Ornis Fennica 90:151–177. 2013

Breeding bird assemblage dynamics of a primaeval temperate mixed forest in the Western Carpathians (Slovakia): support for pluralistic community concept

Martin Korňan

Centre for Ecological Studies, Ústredie 14, 013 62 Veľké Rovné, Slovakia. E-mail: martin.kornan@gmail.com
and Department of Forest Protection and Game Management, Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 20, 960 53 Zvolen, Slovakia

Received 30 October 2012, accepted 11 February 2013

Structure and dynamics of breeding bird assemblages of primaeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts., Slovakia were studied during ten consecutive years 1997–2006. Bird abundances were estimated by the combined version of the mapping method in the 27.5 ha forest interior study plot. Determination of foraging guild structure was done by a posteriori approach by a numerical analysis of random point observations of foraging birds. In total, 53 bird species were recorded as breeders in the study plot, averaging 39.0 species per year. Mean value of population variability coefficient (PV) of density of the 22 most numerous species was 0.33 ± 0.14 SD (CV = 42.05%) indicating a mean difference in density among years of 33%. The highest fluctuations were detected in plant eaters (PV = 0.47, N = 3) followed by flycatchers (PV = 0.44, N = 3), herb layer foragers (PV = 0.33, N = 2), trunk foragers (PV = 0.33, N = 2), foliage gleaners (PV = 0.29, N = 8) and litter foragers (PV = 0.21, N = 4). Cluster analysis of the Pearson's correlation coefficient of species densities showed no consistent grouping according to wintering areas or guild membership. Only seven of 26 simulations by binary null models (9 algorithms, 3 indices) on assemblage level indicated negative associations. None of 9 null model simulations of density assemblage matrix (3 algorithms, 3 indices) or null model analysis of foraging guilds showed negative species associations. The results do not provide evidence for competition in the structuring of this bird assemblage, but instead support a pluralistic model of community functioning.

1. Introduction

The first community concepts proposed by Clements (1916, 1936) and Gleason (1917, 1926) offered sharply differing views on organization and functioning of communities. Clements understood community as a discrete and integrated unit of taxa, a superorganism, repeatable in space and time and possessing fundamental properties analogous to those of an individual organism. Various species were thought to coexist because of similar requirements for habitat and resources and to develop together along a deterministic path of succession, leading eventually to stable climax communities (Underwood 1986). These processes were sometimes considered akin to the ontogenetic development and growth of a single organism. In contrast, Gleason (1917, 1926) argued that communities lacked internal organisation and order, being instead a random aggregation of species that responded to environmental conditions quite independently. The opposing concepts have caused one of the major debates in ecology, and controversy in results and interpretation of scientific studies still remains (McIntosh 1995). Nevertheless, both concepts have had significant impacts on the development of ecological theory. Levin (1988) concluded that the mathematical theory of community ecology emerged from the Clementsian approach and paid attention to equilibrium, constancy, homogeneity and predictability. On the other hand, extreme interpretation of Gleason's view lead to the concept that communities were only random aggregations of species and led to the development and application of null models in ecology (Caswell 1976, Connor & Simberloff 1979, Gotelli 2000, Ulrich & Gotelli 2010).

Independent community concept based on the notion that interspecific competition is the main force of nature influencing structure and functioning of communities has developed in parallel (Wiens 1989) taken the ideas from Gause's (1934) competitive exclusion principle, Mayr's (1942) views on speciation, and the theory of niche (Hutchinson 1957).The theory of competition was dominant in the ecological literature until the beginning of the 1980s. In fact, competition was believed to be the main natural factor affecting survival of species. The theory of competition emphasized the importance of interactions and interdependence among species in producing structured community patterns (Wiens 1989). This lead to the creation of the idea that communities are organized by so called "assembly rules" (Diamond 1975). This notion, in principle, was consistent with the Clementsian community concept.

The theory of competition predicts that guild members (species with similar resource requirements) should have at least partly negative associations in space and time when resources are limited. Many studies of bird assemblages failed to support this prediction (Enemar *et al.* 1984, James & Boecklen 1984, Mountainspring & Scott 1985, Holmes *et al.* 1986, Hogstad 1993, Morozov 1993, Enemar *et al.* 1994, Wesołowski & Tomiałojć 1997, Leito *et al.* 2006, Wesołowski 2007, Houlahan *et al.* 2007). Findings and conclusions of these studies argue against the existence of tightly organized bird assemblages primarily structured by competition, and support what has been referred to as the "pluralistic concept" (Holmes *et al.* 1986, Holmes 2011). This concept views a community as a set of interacting individual populations existing at a variety of spatial and temporal scales. Holmes *et al.* (1986) concluded that the model forest bird assemblage of a deciduous forest in the northeastern USA is influenced and regulated by at least five major factors: (1) food abundance, (2) stochastic weather events, (3) habitat change, (4) interspecific aggression, a form of interspecific competition, and (5) mortality during winter. They further summarize that it appears that the relative importance of these factors differs among species such that the dynamics of each species is driven by a different combination of factors and events. This model can be generalized with certain specific local limitations to other communities. In addition, other factors such as predation (Martin 1993, Wesołowski & Tomiałojć 2005, Weatherhead *et al.* 2010), parasitism (Brown *et al.* 1995, Dudaniec *et al.* 2007), brood parasitism (Goguen & Mathews 1998, Powell & Steidl 2000, Curson *et al.* 2010), multiple density dependent processes (Holmes 2011), environmental disturbance (Fuller 2000, Greenberg *et al.* 2001, Hirao *et al.* 2008, Russell *et al.* 2009), heterospecific attraction (Mönkkönen *et al.* 1990, Forsman *et al.* 1998, Sebastian-Gonzalez *et al.* 2010) and pollution (Flousek 1989, Rheindt 2003, Kempenaers *et al.* 2010) may also affect structure, dynamics and functioning of bird assemblages.

Based on a number of studies, new interactions among species within communities have been described, namely facilitation and indirect effects among competitors (Lortie *et al.* 2004). These findings do not support the Gleasonian individualistic concept. In fact, real communities will hardly ever function as either groups of individual species as understood by Gleason or as communities of perfectly integrated species following the Clementsian concept. Consequently, communities reach a range of different dependencies among species or degrees of integration with variation in space and time (Lortie *et al.* 2004). Applying these notions, Lortie *et al.* (2004) proposed for plant communities the latest concept called the "integrated community concept". The basic principles of this concept can be also applied to ecological communities in general. They predict that community structure is inclusively determined by synergistic (non-linear) interactions among (1) stochastic processes, (2) the specific tolerances of species to a suite of local abiotic conditions, (3) positive and negative direct and indirect interactions among plant species, and (4) direct interactions with other organisms (Lortie *et al.* 2004). For the general community concept, the third point can be generalized across all species and thus the fourth point is redundant and can be omitted.

As an alternative to niche theory, Hubbell (2001) proposed "the unified neutral theory of biodiversity and biogeography" assuming that interactions among species are weak so that abundance patterns are determined by random/stochastic processes alone. The theory has been viewed that species coexist without niche differences, without fitness differences, or simply that all species have equal probability of success (Clark in press). This theory has been shown to be capable of giving reasonable predictions of empirical patterns of natural communities. The theory has many supporters on the one hand and opponents on the other (e.g., Rosindell *et al.* 2011, Clark in press). Houlahan *et al.* (2007) analyzed the Hubbell's theory and reached conclusion that the Hubbell's zero-sum community dynamics implies negative covariance among population abundances within communities. In contrast, a meta-analysis of long term community studies showed positive associations, thus not supporting the unified neutral theory (Houlahan *et al.* 2007).

Primaeval forests are defined as original continuously growing forests influenced and determined only by natural factors without any perceivable direct or indirect human impact (Korpeľ 1989). However, forests without indirect human influences (e.g., air pollution, climate change) do not exist anymore. Some forests remain close to the original state, and these offer a unique opportunity to study ecosystem processes of prehistoric times before human settlement when these forests covered most of the European continent (Wesołowski & Tomiałojć 1997, Wesołowski *et al.* 2010). The Šrámková National Nature Reserve represents one of the largest and best-preserved tracts of primaeval mixed forest in the Western Carpathians (Korpeľ 1989). Primaeval mixed forests in the Western Carpathians are distinctive ecosystems that occur in a transitional zone between the vegetation belts of deciduous and coniferous forests. From a biogeographic view, they represent a "natural ecotone" between these two zones where faunal elements specific for deciduous and coniferous forest occur together. In 1997, a research project was initiated to understand the structure and dynamics of the bird assemblage of this unique ecosystem. The primary aim was to gather data from a reference site for comparison with man-transformed habitats (Korňan 2000, Adamík *et al.* 2003, Adamík & Korňan 2004, Korňan 2004, Korňan & Adamík 2007).

My main objective is to analyse the dynamics of the breeding bird assemblage during ten consecutive years and to evaluate which community concept described above, fits best, with special emphasis on competitionist view of community structure. Here, I address the following questions: (1) What is the overall extent of numerical variation of species richness, total assemblage density and species densities of this bird assemblage in a near-primaeval forest? (2) What are the maximum rates of increase and decrease in the abundances of individual species between years? (3) Do densities among species and guild members vary independently, in parallel or inversely? Do these patterns of variation imply interspecific competition or whether pluralistic factors were operating? (4) Is there relationship between similarity of population dynamics among species and their migratory habits?

2. Material and methods

2.1. Study area

The study was conducted in the Šrámková National Nature Reserve (243.65 ha), Malá Fatra Mts, NW Slovakia (Fig. 1). The geographic coordinates in the system WGS84 corresponding to the bottom line of the 27.5 ha (500 × 550 m) study plot are: 49°11'11.9"–23.2"N; 19°06'37.0–51.3"E. The study plot represents the climax stage of a Western Carpathian beech-fir forest growing on hillside granite till. The forest has all the characteristic fea-

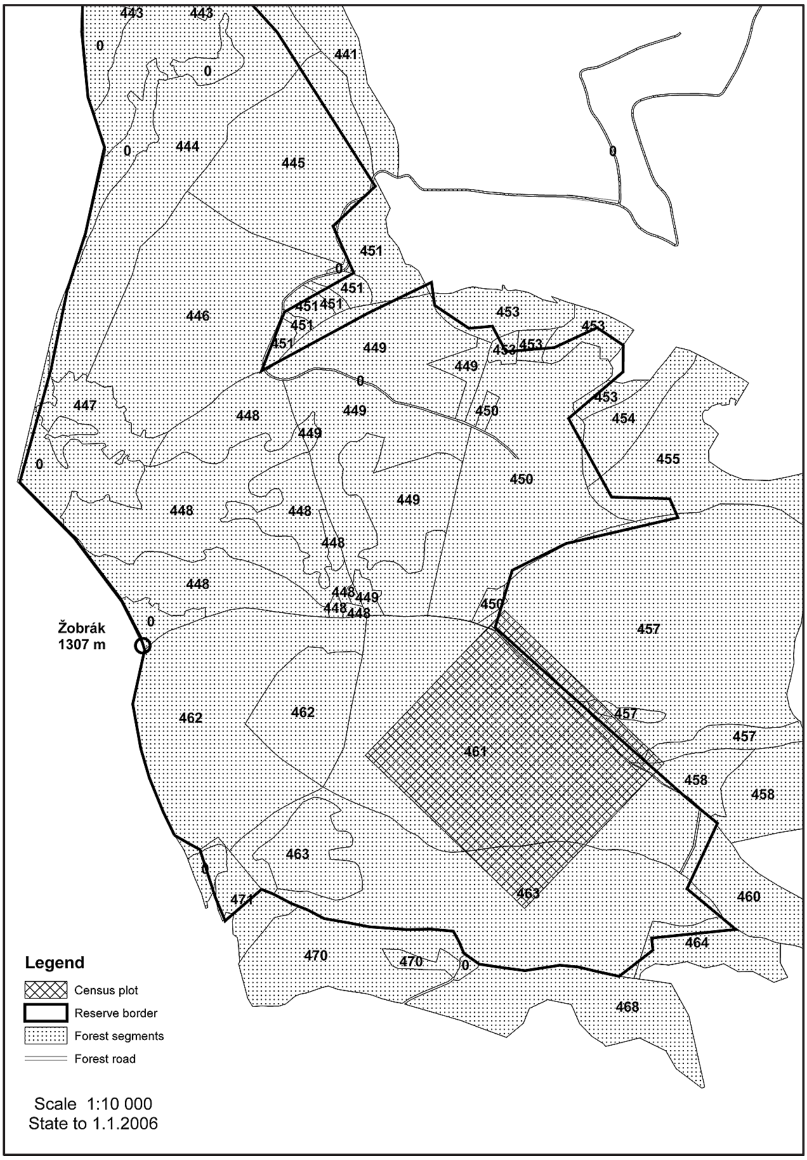

Fig. 1. Map of the 27.5 ha (500 × 550 m) bird census plot in the Šrámková National Nature Reserve, the Malá Fatra Mts., Slovakia. The exact geographic coordinates in WGS 84 of the bottom line of the study plot are indicated in section 2.1. Study area. The digital layers for the map construction were given by the National Forest Centre in Zvolen.

tures of primaeval stands (Korpeľ 1989). The study plot is situated at an elevation 850–1,078 m a.s.l. The plot is located in the central part of the reserve and is well isolated from forest edges. The reserve belongs to a cold mountain climatic zone with mean July air temperatures of 10°–12°C. The total mean annual precipitation varies between 900–1200 mm (Vološčuk 1986). The slope inclination is 20°–60°. A mountain stream intersects the study plot about 250–300 m from the western edge and creates 5–8 m deep channel surrounded by vegetation.

The forest is uneven aged with considerable vertical and horizontal heterogeneity. All developmental stages (growing stage, terminal (optimum) stage, break down stage) of a primaeval beech-fir forest occur in the study plot. The original plant species composition has been preserved. The fitness of the silver fir *Abies alba* population significantly has decreased due to the emission of air pollutants.

