

Interspecific foraging substrate preferences among flycatchers in a primeval mixed forest (Šrámková National Nature Reserve)

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Abstract. The study had two main objectives: (1) to analyze interspecific differences in foraging substrate utilization, foraging strategies, niche breadth, and niche overlap among the five flycatchers, and (2) to test the association between species foraging patterns on trees and the study site tree structure. The study was conducted in a primeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts., in the years 1997–2000. Species specific resource use patterns indicated their position on generalist-specialist gradient. *D. urbica* and *M. striata* showed lower values of niche breadth, but higher values of niche overlap. Foraging patterns of *E. rubecula* and *F. parva* indicated rather opportunistic use of foraging substrates. Their niche breadth reached the highest values, whereas niche overlap was generally lower in comparison to airspace specialists. Niche breadth and overlap values for *F. albicollis* tend to have more or less medium values giving this species a position somewhere between the two groups. Resource partitioning was also well distinguished by foraging height. All species showed considerable opportunism in feeding on tree species. None of the two most dominant tree species was significantly preferred. *Acer pseudoplatanus* was the most selected foraging substrate. This may be result of its relatively large leaf area, thus supporting higher numbers of insects.

Keywords: flycatchers, *Delichon urbica*, *Erithacus rubecula*, *Ficedula albicollis*, *Ficedula parva*, *Muscicapa striata*, foraging niche, niche characteristics, niche overlap, resource partitioning, vegetation structure

Introduction

Theory of resource allocation (MacArthur and Levins 1964, Levins 1968, MacArthur 1970, see Schoener 1974 for review) and limiting similarity (MacArthur and Levins 1967) assumed that species within communities compete for resources that are spread along a continuous gradient. Species segregation along this resource gradient reflects their resource requirements. The degree of segregation or level of specialization

depends on the similarity of resources and their abundance. The models predict that the extent of segregation respectively specialization should be favored if resources are abundant or totally different. In opposite, when resources are similar or are scarcely distributed, generalist strategy or opportunistic use of resources should be more advantageous.

These rather simplistic mathematical models moved significantly forward ideas concerning structure and functioning of ecological communities in the sense of competition and have influenced conceptual framework in ecology until now (Cody and Diamond 1974, Connell 1983, Schoener 1985, Stewart 1996). Currently, interspecific competition as the primary process forming the community structure has faced considerable criticism and the influence of other natural processes such as predation, parasitism, and environmental stochasticity (Tilman 1987; Faivre and Auger 1993; Richter, Oppliger, and Christe 1993) has been viewed as simultaneously important for the mechanisms of community shaping.

The main objective of this study was to analyze resource use patterns among five species of flycatchers in a primeval ecosystem. The following problems of the niche organization in the flycatcher guild were analyzed:

1. Interspecific differences in foraging substrate utilization.
2. Interspecific differences in foraging strategies.
3. Do tree foraging patterns of individual species reflect the species composition of tree layer of the studied ecosystem or are there some species specific tree species preferences?
4. Estimate species niche breadth.
5. How much do species in the guild overlap in their multidimensional foraging substrate niche?

Study area

The data were gathered in the Šrámková National Nature Reserve, the Malá Fatra Mts. The Malá Fatra Mts. lie in the north-western part of Slovakia. The investigation was conducted in a 27.5 ha (500 × 550 m) forest interior study plot representing the climax stage of a Western Carpathian beech-fir forest. The study plot is situated in the elevation 950–1200 m. The site belongs into a cold mountain climatic zone with

Tree species	Density n/ ha	Minimum density	Maximum density	Standard deviation	Standard error	Dominance %
<i>Fagus silvatica</i>	209.398	24.928	598.280	189.557	42.386	44.762
<i>Abies alba</i>	94.728	0.000	299.140	74.989	16.768	20.249
<i>Corylus avellana</i>	27.421	0.000	299.14	76.291	17.059	5.862
<i>Picea abies</i>	22.435	0.000	124.641	31.119	6.958	4.796
<i>Acer pseudoplatanus</i>	19.943	0.000	174.498	47.691	10.664	4.263
<i>Ulmus glabra</i>	13.711	0.000	99.713	27.377	6.122	2.931
<i>Sorbus aucuparia</i>	11.218	0.000	274.212	61.442	13.739	2.398
<i>Betula pendula</i>	0.182	—	—	—	—	0.039
<i>Larix decidua</i>	0.109	—	—	—	—	0.023
<i>Acer platanoides</i>	0.073	—	—	—	—	0.016
<i>Tilia cordata</i>	0.036	—	—	—	—	0.008
Standing dead trees	68.553	0.000	199.427	55.475	12.405	14.654
Sum of live trees	467.806					100.000

