0.5 pair per plot, only breeding presence '+' denoting the stationary occurrence of a part of bird territory within the boundaries of a plot was stated. This symbol was primarily used for the species with territory sizes much larger to the study plot size such as some woodpeckers, owls, birds of prey and corvids (Tomiałojć, 1980; Korňan, 1996). Species with trace population densities that bred in the reserve (the same habitat), but outside the study plot were marked by new symbol "o+" (Korňan 2004).

Statistical analyses

Bird assemblage structure was analyzed on population abundance, density, species diversity, evenness and species–area relationship (rarefaction). Standard deviation was applied to measure the variability between years. The use of $n - 1$ in the denominator was applied instead of n in the SD formula. Coefficient of variation was applied to measure the relative dispersion in the sample. It is the standard deviation divided by the mean ($CV = SD / \bar{x} \cdot {}^*100$). Species with abundance lower that 0.5 pair per study plot had 0 value for the calculations of variation measures.

Species diversity and evenness were measured by two common formulas – Shannon diversity index as information theory measure and Simpson index as measure of concentration (Magurran, 1988). In addition, the rarefaction as an alternative to traditional diversity indices was also applied (Hurlbert, 1971; Heck et al., 1975). To include species with very low population densities (+) to computation of species diversity and evenness, constant numbers of densities (see Table 1 for the constant values) were added to these species. Species diversity indices, rarefaction values and curves, evenness, and variability measures were calculated in MS Excel 2007 and Maxima 5.17.0.

Only the mathematical formulas for computation of rarefaction and evenness are presented further:
Evenness (equitability):

$$E = \frac{DIV}{DIV_{MAX}} \ ,$$

where *DIV*, is the species diversity measured according to Shannon or Simpson formulas and and DIV_{MAX} is the maximal theoretical value of these indices.
Rarefaction (James, Rathbun, 1981):

$$E(Sn) = \sum_{i=1}^{S} \left[1 - \frac{\dbinom{N - N_i}{n}}{\dbinom{N}{n}} \right] \ ,$$

where $E(Sn)$ is an expected number of species in a random sample of n individuals drawn without replacement from N individuals, S is the total number of species found in the study plot in a year and N_i is the number of individuals in species i.

T a b l e 1. Year and mean abundance, density and dominance of the breeding bird assemblage of the natural beech-
-spruce forest in the Šútovská dolina NNR.

