



Convergence in foraging guild structure of forest breeding bird assemblages across three continents is related to habitat structure and foraging opportunities

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Abstract. Comparisons of community structure across sites allow for the detection of convergent patterns and the selective forces that have produced them. In this study, we examined the foraging guild structure of birds breeding in forests on three continents – Europe, North America, and Australia, with largely phylogenetically distinct avifaunas. We examined two hypotheses: (1) the bird assemblages in the three geographically separated forested study sites should have similar foraging guild patterns to the extent to which environmental resources of these forests are similar, and (2) if bird assemblages in structurally similar forest habitats have undergone adaptive evolution, then radiation of species into guilds should have been caused by analogous selective resource gradients (factors). Bootstrapped cluster analysis (UPGMA) and bootstrapped principal coordinate analysis (BPCoA) of chord distances were employed to determine foraging guild structure for each assemblage, and to extract the significantly different factors responsible for segregation of species into guilds. Cluster analyses identified three analogous foraging guilds (ground and litter foragers, foliage gleaners, and trunk foragers) in each of the bird assemblages, supporting the first hypothesis of guild structure convergence. The BPCoA determined that two environmental factors (vertical resource allocation and spatial tree morphology gradients) were primarily responsible for segregation of species into guilds in these three geographically distant but structurally similar forests. These findings support the hypothesis that guild structures in forest bird assemblages largely reflect the similarities and differences in forest structure and the distribution and abundance of foraging resources, and result from largely adaptive evolution.

Nomenclature: Bird nomenclature follows Dickinson (2003).

Abbreviations: BMMDS–Bootstrapped metric multidimensional scaling, BPCoA–Bootstrapped principal coordinate analysis, UPGMA–Unweighted Pair Group Cluster Analysis.

Introduction

One of the main objectives of ecological research is to analyze biodiversity patterns and search for factors determining them (Ricklefs and Schluter 1993). Comparing biodiversity and structural patterns of communities across continents is a common approach to search for similarities in their organization and evolution, which if found indicate ecological convergence. Up to now, convergence has been documented for a variety of taxonomic groups, including fishes (Winemiller 1991), reptiles (Losos 1992), birds (Leisler and Winkler 2001, Korner-Nievergelt and Leisler 2004), and mammals (Mares 1993). If species converge in morphology, behaviour, ecology, and/or physiology, then similar selection

processes may operate on higher levels of organization of ecological systems, that is, to produce similar guilds and communities. This hypothesis was expressed by Cody and Diamond (1975, p. 7) as: "If observed patterns in community structure are products of natural selection, then similar selection by similar environments should produce similar optimal solutions to community structure."

Since the early work of Cody and Diamond, convergence in structural and biodiversity patterns has been documented in a wide range of assemblages and communities (e.g., Ricklefs and Travis 1980, Niemi 1985, Wiens 1991a, Irz et al. 2007, Gido et al. 2009). However, in some cases the detected patterns were ambiguous and interpretation depended on the

parameters being analyzed. For instance, Wiens (1991b) in a comparison of shrub-desert avifaunas between Australia and North America did not detect convergence in life history traits, but did find similarities in ecomorphological characters (Wiens 1991a). Another problem in interpreting convergence can be the scale of comparison. For instance, convergence may emerge on a community or assemblage level, but it may disappear in species to species pairing (Ricklefs and Travis 1980). Additionally, convergence may not evolve in some taxonomic groups due to phylogenetic conservatism and homogenization, as reported for emydid turtle communities by Stephens and Wiens (2004).

Intercontinental comparisons of guild structure of communities based on an *a posteriori* approach have been rarely conducted and the results remain ambiguous because not all studies detected convergence in foraging guild structure. For instance, Irz et al. (2007) detected no sign of convergence in the trophic guild structure of lacustrine fish assemblages between France and north-east U.S.A. Similarly, Kelt et al. (1996) in comparing desert small mammal communities across four continents did not find similar structure of foraging guilds presumably due to major differences in phylogenetic lineages. In contrast, Holmes and Recher (1986) compared foraging guild structure of forest bird assemblages between Australia and North America and detected the presence of three analogous guilds and identified similar determinants of guild structure in both communities. Thus, evidence for convergence of guild structure remains equivocal, and additional comparative community studies are needed to examine for the occurrence and extent of guild convergence among different communities and the selective forces that may produce them.

Holmes et al. (1979) and Holmes and Recher (1986) used the method of random point observations of foraging birds to collect information on use of foraging substrates, foraging maneuvers, and foraging heights in two study sites, one in North America and one in Australia. Both studies used the same analytical procedures (cluster analysis and principal component analysis) to describe guild structure of the bird assemblages. More recently, Korňan and Adamik (2007) applied the same sampling approach in the guild structure study of a European primeval mixed forest bird assemblage. In the present paper, these three data sets are compared using more objective analytical methods, namely bootstrapped cluster analysis and bootstrapped principal coordinate analysis designed for *a posteriori* guild recognition.

Based on the above quoted proposition of Cody and Diamond (1975) about community adaptive evolution, we hypothesized that (1) the bird assemblages in the three geographically separated forested study sites should have similar guild patterns to the extent to which environmental resources of these forests are similar, and (2) if bird assemblages in structurally similar forest habitats have undergone adaptive evolution, then radiation of species into guilds should have been caused by analogous selective resource gradients (factors). Our analytical techniques are then used to identify and

assess these selective forces across these three forest bird communities on different continents.

Characteristics of study sites

North American site

The North American study was conducted in the Hubbard Brook Experimental Forest (hereafter North American site), Woodstock, New Hampshire, USA, on the 10-ha study plot (Supplement 1) described by Holmes and Sturges (1975) and Holmes and Sherry (2001). The plot was located in undisturbed forest, near weir 6 of the Hubbard Brook Experimental Forest (geographic coordinates in WGS84 of plot corners: 43°56'41.92-58.17''N, 71°44'7.69-9.32''W; 43°56'42.69-58.37''N, 71°44'16.90-17.79''W). The plot was on south-southeast facing slope at elevation 500-600 m above sea level. The forest is an uneven aged, well-stocked stand of northern hardwoods, dominated by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marshall), and yellow birch (*Betula alleghaniensis* Britt.), with occasional white ash (*Fraxinus americana* L.), white birch (*B. papyrifera* Marshall), and red spruce (*Picea rubens* Sarg.). The canopy height averaged approximately 25 m. The plot was situated within forest tracts that had been selectively logged in the early 1900s but have remained free of any direct human disturbance since that time. Further details can be found in Holmes (2011).