Table 1. The tree species diversity, density, and dominance in the beech-fir study site in the Šrámková National Nature Reserve. The measurement were carried out by 0.04 ha circular plot method ($n = 24$) following Noon (1980) and Korňan (1996). Densities of *Betula pendula*, *Larix decidua*, *Acer platanoides*, and *Tilia cordata* were estimated.

the average July air temperatures 10–12 °C. Total year precipitation varies from 900–1200 mm (Vološčuk 1986). The slope inclination is 20°–48°.

The forest is unevenaged with considerable spatial heterogeneity. The original plant species composition has been preserved. The study site is dominated (> 5 %, Table 1) by beech (*Fagus silvatica*), silver fir (*Abies alba*), Norway spruce (*Picea abies*), sycamore (*Acer pseudoplatanus*), and elm (*Ulmus glabra*) with admixture of other tree species such as rowan (*Sorbus aucuparia*), silver birch (*Betula pendula*), European larch (*Larix decidua*), maple (*Acer platanoides*), and small-leaved lime (*Tilia cordata*). Dominant tree species have strong regeneration. The canopy height is up to 45 m. The scrub layer mainly consists of hazel (*Corylus avellana*), elder (*Sambucus racemosa*), currant (*Ribes* spp.), and samplings of the dominant tree species. The herb layer is mainly composed of ferns *Dryopteris filix-mas*, *Athyrium filix-femina*, forbs *Rubus* spp., *Impatiens glandulifera*, *Senecio nemorensis*, *Oxalis acetosella*, *Galium odoratum*, *Dentaria bulbifera*, *Lunaria rediviva*, *Homogyne alpina*, grasses *Luzula nemorosa*, *Calamagrostis arundinacea*, and small scrubs *Vaccinium myrtillus*.

According to Braun-Blanquet classification, the study site belongs into the alliance *Luzulo-Fagion*, association *Abieti-Fageta*. Having followed the Zlatník forest phytosociological approach, Vološčuk (1986) defined in the reserve *Fageto-Abietum* and *Fageto-Aceretum* forest types.

Methods

Vegetation sampling

On the quantitative description of the floristics and structure of vegetation cover, the 0.04 ha circular plot method was applied. The method was originally proposed for bird-vegetation relationship studies by James and Shugart (1970) and improved by Noon (1981). The presented

sampling design is based on the Noon's (1981) approach. The original technique was slightly modified in order to include additional variables and to clarify existing ambiguities. The detail description of the sampling approach for each measured resp. estimated variable is described in Korňan (1996).

The circular plots ($r = 11.3$ m) were regularly distributed in the intersections of a rectangular grid system 100 × 100 m, so the sampling intensity was one circular plot per hectare. This sampling design is suitable for mapping variation in tree species abundance across the study site as well as to estimate their total abundance (Greenwood 1996). Totally, 24 circular plots covering the area of 0.963 ha were placed to the study site to measure tree species composition and density (Table 1). Sampling was carried out during the period from August until mid-September in 1998–99. Trees *Betula pendula*, *Larix decidua*, *Acer platanoides*, and *Tilia cordata* were very scarcely dispersed. Due to the insufficient number of circular plots to catch the presence of these species, their population densities were estimated from the area of the whole study site by visual count. These estimates can also be considered as reliable due to a very precise plot checking during bird censuses and foraging observations.

Sampling of bird foraging patterns

The bird foraging data were collected in the period 1997–2000 from the middle of May until end of July. In order to collect foraging observations, two observers crossed the study plot in random manner and observed as many different feeding birds as possible. Individuals were watched as long as they continuously remained in sight. The observations were usually carried out for a whole day. During the observations, different section of the study plot were sampled with approximately equal intensity. Each foraging observation was written to a field cards with the standardized list of foraging substrate and

movement categories (Appendix). When a foraging bird was seen, the following information were recorded to the card: species, sex, time length of observation, the time of day (CET), foraging height, foraging substrate, type of foraging movement, and direction of foraging movement whether it was in vertical or horizontal direction to the three trunk. Foraging heights were estimated by eye.

