Foraging guild structure within a primaeval mixed forest bird assemblage: a comparison of two concepts

M. Korňan[1,3] and P. Adamík[2]

[1] Centre for Ecological Studies, Ústredie 14, 013 62 Veľké Rovné, Slovakia
[2] Department of Zoology, Palacký University, Tř. Svobody 26, 771 46 Olomouc, Czech Republic
[3] Corresponding author. E-mail: mkornan@mail.t-com.sk

Abstract: Two basic concepts of guild definition were developed in community ecology that enable simplification of complex communities or ecosystems into structural building blocks of species with similar niches. Root defined guild as a group of species utilising the same environmental resources by a similar foraging method. MacMahon et al. simplified the original definition even more by excluding a foraging method. This concept is focused on utilisation patterns of resources by species regardless the purpose of use. Our objectives were: (1) to test guild structure within a model ecosystem from matrices reflecting the differences between the two concepts, (2) to compare guild patterns detected by the two concepts, (3) to test whether the mixed forest ecosystem consists of significantly different groups of species representing deciduous and coniferous faunal elements. The study was conducted in a primeval beech-fir forest in NW Slovakia during 1997–2000. In total, 26 bird species were used for further numerical analyses. Two data matrices were constructed reflecting the differences between the two guild concepts. To statistically determine guild structure without arbitrary fusion criteria, a bootstrapped cluster analysis (UPGMA) of chord distances was employed to analyse the data matrices. Symmetric correspondence analysis (CA) was applied for extraction of eigenvectors responsible for the segregation of species into guilds. The classification proposed by Root produced two guild models at the levels of 6 or 9 group partitions at $\alpha = 0.10$, while the classification following MacMahon et al. detected 7 guild types. The guild structures based on the two concepts were significantly different when tested by two-tailed Wilcoxon paired sample tests and the Monte Carlo among-cluster error sum of squares (SSQ) distance simulation test. Six out of the eight interpretable factors (75%) indicated analogous environmental gradients when comparing two CA ordinations. The most important environmental gradients were: (1) vertical foraging substrate – habitat structure, (2) water – terrestrial foraging substrate gradient, (3) spatial tree morphology, (4) terrestrial foraging substrate gradient, (5) arboreal – airspace gradient, and (6) mountain stream environmental gradient. We did not detect significantly different guilds for generalists and for coniferous and deciduous forest specialists.

Introduction

In community ecology, guilds are viewed as one of the basic structural units or building blocks of communities. The concept of ecological guilds was originally proposed by Root (1967), who defined an ecological guild as a group of species that "exploit the same class of environmental resources in a similar way." Members of a guild overlap in their foraging repertoires, foraging beats, and diet (p. 346). Based on Root's definition, this term groups together all sympatric species without regard to their taxonomic position that overlap significantly in their niche dimensions. The guild had an important structural

position in the classification of exploitation patterns in communities comparable to the genus in phylogenetic systems. In terms of ecological niche theory (Hutchinson 1957, MacFadyen 1957), the members of the same guild have similar ecological role within a community; however, they do not have to occupy the same niche.

Since then, the concept has faced criticism and diverse interpretation causing serious dichotomy in the concept, its interpretation, application, and terminology (Wilson 1999, Blondel 2003, Korňan 2005). In contrast to Root's original definition, in which one of the main criteria of

guild definition was the use of resources in a "similar manner", MacMahon et al. (1981) and Jaksić (1981) argue that community guilds should be defined on the basis of resource utilisation patterns of species, and they conclude that the most important is the effect of resource use on the resource itself. Quoting MacMahon et al. (1981, p. 301), "...it does not matter whether an organism removes a tree leaf for nesting material, for food, or as substrate to grow fungi which in turn are eaten; the leaf is gone and the leaf users belong to a common guild." Simberloff and Dayan (1991) do not accept this view and suggest that using a resource in a different way could reduce interspecific competition. Even though it is probably very difficult to make a straightforward conclusion, it is important to notice for further development of the concept that partitioning of resource type utilisation should be in the first place. In addition, it is important to mention that not only ways of resource use may lower interspecific competition, but also day time and seasonal partitioning, habitat partitioning, and other mechanisms not included in Root's original concept may play an equally important role in the definition of guilds (Schoener 1974, Wilson 1999, Korňan 2005).

The concept assumes that communities in identical habitat types are built up by a similar mosaic of guild types composed of the same species so-called assembly rules (Diamond 1975, Gilpin and Diamond 1982, Drake 1990). This concept, furthermore, assumes more or less constant species composition and functional structures, which are responsible for all ecological and biotic processes with some variability in time (Jaksić et al. 1993) and space (Mac Nally 1994, Wilson and Gitay 1999). The concept of assembly rules faces a serious criticism due to the argument that assembly patterns could merely reflect random distributions (Connor and Simberloff 1979). This also directly touches the concept of guild composition within communities, which assumes non-random distribution of species into guilds (Jaksić and Medel 1990, Korňan 2005). This notion significantly influenced development of new statistical techniques based on bootstrap randomisation methods and genetic algorithms that enable testing whether species clusters are non-random (Lawlor 1980, Strauss 1982, Jaksić and Medel 1990, Winemiller and Pianka 1990, Wilson and Roxburgh 1994, Mitchell 1997, Pillar 1999, Gotelli 2000, Pillar 2004). Most of the guild studies failed to meet this criterion of non-randomness, even if they detected and described strong guild structure of assemblages (e.g., Holmes et al. 1979, Wagner 1980, Landres and MacMahon

1983, Holmes and Recher 1986, Mac Nally 1994, Giannini and Kalko 2004). Wilson and Gitay (1999) demonstrated by using genetic algorithms that it is highly probable to reveal at least two independent guild classifications that are simultaneously and orthogonally effective in limiting species coexistence in one community at one time. They concluded that any attempts for application of multivariate methods for guild classification are potentially misleading.

Many studies have sought to identify the most important factors regarding structural and floristic components of habitats that cause segregation of species into guild types (Inger and Colwell 1977, Holmes et al. 1979, Holmes and Rechel 1986, Székely and Moskát 1991, Brandl et al. 1994, Giannini and Kalko 2004, Korňan 2004b, 2005). The main intention of this research was to describe mechanisms of species radiation and resource partitioning within a particular habitat. Various multivariate indirect ordination (factor[1]) analyses (e.g., principal component analysis, multidimensional scaling, correspondence analysis) were applied to meet these objectives in several taxonomical groups (insects, amphibians, reptiles, birds, and mammals). Most of the studies used PCA as the factor extraction technique from data matrices (Inger and Colwell 1977, Holmes et al. 1979, Landres and MacMahon 1983, Holmes and Recher 1986, Cornell and Kahn 1989, Székely and Moskát 1991, Brandl et al. 1994). PCA is defined for a linear response model in which the values of any species either increases or decreases with the value of each of the latent environmental variables (Legendre and Legendre 1983, Jongman et al. 1997). Although being very robust, this technique is not optimal for extraction of eigenvalues and eigenvectors from compositional data matrices. Using such data may lead to detection of a limited number of interpretable factors (e.g., Gauch et al. 1977, Holmes et al. 1979, Holmes and Recher 1986), but also standardisation may lead to artificial correlations among variables causing artifactitious relationships known as the constant-sum constraint problem (Jackson 1997). A solution is correspondence analysis (CA), a distribution free ordination method related to an unimodal response model. It better reflects real ecological data sets and is unaffected by the decision to use either raw or compositional (percentages, proportions, and frequencies) data (Jackson 1997, Jongman et al. 1997).

In order to analyse both guild relationships among species and the mechanisms of resource partitioning in a bird assemblage, a primeval temperate mountain beech-

---

1   The term "factor analysis" is used here in the most general sense, referring to any statistical method for resolving complex relationships by isolating and identifying causal factors (Lincoln et al. 1998).

fir forest was selected as a model study site. Mixed forests composed of deciduous and coniferous faunal elements fill a very specific space in the mid-elevation vegetation belt in the transition between deciduous and coniferous vegetation zones. In a wide sense, they function as ecotones between these two altitudinal zones. They provide an extraordinary ecosystem for studying both deciduous and coniferous forest specialists and generalist species occupying both altitudinal zones.

The main objectives of this study were:

(1) Are species of the primeval bird assemblage randomly distributed in their multidimensional foraging niche space or do they form significantly different and stable multispecies guilds reflecting functional organisation of the assemblage? The definition of statistically significant foraging guilds is a crucial stage for this study since a number of studies based on genetic algorithms failed to detect clear intrinsic guild structures, e.g., in rain forest (Wilson et al. 1995a), in limestone grassland (Wilson et al. 1995b), and in bryophyte carpets (Wilson et al. 1995c). This has led to the conclusion that some communities are not structured into guilds in the sense of Pianka (1988).

(2) Are there any differences in guild structure when Root's original concept of guild definition is compared to MacMahon et al.'s concept? As far as we are aware, this is the first empirical study comparing these concepts in a model ecosystem and taxonomic group.

(3) What are the main structural and floristic habitat components responsible for species division into guilds?

It is important to point out that few studies have delineated animal guilds at the community or assemblage level (e.g., Holmes et al. 1979, Sabo 1980, Landres and MacMahon 1983, Holmes and Recher 1986, Cooper et al. 1990, Winemiller and Pianka 1990, Mac Nally 1994). Only one was statistically designed to objectively detect guild structures using genetic algorithms or bootstrapped multivariate techniques (Winemiller and Pianka 1990). In addition, the majority of studies have dealt only with one or few taxonomic guilds (e.g., Eckhardt 1979, Wagner 1980, Hairstone 1981, Alatalo 1982, Alatalo et al. 1985, Adams 1985, Alatalo and Moreno 1987, Jaksić and Medel 1990, Székely and Moskát 1991, Krištín 1992, Suhonen et al. 1993, Jaksić et al. 1993, Brandl et al. 1994, Muñoz and Ojeda 1998, Cody 2000, Giannini and Kalko 2004). This is the first *a posteriori* study of bird foraging guilds in a primeval ecosystem and probably the first study of bird foraging guilds on an assemblage level in Europe.

Material and methods

Study area

The study was conducted in the Šrámková National Nature Reserve, Malá Fatra Mts (49°11′22′′ N, 19°06′49′′ E), NW Slovakia. The study plot represents the climax stage of a Western Carpathian beech-fir forest growing on hillside granite waste. The forest has all the characteristic features of primeval stands. The study plot is situated at an elevation 825–1123 m a.s.l. (measured by the Magellan GPS ProMARK X). The reserve belongs to a cold mountain climatic zone with mean July air temperature between 10–12°C. The total mean annual precipitation varies between 900–1200 mm (Vološčuk 1986). The slope inclination is 20–60°.