Vegetation structure was quantified within 0.04 ha circular plots (radius 11.3 m) using a method originally proposed for bird-vegetation studies (Noon 1981, Korňan 1996). In total, 24 circular plots (0.96 ha) were sampled from August until the middle of September in 1998–99. The study site is dominated by beech *Fagus sylvatica* (44.8%), silver fir *Abies alba* (20.2%), Norway spruce *Picea abies* (4.8%), sycamore *Acer pseudoplatanus* (4.3%), wych elm *Ulmus glabra* (2.9%), and rowan *Sorbus aucuparia* (2.4%) with admixture of other tree species such as, silver birch *Betula pendula*, European larch *Larix decidua*, Norway maple *Acer platanoides*, and small-leaved lime *Tilia cordata*. The mean canopy height in the forest segment 461 representing the majority of the census plot is 24.7 m (database of the National Forest Centre in Zvolen, state to 1.1.2006). The maximum canopy height is up to 45 m. The rich clumped shrub layer mainly consists of hazel *Corylus avellana*, red-berried elder *Sambucus racemosa*, currant *Ribes* spp., and saplings of the dominant tree species. The herb layer is mainly composed of *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*. For details regarding the density and dominance of tree composition see Korňan (2000).

2.2. Bird censusing

Population densities were estimated by the combined version of the mapping method, which is considered one of the most accurate census techniques (Tomiałojć 1980). 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 rectangular study plot. Breeding bird censuses were carried out in the years 1997–2006 from April to mid-July. A total of 10–11 valid census visits (only bird mapping) per breeding season were performed usually between 04:30 and 09:00 CET (sometimes by 10:00 CET) for morning visits, between 16:00 and 19:30 CET for evening visits, and between 19:00 and 22:00 CET for night visits. The number of evening visits was always two from the total number of valid visits. In the beginning of April one night visit focused on owl registrations was carried out. The censuses were only done when not rainy or windy. Each visit involved walking and mapping the presence of birds on alternate grid lines 100 m apart, beginning at the plot edge and ending at the opposite edge. The starting point and direction of observer movement were regularly switched so that census timing during the season between different parts of the plot was similar. Further details regarding the mapping procedure are given in Korňan (2004).

The registrations of observed individuals and singing males of certain species were plotted cumulatively on a plot map (species map), which then allowed the determination of clusters of points and in many cases locations of territories, and ultimately the number of territories (pairs) occupying the study area. The criteria for territory interpretation were principally based on the IBCC (1969) recommendations. However, in cases of some secretive species or species without well-evolved territorial behaviour (listed in Korňan 2004), a species specific minimum number of registrations (acceptance level of territory), and other criteria required to accept a cluster as a territory, were modified in a way that the minimum number of registrations to accept a territory was lowered by one registration. Other useful information about a territory and nest positions in the plot were gained during independent plot visits when foraging bird observations were being collected. In the case of species with abundances less than 0.5 territory per plot, only breeding presence "+" denoting the stationary occurrence of a part of bird territory within the plot boundaries are indicated. This symbol was primarily used for species with territory sizes much larger than the study plot, this includes some woodpeckers, owls, birds of prey, and corvids (Tomiałojć 1980). 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). Bird nomenclature follows Dickinson (2003).

2.3. Determination of guild structure

Bird foraging data were collected in the core zone of the reserve, but primarily within the 27.5 study site. Sampling was carried out in the period 1997–

Table 1. Mean dominance, mean density and variation measures of density (sample standard deviation – SD, coefficient of variation – CV, coefficient of fluctuation – CF, population variability – PV) of species breeding in the primaeval beech-fir forest in the Šrámková National Nature Reserve in the period 1997–2006. Species included are only those that reached abundance of at least 0.5 breeding pair in at least one year.

Species	Dominance mean (%)	Density (p/ 10 ha)			CF	PV
		mean	SD	CV (%)		
Chaffinch	21.92	13.03	2.41	18.47	1.22	0.192
European Robin	8.60	5.11	1.00	19.59	1.22	0.199
Blackcap	7.20	4.28	1.00	23.47	1.28	0.241
Coal Tit	7.08	4.21	1.10	26.01	1.31	0.256
Goldcrest	5.92	3.52	0.43	12.33	1.13	0.133
Common Chiffchaff	5.87	3.49	0.54	15.46	1.18	0.165
Dunnock	5.23	3.11	0.47	15.05	1.16	0.154
Collared Flycatcher	4.39	2.61	0.72	27.56	1.31	0.263
Eurasian Treecreeper	3.84	2.28	0.57	24.86	1.30	0.250
Winter Wren	3.06	1.82	0.44	24.27	1.39	0.225
Stock Dove	2.87	1.71	1.10	64.21	2.03	0.510
Woodpigeon	2.79	1.66	0.78	47.29	1.66	0.409
Eurasian Blackbird	2.74	1.63	0.38	23.36	1.27	0.233
Song Thrush	2.45	1.46	0.39	26.79	1.38	0.267
Wood Warbler	2.36	1.40	0.75	53.21	3.24	0.470
Eurasian Nuthatch	2.09	1.24	0.58	46.78	1.63	0.404
Red-breasted Flycatcher	1.18	0.70	0.43	61.65	1.89	0.469
Eurasian Bullfinch	1.13	0.67	0.44	65.73	1.79	0.427
Marsh Tit	1.11	0.66	0.26	39.28	1.53	0.350
Spotted Flycatcher	1.00	0.59	0.54	91.73	3.07	0.601
Hawfinch	0.84	0.50	0.33	66.13	2.08	0.490
Willow Warbler	0.79	0.47	0.28	60.65	2.07	0.482
Mistle Thrush	0.75	0.45	0.24	53.25	1.90	0.439
Firecrest	0.73	0.44	0.30	68.61	3.61	0.496
White-backed Woodpecker	0.64	0.38	0.14	37.98	1.53	0.354
Ring Ouzel	0.55	0.33	0.31	94.72	2.95	0.586
Three-toed Woodpecker	0.49	0.29	0.19	65.62	1.73	0.417
Grey Wagtail	0.42	0.25	0.12	49.41	1.56	0.348
Long-tailed Tit	0.41	0.24	0.31	128.39	3.55	0.657
Eurasian Siskin	0.24	0.15	0.29	202.42	6.12	0.494
Red Crossbill	0.24	0.15	0.19	129.10	6.40	0.519
Blue Tit	0.24	0.15	0.34	234.22	5.33	0.642
Eurasian Woodcock	0.18	0.11	0.18	161.02	5.01	0.644
Common Cuckoo	0.17	0.10	0.16	153.20	1.67	0.326
Great Tit	0.15	0.09	0.15	169.97	4.97	0.569
Tree Pipit	0.12	0.07	0.09	129.10	3.12	0.542
Hazel Grouse	0.09	0.05	0.12	224.98	3.66	0.617
Great Spotted Woodpecker	0.06	0.04	0.11	316.23	3.66	0.462
Tawny Owl	0.03	0.02	0.06	316.23	2.99	0.414

2000 from the middle of May until the end of July. In order to collect foraging observations, two observers independently crossed the study plot in a random manner, searching for and observing as many different feeding birds as possible. The sampling of bird foraging behaviour was usually carried out throughout the day from morning (05:00 CET) to evening (19:00 CET). During the observations, different sections of the study plot were sampled with approximately equal intensity. Each foraging observation was written onto field sheets with the standardised list of foraging substrates and movement categories (see Korňan 2000). When a foraging bird was seen, the following information was recorded: species, sex, length of observation, time of day (CET), foraging height, foraging substrate, type of foraging movement, and direction of foraging movement (vertical or horizontal direction to the tree trunk). Foraging heights were estimated by eye. A total of 39 variables were recorded, from which a subset was subsequently used for statistical analyses (see Korňan & Adamík 2007).

A total of 4,214 foraging observations from 41 bird species were collected. Only 26 species with at least 30 observations or a minimum total observation time of 1,500 seconds were used for data analyses. A data matrix (26 species × 47 variables, Supplement A) describing the use of foraging substrate following the MacMahon *et al.* (1981) guild concept were subjected to numerical analyses. In order to objectively determine guild structure of the bird assemblage without arbitrary fusion criteria, the data matrix was analysed by the bootstrapped cluster analysis (UPGMA) of chord distances. Further details regarding the numerical analyses are given by Korňan & Adamík (2007).

The bootstrapped cluster analysis classified seven groups of species with significantly different group partitions at $\alpha = 0.1$. These groups corresponded to six foraging guild types: litter foragers, herb layer foragers, stream foragers, flycatchers, trunk foragers, foliage gleaners and a single species dendrogram branch for the Willow Warbler. Even though the Willow Warbler formed an independent branch, for purposes of this paper it was combined with the foliage gleaning guilds with which it showed the closest relationship. Other breeding species for which I had no or insufficient samples of foraging observations were classified by an a priori approach into the above mentioned guild type pattern, following the scheme in Korňan & Adamík (2002, Appendix 1). Nesting guilds and migratory habits of species were also classified by an a priori approach (Appendix 2).

2.4. Numerical analysis

2.4.1. Assemblage structure and variability

Bird assemblage structure was analysed for abundance, density and dominance (Table 1, Appendix 1). Sample standard deviation (SD), coefficient of variation (CV), coefficient of fluctuation (CF, Whittaker 1975), and population variability (PV, Heath 2006) were applied to estimate variation in density between years. A coefficient of variation was employed to measure the relative dispersion in the sample. CF is considered a better measure of population variability than CV, largely because CV can be biased by rare events, zero counts and other non-Gausian behaviour (Heath 2006). The mathematical formula for the coefficient of fluctuation is (Whittaker 1975):

$$CF = antilog \sqrt{\sum\nolimits_{x=1}^{t} (\log N_x - \log \tilde{N})^2 / (t-1)}, \quad \text{(Eq. 1)}$$

where N_x is population density of a species in a certain year x, $\tilde{N}$ is geometric mean density and t is number of census years (10 years). CF is interpreted multiplicatively (see results).

Population variability (PV) quantifies variability as the average percent difference between all combinations of observed abundances (Heath 2006). PV is measured on a proportional scale that facilitates comparative applications. Heath recommends using PV because while it behaves similarly for normal time series, it is independent of deviation from mean abundance for heavy tailed distributions, its robustness to non-Gaussian behaviour resolves artificial reddened spectrum issues, and variability calculated using PV from short time series is substantially more accurate at estimating known long term variability than standard metrics. The computation background of PV is given in Heath (2006). I computed PV in statistical package R 2.13.1 (R Development Core Team 2011).

Species with abundances lower than 0.5 pair for the study plot had a zero value for the calculations of total density of the assemblage, individual guild densities, dominance, SDs and CVs (Appendix 1). Because the CF is based on logarithms that are sensitive to zero values, the species with zero values of density in the Šrámkova matrix were included for calculating CF by adding constant values of 0.01, except for the species *Strix aluco*, which had constant 0.005. The other density constants are indicated in Appendix 1. PV enabled me to compute values in data with one zero count, however in data with two or more zero counts, I used constant values as in the case of CF. In Kruskall-Wallis ANOVA testing of differences

Table 2. Ratio between maximum and minimum density value (N_{max} / N_{min}, N = the highest / lowest density of a species), maximum rates of decrease (N_t / N_{t+1}, N_t = density of a species in a year t), maximum rates of increase (N_{t+1} / N_t, N_t = density of a species in a year t), mean coefficient of growth and classification of the 22 most numerous species into nesting guilds and migratory habit groups. Species are in alphabetical order. Abbreviations: nesting guilds: B – bush nesters, C – canopy nesters, G – ground nesters, H – hole nesters. Migratory habits were classified based on data from Cepák et al. (2008) into three categories: R – residents, M – short-distance migrants, T – tropical migrants.

Species	Nesting guilds	Migratory habits	Density ratio max / min	Max. between year decrease	Max. between year increase	Mean coefficient of growth (%)
Blackcap	B	M	2.09	1.14	1.63	2.64
Chaffinch	C	M	1.74	1.17	1.34	2.95
Coal Tit	H	R	2.33	2.19	1.66	0.24
Collared Flycatcher	H	T	2.33	1.75	1.75	–5.52
Common Chiffchaff	G	M	1.62	1.08	1.38	0.61
Dunnock	B	M	1.66	1.26	1.31	3.21
Eurasian Blackbird	B	M–R	2.21	1.29	1.72	–5.14
Eurasian Bullfinch	B	M–R	5.63	2.25	2.25	–6.51
Eurasian Nuthatch	H	R	4.07	3.05	2.22	2.76
Eurasian Treecreeper	H	R	2.31	1.56	1.37	–5.35
European Robin	G	M	1.75	1.75	1.66	1.28
Goldcrest	C	M–R	1.40	1.19	1.39	1.06
Hawfinch	C	M	10.91	4.00	8.36	–7.41
Marsh Tit	H	R	2.70	2.50	1.77	9.70
Red-breasted Flycatcher	H	T	8.60	3.50	2.87	–19.44
Song Thrush	B	M	3.06	1.72	3.06	9.28
Spotted Flycatcher	H	T	13.82	13.82	10.91	–4.41
Stock Dove	H	M	11.00	3.15	7.50	–8.86
Willow Warbler	B–G	T	9.09	4.40	6.55	18.84
Winter Wren	G–B	M	3.20	2.50	2.50	2.25
Wood Warbler	G	T	49.45	4.30	24.00	–1.78
Woodpigeon	C	M	3.65	3.25	1.67	–8.84

among guilds and migratory groups, the CF values for species that were classified into two guilds or migratory group categories were included into both categories.

Similarity of species structure of the assemblage between years was calculated by qualitative Sørensen similarity index, whereas similarity of quantitative structure of the assemblage was calculated using Czekanowski-Sørensen similarity index (Huhta 1979, formula 8). Both indices range in value from zero (completely dissimilar) to one (completely similar). In computation of quantitative similarity, density values included only species breeding in the census plot and covered trace species ("+" species with constant values of density in parenthesis in Appendix 1). The index values (mean, SD, CV) were computed in MS Excel 2007, while cluster analysis (UPGMA algorithm) based on the index metrics was performed in the numerical package MVSP 3.13 (Kovach 2007). In the numerical package, Czekanowski-Sørensen similarity index was converted into percentage similarity coefficient. Regressions were run in package NCSS 2001 (Hintze 2001).