Foraging movement was defined as any directed activity whose immediate purpose was to capture a prey item. For the purposes of this study, the foraging movement classification scheme was taken from Remsen and Robinson (1990). Their proposed classification scheme is very detailed, however its application for a study on the community level would give an extremely large data matrix containing high proportion of zero values, thus could cause a serious problems to further statistical analyses. Therefore, the considerable reduction of attack categories was necessary. Attack categories resp. foraging movements were divided into four main types: gleaning, hovering, sallying (hawking), and probing (pecking). Gleaning (included reach, hang, lunge) is a foraging tactics when a stationary prey item is taken from the surface of a nearby substrate by perching or hopping bird. Hovering (included sally-hover, sally-stall) is picking an exposed prey from a substrate by actively flying bird similarly as a hummingbird feeds on nectar from a flower. Sallying (included leap, sally-strike, sally-glide, sally-pounce, flutter-chase, flush-pursue, hawk) is flying from an observation perch to attack a food item usually in longer distance and then returning to a perch. Probing (included peck, hammer) is a maneuver when the bird inserts the bill into the substrate to catch a subsurface prey item. The attack is directed at food that is invisible from the surface without substrate manipulation. Unfortunately, it was impossible to determine by sight the caught prey item, or to distinguish successful from unsuccessful attacks. Consequently, all observations indicate only foraging maneuvers regardless their prey catching efficiency.

The data matrix consists of four variables indicating foraging heights, sixteen foraging substrate variables, eighteen variables reflecting type of foraging movement, and two variables indicating direction of foraging movements.

Even though, the number of studies have showed significant intraspecific, seasonal, yearly, etc. variation in foraging behavior (e.g. Hejl and

Verner 1990, Sakai and Noon 1990), none of these aspects is analyzed in the present paper and will be subjected to future studies. For the purpose of this study, the only pooled data for all individuals of each species collected in the period 1997–2000 were used in the further analyses.

Statistical analyses

Flycatcher guild determination Foraging guild structure of the primeval forest was determined by the posteriori approach (Wiens 1989). A data matrix 25 species \times 39 variables describing foraging behavior, substrates, and heights (Appendix) were analyzed by multivariate statistical procedures such as hierarchical cluster analysis and correspondence analysis in order to illustrate guild structure. Multivariate statistical procedures revealed a pattern representing five guilds: foliage gleaners, flycatchers, ground foragers, bark foragers, and stream foragers. The guild of flycatchers contained five species: *Delichon urbica*, *Erithacus rubecula*, *Ficedula albicollis*, *Ficedula parva*, and *Muscicapa striata*. The flycatcher guild was primarily distinguished by higher use of sally foraging strategy and airspace foraging substrate in comparison to the other guild members (Korňan and Adamik in press).

Niche breadth Foraging substrate niche breadth was estimated from the collected data by using the Levins' index (Feinsinger, Spears, and Poole 1981):

$$B_n = 1 / R \sum_i p_i^2$$

where B_n is Levins' measure of niche breadth, p_i is the proportion of i items, out of all resource categories. Values of the index ranges from $1/R$, when the population uses one resource state exclusively (here foraging substrates), to 1.0, when population uses all available resources in equal proportion.

Niche overlap The niche overlaps of the species pairs were calculated by the following equation (Hurlbert 1978):

$$C_{xy} = 1 - \frac{1}{2} \left(\sum_i |p_{xi} - p_{yi}| \right) = \sum_i \min(p_{xi}, p_{yi})$$

where $p_{xi} = x_i/X$ and $p_{yi} = y_i/Y$; x_i is the number of i items used by population of species x , out of all resource categories (X) used by the

Species	Number and total time (s) of observations	Mean abundance (pairs/ plot)	SD of abundance	Dominance (%)	Mean foraging height (m)	SD of foraging height
<i>Erithacus rubecula</i>	81 (698)	13.60	2.99	8.72	2.83	3.72
<i>Delichon urbica</i>	324 (2800)	—	—	—	76.64	35.44
<i>Ficedula albicollis</i>	107 (531)	6.57	1.13	4.21	16.71	7.24
<i>Ficedula parva</i>	154 (661)	2.00	1.38	1.28	6.54	6.24
<i>Muscicapa striata</i>	75 (730)	3.27	0.00	2.09	18.65	7.34

Table 2. The total number and time of observations, abundance and foraging height of five species belonging to flycatcher guild. The census data were gathered by territory mapping method in the period 1997–99.

population, y_i is the number of i items used by population of species y , out of all resource categories (Y). This measure of overlap ranges from 0 (no overlap) to 1 (complete overlap). The index was calculated for every possible pair of individual species.