Australian site

The study was conducted on the Southern Tablelands, New South Wales and Victoria in southeastern Australia. The three 10 ha study areas (Supplement 2A-C) were located approximately 40 km southeast of Bombala (36°54' S, 149°14' E) at 800-850 m above sea level within and adjacent to Bondi State Forest (hereafter Australian site). The study areas consisted of forest-woodland ecotone grading from a moist, tall open forest through drier, open-forest to woodland at the edge of grazed pastures. Almost all of two of the three plots at Bondi would be described as 'dry sclerophyll' forest. The third plot was mainly dry sclerophyll, with a small area that could be classed as 'wet sclerophyll'. The forest was multi-layered dominated by narrow-leaved peppermint (*Eucalyptus radiata* A. Cunn. ex. DC.), ribbon gum (*E. viminalis* Labill.), mountain gum (*E. dalrympleana* Maiden), and swamp gum (*E. ovata* Labill.). The canopy height averaged 16-22 m depending on the forest plot. In moist areas, the sub-canopy was formed by young eucalypts with scattered Australian blackwood (*Acacia melanoxylon* R.Br.) and silver wattle (*A. dealbata* Link). The shrub layer was diverse and often dense, whereas in the drier parts it was more open due to grazing by sheep and selective logging. Areas of woodland were drier and dominated by snow gum (*E. pauciflora* Sieber ex. Spreng.) and black sallee (*E. stellulata* Sieber ex DC.), with an understory of small eucalypts. The woodland lacked shrubs. Further details regarding the description of the study sites are in Recher et al. (1985) and Holmes and Recher (1986).

European site

The research was carried out in the Šrámková National Nature Reserve (hereafter European site), Malá Fatra Mts., northwestern Slovakia. The study plot (27.5 ha) represents the Western Carpathian primeval beech-fir forest (Supplement 3). The bottom line of the plot was georeferenced in WGS84 (49°11'11.9''-23.2''N; 19°06'37.0-51.3''E). 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 study plot is situated at an elevation 850–1078 m above sea level. The study site is dominated by European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* L.) H. Karst.), sycamore (*Acer pseudoplatanus* L.), wych elm (*Ulmus glabra* Huds.), and rowan (*Sorbus aucuparia* L.) with admixture of other tree species such as silver birch (*Betula pendula* Roth), European larch (*Larix decidua* Mill.), Norway maple (*A. platanoides* L.) and small-leaved lime (*Tilia cordata* Mill.). The canopy height ranges up to 45 m. The mean canopy height in forest segment 461 that represents the majority of the research plot was estimated to be 24.7 m (database of the National Forest Centre in Zvolen, state to 1.1.2006). The shrub layer is locally dense and mainly consists of hazel (*Corylus avellana* Mill.), red-berried elder (*Sambucus racemosa* L.), currant (*Ribes* spp.), and saplings of the dominant tree species. For more details see Korňan (2000, 2004)

Methods

Sampling of bird foraging patterns

At each site foraging data were collected during the peak breeding season (early spring to mid-summer). In the North American site, the sampling of bird foraging patterns was conducted during June and July in 1974–1976, in the Australian site between mid-October 1980 and mid-January 1981, and in the European site the sampling was carried out from mid-May until late July in 1997–2000. Bird foraging data were collected in the study plots in the North American and the Australian sites, and in the case of the European site also in similar habitat on 244 ha surrounding the study plot. Foraging data were collected in the three study areas using similar methods (see Holmes et al. 1979, Holmes and Recher 1986, Korňan and Adamík 2007). Observers searched for, and observed as many different feeding birds as possible throughout the day from early dawn to dusk. After recording a foraging observation, observer moved to search for different foraging bird in order to avoid a pseudoreplication bias. In the North American and Australian studies, several sequential foraging records were sometimes taken on the same individual, especially for species with low population densities. This was justified by statistical analyses that indicated no significant differences between the frequency of different foraging behaviours in the first observation versus all observations in a sequence (Holmes et al. 1979, Recher and GebSKI 1990). Thus, foraging data set for individual species most

likely consists of foraging observations of different birds. However, especially in case of conspicuous species with lower population densities, it is possible that the same individual could have been recorded more than once during the breeding season. For each observation, species, sex, time of day, length of observation, foraging height, foraging substrate, and foraging manoeuvre were recorded. For some observations, we recorded direction of foraging movement (vertical or horizontal direction to the tree trunk). The lists of variables recorded for each site are given in the original papers (Holmes et al. 1979, Table 1, Appendix; Holmes and Recher 1986, Table 1, Appendix; and Korňan and Adamík 2007, Table 2).

A foraging movement was defined as any activity of a bird whose immediate purpose was to detect and capture a food item. Attack categories (foraging manoeuvres) were divided into six main types: glean, hover, sally (hawk), probe (peck, drill), snatch, and pounce. Gleaning was defined as a foraging tactic when a stationary prey item is taken from a surface of a nearby substrate by a perching or hopping bird. Hovering was when an exposed prey is taken from a substrate (e.g., a leaf or a branch) by an actively flying bird in hummingbird manner. Sallying was when a bird flies from an observation perch to attack a food item and then returns to a perch. Probing was a manoeuvre when a bird penetrates its bill into a substrate to locate a subsurface prey item or to take nectar. Snatching was like hover, but the flying bird plucks the food item from the substrate as it flies past, and does not pause or hover. Pouncing involved flying from a perch and grabbing the food item as the bird lands on the substrate (usually the ground). Further information is given in the papers of Holmes et al. (1979), Holmes and Recher (1986), Recher et al. (1985), and Korňan and Adamík (2007).

For most species, and especially insectivorous ones, it was rarely possible to identify a caught prey item or even to distinguish successful from unsuccessful attacks. Therefore, observations indicate the foraging manoeuvres used regardless of outcome. For the purpose of the analyses in this paper, pooled data for all individuals of each species collected over the study period were used, although significant intraspecific, seasonal, and annual variation in foraging behaviour did occur (e.g., see more detailed accounts in Holmes et al. 1978, Holmes 1986, Hejl and Verner 1990, Adamík and Korňan 2004).