The forest is uneven-aged with considerable vertical and horizontal heterogeneity. All developmental stages of a primeval 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 decreases due to the emission of air pollutants.

The quantitative description of vegetation structure was carried out within 0.04 ha ($r = 11.3$ m) circular plots with 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 canopy height is up to 45 m. The shrub layer mainly consists of hazel (*Corylus avellana*), red-berried elder (*Sambucus racemosa*), currant (*Ribes* sp.), and saplings of the dominant tree species. The herb layer is mainly composed of *Dryopteris filix-mas*, *Athyrium filix-femina*, *Rubus* sp., *Impatiens glandulifera*, *Senecio jacobaea*, *Oxalis acetosella*, *Galium odoratum*, *Dentaria bulbifera*, *Lunaria rediviva*, *Homogyne alpina*, *Luzula luzuloides* ssp. *luzuloides*, *Calamagrostis arundinacea*, and *Vaccinium myrtillus*. For details, see Korňan (2000).

Data collection

Bird foraging data were collected in the core zone of the reserve spread on 243.65 ha, but primarily within the 27.5 ha (500 m × 550 m) study site. Sampling was carried out in the period 1997–2000 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, searched for, and observed as many different feeding birds as possible. Individuals were watched as long as they continuously remained in sight. The sampling of bird foraging behaviour was usually carried out for a whole 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 to a field sheet 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, time 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. In total, 39 variables were recorded, which were subsequently used for statistical analyses (Tables 2, 3).

A foraging movement was defined as any activity whose immediate purpose was to detect and capture a food item. The foraging classification scheme follows Remsen and Robinson (1990). They subdivided the attack phase into (1) perch and (2) manoeuvre. Their proposed classification scheme is very detailed. Its application for a study on the assemblage level would give an extremely large data matrix containing a high proportion of zero values. Therefore, a considerable reduction of attack categories was necessary. This was important for comparison with guild studies that had used an identical data collection design (Holmes et al. 1979, Holmes and Rechel 1986). Attack categories (foraging manoeuvres) were divided into four main types: gleaning, hovering, sallying (hawking), and probing (pecking). These combined several other individual categories of Remsen and Robinson (1990) shown in parentheses as follows. Gleaning (included reach, hang, and lunge) is a foraging tactic when a stationary prey item is taken from a surface of a nearby substrate by a perching or hopping bird. Hovering (included sally-hover, and sally-stall) is picking an exposed prey from a substrate by an actively flying bird in hummingbird manner. Sallying (included leap, sally-strike, sally-glide, sally-pounce, flutter-chase, flush-pursue, and hawk) is flying from an observation perch to attack a food item and then returning to a perch. Probing (included are peck and hammer) is a manoeuvre when a bird penetrates a bill into a substrate to catch a subsurface prey item. The latter attack is directed at food that is invisible from the surface without substrate manipulation. It was impossible to determine by sight a caught prey item or to distinguish successful and unsuccessful attacks. Consequently, all observations indicate only foraging manoeuvres regardless of outcome.

For the purpose of this study, pooled data for all individuals of each species collected over the period 1997–2000 were used, although several studies have showed significant intraspecific, seasonal, and annual variation in foraging behaviour (e.g., Ulfstrand 1976, Hejl and Verner 1990, Tebbich et al. 2004, Adamík and Korňan 2004).

Statistical analyses

Matrix preparation. Totally, 4214 foraging observations of 41 bird species were collected during 1997–2000. The data sheet information was typed into databases in the MS Access and MS Excel format. From the total number of recorded species, only 26 species with at least 30 observations or a minimum total observation time of 1 500 s were used for data analyses. This criterion seems satisfactory for a description of general species foraging patterns (see Mac Nally 1994, 10–20 observations). Brennan and Morrison (1990) concluded that the means of samples with at least 30 observations per species were stable and they were significantly similar to the total sample means. In addition, the authors stated that 40–50 observations are satisfactory for the accurate description of the foraging behaviour based on differences of means and their standard deviations. The majority of the species highly exceeded this number (Appendix 1).

In order to compare the ecological guild concepts of Root and MacMahon et al. (objective 2), two data matrices were constructed. The first data matrix (matrix 1) combined both the use of foraging substrates and foraging manoeuvres, whereas the foraging behaviour variables were excluded from the other data matrix (matrix 2). In data matrix 1, a foraging manoeuvre was combined with a morphological part (i.e., leaf, twig, branch, trunk) of a substrate (i.e., plant species) to which it was directed. Data matrix 1 (26 species × 38 variables) consists of two variables indicating foraging heights, sixteen foraging substrate variables, eighteen variables reflecting type of foraging movement, and two variables indicating direction of foraging movements. The matrix structure reflected Root's concept of ecological guilds.

Matrix 2 was based only on the data describing the use of the foraging substrates; the data on the species foraging manoeuvres were ignored. Each type of a foraging substrate (e.g., tree species, standing dead trees, fallen trees, and herb layer) was divided into morphological parts (i.e., leaf, twig, branch, trunk) on which a foraging manoeuvre took place. Data matrix 2 (26 species × 47 variables) con-

sists of 32 tree substrate variables, 1 ground substrate variable, 1 litter substrate variable, 2 herb layer variables, 3 standing dead tree or log variables, 3 fallen dead tree or log variables, 1 rock substrate variable, 1 air substrate variable, and 1 water substrate variable. The variables with lower frequency (< 5) observations (0.001%) in the database were excluded from the further statistical analyses.

Except for two metric variables related to the foraging height, all variables were expressed as proportions based on the foraging frequencies of the individual species in the standardised variable set. The minimal and maximal foraging heights were not used for the description of foraging niches, instead derived variables were used: the mean foraging height and its standard derivation (SD).

Nonparametric distribution free multivariate clustering (bootstrapped UPGMA) and ordination techniques (CA) were selected for numerical analyses. Although the matrices contained variables in different measurement units – percentages and meters, no data transformations were applied since they can seriously damage the original correlation and covariation structure of the data matrix and bias results by data standardisation (Jackson 1997). In any case, two variable types had similar ranges of values that were always in the interval 0–100 for both measurement units, so the standardisation was not necessary due to the similar magnitude of values. Both data matrices were constructed from the same primary data due to the insufficient number of foraging observations to prepare several statistically independent matrices.

Guild determination. The principal problem of guild definition concerns the criteria and method of species cluster delineation. Most studies have identified guilds based on subjectively selected criteria, e.g., certain fusion levels in clustering, a mean Euclidean distance among species, and a ratio of the variation within clusters and between clusters. To objectively determine a foraging guild structure of the assemblage without arbitrary fusion criteria, the data matrices were analysed with a bootstrapped cluster analysis (UPGMA) of chord distances and correspondence analysis (CA). The bootstrapped cluster analysis is based on bootstrap resampling of the basic data matrix (Pillar 1999). The method statistically tests fuzziness of the partition in the cluster analysis of objects (bird species). While computing, partitions found in bootstrap samples are compared to the observed partitions by similarity of the objects that form the groups. The method tests the null hypothesis that the clusters in the bootstrap samples are random samples of their most similar corresponding clusters mapped one to one into the observed data. The resulting probability indicates whether the groups in the

partition are stable enough to reappear consistently in re-sampling (Pillar 1999). We used 10 000 iterations in all computations. Each computation started with a randomly generated number by the program. The critical threshold level on which partition sharpness was tested was set at α = 0.10. All computations were done with MULTIV 2.3.9 (Pillar 2004). This principle is also applied to compute differences among clusters of objects produced by ordination techniques (Pillar 2004). Up to now, bootstrap algorithms were developed only for PCA and principal coordinates analysis (metric multidimensional scaling) which were not suitable for analysis of our data sets. Instead, we used a symmetric correspondence analysis (CA) of non-transformed data matrices. The similarity of dendrograms was tested by Monte Carlo simulation techniques using standard dendrogram descriptors, such as cladistic difference, cophenetic difference, and cluster membership divergence (Podani and Dickinson 1985, Table 4). The differences were tested by the Monte Carlo among-cluster error sum of squares (SSQ) distance simulation test in SYNTAX 5.10 (Podani 1997). The guild structures between dendrograms 1 and 2 were also tested by two-tailed Wilcoxon signed-rank paired-sample tests (Hintze 1997). Node values of all species pairs in dendrogram 1 were paired with their counterparts in dendrogram 2.

Results

Classification based on the concept of Root: foraging substrate and manoeuvres guilds

Hierarchical classification. The bootstrapped cluster analysis (UPGMA) of chord distances (CD) detected a highly structured bird assemblage. Cluster analysis as common for genetic algorithms revealed two independent trenchant models of the guild structure at the levels of 6 and 9 species clusters – guild categories that were statistically different at the threshold α = 0.10 (Fig. 1a). The significance of the guild classification was lost at the level of 7 and 8 clusters (groups), however the significant structure again emerged at the level of 9 clusters (Table 1).

The first and broader guild classification model distinguished 6 categories of foraging guilds: ground foragers, stream foragers, flycatchers, trunk probers, bark gleaners, and foliage gleaners in order from the upper part to the lower part of the dendrogram. This higher-level classification created broader species groups combining several guilds of the lower classification level into one broader group as described below. The broader classification may be a basic guild structure of primeval mixed forests dominated by beech, fir, spruce, and sycamore in the Western Carpathians. It can be assumed because these biotopes have similar habitat and bird species structure (Korňan

Table 1. Probabilities $P(G^0 \leq G^*)$ and averages of sample attributes generated by 10 000 random iterations of bootstrap resampling of two foraging guild data matrices at different partition levels. Initializer of pseudo-random number generator was set to automatic mode (Pillar 2004). In the first data matrix, the classification was sharp at the levels of 6 and 9 groups indicating 6 or 9 significantly different guild types at the critical value of $\alpha = 0.10$. The second classification was sharp at the level of 7 partition groups indicating 7 guild categories. The numbers of significantly different clusters in both classifications are indicated by bold letters.

	Number of groups (clusters)								
Matrix 26 × 38	2	3	4	5	6	7	8	9	10
$P(G^0 \leq G^*)$	**0.2953**	**0.2079**	**0.3987**	**0.1680**	**0.1367**	0.076	0.0814	**0.1426**	0.0639
Average of sample attribute	0.9421	0.9466	0.9798	0.9491	0.9383	0.9231	0.9495	0.9548	0.9549
Matrix 26 × 47									
$P(G^0 \leq G^*)$	**0.3067**	**0.3109**	**0.2936**	**0.3731**	**0.2052**	**0.1473**	0.0736	0.0186	0.0069
Average of sample attribute	0.9589	0.9569	0.9589	0.9719	0.9603	0.9566	0.9456	0.9352	0.9324

2004a). The other classification model detected 9 significantly different foraging guilds that were much narrower and consisted of a smaller number of species. The following guild categories were identified: litter foragers, herb layer foragers, a "solitary guild" of a bush flycatcher, stream foragers, arboreal flycatchers, sweepers, trunk probers, bark gleaners, and foliage gleaners (Fig. 1a).