Statistical tests Between species and pairwise comparisons in use of foraging substrates and movements were statistically tested by Yates chi-square test and Fisher's exact test (FET). All computations were performed on PC statistical package NCSS 97 (Hintze 1997).

Results

Interspecific differences in substrate utilization

Interspecific foraging substrate preferences were illustrated on the proportional use of 14 types of foraging substrates (Fig. 1). For easier interpretation, variables describing foraging affinities to individual tree parts were analyzed separately. The number of used substrates and relative proportion of individual items significantly varied between species.

Delichon urbica used to feed only in the air. Similarly, *Muscicapa striata* significantly preferred air feeding (FET, $P < 0.001$), however it occasionally used to feed on all dominant tree species. Use of other substrates can be considered very rare and probably accidental. *F. albicollis* primarily foraged on the trees and in the air, neither trees nor air foraging was preferred (FET, $P < 0.553$). Few attacks were also seen on litter. In comparison to the above mentioned species, *Ficedula parva* and *Erithacus rubecula* used very large scale of foraging substrates. Both used resources in a very generalist manner. *F. parva* was observed to feed practically on all substrates except rocks (Fig. 1). It preferred to feed on live (55.93 %) and dead trees (5.08 %), ground (6.78 %), and air (31.51 %). *F. parva* favored feeding on trees (pooled data for all species) to any other substrate (pairwise comparisons, FET, $P < 0.02$). *E. rubecula* used less foraging substrate types,

yet their use, on the other hand, was much more even. This slight differences might have been caused by different sample sizes (Table 2). *E. rubecula* favored feeding mainly on trees (55.74 %), bare ground (24.59 %), and litter (6.56 %). It preferred feeding on live trees (pooled data for all species) to other substrates (FET, $P < 0.02$).

Tree space utilization In order to show how individual species differ in the utilization of tree microsites, a tree space was divided into four parts: trunk, branch, twig, and leaf (Fig. 2). *D. urbica* was excluded from the further analyses because it exclusively foraged in airspace. *M. striata* as the second highest airspace specialist foraged on all tree parts. However, it significantly did not prefer any tree parts (pairwise comparisons, FET). Also, *E. rubecula* did not show affinity to utilize any particular tree part. *F. albicollis* significantly more frequently foraged on leaves (47.22 %) than on trunk (13.89 %) and branches (11.11 %), but no further differences were found in pairwise comparisons to the other tree parts. *F. parva* also preferred leaves to any other tree parts (FET, $P < 0.001$). Similarly to the last species, any further significant differences were not detected.

Opportunism versus specialization

In order to analyze whether individual species tend to selectively forage on certain type of tree species, the pairwise comparisons between foraging proportions on trees and the occurrence of tree species were conducted for each species (Table 3). Data on the structure of tree layer were gathered from circular plot sampling (Table 1).

In general, all tested flycatchers showed more or less opportunistic use of resources at least in consideration to tree layer of the forest structure. The main dominant tree species, *Fagus sylvatica* and *Abies alba*, were not selectively utilized by any species (Table 3), so they were utilized in comparable frequencies to their occurrence. *E. rubecula* (FET, $P < 0.01$) and *F. parva* (FET, $P < 0.05$) showed significant association with *Picea abies*. *Acer pseudoplatanus* showed the