Statistical analyses

Matrix preparation

We employed the guild concept as developed by Root (1967), in which guilds are defined on the basis of utilization patterns of resources and foraging tactics. In total, 9285 foraging observations of 22 bird species were collected in the North American site, 26116 observations of 41 species in the Australian site, and 4214 observations of 41 species in the European site during the whole study periods. Only species with at least 30 observations or a minimum total cumulative

observation time of 1500 s were used in the analyses. This criterion seems satisfactory for a description of general species foraging patterns. Brennan and Morrison (1990) studied foraging behaviour of a small passerine bird and concluded that estimates of central tendency and dispersion in foraging samples with at least 30-50 observations per species were stable and were significantly similar to the total sample means. Data for the majority of the species in our data sets greatly exceeded this number (for sample sizes of individual species, see Holmes et al. 1979, Table 1, Holmes and Recher 1986, Table 1, Korňan and Adamík 2007, Appendix 1).

The North American data matrix (22 species \times 26 variables) consisted of two foraging height variables, 14 foraging manoeuvres, 11 foraging substrates, and two indicating direction of foraging movement (distal/proximal to the main axis/trunk of trees). The Australian data matrix (41 species \times 24 variables) contained two variables indicating foraging heights, 15 foraging manoeuvres, and seven foraging substrates. The European data matrix (26 species \times 38 variables) consisted of two foraging height variables, 18 variables reflecting type of foraging movement, 16 foraging substrate variables, and two indicating direction of foraging movement. The North American and Australian data matrices are published in Holmes et al. (1979) and Holmes and Recher (1986). The European data matrix is published in the Supplement 4.

All variables were expressed as proportions based on the foraging frequencies of the individual species in the standardized variable set except for two metric variables related to foraging height (mean, SD). Multivariate clustering (bootstrapped UPGMA) and ordination techniques (bootstrapped principal coordinate analysis) were selected for the numerical analyses. Data matrix was automatically normalized (Pillar 2004, p. 15 and 11) when the resemblance measure chord distance was selected for analysis.

Guild determination

To determine objectively the foraging guild structure of each bird assemblage without arbitrary fusion criteria, the data matrices were subjected to a bootstrapped cluster analysis (UPGMA) of chord distances and a bootstrapped principal coordinate analysis (BPCoA) of chord distances in the program MULTIV 2.3.9 (Pillar 2004). MULTIV is designed to offer an option of bootstrap resampling to generate empirical confidence limits useful in estimation, to evaluate group partition sharpness in cluster analysis (Pillar 1999a) and to evaluate the significance of ordination dimensions (Pillar 1999b).

The bootstrapped cluster analysis is based on bootstrapped resampling of the basic data matrix (Pillar 1999a). The probability $P(G^0 \leq G^*)$ is the proportion of bootstrapped iterations in which G^0 is found smaller than or equal to G^* . If $P(G^0 \leq G^*)$ is not larger than a specified threshold α , we conclude, with a probability $P(G^0 \leq G^*)$ of being wrong, that the k groups in the partition are not sharp enough to consistently reappear in resampling. It means that we reject the null

hypothesis and conclude that the groups are fuzzy. If, instead, we accept the null hypothesis, we conclude that there is not enough evidence to refute that the groups are sharp (Pillar 2004). G^* attribute is computed as the similarity of the k -group partition in the bootstrapped sample to the k -group partition in the original reference sample. G^* attribute can reach values from zero to one when original reference and bootstrap sample coincide. G^0 attribute is computed under the assumption of the null hypothesis that the groups are sharp. Computation of G^0 is more complicated and further details are given in Pillar (1999a, p. 2510). Comparison of attributes G^* and G^0 is one iteration the bootstrapped resampling.

BPCoA (synonym is bootstrapped metric multidimensional scaling – BMMDS) was applied to determine the number of significant factors (dimensions) in the metric ordination of a sample (Pillar 1999b). An iterative algorithm takes bootstrap samples with replacement from the sample. The algorithm for bootstrapped ordination involves Procrustean adjustment. The probability $P(\theta_i^0 \geq \theta_i^*)$ is an indicator of the strength of the structure in an ordination, as compared to the ordination of a null data set containing variables with the observed distribution but zero expected association (Pillar 2004). Setting an α probability threshold will help the interpretation of $P(\theta_i^0 \geq \theta_i^*)$. A smaller $P(\theta_i^0 \geq \theta_i^*)$ than α will indicate that the ordination dimension in consideration is significantly more stable than that would be expected for the same dimension in the ordination of a random data set. In this case we reject the null hypothesis and conclude with a probability $P(\theta_i^0 \geq \theta_i^*)$ of being wrong, that the given ordination dimension is nontrivial and worthy of interpretation. Otherwise, we accept the null hypothesis and consider the ordination dimension unstable and indistinguishable from a random data ordination (Pillar 2004).

When running both statistical procedures, we selected the option of computing bootstrapped samples with increasing sizes and the results were used to evaluate sampling sufficiency (Pillar 2004). An insufficient sample size may cause statistical type II error; that is, the test may not detect significance of clusters or ordination dimensions that would be found significant if the samples were larger (see Supplements 5-7). We used 10 000 iterations in all computations. Each computation started with a randomly generated number by the program. The critical threshold level in all computations was set at $\alpha = 0.10$.

Results

Hierarchical classification

North American site. The bootstrapped cluster analysis (UPGMA) of chord distances detected significant structure in the bird assemblage at the North American site. In total, there were three significantly different species clusters and an independent dendrogram branch at the threshold $\alpha = 0.10$ which we designate here as foraging guilds (Fig. 1a, Table 1). The first cluster (from upper toward lower part of the den-

Table 1. Probabilities $P(G^0 \geq G^*)$ and averages of sample attributes generated by 10 000 random iterations of bootstrap resampling of three foraging guild data matrices (North American, Australian, and European sites) at different partition levels. Initializer of pseudo-random number generator was set on automatic mode (Pillar 2004). In the first data matrix, the classification was sharp at the levels of 4 groups, in the second matrix at levels 3, 9, and 10, and in the third matrix at levels 8 groups, indicating the numbers of different guild types at the critical value $\alpha = 0.10$. The numbers of significantly different clusters in the three classifications are indicated in bold.