Species	Abundance			Density (pairs/10 ha)				Dominance (%)				SD	CV
	2000	2001	2002	2000	2001	2002	$\bar{x}$	2000	2001	2002	$\bar{x}$		(%)
1. F. coelebs	22.6	28.6	32.4	11.30	14.30	16.20	13.93	25.28	23.29	28.62	25.73	2.69	10.47
2. E. rubecula	7.6	13.4	9.4	3.80	6.70	4.70	5.07	8.50	10.91	8.30	9.24	1.45	15.72
3. S. atricapilla	7.6	8.2	8.4	3.80	4.10	4.20	4.03	8.50	6.68	7.42	7.53	0.92	12.17
4. P. ater	7.6	8.6	7.9	3.80	4.30	3.95	4.02	8.50	7.00	6.98	7.49	0.87	11.63
5. R. regulus	5.6	7.5	5.3	2.80	3.75	2.65	3.07	6.26	6.11	4.68	5.68	0.87	15.33
6. C. familiaris	6.2	4.7	6.0	3.10	2.35	3.00	2.82	6.94	3.83	5.30	5.35	1.55	29.03
7. F. albicollis	4.0	6.2	5.5	2.00	3.10	2.75	2.62	4.47	5.05	4.86	4.79	0.29	6.11
8. T. troglodytes	4.0	6.7	5.0	2.00	3.35	2.50	2.62	4.47	5.46	4.42	4.78	0.58	12.21
9. P. modularis	4.4	5.3	5.5	2.20	2.65	2.75	2.53	4.92	4.32	4.86	4.70	0.33	7.09
10. P. collybita	3.0	4.5	5.8	1.50	2.25	2.90	2.22	3.36	3.66	5.12	4.05	0.94	23.33
11. P. sibilatrix	4.2	4.0	4.0	2.10	2.00	2.00	2.03	4.70	3.26	3.53	3.83	0.76	19.97
12. S. europaea	2.6	4.8	2.0	1.30	2.40	1.00	1.57	2.91	3.91	1.77	2.86	1.07	37.46
13. T. merula	1.0	2.8	2.8	0.50	1.40	1.40	1.10	1.12	2.28	2.47	1.96	0.73	37.44
14. T. philomelos	2.0	1.5	2.0	1.00	0.75	1.00	0.92	2.24	1.22	1.77	1.74	0.51	29.18
15. F. parva	–	1.5	2.7	0.00	0.75	1.35	0.70	0.00	1.22	2.39	1.20	1.19	99.21
16. P. pyrrhula	1.0	2.0	1.0	0.50	1.00	0.50	0.67	1.12	1.63	0.88	1.21	0.38	31.48
17. C. coccothraustes	2.0	1.0	1.0	1.00	0.50	0.50	0.67	2.24	0.81	0.88	1.31	0.80	61.17
18. P. phoenicurus	+	2.0	1.5	{0.10}	1.00	0.75	0.62	0.00	1.63	1.33	0.98	0.87	87.96
19. T. viscivorus	+	2.0	1.0	{0.10}	1.00	0.50	0.53	0.00	1.63	0.88	0.84	0.82	97.37
20. C. oenas	1.0	2.0	o+	0.50	1.00	{0.05}	0.52	1.12	1.63	0.00	0.92	0.83	90.97
21. C. palumbus	1.0	2.0	o+	0.50	1.00	{0.05}	0.52	1.12	1.63	0.00	0.92	0.83	90.97
22. T. torquatus	+	1.0	1.0	{0.10}	0.50	0.50	0.37	0.00	0.81	0.88	0.57	0.49	86.82
23. C. spinus	1.0	p	1.0	0.50	0.00	0.50	0.33	1.12	0.00	0.88	0.67	0.59	88.38
24. P. palustris	–	1.0	1.0	0.00	0.50	0.50	0.33	0.00	0.81	0.88	0.57	0.49	86.82
25. A. trivialis	1.0	o+	+	0.50	{0.05}	{0.10}	0.22	1.12	0.00	0.00	0.37	0.65	173.21
26. R. ignicapilla	–	1.0	+	0.00	0.50	{0.10}	0.20	0.00	0.81	0.00	0.27	0.47	173.21
27. C. caeruleus	–	p	1.0	0.00	0.00	0.50	0.17	0.00	0.00	0.88	0.29	0.51	173.21
28. P. montanus	+	0.5	o+	{0.10}	0.25	{0.05}	0.13	0.00	0.41	0.00	0.14	0.24	173.21
29. A. chrysaetos	+	+	+	{0.001}	{0.001}	{0.001}	0.00	–	–	–	–	–	–
30. C. canorus	+	+	+	{0.10}	{0.10}	{0.10}	0.00	–	–	–	–	–	–
31. S. aluco	+	+	+	{0.01}	{0.01}	{0.01}	0.00	–	–	–	–	–	–
32. D. martius	+	+	+	{0.10}	{0.10}	{0.10}	0.00	–	–	–	–	–	–
33. D. leucotos	+	+	+	{0.10}	{0.10}	{0.10}	0.00	–	–	–	–	–	–
34. C. corax	+	+	+	{0.004}	{0.004}	{0.004}	0.00	–	–	–	–	–	–
35. A. nisus	+	+	–	{0.01}	{0.01}	0.00	0.00	–	–	–	–	–	–
36. B. buteo	+	+	–	{0.004}	{0.004}	0.00	0.00	–	–	–	–	–	–
37. P. tridactylus	+	o+	+	{0.10}	{0.05}	{0.10}	0.00	–	–	–	–	–	–
38. P. trochilus	+	o+	+	{0.10}	{0.05}	{0.10}	0.00	–	–	–	–	–	–
39. N. caryocatactes	+	+	–	{0.10}	{0.10}	0.00	0.00	–	–	–	–	–	–
40. T. bonasia	+	o+	o+	{0.10}	{0.05}	{0.05}	0.00	–	–	–	–	–	–
41. S. rusticola	+	o+	–	{0.10}	{0.05}	0.00	0.00	–	–	–	–	–	–
42. P. canus	–	o+	+	0.00	{0.05}	{0.10}	0.00	–	–	–	–	–	–
43. M. striata	–	o+	+	0.00	{0.05}	{0.10}	0.00	–	–	–	–	–	–
44. G. glandarius	+	o+	–	{0.10}	{0.05}	0.00	0.00	–	–	–	–	–	–
45. A. funereus	+	–	–	0.05	0.00	0.00	0.00	–	–	–	–	–	–
46. P. cristatus	–	+	–	0.00	{0.10}	0.00	0.00	–	–	–	–	–	–
47. P. major	+	–	–	{0.10}	0.00	0.00	0.00	–	–	–	–	–	–
48. A. caudatus	–	–	+	0.00	0.00	{0.10}	0.00	–	–	–	–	–	–
49. L. curvirostra	+	p	–	{0.10}	0.00	0.00	0.00	–	–	–	–	–	–
50. D. urbica	p	p	p	0.00	0.00	0.00	0.00	–	–	–	–	–	–
51. T. urogallus	–	p	p	0.00	0.00	0.00	0.00	–	–	–	–	–	–
52. F. peregrinus	–	p	–	0.00	0.00	0.00	0.00	–	–	–	–	–	–
53. M. cinerea	–	–	p	0.00	0.00	0.00	0.00	–	–	–	–	–	–
Total	89.4	122.8	113.2	44.70	61.40	56.60	54.23	100.00	100.00	100.00	100.00	8.60	15.85