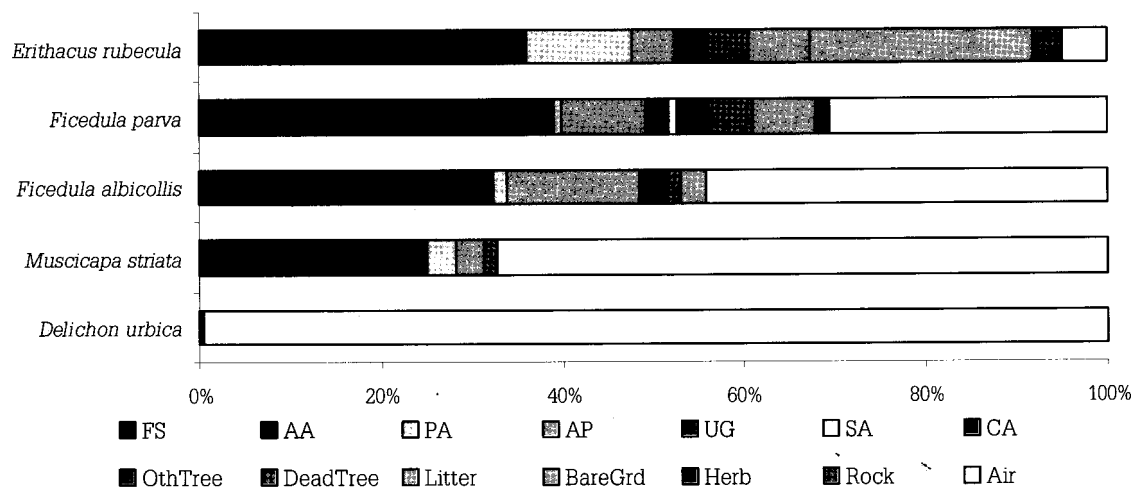


Fig. 1. The foraging substrate preferences between 5 flycatchers in the primeval beech-fir forest. 14 substrate variables were selected to illustrate the substrate utilization patterns. See Appendix for explanations.

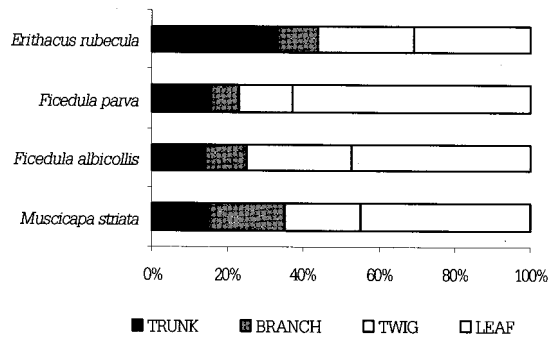


Fig. 2. The preference of tree parts by the five species of flycatcher guild. *D. urbica* as an airspace specialist was excluded from comparisons.

highest level of foraging association. It was preferred by three species: *F. parva*, *F. albicollis*, and *M. striata*. Conversely, *Corylus avellana* was avoided by *F. parva* (FET, $P < 0.01$) and *F. albicollis* (FET, $P < 0.05$). Also, standing dead trees were selected in lower frequency than their occurrence by *F. parva* (FET, $P < 0.01$). There are several other examples of significant associations, however they have to be very carefully interpreted due to the low sample sizes especially when the number of observations undergo critical level of five. Consequently, significant relationships are questionable for the association patterns with rare tree species.

Interspecific foraging movement differences

Foraging movement patterns among species in flycatcher guild considerably varied (Fig. 3), but indicated ecological adaptations on foraging substrates. Specialist foragers such as *D. urbica* and *M. striata* used sallying strategy more frequently than the other three species. There were no significant differences between sally frequencies for these two species (FET, $P < 0.842$). Also, no significant differences in sally frequency were detected between *D. urbica* and *F. albicollis* (FET, $P < 0.307$). *D. urbica* used sallying more frequently than *F. parva* (FET, $P < 0.01$) and, also, *Erithacus rubecula* (FET, $P < 0.01$). However there were no differences between *M. striata* and *F. parva* (FET, $P < 0.122$), but there were be-

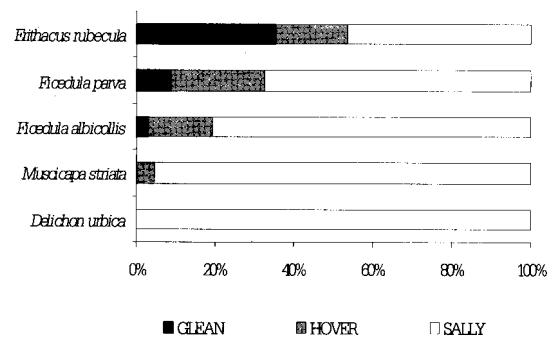


Fig. 3. Interspecific differences in the utilization of foraging strategies between five flycatchers.

tween *M. striata* and *E. rubecula* (FET, $P < 0.01$). No differences were between *M. striata* and *F. albicollis* (FET, $P < 0.528$) and *F. parva* and *E. rubecula* (FET, $P < 0.197$). *F. albicollis* sallied more frequently than *E. rubecula* (FET, $P < 0.05$). No differences were found between species of the genus *Ficedula* (FET, $P < 0.495$).

In general, gleaning and hovering are typical foraging movements for insectivorous foliage gleaning birds such as tits, warblers, and crests. Nevertheless, from the obtained foraging pattern (Fig. 3), it is obvious that these strategies were commonly used by *E. rubecula* and *F. parva*, less by *F. albicollis*, but very rarely by *M. striata*. In fact, *M. striata* was never observed gleaning. No significant difference between frequency of gleaning and hovering was detected for *E. rubecula* (FET, $P < 0.162$), yet *F. parva* (FET, $P < 0.01$) and *F. albicollis* (FAT, $P < 0.02$) used hovering more frequently. No significant differences were found between *Ficedula* species for both strategies (pairwise comparisons, FET). *E. rubecula* used significantly more gleaning than *F. parva* (FET, $P < 0.01$) and *F. albicollis* (FET, $P < 0.01$), whereas there were no interspecific differences between hovering frequencies among these species.