The first guild was identified as the ground foragers. Nonetheless, this guild of 7 species can be further divided into the three tight guilds: litter foragers (trushes), herb layer foragers, and the solitary guild of the bush flycatcher. The guild consists of Ring Quzel (*Turdus torquatus*), Song Thrush (*Turdus philomelos*), Blackbird (*Turdus merula*), Wren (*Troglodytes troglodytes*), Bullfinch (*Pyrrhula pyrrhula*), Dunnock (*Prunella modularis*), and Robin (*Erithacus rubecula*). The species of the genus *Turdus* were highly adapted to foraging from a dead-leaf substrate on a ground, thus forming the specific guild of litter foragers. "Leaf-lifting" by a bill and consequent arthropod gleaning was their principal search/attack manoeuvre in all observed individuals. Wren, Bullfinch, and Dunnock represented the guild of herb layer foragers. Wren was adapted on food searching on decaying trees and logs, on roots, and on the herb vegetation layer. Dunnock primarily gleaned arthropods from litter, the herb, and the bush layers. Bullfinch, a phytophagous species, frequently gleans seeds from the ground, the herb, and the bush layers. A very specific position in this guild is occupied by Robin, forming a one-member "solitary guild". Robin used mainly flycatch attack strategies "leap" and "sally" to catch prey on all types of the substrates except for water. Robin can be classified as a flycatcher of the bush layer (Korňan 2000). In the previous study, this species due to specific foraging strategies was clustered into the flycatcher guild (Adamík et al. 2003). The very specific intermediate position between the

guilds of flycatchers and the ground foragers in the multidimensional foraging niche space is indicated in the correspondence analysis plot (Fig. 2a).

The second guild was represented by two species, Dipper (*Cinclus cinclus*) and Grey Wagtail (*Motacilla cinerea*). Having been tied to the stream habitat due to their foraging adaptations, they form a guild of stream foragers, yet each species has very distinctive foraging behaviour. Dipper was specialised on foraging from the stream bottom dive gleaning aquatic insects, less frequently it gleaned from fallen wooden logs and from stream stones. In contrast, Grey Wagtail fed mainly on the stream bank and the surrounding substrates, e.g., fallen logs and trees. It also frequently sallied flying insects in the air usually from the ground or while perching on a branch.

The third guild, the arboreal and the airspace flycatchers, consists of Red-breasted Flycatcher (*Ficedula parva*), Spotted Flycatcher (*Muscicapa striata*), Collared Flycatcher (*Ficedula albicollis*), and House Martin (*Delichon urbica*). All flycatchers were segregated by the mean foraging height and foraging niche breadth forming a well-developed generalist–specialist gradient (Korňan 2000). Both *Ficedula* species were typically sallying from leaves and twigs in canopies. Spotted Flycatcher foraged in the tree crowns typically perching on the tops of trees hawking mainly on flying insects. House Martin swept flying insects above the canopy and in the upper canopy among trees. It forms a specific guild of airspace sweepers in the model of 9 guild categories. Swift (*Apus apus*) observed only very occasionally also belonged to this guild (Korňan 2004a).

The fourth guild of the trunk probers was represented by two woodpeckers, Three-toed Woodpecker (*Picoides tridactylus*) and White-backed Woodpecker (*Dendro-*
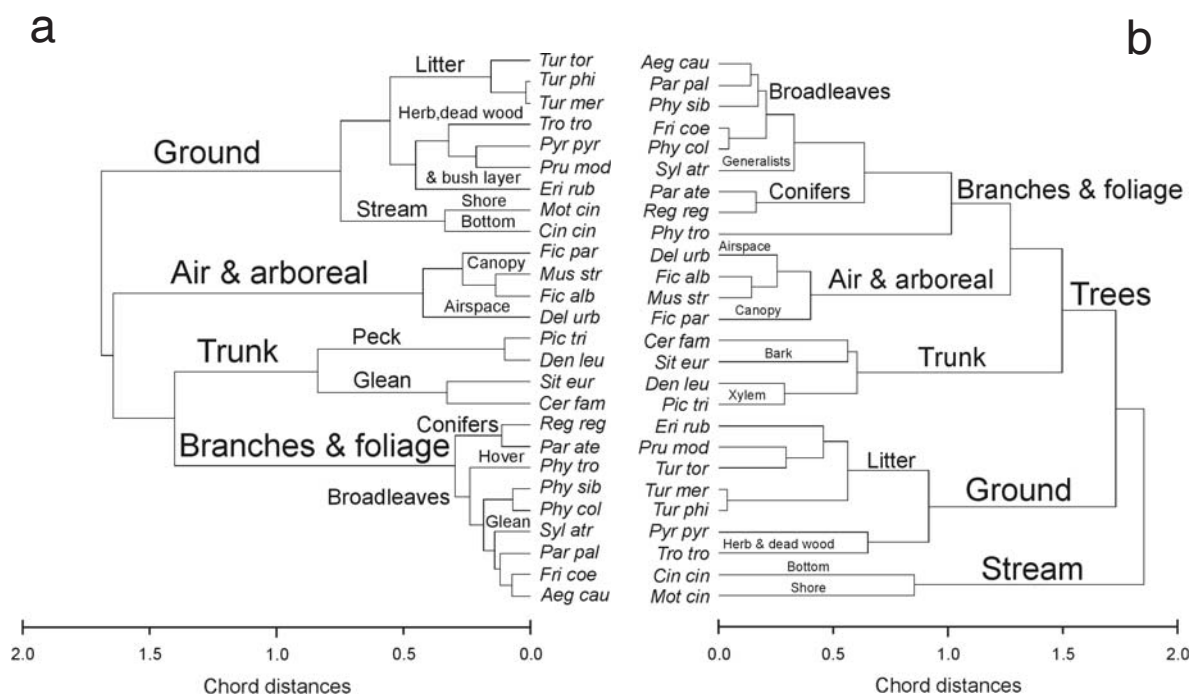
Figure 1. Assemblage dendrograms showing foraging guild structure of the primeval beech-fir forest in the Šrámková National Nature Reserve following two guild concepts. The first dendrogram (**a**) represents the guild concept of Root. Totally, 6 or 9 guild categories were identified based on bootstrap resampling analysis of the original data matrix (Pillar 1999). The second dendrogram (**b**) represents the guild concept of MacMahon et al., where 7 significantly different foraging guild categories were detected. The species abbreviations are listed in Appendix 1.

copos leucotos). However, there were other species of woodpeckers, i.e., Black Woodpecker (*Dryocopus martius*), Grey-headed Woodpecker (*Picus canus*), and Great Spotted Woodpecker (*Dendrocopos major*) in the study site which presumably belong to this guild type (Kornan 2004a). Owing to a high proportion of ground foraging, Grey-headed Woodpecker was classified *a priori* as a ground forager (Kornan 2004b). There were significant differences between these two woodpeckers in foraging substrate preferences (Adamík et al. 2003). Three-toed Woodpecker, a boreal-montane relict species, was highly specialised on foraging from decaying or alive coniferous trees, whereas White-backed Woodpecker was a generalist. Both species almost strictly use search/attack manoeuvres pecking and probing, although they were occasionally observed gleaning from branches.

Bark gleaners formed the fifth delineated guild of the assemblage. It consists of only two species, Nuthatch (*Sitta europaea*) and Treecreeper (*Certhia familiaris*). Nuthatch can be characterised as a generalist with broader foraging niche feeding even from leaves, twigs, and branches (Adamík and Kornan 2004). Treecreeper is highly specialised on bark gleaning. Both species foraged on a wide range of tree species, yet they preferred species with a rough bark structure that have higher abundance

and diversity of insect prey in comparison to species with a smooth bark structure (Adamík and Kornan 2004).

The last guild, foliage gleaners, is the most diverse. It reflected a very high diversity and concentration of food resources in tree crowns. A total of 9 species, i.e., Goldcrest (*Regulus regulus*), Coal Tit (*Parus ater*), Willow Warbler (*Phylloscopus trochilus*), Wood Warbler (*Phylloscopus sibilatrix*), Chiffchaff (*Phylloscopus collybita*), Blackcap (*Sylvia atricapilla*), Marsh Tit (*Parus palustris*), Chaffinch (*Fringilla coelebs*), and Long-tailed Tit (*Aegithalos caudatus*) belong to this guild. Other species, e.g., Firecrest (*Regulus ignicapillus*), Great Tit (*Parus major*), Blue Tit (*Parus caeruleus*), Crested Tit (*Parus cristatus*), Willow Tit (*Parus montanus*), not included in this study due to the low number of registrations, also belong to this guild (Kornan 2004a). All species were adapted to foraging from leaves, twigs, and branches. They frequently attacked prey by gleaning or hovering. The guild can be divided into two groups, yet not significantly different, according to affinity of species to forage from coniferous and deciduous trees. Goldcrest and Coal Tit normally preferred conifers, while the others were generalists or deciduous specialists. Most of the species showed a high temporal opportunism in foraging patterns. For example, Coal Tit, a conifer specialist, preferred for-
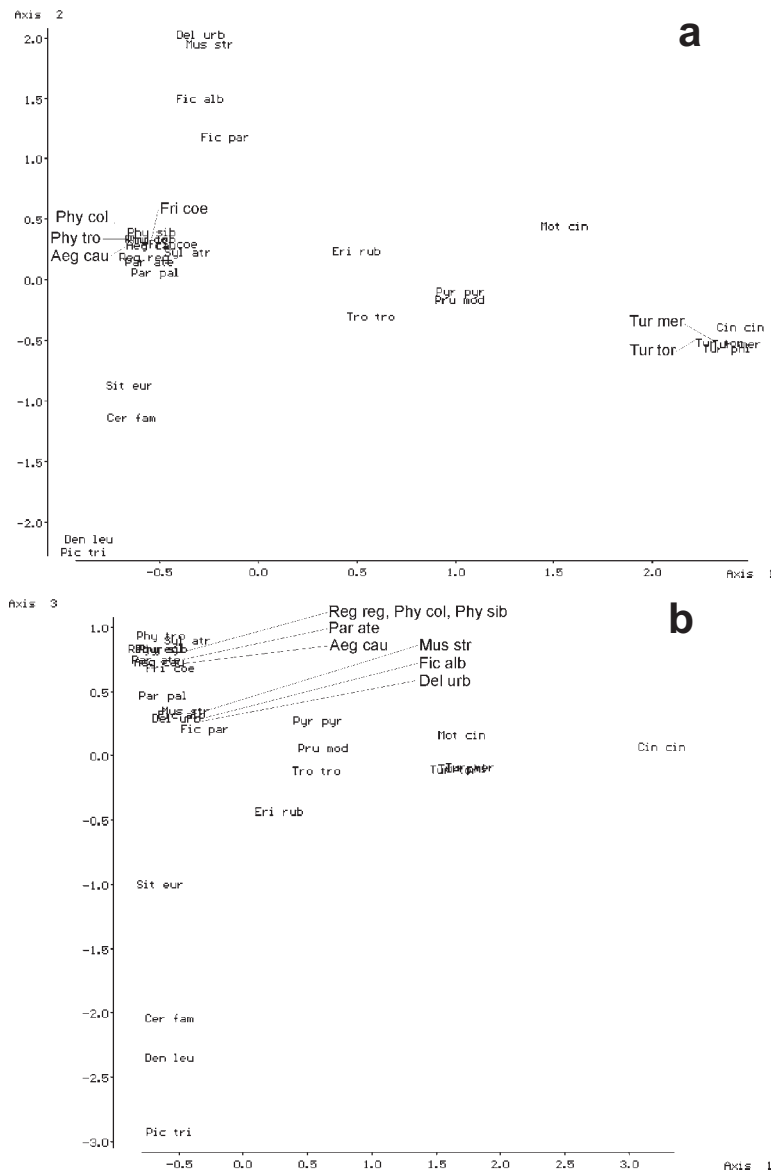
Figure 2. Correspondence analysis ordination of 26 species of the breeding bird assemblage of the primeval beech-fir forest in the Šrámková National Nature Reserve computed from the data matrix following the concept of Root (26 species × 38 variables, **a**) and the data following the concept of MacMahon et al. (26 species × 47 variables, **b**). The indicated species groups correspond to the foraging guilds based on the results of bootstrapped cluster analysis (UPGMA) that revealed two guild models for the guild concept of Root, 6 or 9 guild categories on two dissimilarity levels, and one guild model for the guild concept of MacMahon et al., 7 guild categories. The species abbreviations are listed in Appendix 1.