	Number of species groups (clusters)								
	2	3	4	5	6	7	8	9	10
N. American matrix 22 × 26									
$P(G^0 \leq G^*)$	0.4860	0.2684	0.1295	0.0776	0.080	0.0497	0.0395	0.0274	0.0111
Average of sample attribute	0.9806	0.9374	0.9434	0.9277	0.9312	0.9332	0.9336	0.9320	0.9107
Australian matrix 41 × 24									
$P(G^0 \leq G^*)$	0.3970	0.4204	0.0548	0.0645	0.0920	0.0521	0.0740	0.1135	0.1113
Average of sample attribute	0.9795	0.9848	0.9526	0.9418	0.9502	0.9525	0.9631	0.9684	0.9660
European matrix 26 × 38									
$P(G^0 \leq G^*)$	0.2093	0.3119	0.4569	0.3242	0.2911	0.1930	0.1130	0.0550	0.0186
Average of sample attribute	0.9184	0.9475	0.9857	0.9691	0.9716	0.9672	0.9625	0.9532	0.9397

rogram) consisted of three species and the data show that these species forage extensively on the ground (litter), herbs, beech leaves, and deadwood, and thus we label this group as a ground foraging guild. These species foraged mainly by gleaning and probing. The Wood Thrush formed an independent branch, although it was very similar to the ground foragers in use of foraging substrates and foraging tactics. The second cluster consisted of 14 species. Because all of these species fed extensively on insect prey obtained from leaves, they can be considered as foliage foragers. These species primarily foraged by gleaning, hovering, and some, especially the Least Flycatcher and American Redstart, used hawking manoeuvres to capture flying insect prey. Also, clustered with this foliage foraging group were Swainson’s Thrush, Hermit Thrush, and Dark-eyed Junco, which foraged primarily on ground, herbs and shrubs. The third cluster was composed of four species, including three species of woodpeckers and a nuthatch. These foraged primarily on tree trunks and branches, using probes and gleans, and are classified here as trunk foragers.

Australian site. For the Australian site, the bootstrapped cluster analysis (UPGMA) revealed three independent trenchant models of the guild structure at the levels of 3, 9 and 10 group partitions at the threshold $\alpha = 0.10$ (Fig. 1b, Table 1). The statistical significance of the guild classification was lost at the level of 4-8 clusters. We interpreted the guild structure pattern for this site at the level of 9 partitions that seem ecologically the most reasonable. The first cluster (from the upper part of the dendrogram) contained three species that typically foraged by gleaning on branches and trunks and are labelled as trunk foragers. The second cluster contained eight species, which mostly gleaned insect prey from foliage and branches primarily from rough-barked eucalypts, forest gums, and woodland gums, and thus can be considered the foliage foraging guild. The third cluster had two species that primarily foraged on loose bark by gleaning and are labelled as loose bark gleaners. The fourth cluster had six species, which mostly foraged from the ground and litter by gleaning,

and are considered to be ground-foragers I (gleaners). The fifth cluster consisted of nine species. These can be considered as the arboreal flycatcher guild, with high frequencies of snatching from foliage and sallying (hawking). The sixth cluster had four species, which mainly pounced on prey located on the ground and are labelled as ground foragers II (pouncers). The seventh cluster contained two species, which fed almost exclusively on eucalypt capsules and are characterized as seed eaters. The eighth cluster consisted of three species that were characterized as nectar feeders due to their extensive gleaning (of nectar) from flowers, mainly of gippsland waratah (*Telopea oreades* F. Muell.). The ninth cluster contained four species that foraged on the ground by probing and gleaning (pecking, scratching) and can be referred to as ground-foragers III (probers).

European site. For the third forest bird assemblage, the bootstrapped cluster analysis (UPGMA) of chord distances detected eight significantly different group partitions in the data matrix at the threshold $\alpha = 0.10$ corresponding to seven foraging guilds and one independent dendrogram branch (Fig. 1c, Table 1). The first cluster (from the upper part of dendrogram) consisted of two bark foraging passerines that primarily gleaned and can be classified as bark gleaners. The second cluster had also two woodpecker species that foraged mostly from trunks and branches of standing dead and live trees by probing. The Three-toed Woodpecker foraged mainly on the trunks of conifers. These can be considered as the trunk probers. The third cluster was composed of nine species that were characterized as the foliage foragers due to their foraging primarily from leaves and twigs of trees by gleaning and hovering. The fourth guild consisted of four species were identified as the flycatchers due to high frequencies of foraging by hawking prey from the air, and by sallying and hovering from leaves and twigs. House Martin (*Delichon urbica*) represented an air sweeper branch within this guild. The fifth cluster had three species that mainly foraged in low strata from ground, litter, herbs, logs, and the leaves, twigs and branches of trees. The guild was charac-

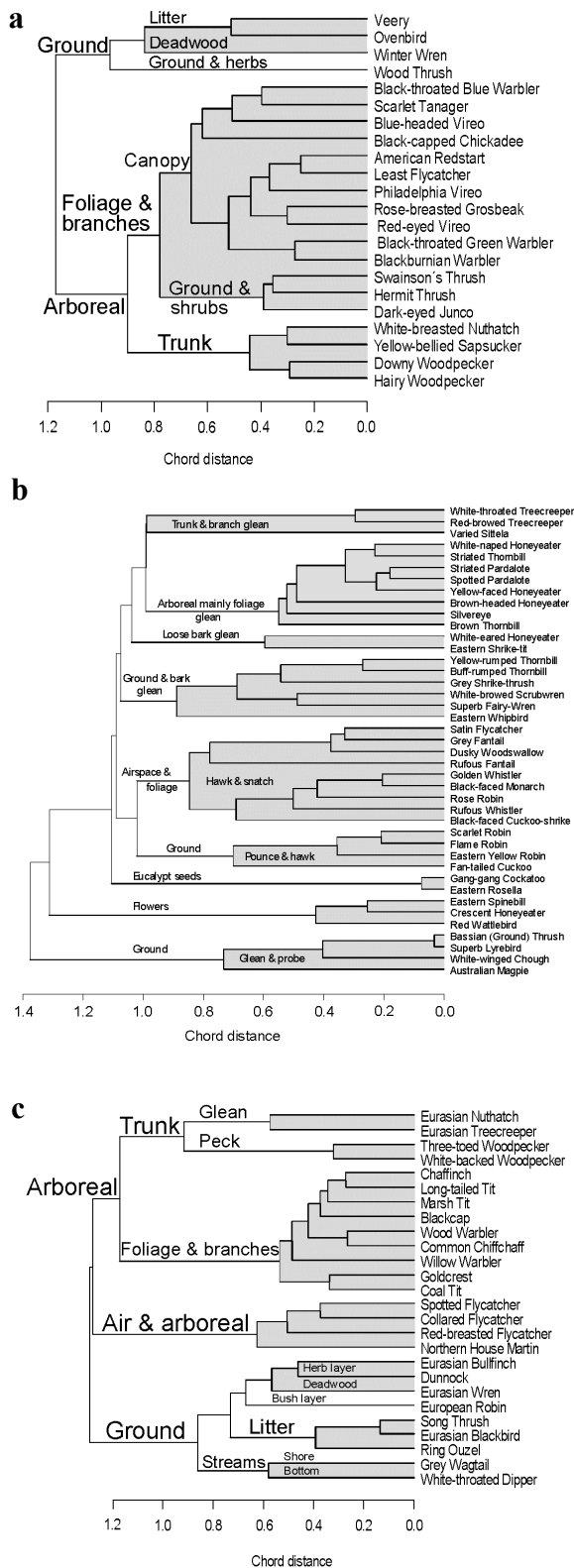


Figure 1. Bird assemblage dendrograms showing foraging guild structure of three forests on different continents: North America (a), Australia (b) and Europe (c). The guilds were determined by the bootstrapped cluster analyses (UPGMA) of chord distances. The individual guilds are highlighted by grey colour. Latin names are given in the Supplement 12.