Niche breadth

Totally, 44 foraging substrates indicating the main structural components and specifics of the beech-fir habitat were used for calculation of

Foraging tree type	<i>Delichon urbica</i>	<i>Erithacus rubecula</i>	<i>Ficedula albicollis</i>	<i>Ficedula parva</i>	<i>Muscicapa striata</i>
<i>Fagus silvatica</i>	—	NS	NS	NS	NS
<i>Abies alba</i>	—	NS	NS	NS	NS
<i>Corylus avellana</i>	—	NS	1.450***	1.525*	NS
<i>Picea abies</i>	—	3.201***	NS	1.280*	NS
<i>Acer pseudoplatanus</i>	—	NS	-4.973***	-3.408***	-1.131*
<i>Ulmus glabra</i>	—	1.040*	NS	NS	NS
<i>Sorbus aucuparia</i>	—	0.941**	0.928**	NS	0.692**
Other live tree species	—	-4.409***	NS	-3.991***	0.131*
Standing dead trees	—	NS	NS	1.286*	NS

Table 3. Pairwise comparisons between foraging proportions on tree species and relative proportion (dominance) of trees occurrence in the study plot. The results of Fisher's exact test are indicated in the table. Z-values of normal approximations are also given. Results of both testing procedures were consistent (* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$, NS - nonsignificant).

niche breadth. Niche breadth values for individual species are presented in Table 4. Out of all species, *E. rubecula* had the widest niche breadth ($B_n = 0.24$). It foraged on 23 substrates representing 52.27 % of the total number of foraging substrates. Even though, *F. parva* totally used the highest number of substrate items (26) representing 59.09 %, its niche breadth 0.19 was lower in comparison to *E. rubecula*. *F. albicollis* as a syngenic species, however, had much lower value 0.10. It used only 15 (34.09 %) foraging substrate types. Highly specialized species on airspace foraging, *M. striata* and *D. urbica*, showed the lowest niche breadth values 0.05 and 0.02 resp. In fact, *D. urbica* was observed to feed only in airspace, thus his niche breadth value reflected one item proportion.

Niche breadth values are very good indicators of foraging specialization of the five flycatcher species. *E. rubecula* and *F. parva* can be characterized from the resource use tactics as generalists, both species used relatively wide range of foraging substrates and feed in pretty much opportunistic manner. Relative proportion of airspace foraging for both species is relatively low. *E. rubecula* foraged in airspace only in 4.41 % out of all observations, whereas in the case of *F. parva*, it was 26.47 %. Conversely, *M. striata* and *D. urbica* representing two specialized species stay on the opposite site of resource use tactics. *M. striata* used airspace substrate (67.19 %) significantly higher compared to any other substrate (pairwise comparisons, FET, $P < 0.001$).

Niche overlap

Niche overlap values between species pairs can be considered relatively low (Table 4) indicating efficient resource partitioning mechanisms within the guild. The higher overlap values than 0.5 were found only for three pairs of species *D. urbica* – *M. striata*, *M. striata* – *F. albicollis*, and *F. albicollis* – *F. parva*. Results indicates that even airspace specialist, *D. urbica* and *M. striata*, had relatively low overlap, thus theoretically speaking, competition for food resources would be low if any. Moreover, their foraging space was very well distinguished by foraging heights (Table 2). Similarly, foraging heights between syngenic *Ficedula* species were well divided. *F. albicollis* favored foraging in upper strata, while *F. parva* preferred foraging in lower strata.

Generalists, *F. parva* and *E. rubecula*, using wide range of foraging substrates had lower overlap values then 0.5.