aging from a beech during an outbreak of leaf-eating caterpillars. When compared to other species, the *Phylloscopus* warblers used hovering more frequently. This enabled them to catch prey from the leaf's inverse side. In the end, it is important to conclude that it was not possible to distinguish coniferous and deciduous forest specialists and generalists as significantly different guilds of foliage gleaners. All of these species have shown very broad foraging patterns.

Correspondence analysis. The primary purpose of this analysis was to identify the main factors that caused specific ecological adaptations for an effective foraging from a certain structural component of the habitat which mainly influence a radiation of species to specific foraging niches. The first five correspondence factors (≥ 5%) explained 79.32% of the total matrix inertia (Table 2).

However, the revealed ordination pattern was so robust that it was possible to interpret up to the first eight factors jointly explaining 89.77% inertia.

The first factor (see Table 2 for eigenvalues and associated percentages) explained 25.17% of the total inertia of the matrix. It was interpreted as a gradient related to the mean foraging height and height related variables (Table 2). Based on the variable loadings of this factor, it was assumed that a vertical structure and partitioning of the forest habitat and allocation of foraging resources along this gradient played the most important role in the development of specific ecomorphological adaptations and a radiation of species. This gradient played a major role in a segregation of foraging niches in relation to the mean foraging height among flycatchers (Korňan 2000).

The second factor was interpreted as a microhabitat gradient connected to the spatial tree morphology reflecting substrates: trunk – branches – twigs – leaves. The factor was primarily responsible for the segregation of the three types of the arboreal foraging guilds: the trunk probers (woodpeckers), the bark gleaners, and the foliage gleaners. This factor reflects one of the most important di-

Table 2. Eigenvalues, contributions to total inertia, cumulative contributions, and individual variable scores for the first eight factors of correspondence analysis (CA) revealed from the data matrix compiled according to the concept of Root (26 species × 38 variables). The variable score values (≥ 0.7) are indicated by bold letters.

| | | FACTORS | | | | | | | |
		I.	II.	III.	IV.	V.	VI.	VII.	VIII.
	Eigenvalues	0.75	0.55	0.51	0.35	0.19	0.13	0.11	0.07
	Factor contribution to total variance (%)	25.17	18.73	17.11	11.91	6.39	4.56	3.56	2.34
	Cumulative percent (%)	25.17	43.90	61.01	72.93	79.32	83.88	87.43	89.77
1.	Mean foraging height	−0.49	**0.83**	**0.90**	−0.22	0.17	−1.64	0.07	−0.72
2.	SD of foraging height	−0.45	**0.74**	**0.87**	−0.22	0.15	−1.62	0.31	−0.82
3.	Foraging on beech *Fagus sylvatica*	−0.42	0.29	−0.38	0.00	−0.09	**0.98**	−0.28	−0.90
4.	Foraging on fir *Abies alba*	−0.60	−0.13	−0.39	0.12	−0.34	−0.30	−0.50	1.10
5.	Foraging on spruce *Picea abies*	−0.58	−0.45	−0.26	0.07	0.30	−0.30	−0.39	1.51
6.	Foraging on sycamore *Acer pseudoplatanus*	−0.49	0.16	−0.23	0.02	−0.11	**0.98**	−0.67	−1.31
7.	Foraging on elm *Ulmus glabra*	−0.53	−0.52	0.21	−0.09	0.03	**0.92**	0.04	−1.70
8.	Foraging on rowan *Sorbus aucuparia*	−0.53	0.38	−1.07	0.20	0.40	**0.94**	−0.91	−1.58
9.	Foraging on hazel *Corylus avellana*	−0.54	0.35	−0.82	0.14	0.55	1.23	0.19	−1.90
10.	Foraging on other live tree species	0.58	−0.27	−0.29	−0.95	−0.75	0.50	−1.19	−0.79
11.	Foraging on or in litter	2.21	−0.47	−0.29	−2.20	0.25	−0.47	−1.35	−0.65
12.	Foraging on bare ground	1.83	−0.37	−0.33	−1.77	−0.21	0.34	0.42	1.38
13.	Foraging on herb or forb layers	0.59	0.05	−0.59	−0.37	−0.45	1.36	6.13	−2.48
14.	Foraging on standing dead wood	**−0.75**	−1.83	1.14	−0.13	0.34	0.48	0.28	0.13
15.	Foraging on fallen dead wood	**0.71**	−0.34	0.32	**0.78**	−0.40	1.80	3.09	0.62
16.	Foraging on or in water	2.69	−0.35	**0.86**	7.31	0.47	−0.13	−2.23	−3.92
17.	Foraging on rocks	1.97	0.12	**0.92**	4.15	0.10	0.08	0.59	4.10
18.	Foraging in airspace	−0.11	1.95	**2.00**	−0.26	0.07	−0.80	0.30	0.18
19.	Foraging movement in horizontal direction	−0.49	0.07	−0.90	0.17	0.27	−0.19	0.12	−0.07
20.	Foraging movement in vertical direction	−0.88	−2.16	1.36	−0.07	−1.11	−0.20	−0.44	−0.14
21.	Glean from trunk	−0.47	−1.14	0.55	0.17	−5.04	−0.24	−0.37	−0.23
22.	Glean from leaf	−0.42	0.21	−1.09	0.16	0.20	−0.34	0.58	0.02
23.	Glean from branch	−0.40	−0.42	−0.38	0.03	−1.63	−0.24	0.26	−0.10
24.	Glean from twig	−0.48	0.17	−1.05	0.19	0.05	−0.62	0.05	1.18
25.	Glean from other substrates*	2.05	−0.34	−0.05	−0.01	0.08	−0.16	0.14	0.01
26.	Hover at trunk	0.04	**0.82**	**0.78**	−0.45	−1.17	3.52	0.47	1.75
27.	Hover at leaf	−0.54	0.50	−0.97	0.19	0.61	0.53	−1.01	−0.68
28.	Hover at branch	−0.47	**0.80**	−0.15	−0.04	0.26	1.34	−1.51	−0.53
29.	Hover at twig	−0.53	0.39	−1.08	0.20	0.58	−0.24	−0.95	1.10
30.	Hover at other substrates*	1.09	0.53	0.59	2.06	0.24	**0.78**	2.05	8.03
31.	Probe or peck into trunk	−1.00	−2.83	1.92	−0.21	3.00	0.34	0.41	0.33
32.	Probe or peck into branch	−0.95	−2.48	1.59	−0.17	2.27	0.33	0.32	−0.81
33.	Probe or peck into other substrates*	2.35	−0.97	−0.08	−2.83	0.95	−1.64	−5.01	−2.90
34.	Hawk or sally to trunk	0.09	1.12	**0.82**	−0.50	−0.37	5.78	−1.24	1.90
35.	Hawk or sally to leaf	−0.19	1.62	1.30	−0.49	−0.17	4.82	−1.42	0.45
36.	Hawk or sally to branch	−0.02	1.27	1.09	−0.55	−0.48	4.15	−0.70	1.34
37.	Hawk or sally to twig	−0.18	1.74	1.50	−0.60	−0.20	5.12	−1.61	0.53
38.	Hawk or sally to other substr.* (mainly air)	−0.13	1.95	**1.97**	−0.32	0.05	−0.37	0.13	0.09

* in combination with one of the listed foraging substrates

mensions of resource concentration for insectivorous species – leaves and twigs as the first spatial area and a trunk as the other spatial area (Alatalo 1982). The high concentration of resources available to these guilds was probably one of the most important factors during evolutionary time which caused the development of specific ecomorphological adaptations and bird foraging behaviour for effective feeding (Moreno and Carrascal 1993). This factor indicated important tree features, i.e., bark roughness/smoothness, xylem rigidity, leaf size, deciduous leaf and branch structure, coniferous leaf and branch structure, which played probably the major role in the segregation of arboricolous species to the guilds. Especially important were behavioural adaptations for foraging on deciduous and coniferous substrates. Both types of forest specialists form only one foliage gleaning guild, yet several species, e.g., Crested Tit, Coal Tit, Goldcrest significantly preferred foraging on conifers, while other species, e.g., Wood Warbler significantly preferred deciduous substrates (Adamík et al. 2003).

The third factor was interpreted as a gradient separating the arboreal species from the airspace specialists. This factor divided the

arboreal foliage gleaning warblers from the arboreal and the airspace foraging flycatchers (i.e., genera *Erithacus* and *Ficedula*) and the airspace specialised flycatchers (i.e., genera *Muscicapa* and *Delichon*).