Notes: SD – standard deviation of density, CV – coefficient of variation of density.
Plus sign (+) indicates breeding abundance <0.5 territory (pair) per study plot; 'o+' indicates breeding presence in the reserve, but the species was not detected as breeder in the study plot; 'p' is used for species detected in the study plot as non-breeders or rare visitors; '–' indicate absence. In the density columns, density estimates for '+' and 'o+' species are given by qualified guess based on observation in the reserve and the national park. The density estimates in parenthesis {} were only roughly estimated for calculation of diversity indices and rarefaction of the assemblage.

Results

Species richness and assemblage structure similarity

Totally, 53 species including vagrants were detected in the reserve during the period 2000–2002, out of which 49 were breeders (Tables 1 and 2). The mean yearly species richness in the reserve was 41.33 species. Forty-nine breeders were also recorded in the study plot; the mean species richness in the plot was 37.33 species. The highest number, 41 species, was found in 2000, while the lowest species richness, 35 species, was recorded in 2001. Thirty-four species were constantly recorded in the study plot in each year of the study period, while 15 species occurred only in some of the years. In fact, five of them bred in the plot in 2 years and 10 species nested only in 1 year of the 3-year study period.

T a b l e 2. Estimates of bird species diversity and evenness of the natural beech-spruce forest in the Šútovská dolina NNR by standard indices and rarefaction.

Diversity measures	2000	2001	2002	Mean	SD	CV
Total number of species	42	47	43	44.00	2.65	6.01
Total number of breeders	41	43	40	41.33	1.53	3.70
Number of breeders in plot	41	35	36	37.33	3.22	8.61
Shannon (H')	3.97	4.04	3.90	3.97	0.07	1.74
Simpson (D)	0.90	0.91	0.89	0.90	0.01	1.15
Rarefaction E ($S_{50\,pairs}$)	16.51	17.32	16.61	16.81	0.44	2.60
Rarefaction E ($S_{100\,pairs}$)	20.70	21.55	20.82	21.02	0.46	2.18
Rarefaction E ($S_{5\,ha}$)	11.64	13.85	12.82	12.77	1.10	8.64
Rarefaction E ($S_{10\,ha}$)	16.00	18.61	17.44	17.35	1.31	7.54
Evenness measures						
Evenness Shannon (J')	0.74	0.79	0.75	0.76	0.02	3.14
Evenness Simpson (ED)	0.24	0.31	0.25	0.27	0.04	13.58

Notes: Only species breeding within the 20 ha study plot were taken into the calculations (including species marked as '+'). Shannon index is calculated in bites.

The similarity of assemblage structure between years was compared by the qualitative Sørensen similarity index and quantitative Czekanowski–Sørensen similarity index. The qualitative Sørensen index had values of 0.75–0.82. The highest similarity (0.82) was found between years 2000 and 2001, whereas the qualitative comparison of the years 2000 and 2002 showed the lowest value of 0.75. A little higher similarity (0.79) was detected between years 2001 and 2002. The Czekanowski–Sørensen similarity index reached values of 0.79–0.87. The highest similarity value 0.87 was detected between the years 2001 and 2002, while the lowest value of quantitative comparison was found between the years 2000 and 2001. Intermediate value (0.83) was found between the years 2000 and 2002. Similarity measurement indicated relatively low between year variability of the assemblage from qualitative and quantitative species structure. Consequently, the studied assemblage seems to be stable regarding species structure.