Discussion

The very principal question raising from the primary objectives of this study is: what species can be considered as specialist and what as generalist? A concept dietary specialization is influenced by all aspects of species life history: niche requirements, ecomorphological adaptations, optimal foraging, and phylogeny. There are several possible ways how to answer these question depending on the objectives of a particular study. Sherry (1990) distinguished two approaches: (1) ecological (tactical) and (2) evolutionary (strategic). The ecological approach emphasizes short-term responses of individual organisms to resource availability and abundance, while the evolutionary approach is based on long-term, genetically based constraints and adaptations of consumers to patterns in the predictability of resources in space and time. In practice, several examples showed that these to approaches may offer opposite conclusions (Sherry 1990). For example, a neotropical flycatcher *Nesotruccus ridgwayi* (Tyrannidae) is ecological generalist, yet specialist from the evolutionary aspect. Generally, neotropical flycatchers are dietary specialists in comparisons to temperate species from evolutionary aspect, however, these two groups do not differ from the ecological view point. Paleotropical and neotropical migratory flycatchers have to be adapted to very wide range of ecological conditions in order to survive migration. Through the year, they occupy a very broad range of ecological conditions, thus have to be adapted to the wide range of ecological factors e.g. breeding versus wintering grounds where they utilize different food resources and interact with different residents. Consequently, from strategic aspect generalist strategy can be evolutionary favored for migratory flycatchers. Why resident tropical species are also generalist remained unclear. The results are very controversial, for instance, Sherry (1984) argues that the differences are raising from taxonomically broad, but ecologically homogeneous diet.

For the purposes of this study, a specialist is a species that uses a narrow range of resources, whereas a generalist uses a broader range of

Species pair	<i>Delichon urbica</i>	<i>Erithacus rubecula</i>	<i>Ficedula albicollis</i>	<i>Ficedula parva</i>	<i>Muscicapa striata</i>
Niche breadth (B_n)	0.02	0.24	0.10	0.19	0.05
<i>Delichon urbica</i>	1.00	0.04	0.43	0.26	0.67
<i>Erithacus rubecula</i>	0.04	1.00	0.35	0.46	0.30
<i>Ficedula albicollis</i>	0.43	0.35	1.00	0.53	0.63
<i>Ficedula parva</i>	0.26	0.46	0.53	1.00	0.48
<i>Muscicapa striata</i>	0.67	0.30	0.63	0.48	1.00

Table 4. Niche breadth and pairwise niche overlap values for the five species of flycatchers. The index calculations were based on 44 variables representing foraging substrates (niche dimensions).

resources (Recher 1990). Nonetheless, this definition can be applied only in exactly defined temporal and spatial conditions. Resource use patterns among the studied flycatchers indicated their position on generalist-specialist gradient. *D. urbica* and *M. striata* utilized lower number of foraging substrates, thus they had lower values of niche breadth, but higher values of niche overlap in comparison to the generalist. Analyses of foraging patterns for *E. rubecula* and *F. parva* indicated rather opportunistic use of foraging substrates. Their niche breadth values reached the highest values, whereas niche overlap was generally lower in comparison to airspace specialists. Niche breadth and overlap values for *F. albicollis* tend to have more or less medium values giving this species a position somewhere between the two groups. Resource partitioning was also very well distinguished by the mean foraging height and its standard deviation.

All species showed considerable opportunism in feeding on tree species. None of the two dominant tree species was significantly preferred by any species. *A. pseudoplatanus* was the most selected foraging substrate. It was favored by *F. parva*, *F. albicollis*, and *M. striata*. This may be result of its relatively large leaf area, thus higher number of insects species can occur on its large leaves. *E. rubecula* and *F. parva* showed significant association with *Picea abies*. In contrast, *Corylus avellana* was avoided by *F. parva* and *F. albicollis*. Also, standing dead trees were selected in lower frequency than their occurrence by *F. parva*. Further studies on mentioned association patterns could give clearer answers on their origin whether it is caused by some ecological phenomena or it is only an effect of small or non-random data set.

The models of resource allocation (MacArthur and Levins 1964, Levins 1968, MacArthur 1970) can, however, be interpreted in other possible ways for specific resource use patterns (see Introduction). For instance, if species are specialized on a certain resource type, more species should be able to co-exist, and thus community diversity should increase. In a community where a generalist would dominate the available resources, there would be much lower probability for co-existence and the species diversity would decline. Nevertheless, the outcomes of models were not very strict, so discussions about other alternative outcomes gave further very valuable inside into the resource partitioning schemes. For example, species diversity would increase even in a community dominated by generalists if overlap among species in the resource use was possible. This specific event may occur in the situation when resources are very abundant compared to species life requirement or other factors such as environmental stochasticity, predation, parasitism, etc. would lower the effects of competition so that one species would not be capable to outcompete another.

The last case seems to elegantly fit the resource partitioning pattern in the studied primeval beech-fir ecosystem. Food availability for birds in the ecosystem probably overcomes life requirements of majority of species in any year.