The fourth factor was interpreted as a gradient of ground microhabitats: water environment – bare stones (stream banks) – fallen wood – herb layer – litter – bare ground. This gradient was primarily responsible for the segregation of the stream foragers from the guild/s of the ground foragers. It is one of the strongest environmental gradients in the forest ecosystem related to high diversity and abundance of food resources. This caused a development of specific ecomorphological adaptations and foraging strategies between distinct guilds: the litter foragers (trushes), the herb layer foragers (wrens, warblers, and finches), a bush forager (Robin), and the stream foragers (Dipper and Grey Wagtail).

The fifth factor can be interpreted as the substrate gradient: xylem (trunk inner space) – trunk bark (trunk cover). This was the crucial factor splitting the guild of the trunk probers from the guild

Table 3. Eigenvalues, contributions to total inertia, cumulative contributions, and individual variable scores for the first seven factors of correspondence analysis (CA) extracted from the data matrix compiled according to the concept of MacMahon et al. (26 species × 47 variables). Important variable score values (≥ 0.7) are indicated by bold letters.

		FACTORS						
		I.	II.	III.	IV.	V.	VI.	VII.
	Eigenvalues	0.77	0.73	0.52	0.40	0.24	0.16	0.13
	Factor contribution to total variance (%)	21.42	20.36	14.39	11.28	6.64	4.47	3.66
	Cumulative percent (%)	21.42	41.78	56.18	67.45	74.09	78.56	82.22
1.	Mean foraging height	−0.61	−0.24	0.10	**0.86**	−0.37	−0.24	−0.60
2.	SD of foraging height	−0.57	−0.21	0.04	**0.79**	−0.22	−0.27	−0.61
3.	Foraging on beech *Fagus sylvatica* leaf	−0.53	−0.03	**0.82**	−0.61	0.28	0.44	−0.45
4.	Foraging on beech *Fagus sylvatica* twig	−0.41	0.02	0.54	−0.16	0.00	**0.90**	−0.10
5.	Foraging on beech *Fagus sylvatica* branch	−0.45	−0.02	**−1.07**	−0.51	0.35	−0.07	−0.39
6.	Foraging on beech *Fagus sylvatica* trunk	−0.35	−0.11	**−1.38**	0.02	0.20	−0.25	**0.93**
7.	Foraging on fir *Abies alba* leaf	−0.65	−0.09	**0.81**	**−1.06**	−0.63	**−1.58**	0.28
8.	Foraging on fir *Abies alba* twig	−0.65	−0.10	**0.78**	**−0.95**	−0.59	**−1.32**	0.21
9.	Foraging on fir *Abies alba* branch	−0.59	−0.14	−0.62	−0.37	−0.35	−0.09	0.04
10.	Foraging on fir *Abies alba* trunk	−0.65	−0.26	**−2.73**	−0.31	−0.31	0.27	0.24
11.	Foraging on spruce *Picea abies* leaf	−0.58	−0.02	**0.80**	**−0.98**	**−0.84**	−0.54	**0.82**
12.	Foraging on spruce *Picea abies* twig	−0.56	−0.02	**0.76**	**−1.05**	**−0.76**	−0.65	**0.78**
13.	Foraging on spruce *Picea abies* branch	−0.49	−0.07	**−1.37**	−0.56	−0.19	0.69	0.12
14.	Foraging on spruce *Picea abies* trunk	−0.59	−0.22	**−3.24**	−0.48	−0.16	0.40	0.16
15.	For. on sycamore *Acer pseudoplatanus* leaf	−0.56	−0.09	**0.92**	−0.48	0.02	**3.65**	0.67
16.	Foraging on *Acer pseudoplatanus* twig	−0.69	−0.10	**0.99**	**−1.10**	−0.37	**3.20**	**0.84**
17.	Foraging on *Acer pseudoplatanus* branch	−0.60	−0.20	**−1.57**	−0.10	−0.21	**1.00**	0.03
18.	Foraging on *Acer pseudoplatanus* trunk	−0.54	−0.16	**−2.36**	−0.41	−0.22	0.02	0.53
19.	Foraging on elm *Ulmus glabra* leaf	−0.37	0.14	**0.80**	**−0.86**	**1.14**	0.92	**−0.85**
20.	Foraging on elm *Ulmus glabra* twig	**−0.73**	−0.13	**0.79**	**−1.13**	−0.68	−0.18	−0.56
21.	Foraging on elm *Ulmus glabra* branch	−0.69	−0.23	**−2.48**	−0.56	−0.21	0.11	**−0.72**
22.	Foraging on elm *Ulmus glabra* trunk	−0.63	−0.24	**−1.86**	0.13	−0.11	0.48	−0.39
23.	Foraging on rowan *Sorbus aucuparia* leaf	−0.68	−0.09	**1.07**	**−1.16**	−0.37	**4.35**	**1.16**
24.	Foraging on rowan *Sorbus aucuparia* twig	**−0.74**	−0.13	**0.91**	**−1.17**	**−0.70**	**5.50**	**1.71**
25.	Foraging on *Sorbus aucuparia* branch	−0.31	0.12	0.38	**−0.83**	−0.12	**1.67**	**1.45**
26.	Foraging on rowan *Sorbus aucuparia* trunk	−0.67	−0.29	**−2.84**	−0.23	−0.58	−0.10	**1.26**
27.	Foraging on hazel *Corylus avellana* leaf	−0.62	−0.07	**0.98**	**−0.95**	0.53	**1.75**	−0.21
28.	Foraging on hazel *Corylus avellana* twig	−0.65	−0.07	**1.06**	**−1.25**	0.50	**1.62**	−0.26
29.	Foraging on hazel *Corylus avellana* branch	−0.49	0.04	**1.26**	**−1.46**	**2.68**	−0.15	**−1.28**
30.	Foraging on hazel *Corylus avellana* trunk	−0.67	−0.25	**−3.26**	−0.44	0.06	0.41	**−0.98**
31.	Foraging on other live tree species leaf	−0.59	−0.06	**0.89**	**−0.97**	**0.72**	−0.07	**−0.80**
32.	Foraging on other live tree species twig	0.02	0.31	−0.14	−0.64	0.05	**−1.64**	**1.92**
33.	Foraging on other live tree species branch	0.16	0.33	0.06	**−0.93**	**4.24**	**−1.77**	−0.07
34.	Foraging on other live tree species trunk	**−0.73**	−0.21	**−1.51**	**−0.74**	**−0.92**	**−1.19**	−0.09
35.	Foraging on or in litter	**1.57**	**1.92**	−0.06	0.21	**−0.84**	0.28	−0.35
36.	Foraging on bare ground	**1.32**	**1.63**	−0.07	0.00	−0.01	−0.38	0.43
37.	Foraging on herb or forb leaf	0.38	0.53	0.40	−0.57	**4.34**	−0.38	**−0.90**
38.	Foraging on herb or forb stem	**−0.78**	−0.14	**1.05**	**−1.28**	**−1.76**	**−3.55**	0.62
39.	Foraging on standing dead wood twig	−0.30	0.09	0.37	**−0.83**	**1.37**	0.02	−0.34
40.	Foraging on standing dead wood branch	**−0.70**	−0.20	**−1.29**	**−0.74**	−0.44	−0.01	−0.51
41.	Foraging on standing dead wood trunk	−0.57	−0.20	**−2.83**	−0.47	0.08	0.12	−0.14
42.	Foraging on fallen dead wood twig	0.36	0.31	0.12	−0.25	**3.74**	**−0.70**	0.42
43.	Foraging on fallen dead wood branch	0.13	0.29	**−0.82**	−0.43	**2.35**	**−1.07**	**0.86**
44.	Foraging on fallen dead wood trunk	**0.97**	−0.55	−0.51	−0.43	**2.22**	−0.59	0.41
45.	Foraging on or in water	**3.47**	**−3.76**	0.13	**−1.08**	**−1.07**	0.31	**−3.60**
46.	Foraging on rocks	**2.33**	**−2.26**	0.11	0.23	0.16	−0.16	**4.01**
47.	Foraging in airspace	−0.29	−0.44	0.39	**2.47**	0.18	−0.04	0.06

of the bark gleaners. Very distinctive ecomorphological features in the shape and size variables as well as foraging behaviour in the guild of the woodpeckers in comparison to the bark gleaners have evolved to effectively utilise these substrates (i.e., bill shape and size, head and leg morphology, probing and pecking versus bark cavity gleaning).

The sixth factor is more or less similar to the third factor. It split the guild of the flycatchers into two sub-guilds: the arboreal flycatchers (i.e., genera *Ficedula*, *Muscicapa*) and the airspace specialists (i.e., genera *Delichon*, *Apus*).

The seventh factor indicated the terrestrial environmental gradient: herb layer – litter substrate – bare ground substrate. The factor separated the guild of the herb layer foragers (genera *Troglodytes*, *Pyrrhula*, *Prunella*) from the guild of the litter foragers (genus *Turdus*).

The eighth factor was interpreted as the environmental gradient of the mountain stream: water environment (stream bottom) – litto-ral zone – supralittoral zone (stream banks). Even though there were no significant differences between Dipper and Grey Wagtail in the guild membership, this factor split foraging niches of these two species. Dipper foraged mainly from the stream bottom, whereas Grey Wagtail foraged mainly in the littoral zone and on the shore.

Classification based on the concept of MacMahon et al.: foraging substrate guilds

Hierarchical classification. Bootstrapped cluster analysis (UPGMA) classified seven groups with significantly different group partitions at α = 0.1. These groups correspond to the seven groups forming 6 foraging guild types: litter foragers, herb layer foragers, stream foragers, flycatchers, trunk foragers, foliage gleaners, and one single species dendrogram branch represented by Willow War-

Table 4. Comparison of dendrograms depicted in Fig. 2 by the Monte Carlo simulations of the cladistic difference and the cluster membership divergence generated by 10 000 iterations. The compared dendrograms were significantly different considering these two dendrogram descriptors at P < 0.01. Indices of dendrogram similarity and ultrametric comparisons are given in the second part of the table.

Similarity indices	Correlation	Distances	Squared distances	Absolute difference
Cladistic difference	0.85	*28.09	789.00	385.00
Cophenetic difference	0.84	329.50	108 573.40	4014.68
Cluster membership divergence	0.86	**76.89	5912.00	858.00
Number of changes in ultrametric relationships			430.00	
Ultrametric dissimilarity			0.17	
Number of interior edges			48	
Number of mismatched edges			24	
Edge matching coefficient			0.50	
Mismatched edge difference			200.30	
Absolute edge difference			730	

*P<0.01, Monte Carlo critical SSQ value = 58.69
**P<0.01, Monte Carlo critical SSQ value = 180.90

bler. In contrast to the classification based on the concept of Root, the model based on the concept of MacMahon et al. produced only one hierarchical pattern. In the next part, individual guilds will be briefly characterised. Special attention will be paid to the guild types that strongly deviate in the internal structure and species composition with the counterpart guilds in the dendrogram of the Root type.