2.4.2. Mean growth coefficient

The mean growth coefficient is calculated as a geometric mean of growth rates ($k_t = y_t / y_{t-1}$, where y_t is a density of a species in a year $t = 2, 3, ..., n$; Scheer 2010):

$$\bar{k} = \sqrt[n-1]{k_1 \times k_2 ... k_{n-1}} \qquad \text{(Eq. 2).}$$

For instance, a growth coefficient of 1.0295 indicates a mean population increase of 2.95% per year (*Fringilla coelebs*, Table 2). The mean growth coefficient was calculated for the 22 most numerous species from data matrix of population densities including trace species values ("+" and "o+" species in Appendix 1).

2.4.3. Species associations

Null model analyses of the binary data matrix (53 species × 10 years) and of the density data matrix (22 species × 10 years) were conducted in statistical packages EcoSim 7.0 (Gotelli & Entsminger 2001) and Turnover 1.0 (Ulrich 2010). The description of applied null models (SIM1 –SIM9) and indices (CHECKER, C-score, V-ratio) used for analysis of binary data matrix is given by Gotelli (2000). Quantitative null models (IT, IA, IR) and indices (CA_{ST}, AA_{ST}, MA) are described by Ulrich & Gotelli (2010). I used 10,000 iterations in null model analysis from binary matrices and 200 iterations from quantitative matrices. Critical threshold level was set on $\alpha = 0.05$.

2.4.4. Population trend estimates

Population trends of breeding birds were analysed by simple linear model (least-squares method) for changing density of each species over time:

$$density_i = year_i(b) + a \qquad \text{(Eq. 3)},$$

where $density_i$ is density of a bird species in pairs/10 ha in $year_i$; $year_i$ is a number from 1–10 corresponding with the ten census years, 1997–2006; a and b are fitted constants for the y-intercept and slope of the linear regression model, respectively.

The trends were evaluated as statistically significant when the linear regressions had slopes that were statistically different from zero, based on t statistics. To avoid computations with zero values, species that reached low population densities ("+" or "o+") in certain years were given constant density values (see Appendix 1 for the constant values) for computation of trends. Data were tested for normality in statistical package NCSS 2001 (Hintze 2001). Dependent variables (species densities) were tested by seven normality tests and regression residuals by five normality tests. In the event that at least one normality test indicated non-normal distribution, randomization tests (10,000 Monte Carlo samples) were performed for computation of statistical probability of regression models instead of standard procedure. All computations were performed in NCSS 2001.

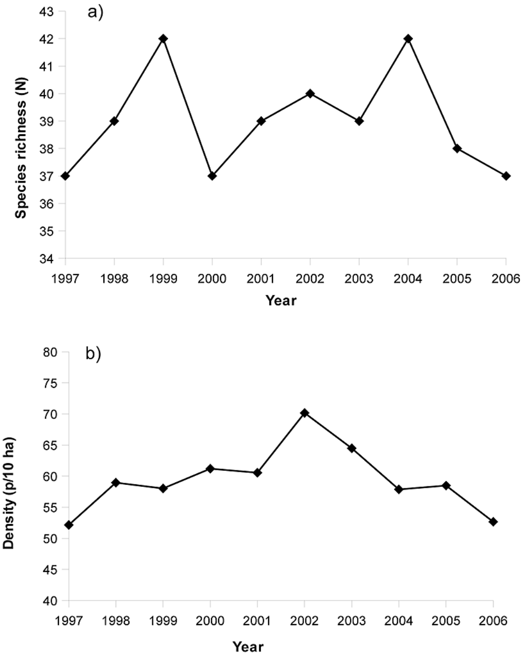

Fig. 2. Species richness (a) and total density (b) of the breeding bird assemblage of the primaeval beech-fir forest in the 27.5 ha study plot in the Šrámková National Nature Reserve from 1997–2006.

To simplify interpretation of the regression analysis, the trends of species were classified into the following categories according to statistical significance and magnitude following Gregory *et al.* (2007). The slope estimate in the linear regression models was converted into one of the following six categories depending on slope value and 95% confidence interval.

(1) Strong increase – increase significantly more than 5% per year. Criterion: lower limit of confidence interval > 1.05. (2) Moderate increase – significant increase, but not significantly more than 5% per year. Criterion: 1.00 < lower limit of confidence interval < 1.05. (3) Stable – no significant increase or decline, and it is certain that trends are less than 5% per year. Criterion: confidence interval encloses 1.00 but lower limit of confidence

Table 3. Trends of species richness, total density, migratory habit groups and foraging and nesting guilds of the breeding bird assemblage in the primaeval beech-fir forest in the Šrámková National Nature Reserve in the period 1997–2006. Trends were computed from linear regression models (SE – standard error). Application of randomization test (10,000 Monte Carlo samples) is indicated by asterisk in the probability (*P*) and confidence interval columns. Trend classification is explained in Material and method: Population trend estimates.

Species	Regression slope ± SE	*t*-test value	*P*	Lower 95% confidence limit	Upper 95% confidence limit	Trend classi-fication
Species richness	0.00 ± 0.22	0.00	1.0000	–0.51	0.51	uncertain
Total assemblage density	0.10 ± 0.62	0.17	0.8697	–1.32	1.53	uncertain
Foraging guilds						
Flycatchers	–0.10 ± 0.10	–1.01	0.3434	–0.33	0.13	uncertain
Foliage gleaners	0.73 ± 0.40	1.80	0.1099*	–0.18*	1.38*	uncertain
Herb layer foragers	–0.12 ± 0.07	–1.86	0.0919*	–0.21*	0.01*	uncertain
Litter foragers	–0.05 ± 0.20	–0.24	0.8182	–0.50	0.41	uncertain
Plant eaters	–0.23 ± 0.11	–2.15	0.0634	–0.47	0.02	uncertain
Trunk foragers	–0.10 ± 0.12	–0.81	0.4417	–0.37	0.18	uncertain
Nesting guilds						
Bush nesters	–0.07 ± 0.21	–0.33	0.7475	–0.54	0.41	uncertain
Canopy nesters	0.38 ± 0.25	1.55	0.1602	–0.19	0.96	uncertain
Ground nesters	–0.11 ± 0.17	–0.64	0.5426	–0.51	0.29	uncertain
Hole nesters	–0.11 ± 0.23	–0.48	0.6431	–0.64	0.42	uncertain
Migratory habits						
Short distance migrants	0.24 ± 0.48	0.51	0.6245	–0.86	1.34	uncertain
Tropical migrants	–0.11 ± 0.16	–0.70	0.5056	–0.49	0.26	uncertain
Residents	–0.02 ± 0.21	–0.11	0.9158	–0.50	0.46	uncertain

interval > 0.95 and upper limit < 1.05. (4) Uncertain – no significant increase or decline, but not certain if trends are less than 5% per year. Criterion: confidence interval encloses 1.00 but lower limit < 0.95 and/or upper limit > 1.05. (5) Moderate decline – significant decline, but not significantly more than 5% per year. Criterion: 0.95 < upper limit of confidence interval < 1.00. (6) Steep decline – decline significantly more than 5% per year. Criterion: upper limit of confidence interval < 0.95.

Similarity in species fluctuations was analysed by cluster analysis (UPGMA) based on metrics of the Pearson's correlation coefficient. Data matrix used for population trend analysis, similarity of fluctuation analysis and amplitude of fluctuation analysis consisted of densities of the 22 most numerous species including trace values ("+" and "o+") that were given constants as indicated in Appendix 1.

3. Results

3.1. Bird species richness

In the period 1997–2006, 53 bird species were recorded as breeders in the 27.5 ha study plot (Appendix 1). The number of breeders in a year varied between 37 in 1997, 2000 and 2006 to 42 in 1999 and 2004; averaging 39.0 species (Fig. 2a). In 2004, the consequences of high bank vole *Myodes glareolus* abundance were observed. In this year, all recorded owl species and the small mammal specialist Eurasian Buzzard bred. In contrast to previous years, two new species of owls (Ural Owl and Tengmalm's Owl) were recorded in 2004. In the same years, 60 species were observed in the reserve, of which 55 species were breeders. Annual species richness in the reserve fluctuated between 40 species in 2000 and 46 species in 2004 averaging 42.4 species. Thirty species were observed to

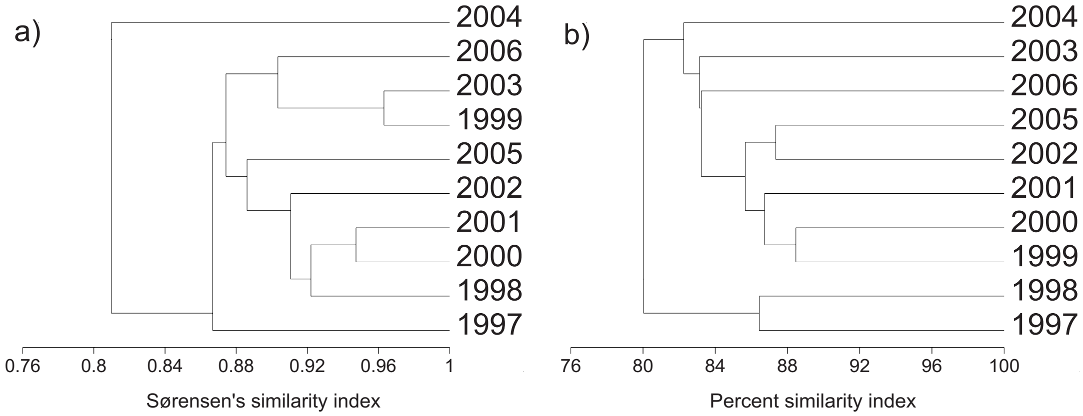

Fig. 3. Qualitative (a) and quantitative (b) structural similarity of the breeding bird assemblage of the primaeval beech-fir forest in the 27.5 ha study plot located in the Šrámková National Nature Reserve tested by Sørensen similarity index and percentage similarity (Czekanowski-Sørensen) index.

breed in the reserve in each year of the study. No relationship between regularity of breeding and population density was detected. Species richness across years showed a neutral trend with zero value of slope and were classified as uncertain (see part Population trend estimates in Material and methods) due to very wide confidence interval (Table 3).

3.2. Bird assemblage density

Total density of the entire bird assemblage on the study area ranged from a low of 52.15 p/10 ha in 1997 to a high of 70.15 p/10 ha in 2002 (Fig. 2b, Appendix 1). Mean value of the total assemblage density was 59.45 ± 5.26 p/10 ha (SD) across all years of study, while the CV = 8.85% indicated relatively low variability. The overall trend in total density for ten years showed an increasing tendency with a slightly positive slope, however it was classified as uncertain due to a wide confidence interval (Table 3).

3.3. Bird assemblage structure

Mean quantitative similarity (species densities within each year compared across years) of assemblages compared among years using the Czekanowski-Sørensen similarity index was 0.83 ± 0.03 SD (CV = 3.91%). Maximum quantitative similarity of 0.88 was detected between year 1999 and 2000, while the minimum similarity 0.75 was found between years 1997 and 2002. Mean qualitative similarity (species structure) compared among years by the Sørensen similarity index was 0.87 ± 0.04 SD (CV = 5.09%). The highest qualitative similarity 0.96 was between years 1999 and 2003, whereas the lowest similarity was 0.76 between years 2000 and 2004. Mean of Czekanowski-Sørensen similarity index between two consecutive years was significantly higher compared to mean of all pairwise combinations except the consecutive years ($t = 3.16$, right-tail test, $df = 43$, $P = 0.0015$) indicating that the structure of assemblages was more similar in sequential years. Similar testing for a difference between means of the Sørensen similarity index did not reveal significant results at $\alpha = 0.05$. The cluster analysis of assemblage similarity among years did not show clear patterns (Fig. 3a, b).

3.4. Species associations

Species associations in the time series data of the breeding bird assemblage from the Šrámková Reserve were tested by binary and quantitative null models using the density data matrix of the 22 most numerous species (three indices), presence/absence (binary) data matrix of the whole assemblage (53 species, three indices) and density data matrices of species from three guilds (foliage foragers – 9 species, flycatchers – 3 species and litter foragers – 4 species; three indices).

Table 4. Observed and simulated values of three indices on estimating species associations derived from nine types of null models (see Material and methods). Computations were carried out in the package EcoSim 7.0 (Gotelli & Entsminger 2001). The probability values at the threshold level α = 0.05 are given in parenthesis behind the simulated index values.

	CHECKER	C score	V ratio
Observed	62	0.73	1.00
SIM1	0.37 (<0.0001)	3.28 (1.000)	0.99 (0.435)
SIM2	65.55 (0.788)	0.69 (0.094)	1.00 (0.458)
SIM3	0.43 (<0.0001)	3.34 (1.000)	0.47 (<0.0001)
SIM4	65.31 (0.773)	0.68 (0.090)	1.02 (0.470)
SIM5	27.34 (0.001)	1.83 (1.000)	0.64 (<0.0001)
SIM6	0.36 (<0.0001)	3.27 (1.000)	1.09 (0.512)
SIM7	26.48 (0.001)	1.76 (1.000)	1.00 (0.429)
SIM8	26.22 (0.007)	1.76 (1.000)	1.07 (0.495)
SIM9	65.09 (0.804)	0.69 (0.003)	N.A.

N.A. – not applicable algorithm.

Table 5. Observed and simulated values of three quantitative indices for estimating species associations derived from three null models. The computations were carried out in the package Turnover 1.0 (Ulrich 2010). One-tailed probability value at the threshold level α = 0.05 computed from the null model distribution are given in parenthesis behind the simulated index values. Description of indices and algorithms is in Ulrich & Gotelli (2010). In parenthesis, there are given abbreviations of indices and algorithms as in Turnover manual.