The total mean breeding bird assemblage density of the beech-fir forest was 54.23 pairs/10 ha (further p/10 ha) in the 3-year period (2000–2002). The highest total assemblage density, 61.40 p/10 ha, was found in 2001, while the lowest value, 44.70 p/10 ha, in 2000. The quantitative species structure of the breeding bird assemblage is presented in Table 1 and the community curve of the assemblage is given in Fig. 2. Standard deviation of total assemblage density was 8.60 p/10 ha and coefficient of variation was 15.85%, which indicate relatively high between year stability.
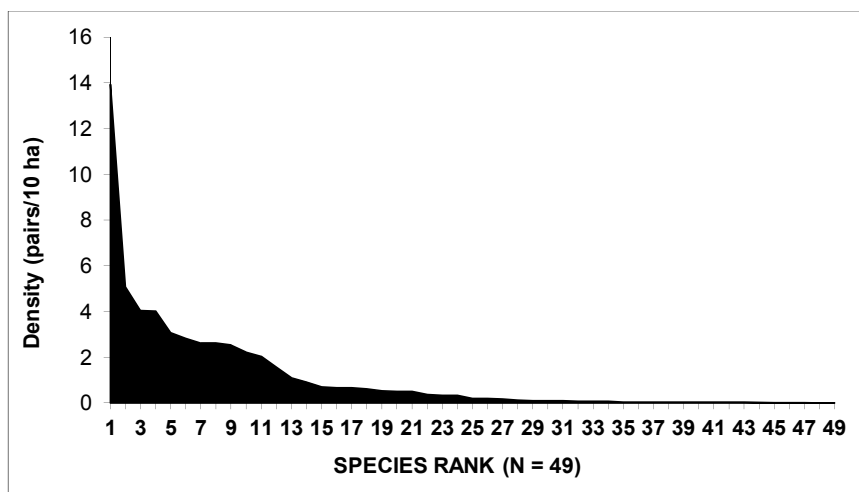
Fig. 2. Assemblage curve of the breeding bird assemblage of the natural mixed forest in the Šútovská dolina NNR. Pooled data from the years 2000–2002 were used. Only species breeding in the 20-ha study plot are ordered. Species are ranked in descending order.

Eudominant species ($x \geq 10\%$) contributed 25.73 % to the total assemblage abundance based on mean values. The yearly variation was 25.28–34.20%. Only one species, *Fringilla coelebs*, belonged to this dominance class when considering the mean values. *Erithacus rubecula* belonged to this class in 2001, when it reached the dominance value of 10.91%. Eudominant species had to reach the minimum year density of 6.70 p/10 ha. Dominant species ($5\% \leq x < 10\%$) contributed by 35.31% to the mean total assemblage abundance, with a yearly variation between 30.29% and 38.70%. In total, five species (*E. rubecula*, *Sylvia atricapilla*, *Periparus ater*, *Regulus regulus* and *Certhia familiaris*) can be characterised as dominants based on the mean values. *Erithacus rubecula* did not belong to this dominance category in 2001 when it was classified as a eudominant. *Regulus regulus* belonged among subdominants in 2002 when it reached dominance only 4.68%. Same happened with *Certhia familiaris* in 2001 when it had dominance only 3.83%. All dominant species reached yearly density at least 3.00 p/10 ha.

Subdominant species ($2\% \leq x < 5\%$) represented 25.01% of the total assemblage abundance with the annual variation between 21.25 and 29.31%. Based on mean dominance val-

ues, six species (*Ficedula albicollis*, *Troglodytes troglodytes*, *Prunella modularis*, *Phylloscopus collybita*, *Phylloscopus sibilatrix*, *Sitta europaea*) can be classified as the subdominants. The first five species belong into this dominance class constantly every year, whereas *S. europaea* reached the dominance of only 1.77% in 2001 and belonged among recedent species. All subdominant species reached population densities at least 1.30 p/10 ha.