terized as herb layer foragers. The European Robin formed an independent dendrogram branch that was characteristic by gleaning, hovering and hawking from herb and shrub layers and ground. The sixth group consisted of three thrush species that fed almost exclusively from the ground and litter by gleaning and were characterized as the guild of ground (litter) foragers. The seventh group was represented by two species. Both were tied to the stream habitat due to their foraging adaptations, thus forming a guild of stream foragers. The wagtail fed mainly along the stream bank and there occurring substrates e.g., rocks, logs. The dipper was specialised on foraging from the stream bottom, dive gleaning for aquatic insects, less frequently by gleaning prey from fallen wood and stones along the stream channel.

Bootstrapped ordination

North American site. The BPCoA of chord distances of the North American foraging matrix revealed two significantly different ordination axes at the threshold $\alpha = 0.10$ (Table 2). We applied the bootstrapped ordination approach and interpreted only the first two axes because the remaining factors seemed intercorrelated. The primary purpose of this analysis was to identify the main habitat components or gradients of resources that were primarily responsible for segregating the foraging guilds and the radiation of species into foraging niches. The first six ordination factors in this analysis for the North American community explained 90.34 % of total matrix variance, with the first two explaining 63.86 % of variance (Supplement 8).

The first factor eigenvalue score was 3.02 and explained 34.48 % of the matrix variance (Supplement 8). The variables mean foraging height, standard deviation of foraging height, maneuver on *Betula* ssp., and maneuver proximal to trunk reached the highest positive correlations with the first ordination axis, whereas the variables related to foraging in low strata (glean from ground, probe into ground, probe into fallen dead wood, and maneuver on herbs and ferns) had the highest negative correlations (Supplement 8). Based on this and position of species within guilds along the first axis (Fig. 2a), the first factor was interpreted as the gradient of resource exploitation related to foraging height. This factor was primarily responsible for separation of ground foragers from arboreal guilds (Fig. 2a).

The eigenvalue score of the second factor for the North American community was 2.57 and explained 29.38 % of matrix variance. The variables hover at leaf, glean from leaf, and maneuver distal to trunk had the highest correlation with the first ordination axis, while variables probe into trunk and maneuver proximal to trunk reached the highest negative loadings. Taking this into consideration and plotting species along the second ordination axis, we interpreted the second factor as a microhabitat gradient connected to the spatial tree morphology reflecting the spatial array of trunks, branches, twigs, and leaves. This factor can be interpreted mainly as being responsible for segregating trunk foragers along the trunks and major branches from the foliage gleaners (Fig. 2a).

Table 2. Probabilities $P(\theta_i^o \geq \theta_i^*)$ and averages of sample attributes generated by 10 000 random iterations of bootstrap resampling for testing the stability of ordination subspaces in the principal coordinates analysis (BPCoA, also called bootstrapped metric multi-dimensional scaling - BMDS) of chord distances of three foraging data matrices (North American, Australian, and European sites). Initializer of pseudo-random number generator was set on automatic mode (Pillar 2004). Probabilities in bold are significant at the critical value $\alpha = 0.10$. Once an axis is considered significant, all axes to the left and corresponding probabilities are ignored and those remaining to the left are considered significant. The BPCoA ordination of the first data matrix (22 species \times 26 variables) yielded the first two meaningful significantly different axes (factors). The ordination of the second data matrix (41 species \times 24 variables) did not show any significantly different axes, the pattern seems fuzzy. The same procedure revealed three meaningful significantly different axes from the third data matrix (26 species \times 38 variables).

	Number of ordination axis									
	1	2	3	4	5	6	7	8	9	10
N. American matrix 22 \times 26										
$P(\theta_i^o \geq \theta_i^*)$	0.5503	0.0953	0.4082	0.4357	0.3560	0.5313	0.4260	0.4522	0.3834	0.4856
Average of sample attribute	0.7592	0.9845	0.8935	0.8948	0.9290	0.8445	0.9107	0.9034	0.9452	0.9356
Australian matrix 41 \times 24										
$P(\theta_i^o \geq \theta_i^*)$	0.4191	0.4155	0.4016	0.5980	0.3819	0.4433	0.2917	0.5065	0.4404	0.3485
Average of sample attribute	0.8593	0.7666	0.7828	0.6539	0.8242	0.8215	0.8909	0.7686	0.8646	0.9029
European matrix 26 \times 38										
$P(\theta_i^o \geq \theta_i^*)$	0.2205	0.2854	0.0553	0.5391	0.3508	0.3475	0.3422	0.4116	0.4727	0.4859
Average of sample attribute	0.9065	0.8925	0.9735	0.7728	0.8932	0.8911	0.9167	0.8937	0.8744	0.9025

Australian site. The BPCoA of chord distances of the Australian data matrix detected a strongly intercorrelated matrix with no significant axes (Table 2). We thus applied the classical approach and tried to interpret the first four ordination axes. The interpretation of remaining axes was difficult because the loadings of variables in the BPCoA did not indicate any clear patterns. The first six ordination axes explained 74.12 % of variance (Supplement 9).

The first factor eigenvalue had a value 5.52 and explained 21.49 % of matrix variance. The first factor was interpreted as a gradient related to foraging height as indicated by the variables with the strongest negative correlation being mean foraging height, the standard deviation of foraging height, and foraging on rough-barked eucalypts, and a positive correlation coefficient with the variable probe ground. Variables describing foraging on the ground and in low vegetation strata tended to have positive correlation coefficients, while variables describing foraging on arboreal substrates had negative coefficients.