	CA_{ST} (WCS)	AA_{ST} (WTog)	MA (Chao)
Observed	0.10	0.49	0.95
IT (rc)	0.12 (0.01)	0.28 (0.01)	0.83 (0.01)
IA (aa)	0.12 (0.08)	0.29 (0.01)	0.83 (0.01)
IR (ss)	0.10 (0.98)	0.17 (0.01)	0.63 (0.01)

3.4.1. Analyses on the assemblage level

3.4.1.1. Binary matrix

Simulated values of the index *checker* by six types of null models were significantly lower than observed (Table 4), which indicates negative species associations (segregation). Mean simulated values of this index in three types of null models (SIM2, SIM4, SIM9) were not different from the observed value suggesting random associations. Note that only two null model algorithms (SIM2 and SIM9) with the index *checker* have acceptable Type 1 error rates (Gotelli 2000). Both algorithms detected independent associations. One null model simulation with the index *C score* reached a significantly lower mean value than the observed, suggesting a negative association. The simulated values in eight null models with the index *C score* were not significantly different from the observed, suggesting independent associations. Six values of the index *V ratio* simulated by six types of null models were not significantly different from 1.0 suggesting random associations (Table 4). In case of two null models (SIM3, SIM5), the simulated *V ratio* values were significantly lower (SIM3 a SIM5) then the observed value suggesting positive associations (aggregation). Computation of this index was not applicable with row and column sums fixed algorithm (SIM9). In summary, only seven of the 26 null model simulations showed negative associations.

3.4.1.2. Quantitative matrix

The observed value of the index CA_{ST} was not significantly different from the mean of simulated values in two cases (Table 5), which suggests random associations. In one case the observed value was significantly lower than the simulated value suggesting positive associations (aggregation). The indices AA_{ST} and MA reached significantly higher values compared to the means of simulated values by all null models. This suggests aggregation in all cases. In summary, none of nine simulations showed a negative species association.

3.4.2. Analyses on the guild level

3.4.2.1. Flycatchers

The simulated values of the index CA_{ST} by three null models were not significantly different from the observed value, indicating random associations (Supplement C). Two simulated values of the index AA_{ST} were significantly lower than the observed, indicating positive associations. The simulated values by the IA null model were not significantly different from the observed suggesting independent associations (Supplement C). All values simulated by the three null model algorithms were significantly lower than the observed values in case of MA index suggesting aggregation. None of the nine null model simulations showed negative species associations within the flycatcher guild.

3.4.2.2. Foliage foragers

The observed value of the index CA_{ST} was not significantly different from the three null model simulations indicating random associations (Supplement C). The observed values of the indices AA_{ST} and MA were significantly higher than the simulated values of the three null models. This suggests positive associations. There were no signs of compensatory dynamics (negative associations or segregation) based on nine null model simulations in the foliage forager guild.

3.4.2.3. Litter foragers

Two simulated values of the CA_{ST} index were significantly higher than the observed value indicating positive associations (Supplement C). The simulated value by the IR null model was not significantly different from the observed value suggesting random associations. The observed values of the indices AA_{ST} and MA were significantly higher than the simulated values by the three null models supporting positive associations. In summary, none of the nine model simulations showed negative species association within the litter forager guild.

3.5. Population variability

3.5.1. Species population variability

The coefficient of variation (CV), coefficient of fluctuation (CF), and population variability coefficient (PV) were employed to estimate population variation in densities during the ten-year period (Table 1). These analyses were made only for the 22 most numerous species because of their larger sample sizes. The value of CV, CF, and PV for the remaining species with low population densities are given only for very rough estimates of their population variation. Mean value of CVs for all species was 38.8 ± 22.0% SD (CV = 56.7%). The highest value of CV 91.7% was found for Spotted Flycatcher, while the lowest value 12.3% was detected for Goldcrest.

Mean value of CF for the 22 most numerous species was 1.64 ± 0.58 SD (CV = 35.2%). This means that species on average fluctuated 64% above and below their geometric means. A minimum CF value of 1.13 was detected for the Goldcrest, while the maximum value of 3.24 was found for the Wood Warbler. High values of CFs were detected for Spotted Flycatcher (3.07), Hawfinch (2.08), Willow Warbler (2.07) and Stock Dove (2.03), whereas low CF values were also found for Dunnock (1.16), Common Chiffchaff (1.18), Chaffinch (1.22), European Robin (1.22), Eurasian Blackbird (1.27) and Blackcap (1.28).

Mean value of PV for 22 most common species was 0.33 ± 0.14 (CV = 42.1%) indicating that mean difference in densities among all years was 33%. A minimum PV value of 0.13 was found for the Goldcrest, whereas the highest PV value 0.60 was detected for the Spotted Flycatcher (Table 1). Low PV values were observed for Dunnock (0.15), Common Chiffchaff (0.16), Chaffinch (0.19), and European Robin (0.19). High population variability was found for Stock Dove (0.51), Hawfinch (0.49), Willow Warbler (0.48), Wood Warbler (0.47), and Red-breasted Flycatcher (0.47). CF and PV showed a relatively high Pearson's correlation coefficient ($r = 0.85$, $t = 7.32$, $P < 0.0001$) indicating a similar tendency in overall species variation. However, differences in the rank of species following the values of these two coefficients were obvious.

3.5.2. Population variability among migratory groups and guilds

Mean values and variation measures (SD, CV) of population variability coefficients were calculated for each group from the nesting and foraging guilds and migratory habits for the 22 most common species (Table 1, Appendix 2). Dynamics of density for individual foraging and nesting guilds and migratory habits is given in Fig. 4a–d. The lowest mean PV value 0.28 ± 0.13 SD (N = 13, CV = 46.9%) was found for short-distance migrants. Similar, but slightly higher values of PV 0.29 ± 0.10 SD (N = 7, CV = 35.8%) were found for residents. The highest mean variability 0.46 ± 0.12 SD (N = 5, CV = 156.1%) was detected for tropical

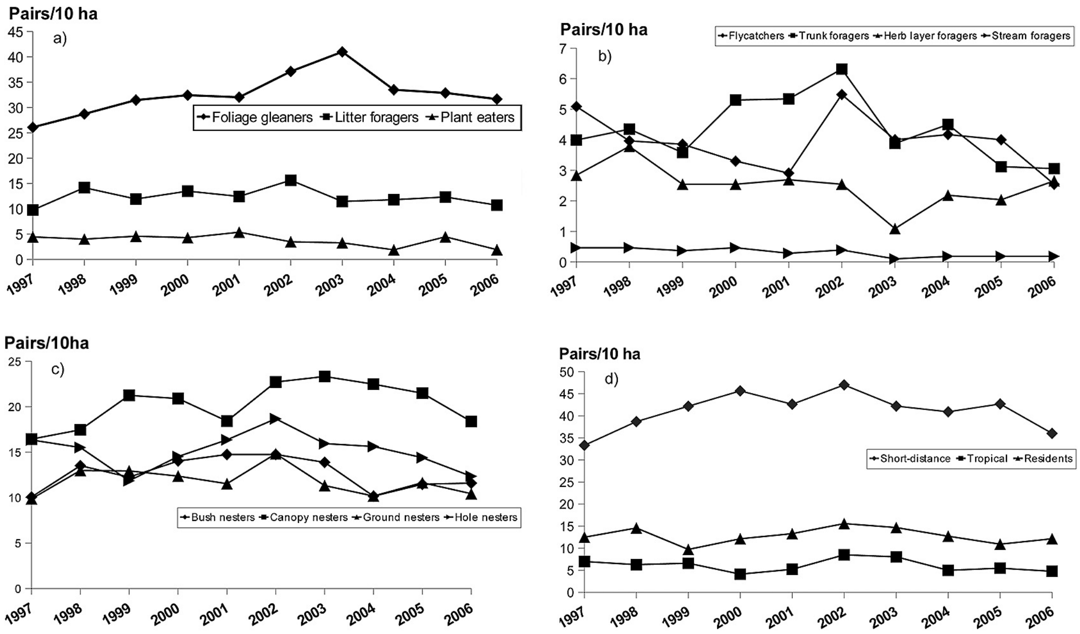

Fig. 4. Time series graphs of guild density (p/10 ha) in the breeding bird assemblage of a primaeval beech-fir forest in the Šrámková National Nature Reserve in the period 1997–2006 (a, b – foraging guilds, c – nesting guilds, d – migratory habits).

migrants. The medians of groups were significantly different (Kruskall-Wallis test on ranks corrected for ties, $H = 6.06$, $df = 2$, $P = 0.048$) indicating that tropical migrants had significantly different median of PV compared to short-distance migrants ($Z = 2.41$) and were almost different from residents ($Z = 1.95$). Differences between residents and short-distance migrants were not found ($Z = 0.26$).

Small differences in PV were found for the four types of nesting guilds (bush nesters – mean = 0.29, SD = 0.12, CV = 41.0%, N = 7; canopy nesters – mean = 0.31, SD = 0.17, CV = 55.8%, N = 4; ground nesters – mean = 0.31, SD = 0.15, CV = 50.2%, N = 5; hole nesters – mean = 0.39, SD = 0.13, CV = 33.8%, N = 8). Differences among guilds were not significant (Kruskall-Wallis test on ranks corrected for ties, $H = 2.89$, $P = 0.236$). Canopy nesters were excluded from testing due to low sample size.

3.6. Amplitude of fluctuation and coefficient of growth

The mean value of max / min ratio of densities was 6.57 ± 10.26 SD (CV = 156.1%). This suggests an almost seven fold difference between population minimum and maximum values for this set of species (Table 2). The highest amplitude, almost 50-fold, was found in Wood Warbler, a species that was common most years but almost absent in the reserve in 2004. High amplitudes, more than tenfold, were also detected for Spotted Flycatcher (13.82), Stock Dove (11.00) and Hawfinch (10.91). These species showed the highest differences between two consecutive years (Table 2). In contrast, the lowest magnitude of amplitudes (1.40) was found for Goldcrest. Low values of max / min ration were also detected for Common Chiffchaff (1.62), Dunnock (1.66), Chaffinch (1.74) and European Robin (1.75).

3.7. Population trends

3.7.1. Trends of species

Population trends were computed for the 22 most numerous species during 10 year period. Based on criteria of trend classifications, 17 species (77.3%)

Table 6. Population trends of the 22 most common species of forest birds breeding in the primaeval beech-fir forest in the Šrámková National Nature Reserve in the period 1997–2006. Trends were computed from linear regression models (SE – standard error). Application of randomization test (10,000 Monte Carlo samples) is indicated by asterisk in the probability (*P*) and confidence interval columns. Rank of birds follows dominance as listed in Appendix 1. Criteria for trend classification are listed Material and methods: Population trend estimates”.

Species	Regression slope ± SE	*t*-test value	*P*	Lower 95% confidence limit	Upper 95% confidence limit	Trend classification
Chaffinch	0.55 ± 0.20	2.70	0.0271	0.08	1.02	strong increase
European Robin	0.02 ± 0.12	0.20	0.8481	–0.25	0.29	uncertain
Blackcap	0.06 ± 0.12	0.53	0.6119	–0.21	0.33	uncertain
Coal Tit	0.02 ± 0.13	0.16	0.8736	–0.27	0.32	uncertain
Goldcrest	0.00 ± 0.05	0.01	0.9889	–0.12	0.12	uncertain
Common Chiffchaff	–0.03 ± 0.06	–0.41	0.6930	–0.17	0.12	uncertain
Dunnock	0.03 ± 0.05	0.58	0.5758	–0.09	0.15	uncertain
Collared Flycatcher	0.03 ± 0.08	0.35	0.7348	–0.16	0.22	uncertain
Eurasian Treecreeper	–0.04 ± 0.06	–0.69	0.5074	–0.19	0.10	uncertain
Winter Wren	–0.03 ± 0.05	–0.53	0.6527*	–0.07*	0.06*	uncertain
Stock Dove	–0.05 ± 0.13	–0.38	0.7215*	–0.22*	0.12*	uncertain
Woodpigeon	–0.20 ± 0.06	–3.42	0.0132*	–0.26*	–0.11*	strong decline
Eurasian Blackbird	–0.01 ± 0.04	–0.31	0.7659	–0.12	0.09	uncertain
Song Thrush	0.01 ± 0.05	0.25	0.8063	–0.09	0.12	uncertain
Wood Warbler	–0.03 ± 0.09	–0.34	0.7416*	–0.15*	0.08	uncertain
Eurasian Nuthatch	–0.03 ± 0.07	–0.38	0.7138	–0.18	0.13	uncertain
Red–breasted Flycatcher	–0.06 ± 0.05	–1.22	0.2612*	–0.13*	–0.002*	moderate decline
Eurasian Bullfinch	–0.10 ± 0.04	–2.48	0.0338*	–0.19†	–0.01†	moderate decline
Marsh Tit	0.08 ± 0.01	5.42	0.0012*	0.05*	0.09*	moderate increase
Spotted Flycatcher	–0.07 ± 0.05	–1.34	0.2076*	–0.15*	0.01*	uncertain
Hawfinch	–0.04 ± 0.03	–1.19	0.2598*	–0.09*	0.01*	uncertain
Willow Warbler	0.00 ± 0.03	0.13	0.9013	–0.07	0.08	uncertain

† bootstrapping was not completed because one of the variables is nearly constant for the values processes. Standard confidence intervals are given.

showed uncertain trends (see Population trend estimates in Material and methods) indicating high population fluctuations (Table 6). Five species showed significant positive or negative trends. Chaffinch showed a strong increase and Marsh Tit a moderate increase. Conversely, Woodpigeon showed a strong decline and Red-breasted Flycatcher and Eurasian Bullfinch a moderate decline.