Recedent species (1% ≤ *x* < 2%) contributed by 7.42% to the total assemblage abundance taking mean values with the yearly variation of 4.86–10.59%. Totally, five species (*Turdus merula*, *T. philomelos*, *Ficedula parva*, *Pyrrhula pyrrhula* and *Coccothraustes coccothraustes*) belong to this group based on mean values. *Ficedula parva* is absent in the year 2000. *Coccothraustes coccothraustes* belonged among subrecedents in 2001–2002 and *Pyrrhula pyrrhula* in 2002. All recedent species reached population density at least 0.5 p/10 ha.

Subrecedent species (*x* < 1) represented 6.53% to the total assemblage abundance (range 0–6.18) based on mean values. In total, 32 species belonged to the subrecedents, however only 9 species (*Phoenicurus phoenicurus*, *Turdus viscivorus*, *T. torquatus*, *Aquila chrysaetos*, *Cuculus canorus*, *Strix aluco*, *Dryocopus martius*, *Dendrocopos leucotos* and *Corvus corax*) bred in the study plot in all years.

Species diversity and evenness

Commonly used diversity indices such as Shannon and Simpson and rarefaction were applied to estimate diversity and evenness of the assemblage in individual years. Relationship between expected species richness estimated by rarefaction and increasing number of territorial pairs and area is displayed in Figs 3a, b. Mean and yearly values of the diversity measures, their SD and CV are presented in Table 2. Both indices and rarefaction detected the highest species diversity in 2001; however the trends of values were different between indices and rarefaction. The indices detected the lowest diversity in 2002, whereas the rarefaction in 2000.
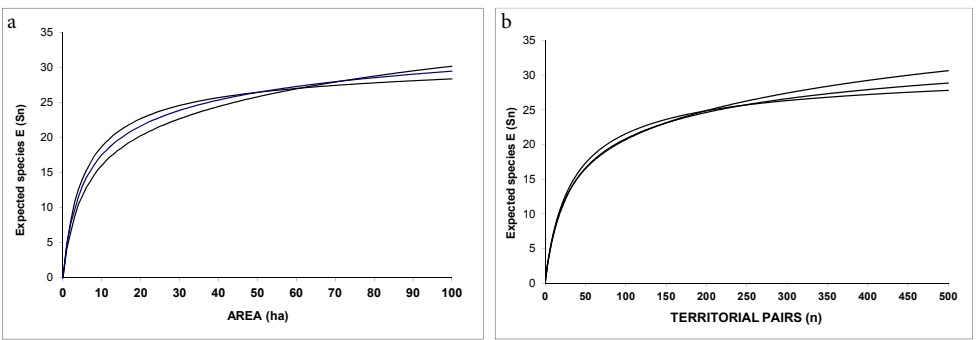

Fig. 3. Rarefaction curves for year samples 2000–2002 of the 20-ha mixed forest census plot in the Šútovská dolina NNR. Figures shows the relationship between expected species richness *E (Sn)* estimated by rarefaction and increasing samples of area (a) and territorial pairs (b). The calculations are based on year density data including species with very low population densities (+). For these species, density estimates given in parenthesis in Table 1 were used for calculations.

Evenness based on Shannon and Simpson diversity indices showed similar trend of values (Table 2). The highest evenness was observed in 2001, while the lowest was detected in 2000. In fact, the differences between the years 2000 and 2002 were very low (Table 2).

Discussion

Comparison of species richness, diversity and evenness with the primeval and natural Western Carpathian mixed forests

Up to now, seven studies of breeding bird assemblages of primeval and natural mixed forest in Slovakia censused by the mapping method was published so far (Table 3). Studies were conducted during the period 1990–2006. Bird censusing in these studies was carried out during three breeding seasons, except the Šrámková NNR where censuses were conducted over 10-year period. Size of census plots varied from 12 to 27.5 ha. All study plots reached relatively high mean species richness of breeders per plot ranging from 32.7 species in the Veľká Stožka NNR and the Osobitá NNR to 39 species in the Šrámková NNR. The Šútovská dolina NNR with the mean species richness of 37.3 species was the second highest in the study. Shannon diversity index is probably the most widely used measure of diversity worldwide, so we used it to compare between sample diversity in our sample size (Table 3) and to enable comparison with other studies. The highest mean Shannon diversity value, 4.45 bites, was observed in the Badín primeval forest NNR, while the lowest value, 3.63 bites, was found in the Osobitá NNR. The breeding bird assemblage in the Šútovská dolina NNR reached second lowest mean Shannon diversity value, 3.97 bites.

