

# **Dlhodobý výskum štruktúry, organizácie a dynamiky ornitocenózy západokarpatského horského zmiešaného pralesa**

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# História dlhodobých výskumov vtáčích zoskupení vo svete

Charles Kendeigh – stredo-východný Illinois, USA – cenzus ornitocenózy javorovo-brestovcovo-jaseňového lesa Wiliama Treleasea, 1924–1976

Anders Enemar – Údolie vtáčieho spevu, provincia Skania, Švédsko – cenzus ornitocenózy dubovo-jaseňového mozaikového lesa, 1953-súčasnosť

Anders Enemar – LUVRE projekt, oblasť Ammarnäs v Laponsku, Švédsko – cenzus ornitocenózy subalpínskeho brezového pralesa a alpínskych vresovísk, 1963-súčasnosť

Richard T. Holmes – Hubbard Brook Ecosystem Study v New Hampshire, USA – cenzus ornitocenózy sekundárneho bukovo-javorovo-brezového lesa, 1969-súčasnosť

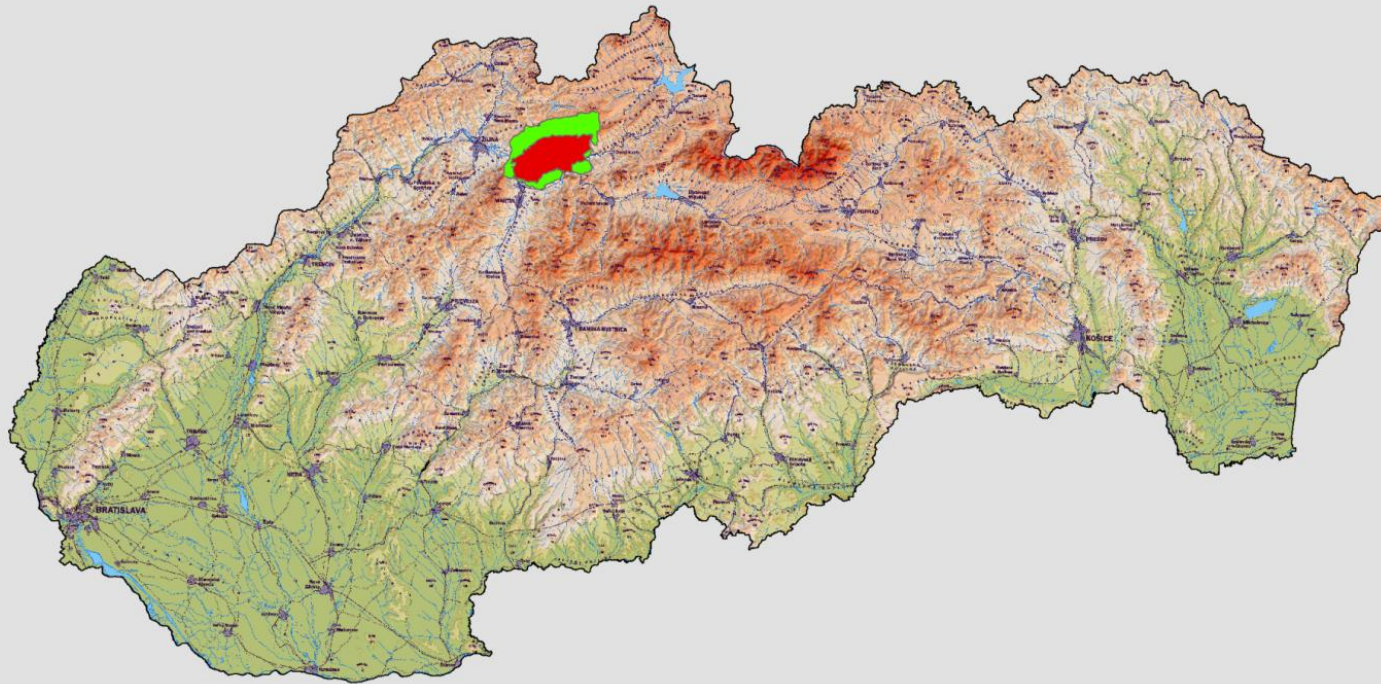
Ludwig Tomiałojć – Białowiezský národný park, Poľsko – cenzus ornitocenóz 7 monitorovacích plôch v rôznych typoch listnatých a zmiešaných pralesov, 1975-súčasnosť