3.7.2. Trends of guilds and migratory groups

Six guilds (flycatchers, foliage gleaners, herb layer foragers, litter foragers, plant eaters and trunk foragers) were tested for general trends in density using the linear regression (Table 3). All guild categories showed no significant trends, however five categories (flycatchers, herb layer foragers, litter foragers, plant eaters and trunk foragers) had slightly negative slopes, suggesting a declining tendency. In contrast, only foliage gleaners showed an increasing tendency with positive slope. Based on 95% confidence intervals, these trends were classified as uncertain.

None of the categories of nesting guilds showed significant trends in population density

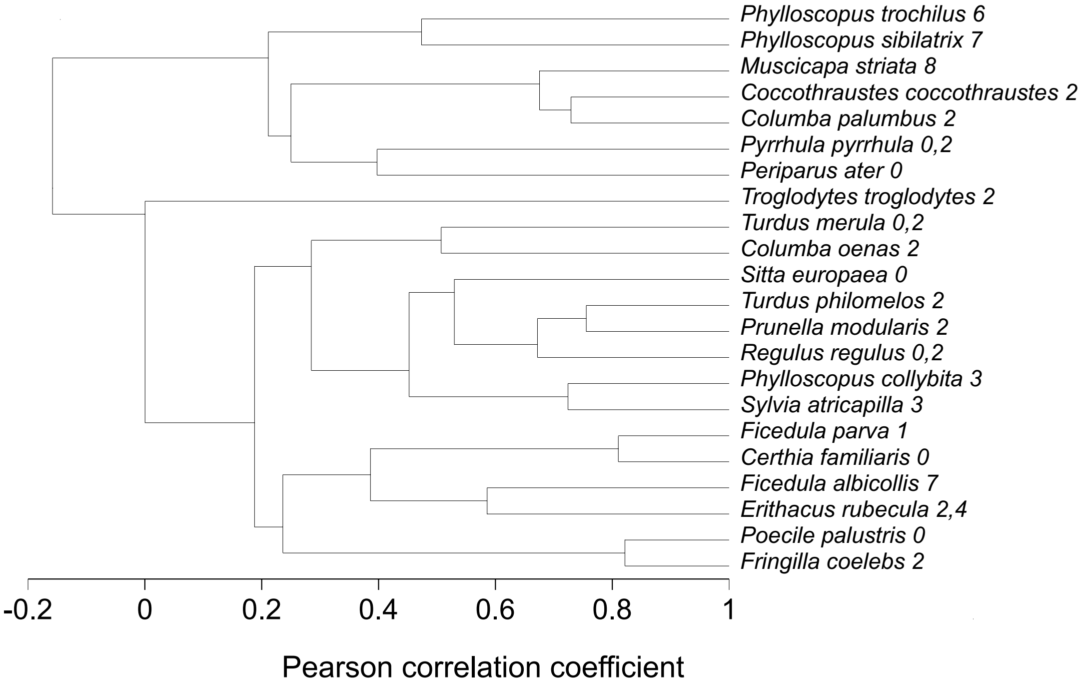

Fig. 5. Dendrogram of the 22 most numerous bird species at the Šrámková National Nature Reserve based on of Pearson's correlation coefficient of densities in the ten year period (1997–2006). The cluster analysis used unweighted pair-group average algorithm (UPGMA). Major wintering areas (Cepák *et al.* 2008) of each species are given with the abbreviation of the species names: 0 – Central Europe (the area Slovakia and Czechia and near surroundings), 1 – Southern and SE Asia, 2 – SW Europe and NW Africa (Switzerland, northern Italy, southern and SW France, the Iberian peninsula, Morocco, Algeria), 3 – Mediterranean (the whole Mediterranean region), 4 – Southern Europe (central and southern Italy), 6 – West Africa (sub-Saharan belt from Senegal to western Nigeria), 7 – Central and east Africa (eastern Nigeria, Tchad, CAR, Sudan, Ethiopia, Kenya, eastern DRC, Uganda, Tanzania), 8 – Cameroon, western DRC, Congo, Gabon, Equatorial Guinea, northern Angola.

and all were classified as uncertain (Table 3). Three categories (bush nesters, ground nesters and hole nesters) showed a negative tendency with negative slopes, whereas canopy nesters showed positive tendency with positive slope.

As with nesting guilds, none of the categories of migratory habit groups accounted for significant trend and were classified as uncertain (Table 3). Tropical migrants and residents showed negative tendency, while the trend for short-distance migrants exhibited a positive slope.

3.8. Similarity of population dynamics

A hierarchical classification of the 22 most common species based on dissimilarity metrics of the Pearson's correlation coefficient of densities did not show any consistent grouping of species according to their wintering areas or guild membership (Fig. 5). The resulting dendrogram contained four species clusters and one single species branch at dissimilarity level 0.22. However, all clusters consisted of a mixture of species from the different winter resident groupings (e.g., residents, short-distance migrants, and tropical migrants) and from different foraging guilds. From a guild membership aspect, the first cluster (from bottom toward up) had species from foliage gleaners, litter foragers, flycatchers and a trunk forager. The second cluster contained foliage gleaners, litter foragers, a trunk forager and a plant eater. Eurasian Wren formed an independent branch in the dendrogram pattern. The third cluster consists of foliage gleaners, a herb layer forager, a plant eater and a flycatcher. The fourth cluster consisted of two foliage

Table 7. Comparisons of mean, standard deviation (SD), minimum and maximum values of population variability coefficients (PV) of selected bird species from assemblages at 15 study sites located in Europe and North America where mapping method was applied for population estimates. Only species that reached measurable abundance (0.5 or higher) at least in half of the years of the study periods and had mean population density equal to or higher than 1.0 p/10 ha were included for computation of PV coefficients. In computation of PV, species with abundance lower than 0.5 territory (pair) per study plot were given constants 0.2 and species with two or more zero counts were given constant 0.01. The citations of studies from which the abundance data were used for computation of fluctuation coefficients are given as superscripts in the column study site.

Study site	Location	Forest type	Time period	Plot size (ha)	Mean PV	SD of PV	Min. PV	Max. PV	Number of analyzed species
Šrámková NNR	Europe, Slovakia	primeval beech-fir	1997–2006 (10)	27.5	0.27	0.11	0.13	0.51	16
Białowieża NP, plot CM[1]	Europe, Poland	primeval oak-lime-hornbeam	1975–2009 (35)	24	0.33	0.11	0.18	0.62	18
Białowieża NP, plot K[1]	Europe, Poland	primeval riverine alder-ash-spruce	1975–2009 (35)	33	0.29	0.07	0.18	0.41	22
Białowieża NP, plot L[1]	Europe, Poland	primeval alder swamp	1976–2009 (32)[9]	25	0.31	0.09	0.17	0.49	20
Białowieża NP, plot MS[1]	Europe, Poland	primeval oak-lime-hornbeam	1975–2009 (35)	30	0.31	0.08	0.21	0.46	16
Białowieża NP, plot NE[1]	Europe, Poland	primeval spruce-pine-birch	1975–2009 (35)	25	0.33	0.10	0.19	0.47	11
Białowieża NP, plot NW[1]	Europe, Poland	primeval spruce-pine-birch	1975–2009 (35)	25	0.34	0.13	0.19	0.63	11
Białowieża NP, plot W[1]	Europe, Poland	primeval oak-lime-hornbeam	1975–2009 (35)	25.5	0.32	0.09	0.19	0.56	22
Gaisatjakke and Valle Mts[2]	Europe, Sweden	primeval subalpine birch	1963–1999 (37)	36–62[14]	0.43	0.12	0.28	0.59	10
Estenstad forest[3]	Europe, Norway	secondary spruce	1960–1972 (12)[10]	100	0.24	0.12	0.12	0.54	13
Birdsong valley[4]	Europe, Sweden	isolated secondary oak-ash	1953–2009 (57)	13	0.45	0.14	0.23	0.67	19
Dalby Söderskog NP[5]	Europe, Sweden	secondary ash-elm-oak-beech	1980–1993 (13)[11]	37	0.38	0.14	0.18	0.71	20
Bookham Common[6]	Europe, England	isolated secondary oak	1949–1975 (26)[12]	16.19	0.39	0.13	0.21	0.67	21
Hubbard Brook[7]	North America, New Hampshire	secondary beech-maple-birch	1969–2004 (36)	10	0.47	0.16	0.19	0.71	18
William Trelease Woods[8]	North America, Illinois	isolated original maple-hackberry-ash	1927–1976 (44)[13]	24	0.53	0.13	0.34	0.72	16

1 Abundance data for the whole study period are given is studies of Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1994, Tomiałojć & Wesołowski 1996, Wesołowski et al. 2002, Wesołowski et al. 2006, Wesołowski et al. 2010.

2 Enemar et al. 2004 (Densities from the period 1963-1982 are also given in Enemar et al. (1984), however the numbers are not identical.)

3 Hogstad 1993

4 Svensson et al. 2010

5 Svensson 2009

6 Beven 1976

7 Abundance data downloaded from the Internet site http://www.hubbardbrook.org/data/dataset_search.php

8 Kendeigh 1982

9 Years 1978 and 1979 are missing.

10 Year 1961 is missing.

11 Year 1981 is missing.

12 Species *Parus caeruleus* and *Prunella modularis* were not censused in 1949. This year is not included to computation of fluctuation coefficient for these two species.

13 Period 1929–1933 and year 1938 are missing.

14 Data published in the paper represent pooled data from six study plots (8–12.8 ha each) censused in the study period. The total area of the censused study plots in a year varied as indicated.

gleaners. It seems probable that each population is regulated by a specific set of factors operating on several geographical levels (breeding site, migratory routes, wintering areas) and causing complex interactions that determine specific patterns of population dynamics. The dendrogram also clearly shows that the foraging substrate niche similarity (guild membership) is not related to similarity of population dynamics.

4. Discussion

4.1. Assemblage variability

Mean population variability (PV) of the breeding species in the primaeval beech-fir in the Šrámková National Nature Reserve was 0.27 ± 0.11 SD (Table 7). Is this extent comparable, higher or lower to other model forest study sites? To answer these questions, I reanalysed data from the published studies on dynamics of breeding bird assemblages worldwide compared them with the results of this study (Table 7). From this comparison, I conclude that the mean value of PV for birds in the Šrámková National Nature Reserve is similar to the mean PV values (0.29–0.34) from other types of primaeval forest in the Białowieża National Park in Poland. A higher mean PV value (0.43 ± 0.12 SD) was detected in a primaeval subalpine birch forest in Sweden. The value detected in the Šrámková forest was the lowest of all temperate primaeval forest bird communities for which data were available, suggesting high population stability from year to year. Mean values of PV in secondary forests (except Estenstad forest dominated by spruce in Norway) and especially in isolated forests were notably higher (0.38–0.53). Such values can result from high turnover and extinction rates of populations in isolated habitat patches as documented in numerous studies (e.g., Hinsley *et al.* 1995, Crooks *et al.* 2001).

Based on statistical testing, the PV medians of compared samples from Table 7 were significantly different (Kruskall-Wallis test on ranks corrected for ties, $H = 72.5$, $df = 14$, $P < 0.0001$). In multiple comparison tests (regular Z-value test) of primaeval forests, the Šrámkova forest was not significantly different from the study plots in the Białowieża forest, but was different from subalpine birch forest in Sweden. The Białowieża study plots did not show significant differences in PVs in pairwise comparisons. The beech-fir forest in the Šrámková forest showed significant differences in medians of PV values on density in pairwise comparisons with the remaining secondary forests except the Estenstad spruce forest in Norway.

4.2. Species variability

In Šrámková forest, the Goldcrest had the lowest PV value (0.13), while Spotted Flycatcher had the highest (0.60). Dunnock (0.15), Common Chiffchaff (0.16), Chaffinch (0.19), and European Robin (0.20) had low PV values. High population variability was found for Stock Dove (0.51), Hawfinch (0.49), Willow Warbler (0.48), Wood Warbler (0.47), and Red-breasted Flycatcher (0.47).

Patterns of species variations were compared by their means from the 13 European studies, but only species with at least 5 PV estimates (5 sites) were included in the comparison (Supplement B). The lowest temporal variation (mean PV ≤ 0.3) was detected in Chaffinch (0.21, N = 12), European Robin (0.24, N = 12), Eurasian Treecreeper (0.27, N = 10), Song Thrush (0.28, N = 11), Great Tit (0.28, N = 8), and Eurasian Blackbird (0.29, N = 11). All listed species are widespread and can be characterized as habitat and niche generalists occupying very wide range of habitats. Low mean PV values across sites of the six above listed species are consistent with the variation patterns described in Šrámková, where five of these species (Great Tit were not measured) had PV values below 0.3 (Table 1). In contrast, high fluctuation pattern (mean PV ≥ 0.4) was found in Willow Warbler (0.43, N = 5) and Wood Warbler (0.43, N = 8). These results are again consistent with findings in the Šrámková forest where both species were among those fluctuating in density the most.

Wood Warbler can be considered as a species with high temporal variability. This species reached the highest values of PV in four study plots (Białowieża NP – plots CM, K, MS; Šrámková NNR). Wesołowski *et al.* (2009) explained high fluctuations of the Wood Warbler as a result of nomadic behaviour in which the birds search for safe breeding grounds. This species searches for sites with low population densities of rodents because rodents cause direct nest depredation of eggs and nestlings and also attract rodent predators that further increase nest depredation. High fluctuations of the Wood Warbler in the Šrámková forest can be attributed to population dynamics of the Bank Vole (*Myodes glareolus*) and is consistent with the conclusions of Wesołowski *et al.* (2009). In 2004, the population of Bank Vole reached peak high densities, and in this year warblers reached their lowest numbers. The explanation as to why other ground nesting species are not negatively correlated with high abundance of rodents remains unknown (Wesołowski & Tomiałojć 1997).

4.3. Population fluctuation patterns

The twenty-two most numerous species breeding in the beech-fir forest in the Šrámková National Nature Reserve fluctuated independently of each other. The four clusters that emerged in the dendrogram structure (Fig. 5) contained a combination of species with different migration strategies and/or relationship to wintering grounds. This support the hypothesis that populations of individual species are driven by a specific and often differing set of environmental factors operating on various geographic scales influencing survivorship in breeding and wintering grounds and along migratory routes and affecting differentially each species.