It is questionable whether Willow Warbler forms a specific foliage gleaning guild, or its split from the other foliage gleaners is a sampling artefact. Based on the distribution of its territories in 1998, they were placed in microhabitats with high dominance of sycamore. In line with this, it had a high proportion of foraging observations on this tree species.

The first guild, litter foragers, was formed by five species: Robin, Dunnock, Ring Quzel, Blackbird, and Song Thrush. The first two species were not members of this guild in the classification that followed the concept of Root. Robin formed a very specific single branch of a bush flycatcher, whereas Dunnock joined the herb layer foragers. Foraging manoeuvre variables heavily influenced the structure of this guild in the Rootian classification. The observed pattern in this classification was caused by the high frequency of foraging on litter.

The second guild, herb foragers, consisted of two species: Bullfinch and Wren. Both species were the members of the same guild in the Rootian classification, yet Bullfinch was paired with Dunnock.

The third guild of stream foragers, was represented by two stream dependent species: Dipper and Grey Wagtail. There were no differences in species composition between the classifications. However, in the classification that follows the concept of MacMahon et al., the guild formed the most independent and distinct branch in the tree structure.

The fourth guild, flycatchers, was formed by four species: House Martin, Spotted Flycatcher, Collared Flycatcher, and Red-breasted Flycatcher. The species composition was the same compared to the Rootian classification.

Trunk foragers represented the fifth delineated guild in this classification. The guild was composed of four species: White-backed Woodpecker, Three-toed Woodpecker, Nuthatch, and Treecreeper. In the Rootian classification, this guild was split into two guilds: trunk probers and bark gleaners due to the effect of foraging variables. We believe that this guild may be naturally divided into these two types according to the substrate classification into bark foragers and xylem foragers.

The foliage gleaners represented the largest guild with nine species. The species composition was identical in both approaches. The main difference is in the internal structure of the classification based on the concept of MacMahon et al. The guild is divided into three nonsignificant groups creating a gradient: deciduous tree specialised species, generalists, and conifer specialised species. This gradient was indicated in eigenvector 6 of CA (Table 3). In the classification following the concept of Root, only conifer specialists were clearly separated in the guild, while generalists and deciduous tree specialists formed mixed species pairs. The presence of coniferous and deciduous tree preferring faunal elements in the mixed forest was not evident in any of the classifications at the guild level. Nevertheless, this pattern was detected when comparing species foraging substrate niches (Adamík et al. 2003).

Correspondence analysis. The first 5 correspondence factors ($\geq 5\%$) explained 74.09% of the total matrix inertia (Table 3). The emerged ordination pattern was robust and clearly interpretable, and comparable to the ordination from the Rootian matrix. The first seven eigenvectors (factors) were interpretable so that it was possible to identify the main environmental gradients responsible for species segregation into guilds. The noise in the remaining factors was so high that it did not permit a detection of any other environmental gradient.

Similarly to the interpretation of the first factor in the Rootian ordination, the first eigenvector (see Table 3 for eigenvalues and associated percentages) was identified as the height gradient of foraging strata reflected in vertical height segregation of the most important foraging substrates. The heaviest variable score loadings of this factor determined the strongest gradient that visibly suppressed the classification power of the second factor. Extreme position of stream foraging substates (water, stones) in the ordination hyperspace is reflected in the extreme positions of stream dependent species Grey Wagtail and Dipper. This is the main reason why the internal guild structure of arboreal birds was not visible and the classification seemed fuzzy when plotting bird species along the first and second axis. The guilds of bark foragers, foliage gleaners, and flycatchers were clumped into one group in the ordination space. To identify clearly the arboreal guild structure, 26 species were plotted along the first and third ordination axes (Fig. 2b).

The second factor was interpreted as the gradient: water environment – bare stones – fallen wood – herb layer – bare ground – litter. This is the major difference when compared to the second factor in the Rootian ordination identified as the spatial tree morphology. The second factor is visible in the dendrogram structure in which the three main partitions are related to this gradient, and they separate arboreal foragers from ground, herb layer, and stream foragers. These principal groups of resource substrates may represent the main areas of food concentration that may have played the major role in ecological radiation of species.

The third factor was assumed to be a gradient of the spatial tree morphology based on the position of variables in ordination space. The gradient reflects the horizontal positions of the main tree substrates: trunk – branches – twigs – leaves. This factor is assumed to be primarily responsible for niche segregation of arboricolous species into the three main groups: bark foragers, foliage gleaners, and flycatchers. Distinction between flycatchers and foliage gleaners is not as sharp as in the Rootian classification presumably due to effects of foraging method variables such as probe into trunk, glean from trunk, hawk and sally to the arboricolous substrates. Interpretation of this gradient is analogous to the second factor in the factor analysis based on Root's concept.

The fourth factor was responsible for segregation of arboreal species from airspace foragers. The substrate gradient clearly separates arboreal foliage gleaning passerines from arboreal and airspace flycatchers and airspace specialised flycatchers. This substrate gradient segregates foraging space of flycatchers in combination with the mean foraging height (Korňan 2000). The fourth factor represents the same gradient as the third factor in the Rootian ordination.

The fifth factor was interpreted as a gradient of terrestrial environment: litter – bare ground – fallen wood – herb layer dividing litter foragers from herb layer and bush foragers. It is analogous to factor 7 in the Rootian classification. Surprisingly, Ring Ouzel joined Dunnock that formed the guild of ground and herb layer

foragers. In the Rootian classification, all species of the genus *Turdus* formed the guild of litter foragers.

The variable positions along the sixth factor indicated an environmental gradient from coniferous foraging substrates to deciduous foraging substrates. The factor splits passerine birds into three main ecological groups: coniferous specialists (Coal Tit, Goldcrest) – generalists – deciduous specialists (Wood Warbler, Willow Warbler, Marsh Tit, Long-tailed Tit). This pattern is also visible in the internal guild structure of the foliage-gleaning guild. However, these three separate ecological groups did not form significantly different structural groups – guilds. This factor was not detected in the Rootian ordination.

On the seventh factor, the opposite position of substrate variables water and bare stones caused separation of two stream dependent species Dipper and Grey Wagtail. It indicates the environmental gradient of mountain stream: water environment (stream bottom) – littoral zone – supralittoral zone. The factor is analogous to the eight factor in the factor analysis based on Root's concept.

Comparison of guild structures between two concepts

Both concepts revealed different structures. This is indicated by the different numbers of guild categories, internal guild category structures, species-specific guild memberships, and differences in species node pairing within dendrograms. When comparing the total number of species-paired nodes between two dendrograms, dissimilarity levels of guild nodes were significantly different ($W = 38467$, $Z = 7.11$, $N = 325$, $P < 0.001$). Means of nodes were significantly higher in the dendrogram based on the concept of MacMahon et al., indicating higher dissimilarity of bird foraging among substrate guilds ($x_1 = 1.15$, $x_2 = 1.10$, $N = 325$).

An alternative way to test for dendrogram similarity is a multivariate analysis of dendrogram resemblance indices (Rohlf 1974, Podani 1997, 2000). Monte Carlo simulations of cladistic difference and cluster membership divergence for 26 dendrogram objects were performed by the SYNTAX 5.10 module DENCOM (Podani 1997). The Monte Carlo SSQ distance simulation test showed significantly different structure between two dendrograms when comparing cladistic difference value 28.09 (SSQ critical value = 58.69, $P < 0.01$) and cluster membership divergence value 76.89 (SSQ critical value = 180.90, $P < 0.01$). The other eight indices of dendrogram paired comparisons are listed in Table 4.

Discussion

Previous bird guild studies (Holmes et al. 1979, Sabo 1980, Holmes and Recher 1986, Korňan 2004b) identified a vertical height gradient (from terrestrial to arboreal and air substrates) as the main factor responsible for partitioning species into guilds in floristically and structurally distinct forests in multicontinental comparisons. The

second most important gradient seems to be the horizontal spatial tree morphology: trunk – branches – twigs – leaves. This gradient reflecting the spatial resource niche partitioning along tree branches was detected in all studies except for Holmes and Recher (1986). These authors concluded (p. 434) that foraging methods are the second major set of characteristics that segregate guilds. Even after the application of the varimax factor rotation of PCA ordination space in their study, the remaining lower-level factors were difficult to interpret and a high amount of repeatability in the interpretation of axes occurred. Similarly, the interpretation of the lower-level factors III–V, differential use of tree species and foraging manoeuvres, with the same numerical design was problematic but clearer in a mixed bird assemblage at Hubbard Brook (Holmes et al. 1979). This could have been partly caused by the parametric design and transformation of raw data (Jackson 1997). The application of correspondence analysis (CA) or detrended correspondence analysis (DCA) can enormously improve an interpretability of axes and a logical structure of ordination patterns as presented in this study.

The final species foraging patterns and the guild structures could have been influenced by interobserver differences in recording foraging behaviour. Due to insufficient samples for 26 selected species, we did not attempt to test such differences between the authors. Ford at al. (1990) detected significant differences among three observers in the use of some substrate categories and foraging manoeuvres. Nevertheless, the observers presented the same general patterns of foraging. We assume that interobserver differences have not significantly influenced the described foraging patterns and guild structure. In addition, foraging data can be seriously effected by seasonal and yearly variations caused by plant phenological stages and concentration of food on foraging substrates (Hejl and Verner 1990, Keane and Morrison 1999). In this study, sampling dates and daytime were relatively evenly distributed throughout the breeding season to minimise these effects. However, bird detectability was much higher in the postfledgling period of the breeding cycle when the highest number of observations was recorded. This could slightly bias the data set. Furthermore, horizontal and vertical differences in structural features of the habitat, for example, bird detectability in open and dense patches and bird detectability on different plants could also bias the foraging patterns. Logically, a higher number of observations were collected in open microhabitats. Yet, it is impossible to estimate possible sampling errors caused by habitat heterogeneity. We are not aware of any study dealing with this type of sampling bias. After all, we do not assume that the combined extend of these effects could

significantly influence the study results. Our strongest supporting point is in the relief shape of the reserve and a very open forest structure typical for a late decaying developmental stage. The study site is located on a very steep slope of 20–60° inclination that enabled excellent visibility into all parts of canopy when watching downhill. This relief feature and low density of trees enabled detection of a foraging bird with similar probability at any height.