# Ciele výskumu

## Dlhodobý 20-ročný (1997-2016) výskum ornitocenózy

1. Druhovú štruktúru, populačné hustoty, druhovú bohatosť, diverzitu, vyrovnanosť v dvoch rezerváciách
2. Štruktúra potravných a hniezdnych gíld a migračných zoskupení
3. Dynamika populácií, gíld a ornitocenózy
4. Druhovú asociáciu na úrovni spoločenstva, gíld a druhových párov
5. Kompetičná teória a kompenzačná dynamika
6. Rozdeľovanie zdrojov, šírka substrátových ník a stromové preferencie
7. Zhodnotenie apriórnych a posteriórnych prístupov determinácie gíld
8. Aplikácie pre manažment lesov, vtákov a prírody

# Geografická poloha študijnej plochy



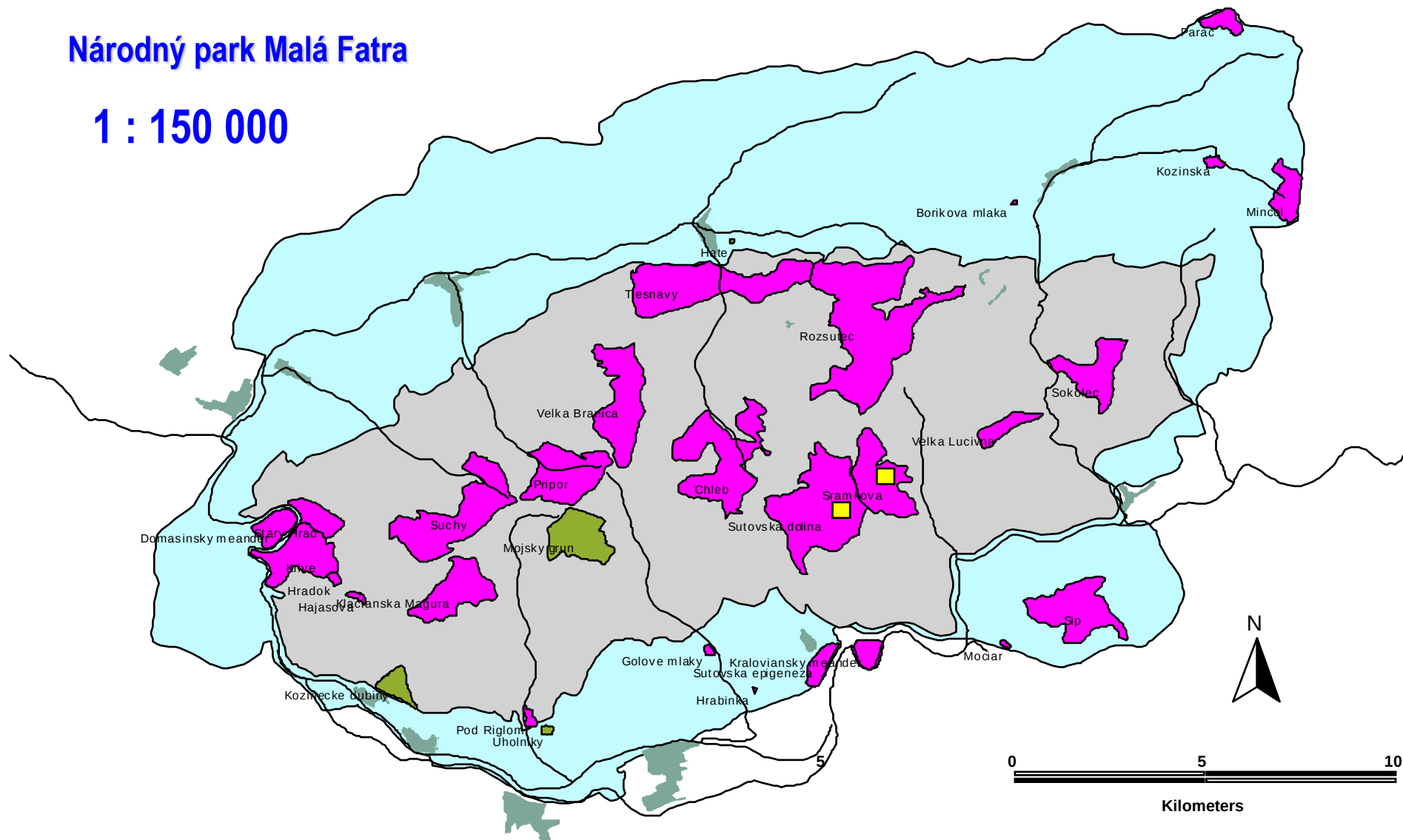
 Jadrová zóna Národného parku Malá Fatra