In contrast, several studies have described correlations between population fluctuation patterns and migratory strategies and wintering locations (Enemar *et al.* 1984, Holmes *et al.* 1986, partly Hogstad 1993, Enemar *et al.* 1994). The correlation dendrograms in these studies clumped species with generally similar migration strategies and wintering grounds. Even though some of these species fluctuated independently, these results suggest that migratory groups of birds may be regulated by similar factors operating on migratory routes and wintering and breeding grounds. Similarly, Morozov (1993) described parallel fluctuation patterns among residents (including partial migrants) and tropical migrants based on data pooled from three habitat types in Valdai Uplands in Russia. Parallel fluctuations in short distance migrants almost significantly prevailed. In contrast to these studies, Wesołowski & Tomiałojć (1997) did not find clear correlation pattern of numerical variation of the 26 most numerous species in the Białowieża National Park in Poland. Instead, they found that species had a strong tendency to fluctuate independently of each other regardless of migration strategy and/or relationship to wintering grounds. The results of the current study are consistent with the conclusions of Wesołowski & Tomiałojć (1997).

The question remaining is why such a huge discrepancy arises between these two groups of studies? To assess this discrepancy, I first analyzed results of the studies showing correlation relationship between fluctuation patterns and migration strategy/ wintering grounds. From the cited studies, only Enemar *et al.* (1984) showed a relatively clear pattern of three groups of species that were interpreted as long-distance (tropical), short-distance irruptive, and short-distance non-irruptive migrants. The only exceptions were *Turdus philomelos*, a short distance non-irruptive migrant that belonged to the group of Afro-tropical migrants; and *Turdus iliacus*, a short distance non-irruptive migrant that belonged among short-distance irruptive migrants.

In addition, Hogstad (1993) and Enemar *et al.* (1994) described a correlative relationship between population fluctuations and migratory strategy and wintering ground that is contrary to the conclusion of this paper. A major problem in Hogstad's (1993) study involved the interpretation of the classification pattern. Fluctuation patterns of only nine species (50%) of 18 compared species were logically merged, while the other half showed independent fluctuations. At least as questionable is Hogstad's interpretation of the second cluster comprising *Turdus philomelos* and *Turdus iliacus* from the aspect of their migratory ecology since *T. iliacus* was classified as an irruptive migrant in Enemar *et al.* (1984). The real ecological meaning of the Hogstad (1993) dendrogram pattern is at least questionable and may be the result of chance alone, thus supporting hypothesis of species specific factors influencing population dynamics, at least partly. A serious problem can be seen in the interpretation of the dendrogram in the study of Enemar *et al.* (1994). Firstly, a combination of short-distance and resident species into one cluster is arbitrary because environmental factors operating on the wintering grounds (mainly Mediterranean region and North Africa in the case of short distance migrants) cannot be intuitively linked with factors operating year-round in Scandinavia. Secondly, there are exceptions in the pattern that questions whether the classification made is ecologically meaningful. In fact, three tropical migrants *Acrocephalus palustris*, *Hippolais icterina* and partly *Sylvia atricapilla* were clustered to the group of residents and short-distance migrants. Taking this into consideration, a species specific set of factors operating on breeding and wintering grounds and along migratory corridors specifically regulates populations of each species thus producing specific population dynamics patterns. This may be responsible for independent fluctuations of species. It seems a more acceptable explanation of fluctuation patterns than the notion of synchronic fluctuations of species from the same migratory groups influenced by factors similarly operating at wintering grounds. The latest findings from population regulation studies of long-distance migrants in North America support this idea (Holmes 2011).

4.4. Species associations and competition theory

Only seven of the 26 null model simulations from binary bird assemblage matrix (53 species × 10 years) of the Šrámková forest showed negative associations. Six of those null model algorithms were prone to Type 1 statistical error (see Results), thus the six negative results are questionable. None of nine null model simulations from the bird density assemblage matrix (22 species × 10 years) showed negative species association. Similarly, the analysis of species association (27 simulations) in three foraging guilds (flycatchers, foliage foragers, and litter foragers) provided no evidence of negative associations. In summary, the results offer little support for the hypothesis of compensatory dynamics, which would be expected if this assemblage was a competitively organized community.

Interspecific competition has been viewed as a primary force of nature shaping structure and dynamics of communities for several decades. This hypothesis, however, lacks support from many empirical studies of bird assemblage structure and dynamics (e.g., Enemar *et al.* 1984, Holmes *et al.* 1986, Morozov 1993, Enemar *et al.* 1994, Wesołowski & Tomiałojć 1997, Leito *et al.* 2006, Houlahan *et al.* 2007). Holmes *et al.* (1986) applied the variance test of Schluter (1984) for estimating synchrony of fluctuation of different species during a 16-year period. Their results indicate significantly positive covariation for all species taken together, not negative covariation as would occur with strong interspecific competitive effects. In addition, covariation among species within guilds was also positive, yet not statistically significant. Enemar *et al.* (1984) using Järvinen's variance V-test also detected clear parallel fluctuations. Morozov (1993) used the same approach and described preponderance of parallel density fluctuations in pool data set from short term study (1985–1989) of bird assemblages of three habitat types. Studies based on pair-wise comparison of correlation coefficients came to similar conclusions (Enemar *et al.* 1994, Wesołowski & Tomiałojć 1997, Leito *et al.* 2006). Correlations mainly indicated independent or positive fluctuations among species within studied assemblages. Houlahan *et al.* (2007) used Schluter's (1984) variance ratio as a measure of community covariance to assess the prevalence of negative associations in 41 patterns of community dynamics from published studies comprising different taxa at a range of spatial scales. They found prevalence of positive associations what is the opposite of what would be expected if compensatory dynamics were important. From my study and this review of other similar studies, we can conclude that dynamic patterns of bird assemblages do not support the competitionist view for bird assemblage structure. On the other hand, this conclusion does not discount the possibility that interspecific competition can operate between similar species just that it does not lead to measureable negative effect on overall assemblage pattern.

4.5. Implications for community concepts

None of the species showed a stable population trend. The population variability of all species was higher than 5% (Table 6). Similarly, CF and PV values highly exceeded 10% fluctuations (Table 1). This does not support the equilibrium model of a stable community.

The bootstapped cluster analysis of the bird foraging data matrix showed presence of significantly different structural units of the assemblage – guilds. Thus, data supports a model of a community composed functionally with habitat structure.

Only seven of 26 simulations by null models from binary data matrices showed negative associations (segregation), however six of these were prone to Type 1 error with the used index. None of the nine null model simulation from quantitative matrices showed segregation. In contrast, positive associations prevailed. These findings do not support the concept of a community organized by competition, but instead underlines the alternative explanations, i.e., the pluralistic idea that many factors operate independently on populations within communities.

Acknowledgements. The long term bird assemblage data from the 10 ha study plot in the Hubbard Brook Experimental Forest were obtained from Richard T. Holmes and I am very grateful to the Northeastern Research Station, U.S. Department of Agriculture, Newtown Square, Pennsylvania for permission to use them for this study. I thank the National Forest Centre in Zvolen for providing the digital forestry map and database of forest segments of the Šrámková National Nature Reserve. I also thank to an anonymous referee for providing me the R code for computing population variability coefficient. I value stimulating discussions regarding null model analysis and help from Nicholas Gotelli and Werner Ulrich. I would like to thank to Matthew G. Betts, Yrjö Haila, Ľudovít Kocian, Matti J. Koivula, Anton Krištín, Andreas Lindén, Marek Svitok, Ludwik Tomiałojć and Tomasz Wesołowski for helpful comments on earlier versions of the manuscript. In the very end, I am especially grateful to Richard T. Holmes for double review of the manuscript and final linguistic corrections.

Pesimälinnuston yhteisödynamiikka lauhkean lämpövyöhykkeen aarnisekametsässä länsi-Karpaateilla (Slovakia): tukea pluralistiselle yhteisöajattelulle

Pesimälintuyhteisön rakennetta ja dynamiikkaa tutkittiin Slovakialaisessa pyökki-pihta aarnimetsässä kymmenen peräkkäisen vuoden aikana 1997–2006, Šrámkován luonnonsuojelualueella Malá Fatran vuorissa. Lintujen tiheydet arvioitiin kartoitusmenetelmällä 27,5 hehtaarin kokoisella tutkimusalueella metsän sisäosissa. Killan rakenne määriteltiin *a posteriori*, numeerisella analyysillä, perustuen ruokailevien lintujen satunnaisiin pistehavaintoihin. Yhteensä alueella havaittiin 53 pesimälajia ja keskimärin 39 lajia vuodessa.

Populaatiotiheyden vaihtelukerroin (PV) oli 22 tavallisimmilla lajeilla 0,33 ± 0,14 SD (CV = 42,05 %), viitaten 33 % keskimääräiseen vuosienväliseen eroon. Suurimmat kannanvaihtelut havaittiin kasvissyöjillä (PV = 0,47; N = 3), tämän jälkeen siepoilla (PV = 0,44; N = 3), kenttäkerroksessa ruokailevilla lajeilla (PV = 0,33; N = 2), puunrungoilla ruokailevilla lajeilla (PV = 0,33; N = 2), lehvästössä ruokailevilla lajeilla (PV = 0,29; N = 8) ja karikkeen seassa ruokailevilla lajeilla (PV = 0,21; N = 4).

Lajien tiehyksien välisen Pearsonin korrelaatiokertoimeen perustuvan ryhmittelyanalyysin tulokset eivät yksiselitteisesti ryhmittäneet samaan talvehtimisalueeseen tai ruokailukiltaan kuuluvia lajeja. Vain seitsemän 26:sta binaarisiin nollamalleihin perustuvista simulaatioista (9 algoritmia, 3 indeksiä) yhteisötasolla viittasi negatiivisiin suhteisiin. Yksikään yhdeksästä yhteisön tiheysmatriisin nollamallin simulaatiosta (3 algoritmia, 3 indeksiä), tai killan nollamallin analyysista, ei viitannut negatiivisiin suhteisiin. Tulokset eivät tue oletusta, että kilpailu muovaa lintuyhteisöjen rakennetta, vaan tukevat pikemminkin pluralistista mallia yhteisön toiminnalle.

References

Adamík, P. & Korňan, M. 2004: Foraging ecology of two bark foraging passerine birds in an old-growth temperate forest. — Ornis Fennica 81: 13–22.

Adamík, P., Korňan, M. & Vojtek J. 2003: The effect of habitat structure on guild patterns and foraging strategies of insectivorous birds in forests. — Biologia, Bratislava 58: 275–285.

Beven, G. 1976: Changes in breeding bird populations of an oak-wood on Bookham Common, Surrey, over twenty-seven years. — London Naturalist 55: 23–42.

Brown, C.R., Brown, M.B. & Rannala B. 1995: Ectoparasites reduce long-term survival of their avian host. — Proceedings of the Royal Society of London B 262: 313–319.

Caswell, H. 1976: Community structure: a neutral model analysis. — Ecological Monographs 46: 327–354.

Cepák, J., Klvaňa, P., Formánek, J., Horák, D., Jelínek, M., Schröpfer, L., Škopek, J. & Zárybnický J. 2008: Czech and Slovak bird migration atlas. — Aventinum, Praha.

Clark, J.S. in press. The coherence problem with the unified neutral theory of biodiversity. — Trends in Ecology and Evolution.

Clements, F.E. 1916: Plant succession: an analysis of the development of vegetation. — Publication no. 242, Carnegie Institute.

Clements, F.E. 1936: Nature and structure of the climax. — Journal of Ecology 24: 252–284.

Connor, E.F. & Simberloff, D. 1979: The assembly of species communities: chance or competition? — Ecology 60: 1132–1140.

Crooks, K.R., Suarez, A.V., Bolger, D.T. & Soulé, M.E. 2001: Extinction and colonization of birds on habitat islands. — Conservation Biology 15: 159–172.

Curson, D.R., Goguen, C.B. & Mathews, N.E. 2010: Community-level patterns of population recruitment in a generalist avian brood parasite, the brown-headed cowbird. — Oecologia 163: 601–612.

Diamond, J.M. 1975: Assembly of species communities. — In Ecology and evolution of communities (eds. Cody, M. & Diamond, J.M.): 342–444. Harvard Univ. Press, Cambridge.

Dickinson E.C. (ed.) 2003. The Howard and Moore complete checklist of the birds of the world. — Christopher Helm, London.

Dudaniec, R.Y., Fessl, B. & Kleindorfer, S. 2007: Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. — Biological Conservation 139: 325–332.

Enemar, A., Nilsson, L. & Sjöstrand, B. 1984: The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. — Annales Zoologici Fennici 21: 321–338.

Enemar, A., Cavallin, B., Nyholm, E., Rudebeck, I. & Thorner, A.M. 1994: Dynamics of a passerine bird community in a small deciduous wood, S Sweden, during 40 years. — Ornis Svecica 4: 65–104.

Enemar, A., Sjöstrand, B., Anderson, G. & Proschwitz, T. von 2004: The 37-year dynamics of a subalpine passerine bird community, with special emphasis on the influence of environmental temperature and *Epirrita autumnata* cycles. — Ornis Svecica 14: 63–106.

Flousek, J. 1989: Impact of industrial emissions on bird populations breeding in mountain spruce forests in Central Europe. — Annales Zoologici Fennici 26: 255–263.

Forsman, J.T., Mönkkönen, M., Helle, P. & Inkeröinen, J. 1998: Heterospecific attraction and food resources in migrant's breeding patch selection in northern boreal forest. — Oecologia 115: 278–286.

Fuller, R.J. 2000: Influence of treefall gaps on distributions of breeding birds within interior old-growth stands in Białowieża forest, Poland. — Condor 102: 267–274.

Gause, G.F. 1934: The struggle for existence. — Williams and Wilkins, Baltimore.

Gleason, H.A. 1917: The structure and development of the plant association. — Bulletin of the Torrey Botanical Club 44: 463–481.