Several authors (e.g. Hurlbert, 1971; James, Rathbun, 1981) concluded that most of these commonly used measures of biological diversity including Shannon index are in many situations inappropriately used as indicators of biological diversity. In addition, their application involves a significant loss of information, because indices confound several community parameters, e.g. number of species, their relative abundances and area sampled into one non-metric number. In summary, differences attributable to the accumulation of species with increasing area are ignored, and many combinations of species richness and relative abundance can produce the same value of the index (James, Ratbun, 1981). One of the alternatives to overcome this problem is the application of rarefaction (Hurlbert, 1971; Heck et al., 1975). In this study, rarefaction was applied in order to compare between season species richness by standardising samples to equal number of individuals and equal-sized plots (Table 3). Rarefaction estimated on a standardised number of pairs reached the highest value, 20.23 species, in the Badín primeval forest NNR, yet the lowest value, 14.67 species, was found in the Osobitá NNR. The breeding bird assemblage in the Šútovská dolina NNR had second lowest rarefaction value, 16.81 species estimated in a sample of 50 pairs. The rarefaction calculated on standardised area of 10 ha showed different rank of sites (Table 3). The highest value, 23.03 species was found in the Badin primeval forest NNR, while the lowest rarefaction value, 15.96 species, was detected in the Osobitá NNR. The rarefaction diversity estimate, 17.35 species on 10 ha area, of the breeding bird assemblage in the Šútovská dolina NNR stayed on the fifth place in the sample of mixed forests. Taking into consideration the diversity values

T a b l e 3. Comparison of breeding bird assemblage structure of primeval and natural mixed forests in Slovakia.

Sites	Šútovská dolina NNR	Šrámková NNR	Badín primeval forest NNR	Dobroč primeval forest NNR	Veľká Stožka NNR	Pod Latiborskou hoľou NNR	Osobitá NNR
Author/s	This study	Korňan (2004, 2013)	Kropil (1996b)	Kropil (1996a)	Pochopová, Kropil (2002)	Čeluch, Kropil (2004)	Baláž, Kocian (2006)
Orographic range	Malá Fatra Mts.	Malá Fatra Mts.	Kremnické Hills	Veporské Hills	Muránska planina	Low Tatras Mts.	Western Tatras Mts.
Area (ha)	20	27.5	16	24	20.36	150	12
Age of forest stand/s	130–160	200–250	210–400	220–450	140–150	100–120	100–120
Dominant trees	F. sylvatica 69%, P. abies 22%, A. alba 6%, A. pseudopla. 3%	F. sylvatica 45%, A. alba 20%, P. abies 5%, A. pseudopla. 4%	F. sylvatica 74%, A. alba 18%	F. sylvatica 45%, A. alba 30%, P. abies 23%	P. abies 36%, F. sylvatica 33%, L. decidua 25%	F. sylvatica 48%, P. abies 23%, A. alba 14%, A. pseudopla. 13%	F. sylvatica 45%, Picea abies 40%, A. alba 5%, A. pseudopla. 5%
Census years	2000–2002	1997–2006	1990–1992	1990–1992	1999–2001	1999–2001	2004–2006
Total density (p/10 ha)	54.2	59.5	71.0	62.6	37.5	63.3	64.6
Rarefaction E ($S_{10\,ha}$)	17.35	19.36	23.03	20.35	16.07	19.44	15.96
Rarefaction E ($S_{5\,ha}$)	12.77	14.20	17.17	14.83	10.94	14.31	12.13
Rarefaction E ($S_{50\,pairs}$)	16.81	18.23	20.23	18.60	18.20	17.75	14.67
Evenness (J)	0.76	0.79	0.86	0.82	0.83	0.82	0.72
Species diversity (H)	3.97	4.17	4.45	4.23	4.16	4.06	3.63
Mean breeder richness per plot	37.3	39.0	36.0	36.0	32.7	31.3	32.7
Density of dominants (p/10 ha)							
1. F. coelebs	13.9	13.0	10.6	10.9	6.4	14.8	17.8*
2. E. rubecula	5.1	5.1	7.3	7.6	5.0	7.1	5.5
3. S. atricapilla	4.0	4.3	—	—	—	—	3.8
4. P. ater	4.0	4.2	—	7.2	4.8	5.0	10.3
5. R. regulus	3.1	3.5	—	4.0	—	3.4	4.4
6. C. familiaris	2.8	—	—	—	—	—	—
7. P. collybita	—	5.9	—	—	—	—	—
8. P. modularis	—	3.1	—	—	3.2	—	—
9. P. sibilatrix	—	—	—	—	—	—	—
10. C. oenas	—	—	5.8	—	—	—	—
11. T. troglodytes	—	—	4.3	—	—	5.1	—
12. F. albicollis	—	—	3.9	—	—	—	—
13. S. europaea	—	—	—	3.2	—	—	—