The second eigenvalue was 3.66 and explained 14.26 % of the matrix variance. This axis factor was best interpreted as being related to the spatial tree morphology related to the birds' use of substrates near to the axis (trunk, branch) of the tree versus more distal (leaf) substrates. This was evidenced by the variable glean leaf having the highest positive correlation, whereas the variables snatch trunk and snatch branch had negative correlations. However, the pattern was not very clear.

The third factor had an eigenvalue of 3.22 and explained 12.52 % of the matrix variance. The variable gleaning flowers mainly on the shrub *Waratah* had strongest negative value, while glean ground had the highest positive value. The factor seem to be related to behavioural gradient of gleaning

from various substrates. The factor separated nectar feeders from ground foragers, but also separated gleaners from snatchers and hawkers.

The score of the fourth factor eigenvalue was 2.55 and explained 9.91 % of the matrix variance. The factor was probably related to a behavioural gradient of ground foraging strategies because the variable 'glean from ground' had a strongest positive correlation, whereas the variable 'probe into ground' had a strongest negative correlation. However, both variables had weak correlation coefficients and this result needs to be interpreted cautiously.

European site. The BPCoA of chord distances of the European foraging matrix revealed three significantly different ordination axes at the threshold $\alpha = 0.10$ (Table 2). The first six ordination factors explained 89.84 % of total matrix variance, with the first three explaining 77.18 % of variance (Supplement 10).

The first factor eigenvalue was 6.17 and explained 37.42 % of the matrix variance. The variables foraging on or in litter and foraging on bare ground showed the highest positive correlations, while those describing foraging on trees and arboreal substrates had the highest negative scores. Thus this axis (factor) was interpreted as related to foraging height. The factor separated ground foragers, stream foragers, bush, and herb layer foragers from arboreal guilds.

The eigenvalue of the second factor had a score of 3.82 and explained 23.14 % of the variance. The second factor was interpreted as a gradient of arboreal substrates and airspace due to the highest positive correlation score of foraging in airspace and hawking in airspace and the highest negative correlation coefficient of variables glean from leaf and glean from twig. Most arboreal variables tended to have negative

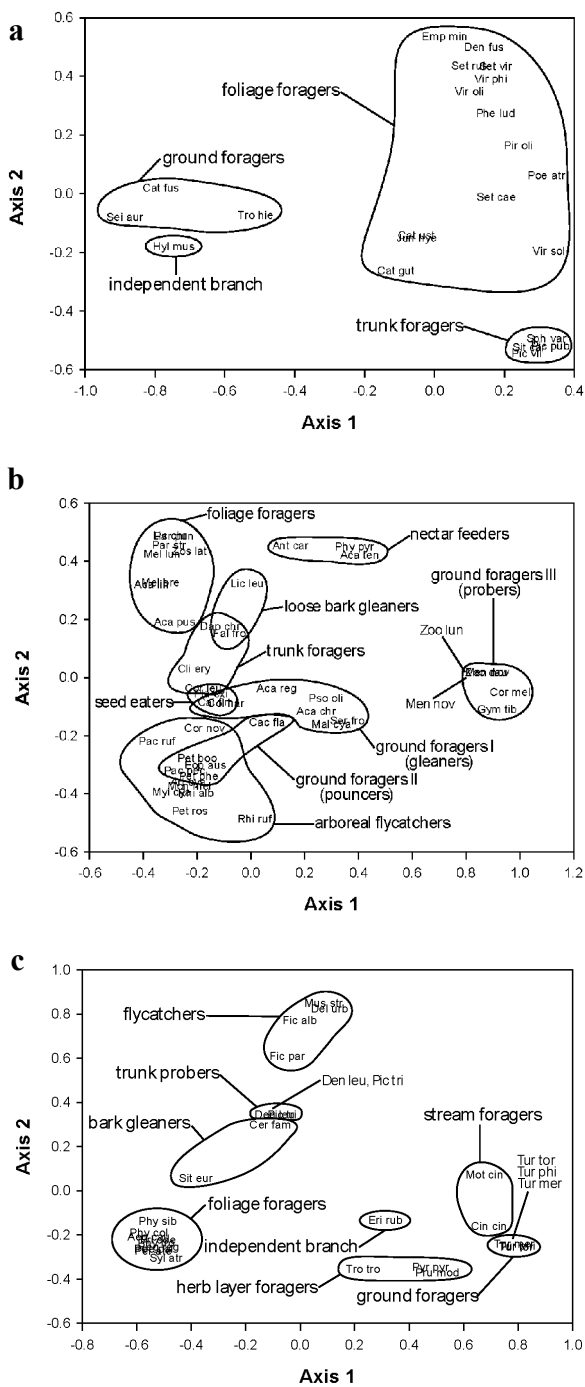


Figure 2. The bootstrapped principal coordinate analysis (BPCoA) of chord distances ordination diagrams showing major groupings (guild structure) of breeding bird assemblages of three forests: North America (a), Australia (b) and Europe (c). The details of these figures visualizing the clumped species are given in Supplementary materials (Supplement 11, a – detail on Fig. 2a (North America), b – detail on Fig. 2b (Australia), c – detail on Fig. 2c (Europe)). The guilds were determined by the bootstrapped cluster analyses (UPGMA) of chord distances (see Fig. 1). The species belonging to individual guilds are grouped into species groups and are named in concordance with the guild structure dendrograms (see Fig. 1). The key for abbreviation of Latin names, common names and full Latin names are given in Supplement 12.

correlation coefficients. The factor was therefore responsible for separating flycatchers from other arboreal guilds.

The eigenvalue of the third factor was 2.74 and explained 16.63 % of the variance. The variables related to foraging on trunk and branch had the highest positive scores, while variables describing foraging on twigs and leaves had negative scores. The factor was interpreted as the microhabitat gradient related to the spatial tree morphology reflecting the substrate gradient arrayed along the horizontal tree axes (trunk, branch, twig, and leaf). The factor separated trunk probers, bark gleaners, and foliage gleaners.

Discussion

Comparison of bird guild assemblage patterns

The following conclusions can be drawn from the above comparative analyses of guild structure of bird assemblages in three different zoogeographic regions:

1. Each assemblage has a specific guild structure that reflects the diversity of resources used by birds.
2. Partial convergence can be implied from the presence of three basic analogous guilds: ground and litter foragers, foliage foragers, and trunk foragers. This partial convergence supports, in general, the hypothesis that the selective forces, such as environmental (vegetation) structure and prey resources in these three geographically separated areas are generally similar.
3. This basic guild structure is likely to be common to bird assemblages in most forest ecosystems worldwide since it is related to the main foraging substrates characteristic of all mature forests.
4. Vertical allocation of resources (foraging height gradient) and gradient of spatial tree morphology connected to specific microhabitats spread along horizontal tree axes (trunk→branch→twig→leaf) probably play the most important role in segregation of guilds and radiation of dietary niches of forest birds.