Gleason, H.A. 1926: The individualistic concept of the plant association. — Bulletin of the Torrey Botanical Club 53: 7–26.

Goguen, C.B. & Mathews, N.E. 1998: Songbird community composition and nestling success in grazed and ungrazed pinyon-juniper woodlands. — Journal of Wildlife Management 62: 474–484.

Gotelli, N.J. 2000: Null model analysis of species co-occurrence patterns. — Ecology 81: 2606–2621.

Gotelli, N.J. & Entsminger, G.L. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey Bear. http://homepages.togethe.net/~gentsmin/ecosim.htm

Greenberg, C.H. & Lanham, J.D. 2001: Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. — Forest Ecology and Management 154: 251–260.

Gregory, R.D., Vorišek, P., van Strien, A., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki P. & Burfield, I.J. 2007. Population trends of widespread woodland birds in Europe. — Ibis 149, Suppl. 2: 78–97.

Heath, J.P. 2006: Quantifying temporal variability in population abundance. — Oikos 115: 573–581.

Hinsley, S.A., Bellamy, P.E. & Newton, I. 1995: Bird species turnover and stochastic extinction in woodland fragments. — Ecography 18: 41–50.

Hintze, J.L. 2001: NCSS 2001, User's guide. — Kaysville.

Hirao, T., Murakami, M. & Oguma, H. 2008: Functional spatial scale of community composition change in response to windthrow disturbance in a deciduous temperate forest. — Ecological Research 23: 249–258.

Hogstad, O. 1993: Structure and dynamics of passerine bird community in a spruce-dominated boreal forest. A 12-year study. — Annales Zoologici Fennici 30: 43–54.

Holmes, R.T. 2011: Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. — Forest Ecology and Management 262: 20–32.

Holmes, R.T., Sherry, T.W. & Sturges, F.W. 1986: Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. — Ecological Monographs 56: 201–220.

Houlahan, J.E., Currie, D.J., Cottenie K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S., Fuhlendorf, S.D., Gaedke U., Legendre, P., Magnuson, J.J., McArdle, B.H., Muldavin, E.H., Noble, D., Russell, R., Stevens, R.D., Willis, T.J., Woiwood, I.P. & Wondzell, S.M. 2007: Compensatory dynamics are rare in natural ecological communities. — Proceedings of the National Academy of Sciences of the USA 104: 3273–3277.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. — Princeton Univ. Press, Princeton.

Huhta, V. 1979: Evaluation of different similarity indices as measures of succession in arthropod communities of the forest floor after clear-cutting. — Oecologia 41: 11–23.

Hutchinson, G.E. 1957: Concluding remarks. — Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427.

IBCC 1969: Recommendations for an international standard for a mapping method in bird census work. — Bird Study 16: 249–255.

James, F.C. & Boecken, W.J. 1984: Interspecific morphological relationship and the densities of birds. — In Ecological communities: conceptual issues and the evidence (eds. Strong, D.R., Simberloff, D., Abele, L.G. & Thistle, A.B.): 458–477. Princeton Univ. Press, Princeton.

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E. & Valcu, M. 2010: Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. — Current Biology 20: 1735–1739.

Kendeigh, S.C. 1982: Bird populations in east central Illinois: fluctuations, variations, and development over a half-century. — Illinois Biological Monographs 52: 1–137.

Korňan, M. 1996: Analyses of lowland forest bird communities in Slovakia and effect of migratory guilds on forming forest bird community structure in an elevational gradient. — MSc. thesis, Faculty of Sciences, Comenius University, Bratislava. (in Slovak)

Korňan, M. 2000: Interspecific foraging substrate preferences among flycatchers in a primeval mixed forest (Šrámková National Nature Reserve). — Oecologia Montana 9: 36–43.

Korňan, M. 2004: Structure of the breeding bird assemblage of a primaeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts. — Biologia, Bratislava 59: 219–231.

Korňan, M. & Adamík, P. 2002: Comparison of a priori and a posteriori approaches in foraging guild analysis in bird communities: a case study. — Oecologia Montana 11: 82–93. (in Slovak with English abstract)

Korňan, M. & Adamík, P. 2007: Foraging guild structure within a primaeval mixed forest bird assemblage: a comparison of two concepts. — Community Ecology 8: 133–149.

Korpel', Š. 1989: Primeval forests of Slovakia. —Veda, Bratislava. (in Slovak)

Kovach, W.L. 2007: MVSP – A multivariate statistical package for Windows, ver. 3.1. —Kovach Computing Services, Pentraeth.

Leito, A., Truu, J., Roosaluste, E., Sepp, K. & Põder, I. 2006: Long-term dynamics of breeding birds in broad-leaved deciduous forest on Hanikatsi Island in the West-Estonian archipelago. — Ornis Fennica 83: 124–130.

Levin, S.A. 1988: Pattern, scale and variability: an ecological perspective. — In Community ecology. (ed. Hastings, A.): 1–12. Springer-Verlag, Berlin.

Lortie, J.C., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I. & Callaway R.M. 2004: Rethinking plant community theory. — Oikos 107: 433–438.

Martin, T.E. 1993: Nest predation among vegetation layers and habitat types: revising the dogmas. — American Naturalist 141: 897–913.

MacMahon, J.A., Schimpf, D.J., Andersen, D.C., Smith, K.G. & Bayn, R.L.Jr. 1981: An organism-centered approach to some community and ecosystem concepts. — Journal of Theoretical Biology 29: 287–307.

Mayr, E. 1942: Systematics and the origin of species. — Columbia Univ. Press, New York.

McIntosh, R.P. 1995: H.A. Gleason's 'individualistic concept' and theory of animal communities: a continuing controversy. — Biological Reviews 70: 317–357.

Morozov, N.S. 1993: Short-term fluctuations in a south-taiga bird assemblage: support for an "individualistic" view. — Ornis Fennica 70: 177–188.

Mountainspring, S. & Scott, J.M. 1985: Interspecific competition among Hawaiian forest birds. — Ecological Monographs 55: 219–239.

Mönkkönen, M., Helle, P. & Soppela, K. 1990: Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? — Oecologia 85: 218–225.

Noon, B.R. 1981: Techniques for mapping avian habitats. — In The use of multivariate statistics in studies of wildlife habitat (ed. Copen, D.E.): 42–49. USDA Forest Service General Technical Report RM–87, Fort Collins.

Powell, B.F. & Steidl, R.J. 2000: Nesting habitat and reproductive success of southwestern riparian birds. — Condor 102: 823–831.

R Development Core Team 2011: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rheindt, F.E. 2003: The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution. — Journal of Ornithology 144: 295–306.

Rosindell, J., Hubbell, S.P. & Etienne S. 2011. The unified neutral theory of biodiversity and biogeography at age ten. — Trends in Ecology and Evolution 26: 340–348.

Russell, R.E., Royle, J.A., Saab, V.A., Lehmkuhl, J.F., Block, W.M. & Sauer, J.R. 2009: Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. — Ecological Application 19: 1253–1263.

Scheer, Ľ. 2010: Biometry. — Technical University in Zvolen, Zvolen. (in Slovak)

Schluter, D. 1984: A variance test for detecting species associations, with some example applications. — Ecology 65: 998–1005.

Sebastian-Gonzalez, E., Sanchez-Zapata, J.A., Botella, F. & Ovaskainen, O. 2010: Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. — Proceedings of the Royal Society of London B 277: 2983–2990.

Svensson, S. 2009: A stable bird community during 27 years (1980–2006) in the nemoral broadleaf wood Dalby Söderskog National Park. — Ornis Svecica 19: 237–243.

Svensson, S., Thorner, A.M. & Nyholm, N.E. 2010: Species trends, turnover and composition of a woodland bird community in southern Sweden during a period of fifty-seven years. — Ornis Svecica 20: 31–44.

Tomiałojć, L. 1980: The combined version of the mapping method. — In Bird census work and nature conservation. Proc. VI. int. conf. on bird census work. (ed. Oelke H.): 92–106. University Göttingen, Göttingen.

Tomiałojć, L. & Wesołowski, T. 1994: Die Stabilität der Vogelgemeinschaft in einem Urwald der gemässigten Zone: Ergebnisse einer 15jährigen Studie aus dem Nationalpark von Białowieża (Polen). — Ornithologische Beobachter 91: 73–110.

Tomiałojć, L. & Wesołowski, T. 1996: Structure of a primaeval forest bird community during 1970s and 1990s (Białowieża National Park, Poland). — Acta Ornithologica 31: 133–154.

Tomiałojć, L., Wesołowski, T. & Walankiewicz, W. 1984: Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). — Acta Ornithologica 20: 241–310.

Ulrich, W. 2010. Turnover – a FORTRAN program for analysis of species associations. Version 1. www.umk.pl/~ulrichw.

Ulrich, W. & Gotelli, N.J. 2010. Null model analysis of species association using abundance data. — Ecology 91: 3384–3397.

Underwood, A.J. 1986: What is a community? — In Patterns and processes in the history of life (eds. Raup, D.M. & Jablonski, D.): 259–276. Springer-Verlag, Berlin.

Vološčuk, I. 1986: The forest vegetation of the State Nature Reserve Šrámková. — Ochrana prírody 7: 237–251. (in Slovak)

Weatherhead, P.J., Carfagno, G.L.F., Sperry, J.H., Brawn, J.D. & Robinson, S.K. 2010: Linking snake behaviour to nest predation in a Midwestern bird community. — Ecological Applications 20: 234–241.

Wesołowski, T. 2007: Primeval conditions – what can we learn from them? — Ibis 149, Suppl. 2: 64–77.

Wesołowski, T., Mitrus, C., Czeszczewik, D. & Rowiński, P. 2010: Breeding bird dynamics in a primeval temperate forest over thirty-five years: variation and stability in the changing world. — Acta Ornithologica 45: 209–232.

Wesołowski, T., Rowiński, P. & Maziarz, M. 2009: Wood Warbler *Phylloscopus sibilatrix*: a nomadic insectivore in search of safe breeding grounds? — Bird Study 56: 26–33.

Wesołowski, T., Rowiński, P., Mitrus, C. & Czeszczewik, D. 2006: Breeding bird community of a primeval temperate forest (Białowieża National Park, Poland) at the beginning of the 21st century. — Acta Ornithologica 41: 55–70.

Wesołowski, T. & Tomiałojć, L. 1997: Breeding bird dynamics in a primaeval temperate forest: long-term trends in Białowieża National Park (Poland). — Ecography 20: 432–453.

Wesołowski, T. & Tomiałojć, L. 2005: Nest sites, nest depredation, and productivity of avian broods in a primeval forest: do the generalisations hold? — Journal of Avian Biology 36: 361–367.

Wesołowski, T., Tomiałojć, L., Mitrus, C., Rowiński, P. & Czeszczewik, D. 2002: The breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland) at the end of the 20th century. — Acta Ornithologica 37: 27–45.

Whittaker, R.H. 1975: Communities and ecosystems. — Macmillan Publishing, New York.

Wiens, J.A. 1989: The ecology of bird communities. Vol. I. Foundation and patterns. — Cambridge Univ. Press, Cambridge.

Appendix 1. Species abundance and density of the breeding bird assemblage of primaeval beech-fir forest in the Šrámková National Nature Reserve during ten year period (1997–2006) in the 27.5 ha census plot as determined by the combined version of the mapping method.