Notes: *The values of mean species density were mistakenly calculated in the original paper; the recalculated values are presented.
Only studies in which the mapping method was applied to estimate population densities were selected. List of dominant species and basic assemblage parameters are given. The presented assemblage parameters were not calculated in all studies. Therefore, the published primary data were reanalysed and the parameters were computed. Logarithms with the base two were used for calculation of Shannon diversity index and evenness. The assemblage parameters were firstly calculated for individual years and then averaged for mean values. In cases, when tracing species (marked '+') were listed as breeders in an assemblage in any study, a constant values of density (see Table 1 for the constant values) were added to these species to include them for computations of diversity, evenness and rarefaction.

of Shannon index and rarefaction, the studied breeding bird assemblage belongs among assemblages with lower diversity in the compared sample, yet the species richness of breeders in census plot was the second highest.

Evenness based on the Shannon diversity index was the highest (0.86) in the Badín primeval forest NNR. The lowest equitability value (0.72) was found in the breeding bird assemblage of the Osobitá NNR. Our studied bird assemblage reached the second lowest evenness (0.76) from the sample.

Comparison of total density and dominant species with the primeval and natural Western Carpathian mixed forests

From the seven compared breeding bird assemblages, the highest mean total assemblage density, 71.0 p/10 ha, was detected in the Badín primeval forest NNR, while the lowest total density, 37.5 p/10 ha, was found in the Veľká Stožka NNR (Table 3). The breeding bird assemblage in the Šútovská dolina NNR reached the mean total density of 54.2 p/10 ha was the second lowest value in the sample.

In total, 13 bird species (*Certhia familiaris*, *Columba oenas*, *Erithacus rubecula*, *Ficedula albicollis*, *Fringilla coelebs*, *Periparus ater*, *Phylloscopus collybita*, *P. sibilatrix*, *Prunella modularis*, *Regulus regulus*, *Sitta europaea*, *Sylvia atricapilla* and *Troglodytes troglodytes*) were detected as dominants ($x \geq 5\%$) in the seven compared breeding bird assemblages of the mixed forests (Table 3). Only two species *Fringilla coelebs* and *Erithacus rubecula* were observed as dominants in all study plots. Both species are characterised as habitat generalists occupying wide range of habitat types in the Western Carpathians from lowlands to dwarf pine communities (Kocian, 1998; Kropil, 2002a, b; Imbeau et al., 2003). Two species *Periparus ater* and *Regulus regulus* were dominant in more than 50% of samples (Table 3). Both species can be characterised as mature forest species and coniferous specialist preferring foraging on coniferous species (Karaska, Kropil, 2002; Adamík et al., 2003; Imbeau et al., 2003) so that they represent the coniferous component of diversity. However, Krištín (2002a) stated that occurrence of *Periparus ater* in lower elevations is tied to beech. Other three species *Columba oenas*, *Ficedula albicollis* and *Phylloscopus sibilatrix* were detected as dominants only in one study plot (FA – Badín primeval forest NNR, PS – Veľká Stožka NNR, CO – Badín primeval forest NNR), yet they were detected in all study sites but with lower dominance status. Both can be characterised as mature forest species preferring broadleaved and mixed forests (Krištín, Kropil, 2002; Krištín, 2002b, Kropil, 2002c). *Ficedula albicollis* can be characterised as foraging generalist preferring wide range of foraging substrates (Korňan, 2000), whereas *Phylloscopus sibilatrix* was tied to foraging on deciduous tree species (Adamík et al., 2003). These three species can be characterised as the deciduous component of diversity of mixed forests. The other dominant species *Certhia familiaris*, *Phylloscopus collybita*, *Prunella modularis*, *Sylvia atricapilla*, *Troglodytes troglodytes*, and *Sitta europaea* can be also characterised as habitat generalists occurring in all types of forests from lowlands to dwarf pine communities.

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