Differences in guild patterns among sites: effect of resources and habitat characteristics

Our analyses identified differences in the number and types of guilds present in these three types of forest, which are due at least in part to the types and abundances of food resources available to birds and to habitat characteristics that influence bird foraging. The greater number of guilds in the eucalypt forest is related to the greater diversity of food resources there, compared to those in temperate forests in Nearctic and Palearctic regions. One example is the Australian nectarivore guild. Many plants that dominate Australian eucalypt forests, for instance, *Eucalyptus*, *Corymbia*, and *Banksia*, produce large quantities of flowers that provide copious quantities of nectar (Holmes and Recher 1986, Holmes

1990). This resource is utilized extensively by numerous species of meliphagid honeyeaters (Meliphagidae) and a number of other species. This resource in eucalypt forests can drive bird assemblage dynamics, as evidenced by seasonal fluxes of huge numbers of nectarivorous birds among habitats and regions (McGoldrick and MacNally 1998). Trees in northern temperate regions are mostly wind pollinated and flowers are usually small and not nectar rich; consequently there are no nectar feeding birds in European temperate forests and only one, a hummingbird *Archilochus colubris*, in temperate forests of eastern North America (Holmes 1990). Even this species, however, does not depend strongly on nectar in these forests, but takes sap oozing from trees, mostly from holes drilled by yellow-bellied sapsucker or on small insects attracted thereto (Miller and Nero 1983).

Plant exudates, other than nectar, are also available to and used by birds in the Australian forests. The carbohydrate-rich exudates of psyllid insects (lerp), sugary secretions of aphids (honeydew), and plant exudates (manna) are important food resources for honeyeaters, pardalotes, thornbills, silvereyes, and variety of other species (Recher et al. 1985, Holmes and Recher 1986, Holmes 1990, Recher and Davis 2010). Because the guilds described in the results are based on foraging methods and on utilization of foraging substrates and not on foods taken, we have not listed a “plant exudate-feeding” guild, but included these species within the foliage foraging guild.

The occurrence of yet other resources in Australian forests also provide unique feeding opportunities for foraging birds. For example, Watson et al. (2011) described that the occurrence of the hemiparasitic shrub *Exocarpos strictus* R.Br. in understory of eucalypt forests that significantly increases resource availability and multi-tropic diversity of those ecosystems. They found that eucalypt forests with *Exocarpos* support a more diverse bird assemblage. This is probably related to the availability of *Exocarpos* fruits to frugivores and omnivores, a rich arthropod fauna, better structure of habitat related to higher quality of perches for sallying and/or increased cover afforded by the low and dense foliage, and/or greater availability of arthropod prey for ground insectivores.

Another important food resource leading to a higher diversity of foraging guilds at the Australian site is the presence of large numbers and diversity of seeds. The eucalypts produce seeds in large and hard capsules, which are utilized almost exclusively by the two species of parrots (Holmes and Recher 1986), and these are available to birds throughout their breeding period. In the north temperate forests, trees produce seeds, but most are small and only become available in the autumn or winter, therefore generally not available or used by birds during the breeding period. Thus, there is no comparable food resource in the North American site and the bird assemblage there during the breeding season does not contain a seed foraging guild. In the temperate mixed forest in Europe, where firs and spruces produce seeds in cones, some of these persist into the following summer and provide

a food resource. Only two passerine species, Eurasian Siskin (*Carduelis spinus*) and Common Crossbill (*Loxia curvirostris*), however, were observed to use this resource, and they bred irregularly and in low densities (Korňan 2004). They are potentially members of a seed foraging guild. However, we have few observations of these species and they were not included in the statistical analysis. This guild of small conifer seed eaters is phylogenetically and ecomorphologically distinct from the parrots in Australia.

Exfoliating bark of forest and woodland gums at our Australian study site is another example of a foraging substrate that offer specialized foraging opportunities. The strips of peeling bark are inhabited by many species of insects and spiders that are searched for by white-eared and brown-headed honeyeaters, eastern shrike-tits, and whipbirds (Holmes and Recher 1986). The first three species utilize this foraging substrate high in the canopy, whereas the whipbird feeds for invertebrate prey among piles of fallen bark on the ground. There is no comparable foraging substrate in temperate forests of Europe and North America. Eurasian wren and its new-world ecological equivalent, winter wren, search for prey on the bark of fallen branches and boles and to this extent are similar to the above mentioned Australian birds especially the whipbird.

From our analyses, we did not identify a distinct an arboreal flycatcher guild at the North American site. Only two species of the new world flycatcher family Tyrannidae, least flycatcher and eastern wood pewee (*Contopus virens*), occurred in our northern hardwoods study site. The least flycatcher often hovered to catch insects from leaves and in the cluster analysis it was grouped in the dendrogram with the foliage gleaners. The eastern wood pewee occurs at low population densities in the study plot at Hubbard Brook (Holmes and Sherry 2001) and was not included in statistical analyses due to inadequate sample sizes. Pewees prefer open forest gaps where they typically sit on open perches and prey on flying insects (Holmes, unpubl. data). Thus, with sufficient data, the pewee would have formed an independent branch of an arboreal flycatcher in the dendrogram structure of our analysis. One other species, the American redstart (*Setophaga ruticilla*) uses flycatching maneuvers (aerial hawking) almost as often as the least flycatcher (Holmes et al. 1979). However, this parulid warbler forages more often by hovering for prey at foliage and in the analyses presented here was clustered with the foliage foragers (Fig. 1). In the European site, the arboreal flycatchers partitioned foraging space along a height gradient and were relatively well segregated (Korňan 2000). Moreover, another ecological group not included in our analyses, is one referred to as “aerial sweepers,” those species that fly above the canopy and catch prey from the air space, while swooping back and forth. At the North American site, this ecological group consisted of one species, the chimney swift (*Apus pelagica*) and at the European site, of two species, the house martin (*Delichon urbica*) and common swift (*Apus apus*) (Korňan and Adamik 2007). This ecological group was absent from the Australian site, but occurs elsewhere in Australia (Recher unpubl.).