Species	Abundance										Density (pairs/10 ha)									
	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Fringilla coelebs	25.7	25.6	34.3	35.7	34.5	42.9	41.3	44.6	40.3	33.4	9.35	9.31	12.47	12.98	12.55	15.60	15.02	16.22	14.65	12.15
Erithacus rubecula	10.7	14.5	15.6	16.2	11.2	18.6	10.6	15.4	15.8	12.0	3.89	5.27	5.67	5.89	4.07	6.76	3.85	5.60	5.75	4.36
Sylvia atricapilla	8.7	7.6	12.4	15.9	14.0	12.7	14.8	8.8	11.8	11.0	3.16	2.76	4.51	5.78	5.09	4.62	5.38	3.20	4.29	4.00
Parus ater	13.5	15.3	7.0	8.8	10.0	9.8	16.3	11.3	10.0	13.8	4.91	5.56	2.55	3.20	3.64	3.56	5.93	4.11	3.64	5.02
Regulus regulus	8.0	11.1	9.3	9.7	9.3	11.2	11.2	8.2	10.0	8.8	2.91	4.04	3.38	3.53	3.38	4.07	4.07	2.98	3.64	3.20
Phylloscopus collybita	7.1	9.8	10.3	11.5	10.6	10.8	10.7	8.5	9.2	7.5	2.58	3.56	3.75	4.18	3.85	3.93	3.89	3.09	3.35	2.73
Prunella modularis	6.7	8.8	7.5	9.0	9.5	11.1	8.8	7.0	8.2	8.9	2.44	3.20	2.73	3.27	3.45	4.04	3.20	2.55	2.98	3.24
Ficedula albicollis	7.5	6.9	5.3	6.3	6.0	10.5	6.0	9.7	9.0	4.5	2.73	2.51	1.93	2.29	2.18	3.82	2.18	3.53	3.27	1.64
Certhia familiaris	6.4	4.9	5.7	7.8	7.0	9.0	6.6	7.0	4.5	3.9	2.33	1.78	2.07	2.84	2.55	3.27	2.40	2.55	1.64	1.42
Troglodytes troglodytes	4.5	5.9	5.0	6.0	6.4	5.0	2.0	5.0	4.8	5.5	1.64	2.15	1.82	2.18	2.33	1.82	0.73	1.82	1.75	2.00
Columba oenas	5.3	3.0	3.5	5.0	11.0	6.3	2.0	1.0	7.5	2.3	1.93	1.09	1.27	1.82	4.00	2.29	0.73	0.36	2.73	0.84
Columba palumbus	6.9	7.0	7.3	6.5	2.0	2.7	4.5	2.2	3.5	3.0	2.51	2.55	2.65	2.36	0.73	0.98	1.64	0.80	1.27	1.09
Turdus merula	4.5	4.5	3.5	3.6	6.2	5.2	5.8	4.2	4.5	2.8	1.64	1.64	1.27	1.31	2.25	1.89	2.11	1.53	1.64	1.02
Turdus philomelos	1.8	5.5	3.2	4.8	4.7	5.0	4.0	3.8	3.3	4.0	0.65	2.00	1.16	1.75	1.71	1.82	1.45	1.38	1.20	1.45
Phylloscopus sibilatrix	4.7	4.0	4.3	1.0	4.5	6.0	6.8	o+	3.3	4.0	1.71	1.45	1.56	0.36	1.64	2.18	2.47	(0.05)	1.20	1.45
Sitta europaea	1.8	4.0	2.8	4.0	5.6	6.1	2.0	4.1	1.5	2.3	0.65	1.45	1.02	1.45	2.04	2.22	0.73	1.49	0.55	0.84
Ficedula parva	3.5	1.0	1.5	2.5	1.5	4.3	2.0	1.5	1.0	0.5	1.27	0.36	0.55	0.91	0.55	1.56	0.73	0.55	0.36	0.18
Pyrrhula pyrrhula	3.3	4.5	2.0	1.0	1.0	2.0	1.0	1.0	0.8	1.8	1.20	1.64	0.73	0.36	0.36	0.73	0.36	0.36	0.29	0.65
Parus palustris	1.0	1.0	1.0	1.5	1.3	2.3	2.7	2.5	2.5	2.3	0.36	0.36	0.36	0.55	0.47	0.84	0.98	0.91	0.91	0.84
Muscicapa striata	3.0	3.0	3.8	o+	0.5	o+	3.0	+	1.0	2.0	1.09	1.09	1.38	(0.10)	0.18	(0.10)	1.09	(0.10)	0.36	0.73
Coccothraustes coccothraustes	2.0	1.0	3.0	2.0	0.5	o+	2.3	1.0	1.0	1.0	0.73	0.36	1.09	0.73	0.18	(0.10)	0.84	0.36	0.36	0.36
Phylloscopus trochilus	+	1.8	2.2	0.5	1.3	1.5	2.5	1.3	0.5	1.3	(0.10)	0.65	0.80	0.18	0.47	0.55	0.91	0.47	0.18	0.47
Turdus viscivorus	1.8	2.0	1.0	2.0	1.0	1.0	+	1.5	1.5	0.5	0.65	0.73	0.36	0.73	0.36	0.36	(0.10)	0.55	0.55	0.18
Regulus ignicapilla	–	1.0	1.5	1.0	1.0	1.0	0.5	2.0	1.0	3.0	0.00	0.36	0.55	0.36	0.36	0.36	0.18	0.73	0.36	1.09
Dendrocopos leucotos	1.0	0.5	0.8	1.5	0.8	1.0	1.3	0.5	1.5	1.5	0.36	0.18	0.29	0.55	0.29	0.36	0.47	0.18	0.55	0.55
Turdus torquatus	+	2.4	1.5	1.0	1.3	1.3	1.5	o+	+	o+	(0.10)	0.87	0.55	0.36	0.47	0.47	0.55	(0.05)	(0.10)	(0.05)
Picoides tridactylus	0.5	2.0	+	1.0	1.0	1.0	0.5	0.5	0.8	0.7	0.18	0.73	(0.10)	0.36	0.36	0.36	0.18	0.18	0.29	0.25
Motacilla cinerea	1.0	1.0	1.0	1.0	0.5	0.8	+	0.5	0.5	0.5	0.36	0.36	0.36	0.36	0.18	0.29	(0.10)	0.18	0.18	0.18
Aegithalos caudatus	0.5	–	†0.25	+	0.8	2.8	1.3	o+	0.5	0.5	0.18	0.00	0.09	(0.10)	0.29	1.02	0.47	(0.05)	0.18	0.18
Carduelis spinus	p	p	0.5	p	p	p	2.5	1.0	p	p	0.00	0.00	0.18	0.00	0.00	0.00	0.91	0.36	0.00	0.00
Loxia curvirostra	–	p	1.0	p	1.0	–	p	1.0	1.0	p	0.00	0.00	0.36	0.00	0.36	0.00	0.00	0.36	0.36	0.00
Parus caeruleus	–	0.5	–	–	o+	0.5	–	3.0	p	o+	0.00	0.18	0.00	0.00	(0.05)	0.18	0.00	1.09	0.00	(0.05)
Scolopax rusticola	1.0	1.0	p	p	p	+	p	+	+	1.0	0.36	0.36	0.00	0.00	0.00	(0.10)	0.00	(0.10)	(0.10)	0.36
Cuculus canorus	+	+	0.5	+	+	+	1.3	0.5	+	0.5	(0.10)	(0.10)	0.18	(0.10)	(0.10)	(0.10)	0.47	0.18	(0.10)	0.18
Parus major	–	–	0.5	1.0	–	–	1.0	–	o+	p	0.00	0.00	0.18	0.36	0.00	0.00	0.36	0.00	(0.05)	0.00
Anthus trivialis	–	+	0.5	0.5	+	0.5	0.5	–	o+	+	0.00	(0.10)	0.18	0.18	(0.10)	0.18	0.18	0.00	(0.05)	(0.10)
Bonasa bonasia	–	1.0	+	+	0.5	+	o+	–	+	–	0.00	0.36	(0.10)	(0.10)	0.18	(0.10)	(0.05)	0.00	(0.10)	0.00
Dendrocopos major	1.0	+	–	–	o+	–	–	–	–	–	0.36	(0.10)	0.00	0.00	(0.05)	0.00	0.00	0.00	0.00	0.00
Strix aluco	–	o+	+	o+	–	–	+	0.5	–	+	0.00	(0.01)	(0.01)	(0.01)	0.00	0.00	(0.01)	0.18	0.00	(0.01)
Garrulus glandarius	+	+	+	+	+	+	+	+	+	+	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)
Dryocopus martius	+	+	+	+	+	+	+	+	+	o+	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.10)	(0.05)
Aquila chrysaëtos	p	+	+	+	+	+	+	+	+	+	0.00	(0.001)	(0.001)	(0.001)	(0.001)	(0.001)	(0.001)	(0.001)	(0.001)	(0.001)
Accipiter gentilis	+	+	+	+	+	+	+	+	–	+	(0.004)	(0.004)	(0.004)	(0.004)	(0.004)	(0.004)	(0.004)	(0.004)	0.00	(0.004)
Glaucidium passerinum	+	p	+	o+	–	–	+	+	–	+	(0.05)	0.00	(0.05)	(0.05)	0.00	0.00	(0.05)	(0.05)	0.00	(0.05)
Cinclus cinclus	+	+	p	+	+	+	p	p	p	–	(0.10)	(0.10)	0.00	(0.10)	(0.10)	(0.10)	0.00	0.00	0.00	0.00
Buteo buteo	+	–	–	–	p	–	p	+	+	+	(0.004)	0.00	0.00	0.00	0.00	0.00	0.00	(0.004)	(0.004)	(0.004)
Nucifraga caryocatactes	o+	o+	o+	–	+	+	–	o+	–	o+	(0.10)	(0.10)	(0.10)	0.00	(0.10)	(0.10)	0.00	(0.10)	0.00	(0.10)
Accipiter nisus	–	–	–	–	–	+	p	–	+	–	0.00	0.00	0.00	0.00	0.00	(0.004)	0.00	0.00	(0.004)	0.00
Pernis apivorus	–	–	+	–	–	+	–	–	–	–	0.00	0.00	(0.004)	0.00	0.00	(0.004)	0.00	0.00	0.00	0.00
Phoenicurus phoenicurus	o+	o+	–	–	–	–	o+	+	o+	o+	(0.10)	(0.10)	0.00	0.00	0.00	0.00	(0.10)	(0.10)	(0.10)	(0.10)
Picus canus	o+	o+	–	–	p	–	p	+	p	o+	(0.10)	(0.10)	0.00	0.00	0.00	0.00	0.00	(0.10)	0.00	(0.10)
Strix uralensis	–	–	–	–	–	–	–	+	–	p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	(0.001)	0.00	0.00
Aegolius funereus	–	–	–	–	–	–	–	+	–	–	0.00	0.00	0.00	0.00	0.00	0.00	0.00	(0.05)	0.00	0.00
Parus cristatus	–	o+	–	–	–	p	–	–	o+	p	0.00	(0.05)	0.00	0.00	0.00	0.00	0.00	0.00	(0.05)	0.00
Corvus corone cornix	o+	o+	–	–	–	–	–	–	–	–	(0.05)	(0.05)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 1, continued

Delichon urbica	p	p	p	p	p	p	p	p	p	p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tetrao urogallus	p	p	p	p	p	p	p	p	–	p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corvus corax	p	–	–	–	p	–	–	–	–	–	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Parus montanus	p	–	–	–	–	–	–	–	–	p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Apus apus	–	–	p	–	–	–	–	–	–	–	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total (60 species)	143.4	162.1	159.6	168.3	166.5	192.9	177.3	159.1	160.8	144.8	52.15	58.95	58.02	61.20	60.55	70.15	64.47	57.85	58.47	52.65

Explanations: Plus ("+") indicates breeding abundance of less than 0.5 territory (pair) per study plot; "o+" indicates breeding presence in the reserve but not detected as breeder in the study plot; "p" is used for species detected in the study plot as none breeders or as rare visitors; "–" indicates absence; "†"– polygamous pair, three adult birds. In the density columns, density estimates for "+" and "o+" species are given by qualified guess based on observations in the reserve and the Krivánska Fatra Mts. The density estimates in parenthesis ( ) are rough density estimates for calculation of several numerical parameters as explained in Material and Methods.

Appendix 2. A classification of species into guild and migratory habit categories detected in the primaeval beech-fir forest in the Šrámková National Nature Reserve in the period 1997–2006. Guild and migratory habit categories: foraging guilds: F – flycatchers, FG – foliage gleaners, HF – herb layer foragers, LF – litter foragers, BG – bark gleaners, O – omnivorous, PE – plant eaters (vegetarians), R – raptorial guild (vertebratophags), SF – stream foragers, S – sweepers, TF – trunk foragers; nesting guilds: B – bush nesters, C – canopy nesters, G – ground nesters, H – hole nesters; migratory habits: R – residents, S – short-distance migrants, T – tropical migrants.

Species	Guild types		Migratory habits
	foraging	nesting	
Accipiter gentilis Northern Goshawk	R	C	R
Accipiter nisus Eurasian Sparrowhawk	R	C	S
Aegithalos caudatus Long-tailed Tit	FG	C	R
Aegolius funereus Tengmalm's Owl/Boreal Owl	R	H	R
Anthus trivialis Tree Pipit	LF	G	T
Apus apus Common Swift	S	–	T
Aquila chrysaetos Golden Eagle	R	C	R
Bonasa bonasia Hazel Grouse	PE	G	R
Buteo buteo Eurasian Buzzard	R	C	S
Carduelis spinus Eurasian Siskin	PE	C	S
Certhia familiaris Eurasian Treecreeper	TF	H	R
Cinclus cinclus White-throated Dipper	SF	G	R
Coccothraustes coccothraustes Hawfinch	FG	C	S
Columba oenas Stock Dove	PE	H	S
Columba palumbus Woodpigeon	PE	C	S
Corvus corax Common Raven	O	C	R
Corvus corone cornix Carrion Crow	O	C	R
Cuculus canorus Common Cuckoo	FG	–	T
Delichon urbica Northern House Martin	S	–	T
Dendrocopos leucotos White-backed Woodpecker	TF	H	R
Dendrocopos major Great Spotted Woodpecker	TF	H	R
Dryocopus martius Black Woodpecker	TF	H	R
Erithacus rubecula European Robin	LF	G	S
Ficedula albicollis Collared Flycatcher	F	H	T
Ficedula parva Red-breasted Flycatcher	F	H	T
Fringilla coelebs Chaffinch	FG	C	S
Garrulus glandarius Eurasian Jay	O	C	S
Glaucidium passerinum Eurasian Pygmy Owl	R	H	R
Loxia curvirostra Red Crossbill	PE	C	S

Appendix 2, continued

Motacilla cinerea Grey Wagtail	SF	G	S
Muscicapa striata Spotted Flycatcher	F	C	T
Nucifraga caryocatactes Eurasian Nutcracker	PE	C	R
Parus ater Coal Tit	FG	H	R
Parus caeruleus Blue Tit	FG	H	S
Parus cristatus Crested Tit	FG	H	R
Parus major Great Tit	FG	H	S
Parus montanus Willow Tit	FG	H	R
Parus palustris Marsh Tit	FG	H	R
Pernis apivorus European Honey Buzzard	LF	C	T
Phoenicurus phoenicurus Common Redstart	FG	H	T
Phylloscopus collybita Common Chiffchaff	FG	G	S
Phylloscopus sibilatrix Wood Warbler	FG	G	T
Phylloscopus trochilus Willow Warbler	FG	B–G	T
Picoides tridactylus Three-toed Woodpecker	TF	H	R
Picus canus Grey-headed Woodpecker	LF	H	R
Prunella modularis Dunnock	LF	B	S
Pyrrhula pyrrhula Eurasian Bullfinch	HF	B	S–R
Regulus ignicapilla Firecrest	FG	C	S–R
Regulus regulus Goldcrest	FG	C	S–R
Scolopax rusticola Eurasian Woodcock	LF	G	S
Sitta europaea Eurasian Nuthatch	TF	H	R
Strix aluco Towny Owl	R	H	R
Strix uralensis Ural Owl	R	C	R
Sylvia atricapilla Blackcap	FG	B	S
Tetrao urogallus Western Capercaillie	PE	G	R
Troglodytes troglodytes Winter Wren	HF	B–G	S
Turdus merula Eurasian Blackbird	LF	B	S–R
Turdus philomelos Song Thrush	LF	B	S
Turdus torquatus Ring Ouzel	LF	B	S
Turdus viscivorus Mistle Thrush	LF	C	S