This assumption can be supported by very low variations in population abundances in the bird assemblage between year of caterpillar outbreak and normal years (unpublished data). In the caterpillar outbreak year several species e.g. *P. ater* were feeding more frequently on beech leaves, which were the main feeding substrate for caterpillars during the outbreak period, then in normal years when it favored conifers. This facts underline strong foraging opportunism even for some specialized species, thus supporting view that probably majority of species utilize food what is currently the most available and accessible to their ecomorphological adaptations. Primeval ecosystem in general have very complex food web dynamics, therefore, even in the year when abundance of "optimal" food items is low species are capable to switch on less suitable food types. Consequently, mechanisms of inter-specific competition do not seem to play the dominant role in shaping structure of primeval ecosystems at least of this particular type. Similar results were reported from long-term studies of bird community dynamics in the Białowieża National Park in Poland (Tomiałojc and Wesolowski 1994).

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Variable	Variable description	Measurement unit
1. HeightMin	Minimal foraging height during a single foraging observation	meter (m)
2. HeightMax	Maximal foraging height during a single foraging observation	meter (m)
3. HeightAver	Average foraging height during a single foraging observation	meter (m)
4. FS	Foraging maneuver on beech <i>Fagus sylvatica</i>	presence/ absence (1, 0)
5. AA	Foraging maneuver on silver fir <i>Abies alba</i>	presence/ absence (1, 0)
6. PA	Foraging maneuver on Norway spruce <i>Picea abies</i>	presence/ absence (1, 0)
7. AP	Foraging maneuver on sycamore <i>Acer pseudoplatanus</i>	presence/ absence (1, 0)
8. UG	Foraging maneuver on elm <i>Ulmus glabra</i>	presence/ absence (1, 0)
9. SA	Foraging maneuver on rowan <i>Sorbus aucuparia</i>	presence/ absence (1, 0)
10. CA	Foraging maneuver on hazel <i>Corylus avellana</i>	presence/ absence (1, 0)
11. OthTree	Foraging maneuver on other live tree species	presence/ absence (1, 0)
12. Litter	Foraging maneuver on litter	presence/ absence (1, 0)
13. BareGrd	Foraging maneuver on bare ground	presence/ absence (1, 0)
14. Herb	Foraging maneuver on herb layer	presence/ absence (1, 0)
15. DeadTree	Foraging maneuver on dead standing tree	presence/ absence (1, 0)
16. FallTree	Foraging maneuver on fallen dead tree	presence/ absence (1, 0)
17. Water	Foraging maneuver on or in water	presence/ absence (1, 0)
18. Rock	Foraging maneuver on rock	presence/ absence (1, 0)
19. Air	Foraging maneuver in airspace	presence/ absence (1, 0)
20. Hor	Foraging movement in horizontal direction	presence/ absence (1, 0)
21. Ver	Foraging movement in vertical direction	presence/ absence (1, 0)
22. GTrunk	Glean from trunk	presence/ absence (1, 0)
23. GLeaf	Glean from leaf	presence/ absence (1, 0)
24. GBranch	Glean from branch*	presence/ absence (1, 0)
25. GTwig	Glean from twig**	presence/ absence (1, 0)
26. GLEAN	Glean in combination with other foraging substrate	presence/ absence (1, 0)
27. HTrunk	Hover at trunk	presence/ absence (1, 0)
28. HLeaf	Hover at leaf	presence/ absence (1, 0)
29. HBranch	Hover at branch*	presence/ absence (1, 0)
30. HTwig	Hover at twig**	presence/ absence (1, 0)
31. HOVER	Hover in combination with other foraging substrate	presence/ absence (1, 0)
32. PTrunk	Probe or peck into trunk	presence/ absence (1, 0)
33. PBranch	Probe or peck into branch*	presence/ absence (1, 0)
34. PROBE	Probe or peck into other foraging substrate	presence/ absence (1, 0)
35. HwTrunk	Hawk or sally to trunk	presence/ absence (1, 0)
36. HwLeaf	Hawk or sally to leaf	presence/ absence (1, 0)
37. HwBranch	Hawk or sally to branch*	presence/ absence (1, 0)
38. HwTwig	Hawk or sally to twig**	presence/ absence (1, 0)
39. HAWK	Hawk or sally in combination with other substrate (usually air)	presence/ absence (1, 0)

Appendix. List and characteristics of used variables of foraging substrates and movements with the indication of measurement units (* branches are understood as the main branches growing from the tree trunk, ** twigs are understood as smaller branches growing from the main branches).