The concept of ecological guilds and functional groups has a strong impetus on both theoretical and applied ecology and on the understanding of the structure and functioning of ecological systems and processes (Root 1967, Cummins 1974, Simberloff and Dayan 1991, Wilson 1999, Blondel 2003, Korňan 2005). However, there are still misunderstandings in the definitions of ecological guilds (MacMahon et al. 1981, Jaksić 1981, Wilson 1999, Blondel 2003, Korňan 2005). We showed that the comparison of the two concepts of guild definition by the same rigorous statistical approach in this study led to different results reflected in different guild structures and species-specific guild memberships in the same assemblage. Here, it is important to stress that the differences were found in the total number of guild categories, internal guild structures, and species pairing within guilds. The differences were caused by species-specific foraging modes following the concept of Root.

It seems that the important factor influencing the final guild structure is the foraging behaviour of the studied species. It is a very crucial part of the original definition suggested by Root ("using resources in a similar manner"). The main question arises whether behaviour is an obligatory part of the definition in the concept as criticised by MacMahon et al. (1981), Jaksić (1981), and Korňan (2005). Nevertheless, the majority of the guild studies included species foraging behaviour as an equally important part of guild definition as resource use (e.g., Holmes et al. 1979, Eckhardt 1979, Sabo 1980, Holmes and Recher 1986, Székely and Moskát 1991, Brandl et al. 1994, Mac Nally 1994, Adamík et al. 2003). It is important to address this question both from theoretical and methodological aspects.

An excellent example of the effect of foraging behaviour on guild type determination and definition can be seen in the case of bark foragers. In this guild, the foraging behaviour caused a split of the guild members in the Rootian classification into two significantly separate groups: bark probers and bark foragers. After excluding foraging variables from the classification based on the concept of MacMahon et al., two guild categories form one compact guild of trunk foragers. Firstly, we have to

find an accurate answer to the question of whether foraging behaviour is an important factor or a dimension that somehow affects a species niche. Foraging behaviour can be characterised as a set of movements determined by ecomorphological adaptations of a species with the purpose to detect, catch and swallow food items. The object of the niche and competition theories is a resource that can be understood as a food item that limits a population in a certain way. Foraging behaviour by itself does not characterise a species niche, but it reflects a species niche together with ecomorphological adaptations. From an evolutionary perspective, foraging strategies and ecomorphological adaptations play a major role in the evolutionary race among species to find the most efficient strategy of resource utilisation. Nonetheless, strategies and adaptations by themselves do not characterise niche, yet they can change it. Here, when speaking about a general theory of ecological guilds applicable not just to the regnum of animals but also to the regnum of plants and fungi, behaviour as part of the process of guild determination should be excluded.

In the theory of niche, a species niche is understood as a multidimensional hyperspace of the life environment defined by all ecophysiological requirements and factors, i.e., nutrition, microelements, life gases, etc. If we understand guilds as groups of species with significantly different overlaps in niche hyperspace, a community can be divided into clusters of species in environmental hyperspace of high niche overlaps. From the competition theory aspect, we can assume much higher interspecific competitive interactions among species within guilds than between guilds if environmental conditions are stable and resources are limited (Mac Nally 1983). Thus, under stable conditions, we can assume a stable guild structure in terms of the number of guild types and species guild memberships. Yet, in a stochastic model in a dynamic environment with changing temporal and spatial resource availability, a dynamic guild structure can be assumed. This hypothesis of a temporal variation in a guild structure in real communities is supported by some studies (Jaksić et al. 1993). Guild variation and instability were also detected within the same ecosystem type among replicates at different spatial scales (Mac Nally 1994). The hypothesis can be tested by computer simulations in a virtual community with a species set with niche characteristics and defined life strategies in the sense of opportunistic and specialised foraging behaviour dependent on a dynamic model of resource fluctuations in a temporal scale that would produce certain guild outcomes, e.g., in annual cycle. Finally, to fully understand the complexity of guild delineation, it is important to note that a guild membership of many taxa changes through an ontoge-

netic development, i.e., ontogenetic niche shifts (Muñoz and Ojeda 1998).

Root (1967) originally proposed the use of the term "niche" for habitat requirements and established "guild" as the functional role of a group of species. This caused problems to the current understanding of community and ecosystem structure in which guilds are basic building blocks. In this context, species with significantly similar niches are members of the same guild. As concluded by Wilson and Gitay (1999), Wilson (1999) and Korňan (2004b, 2005), a true guild structure in nature is probably hierarchical if trophic levels are accepted as guilds of a higher hierarchy and there is a lower hierarchy within trophic levels. It is also probable that guild structure is orthogonal, with alternative and equally valid classifications functioning in different ways. In contrast to the hierarchical model of an ecosystem organisation, several empirical studies (Wilson et al. 1995abc) failed to detect a clear guild structure in several types of plant communities assuming that this does not have to be generally true if methodically correct.

A number of authors discussed guild terminology, definitions, and applications of the concept in ecological studies (MacMahon et al. 1981, Jaksić 1981, Wiens 1989, Simberloff and Dayan 1991, Wilson 1999, Blondel 2003, Korňan 2005). The term guild is presently accepted as a panchreston with a much broader meaning and an application contrary to the original meaning. Some authors (e.g., Simberloff and Dayan 1991, Wilson 1999) argue that it is too late to restrict the term to any narrow meaning. Wilson (1999) proposed a new classification of guild types with two basic guild classes (beta and alpha guilds) and nine guild types. Only alpha guilds are understood in the original Rootian sense as the resource utilisation structural units of communities. The Beta guilds deviate from the original definition, and they group species with a similar habitat distribution, a temporal distribution, a response to environmental factors, etc. Beta guild concept is a combination of rather arbitrary criteria to classify communities such as spatial and temporal distribution of guilds and ecological criteria such as environmental factors, dimensions in niche space, and methodological criteria of guild delineation. We propose that the development of a strict international ecological terminology, a standardised ecological alphabet, is needed in this area of community ecology. Moreover, we suggest that it would be better to define guilds as building blocks of both communities and ecosystems and suggest the development of new terms for other "deviated" meanings of the term.

Wilson (1999) in his terminological study of the guild classification scheme proposed the notion of an intrinsic

guild based on a co-occurrence of species upon several spatial scales. Wilson and Roxburgh (1994) and Wilson (1999) argue that this is the most objective approach to guild determination since other approaches based on niche measurements are influenced by subjectivity of a variable selection. The subjectivity is a risk of selecting a variable and/or a niche parameter that in fact does not play any role in a species niche. From a statistical point of view, correlative studies are subjected to this error because there is no information on the "cause and effect" relationship between the selected variables and species life history. The Wilsonian approach studies the final organisation of a community; however, it lacks a mechanism of a niche organisation and a separation of the final community structure. One of the possible solutions to this problem is to analyse guilds from the diet of species because eaten items were selected by a species itself, thus these data are free from the factor of subjective variable selection (e.g., Jaksić and Medel 1990, Winemiller and Pianka 1990, Krištín 1992, Jaksić et al. 1993, Brandl et al. 1994, Muñoz and Ojeda 1998, Giannini and Kalko 2004). Consequently, there is no difference in objectivity between the Rootian "diet" guilds and the Wilsonian "intrinsic" guilds. Both study communities from different aspects. The Wilsonian approach to guilds reflects the final structure of a community but lacks any causal explanation of a species co-occurrence from an evolutionary perspective. After all, it would be empirically important to compare both approaches and a fit of their guild classification results on a model community. The future may be surprising!

References

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

Adamík, P., M. Korňan and J. Vojtek 2003. The effect of habitat structure on guild patterns and the foraging strategies of insectivorous birds in forests. *Biologia*, Bratislava 58:275–286.

Adams, J. 1985. The definition and interpretation of guild structure in ecological communities. *J. Anim. Ecol.* 54:43–59.

Alatalo, R.V. 1982. Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland. *Ornis Scand.* 13:56–71.

Alatalo, R.V., L. Gustafsson, M. Lindén and A. Lundberg. 1985. Interspecific competition and niche shifts in tits and the goldcrest: an experiment. *J. Anim. Ecol.* 54:977–984.

Alatalo, R.V. and J. Moreno. 1987. Body size, interspecific interactions, and use of foraging sites in tits (Paridae). *Ecology* 68:1773–1777.

Blondel, J. 2003. Guilds or functional groups: does it matter? *Oikos* 100:223–231.

Brandl, R., A. Krištín and B. Leisler. 1994. Dietary niche breadth in a local community of passerine birds: an analysis using phylogenetic contrasts. *Oecologia* 98:109–116.

Brennan, L.A. and M.L. Morrison. 1990. Influence of sample size on interpretations of foraging patterns by Chestnut-backed Chickadees. *Stud. in Avian. Biol.* 13:187–192.

Cody, M.L. 2000. Antbird guilds in the lowland Carribbean rainforest of souteast Nicaragua. *Condor* 102:784–794.

Cummins, K.W. 1974. Structure and function of stream ecosystems. *Bioscience* 24:631–641.

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

Cornell, H.V. and D.M. Kahn. 1989. Guild structure in the British arboreal arthropods: is it stable and predictable? *J. Anim. Ecol.* 58:1003–1020.

Cooper, R.J., P.J. Martinat and R.C. Whitmore. 1990. Dietary similarity among insectivorous birds: influence of taxonomic versus ecological categorization of prey. *Stud. in Avian. Biol.* 13:104–109.

Diamond, J.M. 1975. Assembly of species communities. In: Cody, M.L. and J.M. Diamond (eds), *Ecology and Evolution of Communities*. Harvard Univ. Press, Cambridge, pp. 342–444.

Drake, J.A. 1990. Communities as assembled structures: do rules govern pattern? *Trend. Ecol. Evol.* 5:159–164.

Eckhardt, R.C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecol. Monogr.* 49:129–149.

Ford, H.A., L. Bridges and S. Noske. 1990. Interobserver differences in recording foraging behavior of Fuscous Honeyeaters. *Stud. in Avian Biol.* 13:199–201.

Gauch, H.G., Jr., R.H. Whittaker and T.R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.* 65:157–174.

Giannini, N.P. and E.K.V. Kalko 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos* 105:209–220.

Gilpin, M.E. and J.M. Diamond. 1982. Factor contributing to nonrandomness in species co-occurrences on islands. *Oecologia* 52:75–84.

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

Hairston, N.G. 1981. An experimental test of a guild: salamander competition. *Ecology* 62:65–72.

Hejl, S.J. and J. Verner. 1990. Within-season and yearly variations in foraging locations. *Stud. in Avian Biol.* 13:202–209.

Hintze, J.L. 1997. *NCSS '97*. User's guide. Kaysville.

Holmes, R.T., R.E. Bonney, Jr. and S.W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* 60:512–520.