 Ochranné pásmo Národného parku Malá Fatra

# GEOGRAFICKÁ POLOHA MONITOROVACEJ PLOCHY

Národný park Malá Fatra

1 : 150 000



# Charakteristika študijnej plochy

## (Národná prírodná rezervácia Šrámková)

### 1. Geografická poloha

- Severozápadné Slovensko, Národný park Malá Fatra
- situovaná v doline Bystrička, nadmorská výška plochy 950–1123 m
- juhovýchodná až južná orientácia, sklonitosť 20°–48°
- mierne chladné až chladné podnebie, ročný úhrn žrážok 900–1000 mm

### 2. Charakteristika študijného kvadrátu

- 27,5 ha lesný interiér (500 × 550 m); 11,3 % rozlohy rezervácie
- modelový príklad západokarpatského zmiešaného pralesa na žulovom podloží
- vek stromov do 250–300 rokov, výška porastu do 45 m
- zväz *Luzulo-Fagion*, asociácia *Abieti-Fageta* v zmysle Braun-Blanquet klasifikácie
- dominantné stromy : buk lesný (*Fagus sylvatica*), jedľa biela (*Abies alba*), smrek obyčajný (*Picea abies*) a javor horský (*Acer pseudoplatanus*)

# Interiér NPR Šrámková: aprílový a júnový aspekt



# Interiér NPR Šrámková



# Interiér NPR Šrámková



# Metodika výskumu

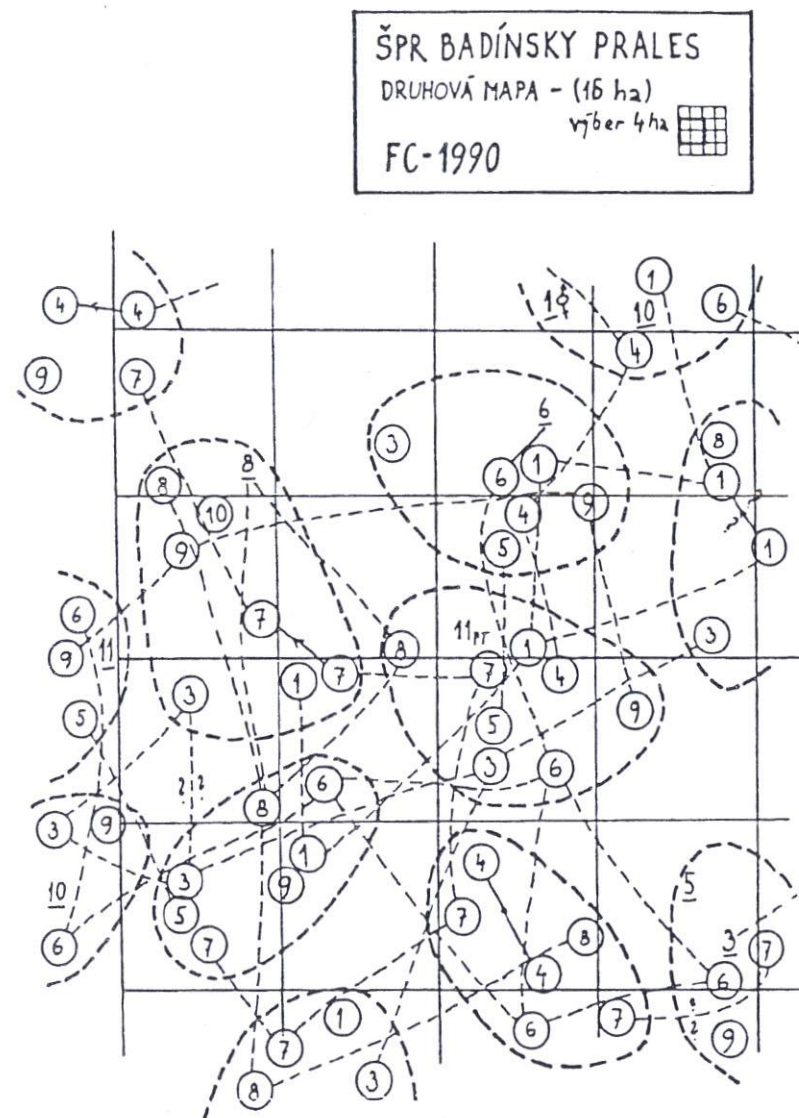
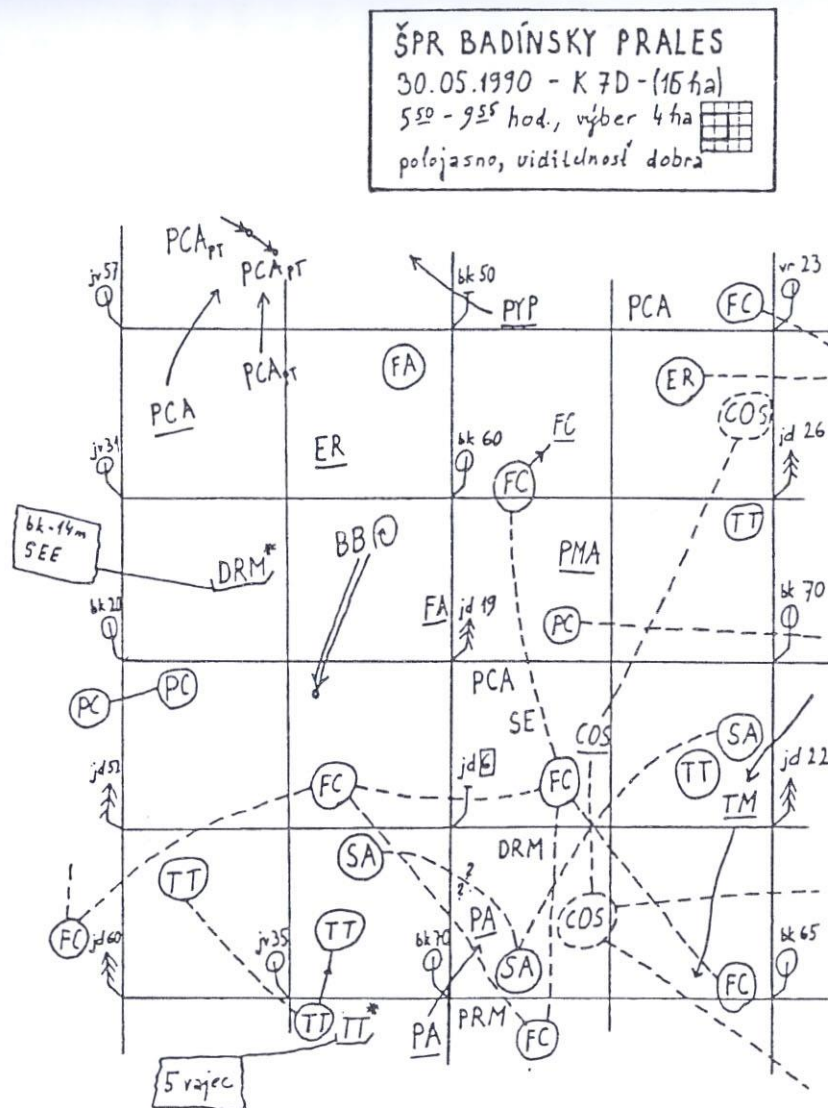
## 1. Kvantitatívny výskum ornitocenózy