Another notable difference between temperate forests of the Northern Hemisphere and Australian eucalypt forests is the absence of wood-probing or drilling guild in Australia. In north temperate forests, woodpeckers (Picidae) radiated into several genera and are adapted to excavate or burrowing insects from bark or dead wood. Although foraging on bark is common in Australian forests (Recher and Holmes 1985, Recher and Davis 1998), most bark-foragers there feed by gleaning, probing into crevices, tearing, and/or flaking loose bark. Some cockatoos (Psittacidae) tear wood apart to obtain wood boring beetle larvae, but no birds drill into wood as do woodpeckers in the north temperate sites.

The occurrence of species that feed specifically along or in streams was unique to the European site. There, this stream foraging guild consisted of two species, grey wagtail and white-throated dipper. Although streams also cross the study site in the Hubbard Brook and occur throughout the Hubbard Brook valley, there is no ecological equivalent of either the dipper or the wagtail. Note, however, that in western North America, there is a species of dipper (*C. mexicanus*) that does occur along forest streams and feed primarily on stream invertebrates. In Australia, there are no bird species that have specialized in foraging in or along streams.

Factors determining guild structure

The factor analysis determined two habitat gradients (vertical allocation of resources and a spatial tree morphology gradient) that occurred in all three study sites and were of importance in affecting bird foraging guild structure. In the case of Bondi Forest, these gradients were determined by a classical interpretation of axes not by bootstrapping. In the previous studies of bird assemblages (Holmes et al. 1979, Holmes and Recher 1986, Korňan and Adamik 2007), the application of classical factor analyses (PCA, CA) led to the interpretation of a relatively large number of axes (2-8) that were probably strongly intercorrelated. In the bootstrapped approach used in this study, only 0-3 axes were significantly different.

The first factor was related to the vertical allocation of resources among forest strata, which was primarily responsible for segregation of species into guilds. The hypothesis that foliage height diversity is a determinant of bird species diversity was proposed by MacArthur and MacArthur (1961) and has been widely tested (e.g., Recher 1969, Jayapal et al. 2009). The results of our study provide further support for this hypothesis that forest height and the corresponding stratification that results is important in the segregation of species into guilds and probably the diversification of species. In contrast, several studies have shown that vegetation composition is an important determinant of bird assemblage structure (e.g., Lopez and Moro 1997, Fleishmann et al. 2003, Lee and Rotenberry 2005). Finally, a combination of both physiognomy and floristics have been shown to be important (e.g., Arnold 1988, Bersier and Meyer 1994, Jayapal et al. 2009). The latter was supported by Cueto and Casenave (2000), who described significant associations between for-

est structure and insectivore guilds, and between forest composition and frugivore-insectivore guilds. An association between forest floristic diversity and a frugivore guild is further supported by the investigation of Wheelwright (1985), who detected that species with large gapes feed on greater variety of fruits than did species with small gape and that the mean size of fruits in the diet correlated with gape width. Consequently, the greater diversity of plant species producing a variety of different sized and kinds of fruits and seeds can be a determinant of greater diversity of fruit and seed consuming guilds. The results presented here only indirectly test the role of floristics in determining guild structure in avian communities. At Hubbard Brook, Holmes and Robinson (1981) and Holmes and Schultz (1988) found that birds foraged differentially among plant species, suggesting that trees of different species provide different foraging opportunities for forest birds (see below). This is also the case in Australia where birds also forage differentially among plant species whether for arthropods, nectar, lerp, or seeds (e.g., Recher et al. 1991, Recher and Davis 2011).

Tree morphology along the horizontal tree axis (trunk-branch-twig-leaf) separating species foraging on trunks and branches (bark) from those foraging more distally from twigs and foliage was the second most important factor determining guild structure. This horizontal separation seems to be an important resource allocation gradient influencing resource partitioning by birds, and probably is characteristic of all forests of mature age. Differences among bird species in resource use pattern in horizontal tree stratification in the canopy of a temperate alluvial forest in Germany was also described by Böhm and Kalko (2009).

The primary question of this study can be put in the following way: "To what extent can we generalize the conclusion of the vertical and horizontal resource gradients on other types of forests worldwide? We assume that bird assemblages of vast majority of mature forest in all climatic zones consists of this basic guild structure as indicated in the point two of the first paragraph in the discussion. We can support this assumption by large number of bird assemblage studies of forest in Eurasia and North America, where the basic bird assemblage guild structure is composed of these three guilds (*a priori* analysis). Consequently, we can assume that there existed similar factors, most likely the two common factors present in the three study plots in this study, causing this spatial pattern of guild structure and these two factors might play crucial role in segregation of bird guilds in most mature forests worldwide.

Guild structure as described in this study is primarily defined by the frequencies of use of foraging substrates and strategies by forest birds during their breeding seasons. Several studies have shown that leaf morphology and arrangement (e.g., size, shape, petiole length, distribution along branches, and elevation above twig), distance between twigs, physiognomy along vertical stratification of vegetation layers are important in influencing bird foraging behaviour, especially those that primarily glean and hover for prey among

leaves and twigs (Holmes and Robinson 1981, Robinson and Holmes 1982, Robinson and Holmes 1984, Holmes and Schultz 1988, Whelan 2001). Furthermore, canopy dwelling passerines in the North American site have been shown to exhibit distinct feeding preferences and/or aversions for foraging on specific tree species. Yellow birch was shown to be clearly preferred as a foraging site by most bird species (Holmes and Robinson 1981, Holmes and Schultz 1988). This appeared to be due to a higher density of arthropods on this tree species especially the leaf-dwelling free-living lepidopteran larvae favoured by birds, as well as to a foliage structure that facilitated the success of birds in seeing and capturing those prey (Holmes and Robinson 1981, Holmes and Schultz 1988). In the European forest, several species favoured foraging from sycamore and conifer-dwelling species from fir and spruce (Korňan 2000, Adamík et al. 2003). These findings again underline the importance of floristics and tree morphologies for influencing bird foraging and consequently bird assemblage structure.

In summary, from our analyses and discussion above, we conclude that the vertical allocation of resources, spatial tree morphology, and vegetation composition connected to species-specific plant architecture appear to be the major factors determining guild structure in the three forest bird communities investigated. Ecomorphological adaptations of birds determine how successfully a species can utilize food resources within the particular vegetation structure and physiognomy of a forest. We hypothesize that the ability of species to use resources successfully affects their demography, which in turn determines the structure and dynamics of bird assemblages. This hypothesis is in need of further testing in other forest types and environments.

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