Holmes, R.T. and H.F. Recher. 1986. Determinants of guild structure in forest bird communities: an intercontinental comparison. *Condor* 88:427–439.

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

Inger, R.F. and R.K. Colwell. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecol. Monogr.* 47:229–253.

Jackson, D.A. 1997. Compositional data in community ecology: the paradigm or peril of proportions? *Ecology* 78:929–940.

Jaksić, F.M. 1981. Abuse and misuse of the term "guild" in ecological studies. *Oikos* 37:397–400.

Jaksić, F.M. and R.G. Medel. 1990. Objective recognition of guilds: testing for statistically significant species clusters. *Oecologia* 82:87–92.

Jaksić, F.M., P. Feinsinger and J.E. Jiménez. 1993. A long-term study on the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site. *Oikos* 67:87–96.

Jongman, R.H.G., C.J.F. Ter Braak and O.F.R. Van Tongeren. 1997. *Data Analysis in Community and Landscape Ecology.* Cambridge Univ. Press, Cambridge.

Keane, J.J. and M.L. Morrison. 1999. Temporal variation in resource use by Black-throated Gray Warblers. *Condor* 101:67–75.

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.* M.Sc. thesis, Faculty of Sciences of Comenius University, Bratislava.

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. 2004a. 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. 2004b. *Structure of Bird Foraging Guilds and Resource Partitioning in a Primaeval Beech-fir Forest.* PhD dissertation, Faculty of Sciences of Comenius University, Bratislava.

Korňan, M. 2005. Concept of structural and functional organization of communities: guilds and functional groups. *Biological papers* 70:81–106.

Krištín, A. 1992. Trophische beziehungen zwischen singvögeln und wirbellosen im eichen-buchenwald zur brutzeit. *Orn. Beob.* 89:157–169.

Landres, P.B. and J.A. MacMahon. 1983. Community organization of arboreal birds in some oak woodlands of western North America. *Ecol. Monogr.* 53:183–208.

Lawlor, L.R. 1980. Structure and stability in natural and randomly constructed competitive communities. *Am. Nat.* 116:394–408.

Legendre, L. and P. Legendre. 1983. *Numerical Ecology.* Elsevier Scientific Publishing Company, Amsterdam.

Lincoln, R., R. Boxshall and P. Clark. 1998. *A Dictionary of Ecology, Evolution and Systematics.* Cambridge Univ. Press, Cambridge.

MacFadyen, A. 1957. *Animal ecology: Aims and Methods.* Pitman and Sons, London.

MacMahon, J.A., D.J. Schimpf, D.C. Andersen, K.G. Smith and R.L. Bayn, Jr. 1981. An organism-centered approach to some community and ecosystem concepts. *J. Theor. Biol.* 29:287–307.

Mac Nally, R.C. 1983. On assessing the significance of interspecific competition to guild structure. *Ecology* 64:1646–1652.

Mac Nally, R.C. 1994. Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. *J. Anim. Ecol.* 63:988–1001.

Marhold, K. and F. Hindák. (eds) 1998. *Checklist of Non-vascular and Vascular Plants of Slovakia.* Veda, Bratislava.

Mitchell, M. 1997. *An Introduction to Genetic Algorithms.* MIT Press, Cambridge.

Moreno, E. and L.M. Carrascal. 1993. Leg morphology and feeding postures in four *Parus* species: an experimental ecomorphological approach. *Ecology* 74:2037–2044.

Muñoz, A.A. and F.P. Ojeda. 1998. Guild structure of carnivorous intertidal fishes of the Chilean coast: implications of ontogenetic dietary shifts. *Oecologia* 114:563–573.

Noon, B. R. 1981. Techniques for mapping avian habitats. In: Copen, D.E. (ed), *The Use of Multivariate Statistics in Studies of Wildlife Habitat.* USDA Forest Service General Technical Report RM–87, Fort Collins. pp. 42–49.

Pillar, V.D. 1999. How sharp are classifications? *Ecology* 80:2508–2516.

Pillar, V.D. 2004. *MULTIV – Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling.* User's guide v.2.3.9. Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Pianka, E.R. 1988. *Evolutionary Ecology.* Harper and Row, New York.

Podani, J. 1997. *SYN-TAX 5.10-pc. Supplement to the User's Manual.* Scientia Publishing, Budapest.

Podani, J. 2000. Simulation of random dendrograms and comparison tests: some comments. *J. Classif.* 17:123–142.

Podani, J. and T. A. Dickinson. 1985. Comparison of dendrograms: a multivariate approach. *Can. J. Bot.* 62:2765-2778.

Remsen, J.V.,Jr. and S.K. Robinson. 1990. A classification scheme for foraging behaviour of birds in terrestrial habitats. *Stud. in Avian Biol.* 13:144–160.

Rohlf, F.J. 1974. Methods of comparing classifications. *Annu. Rev. Ecol. Syst.* 5:101–113.

Root, R.B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecol. Monogr.* 37:317–350.

Sabo, S.R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. *Ecol. Monogr.* 50:241–259.

Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.

Simberloff, D. and T. Dayan. 1991. The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst.* 22:115–143.

Snow, D.W. and C.M. Perrins. 1998. *Birds of the Western Palearctic. Concise Edition.* Oxford Univ. Press, Oxford.

Strauss, R.E. 1982. Statistical significance of species clusters in association analysis. *Ecology* 63:634–639.

Suhonen, J., M. Halonen and T. Mappes. 1993. Predation risk and the organization of the *Parus* guild. *Oikos* 66:94–100.

Székely, T. and C. Moskát. 1991. Guild structure and seasonal changes in foraging behaviour of birds in a Central-European oak forest. *Ornis Hungarica* 1:10–28.

Tebbich, S., M. Taborsky, B. Fessl, M. Dvorak and H. Winkler. 2004. Feeding behaviour of four arboreal Darwin's finches: adaptations to spatial and seasonal variability. *Condor* 106:95–106.

Ulfstrand, S. 1976. Feeding niches of some passerine birds in a South Swedish coniferous plantation in winter and summer. *Ornis Scand.* 7:21–27.

Vološčuk, I. 1986. The forest vegetation of the State Nature Reserve Šrámková. *Ochrana prírody* 7:237–251.

Wagner, J.L. 1980. Seasonal change in guild structure: oak wood-land insektivorous birds. *Ecology* 62:973–981.

Wiens, J.A. 1989. *The Ecology of Bird Communities. Vol. I. Foundations and Patterns.* Cambridge Univ. Press, Cambridge.

Winemiller, K.O. and E.R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monogr.* 60:27–55.

Wilson, J.B. 1999. Guilds, functional types and ecological groups. *Oikos* 86:507–522.

Wilson, J.B. and Roxburgh. 1994. A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. *Oikos* 69:267–276.

Wilson, J.B., R.B. Allen and W.G. Lee. 1995a. An assembly rule in the ground and herbaceous strata of a New Zealand rainforest. *Funct. Ecol.* 9: 61–64.

Wilson, J.B., M.T. Sykes and R.K. Peet. 1995b. Time and space in the community structure of a species-rich grassland. *J. Veg. Sci.* 6:729–740.

Wilson, J.B., J.B. Steel, J.E. Newman and R.S.Tangney. 1995c. Are bryophyte communities different? *J. Bryol.* 18:689–705.

Wilson, J.B. and H. Gitay. 1999. Alternative classifications in the intrinsic guild structure of a New Zealand tussock grassland. *Oikos* 86:566–572.

Appendix 1. List of species that were observed while foraging in the primeval beech-fir forest in the Šrámková National Nature Reserve in the period 1997–2000. Total number of point foraging observations and time are indicated. Only 26 species with minimum of 30 observations or total time of 1500 s were included in the further analyses.

SPECIES Latin and common names	ABBREVIATION	NUMBER OF OBSERVATIONS	TOTAL TIME (s)
Accipiter gentilis Goshawk	*Acc gen*	1	3
Aegithalos caudatus Long-tailed Tit	*Aeg cau*	60	604
Bonasa bonasia Hazel Grouse	*Bon bon*	16	68
Carduelis spinus Siskin	*Car spi*	12	246
Certhia familiaris Treecreeper	*Cer fam*	337	6 183
Cinclus cinclus Dipper	*Cin cin*	67	2 044
Coccothraustes coccothraustes Hawfinch	*Coc coc*	11	941
Delichon urbica House Martin	*Del urb*	247	2 288
Dendrocopus leucotos White-backed Woodpecker	*Den leu*	86	9 919
Dendrocopus major Great Spotted Woodpecker	*Den maj*	10	380
Dryocopus martius Black Woodpecker	*Dry mar*	12	572
Erithacus rubecula Robin	*Eri rub*	115	908
Ficedula albicollis Collared Flycatcher	*Fic alb*	70	477
Ficedula parva Red-breasted Flycatcher	*Fic par*	179	745
Fringilla coelebs Chaffinch	*Fri coe*	335	4 798
Garrulus glandarius Jay	*Gar gla*	4	25
Loxia curvirostra Crossbill	*Lox cur*	20	780
Motacilla cinerea Grey Wagtail	*Mot cin*	121	2 515
Muscicapa striata Spotted Flycatcher	*Mus str*	65	649
Nucifraga caryocatactes Nutcracker	*Nuc car*	3	99
Parus ater Coal Tit	*Par ate*	547	7 217
Parus careuleus Blue Tit	*Par cae*	16	144
Parus cristatus Crested Tit	*Par cri*	17	335
Parus major Great Tit	*Par maj*	6	27
Parus palustris March Tit	*Par pal*	179	2 525
Phylloscopus collybita Chiffchaff	*Phy col*	297	2 645
Phylloscopus sibilatrix Wood Warbler	*Phy sib*	156	1 402
Phylloscopus trochilus Willow Warbler	*Phy tro*	110	1 441
Picoides tridactylus Three-toed Woodpecker	*Pic tri*	45	11 222
Prunella modularis Dunnock	*Pru mod*	31	455
Pyrrhula pyrrhula Bullfinch	*Pyr pyr*	36	1 256
Regulus ignicapileus Firecrest	*Reg ign*	18	408
Regulus regulus Goldcrest	*Reg reg*	321	4 590
Scolopax rusticola Woodcock	*Sco rus*	1	2
Sitta europaea Nuthatch	*Sit eur*	305	4 615
Sylvia atricapilla Blackcap	*Syl atr*	178	1 955
Troglodytes troglodytes Wren	*Tro tro*	102	1 998
Turdus merula Blackbird	*Tur mer*	36	3 038
Turdus philomelos Song Thrush	*Tur phi*	20	1 887
Turdus torquatus Ring Quzel	*Tur tor*	21	2 244
Turdus viscivorus Mistle Thrush	*Tur vis*	1	3
TOTAL		4 214	83 653