- kombinovaná (zlepšená) verzia mapovacej metódy
- štvorcová sieť  $50 \times 50$  m s farebným vyznačením hraničných stromov
- vyhľadávanie hniezd a druhovo orientovaný prístup pri snímkaní
- obdobie snímkovania: apríl–polovica júla
- 10–11 snímkov; ranné (4:30–10:00), večerné (16:00–19:30) a nočné (19:00–22:00)

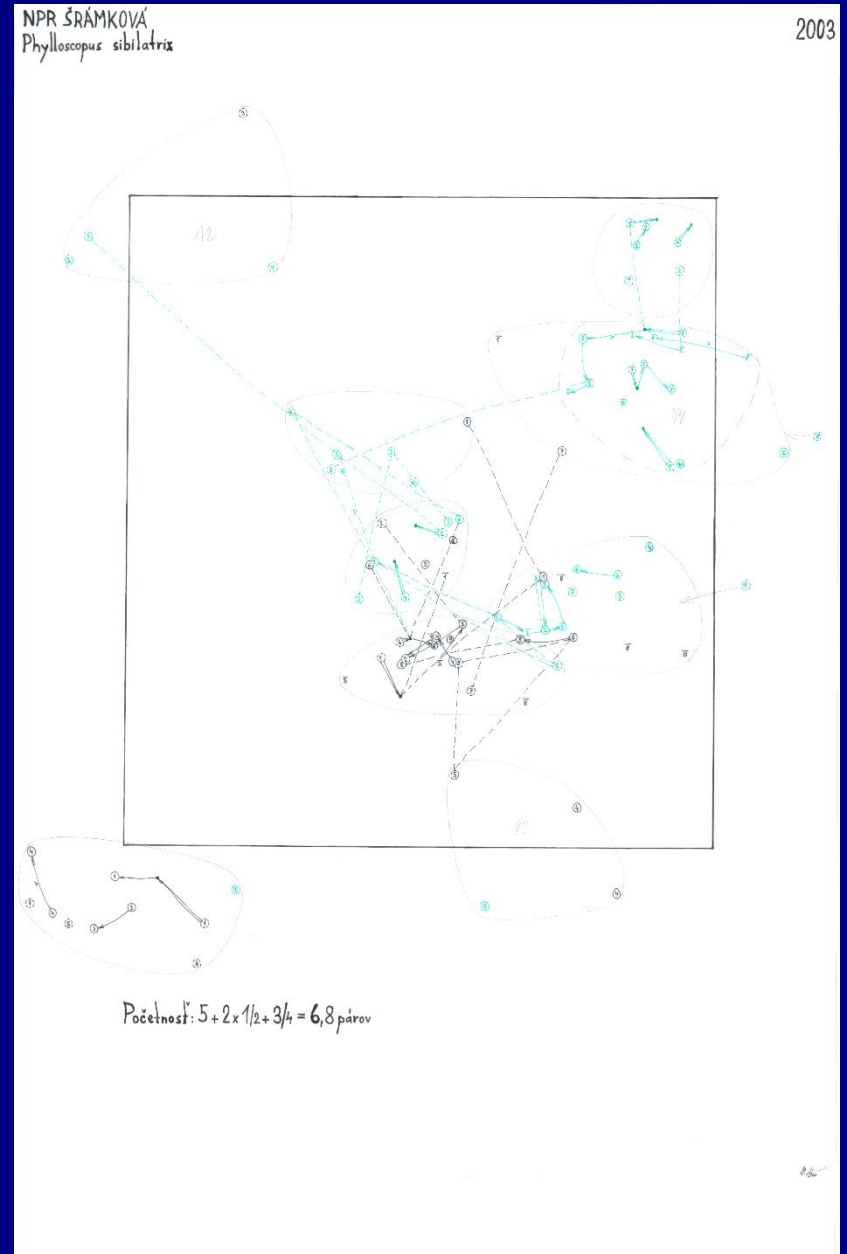
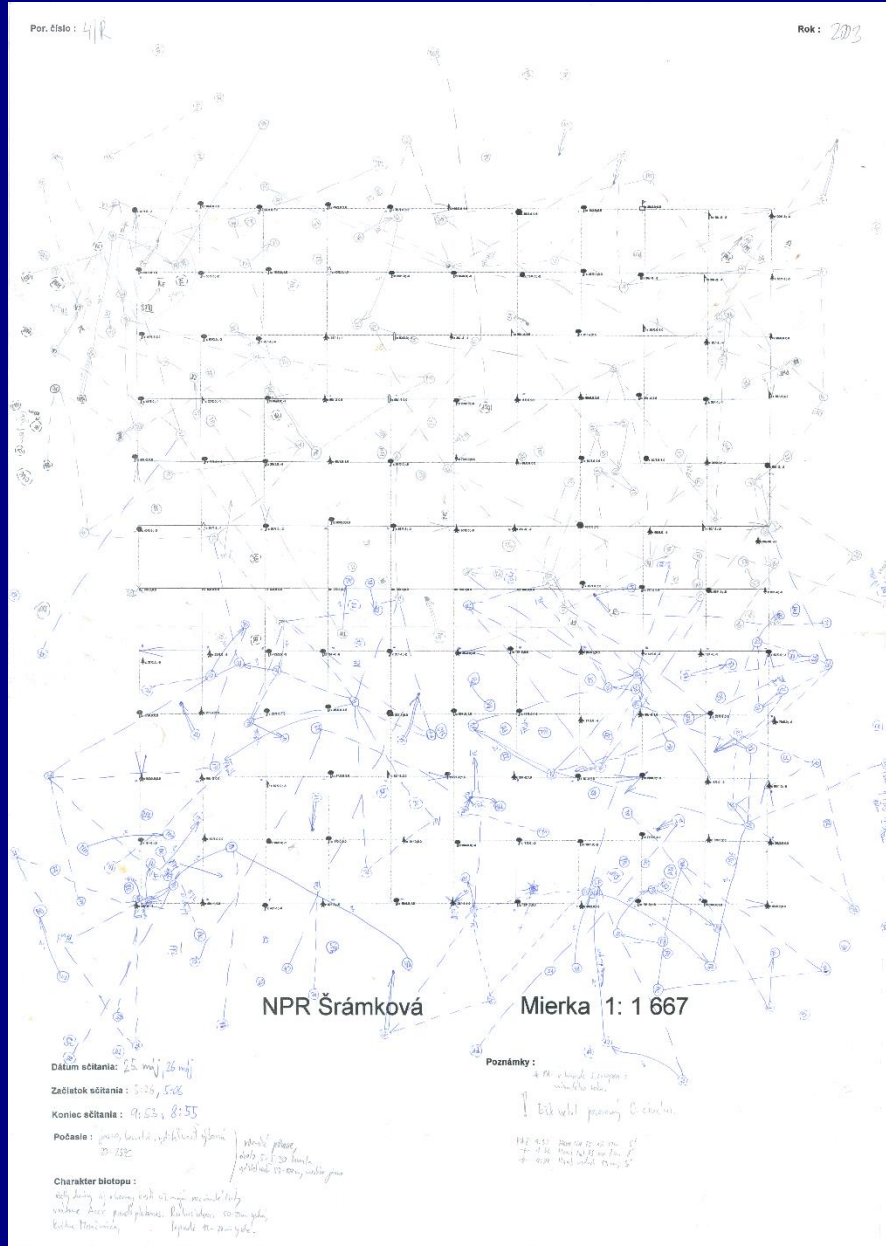
## 2. Vegetačné snímkovanie

- metóda kruhových plôch s polomerom 11,3 m ( $n = 51$ ; plocha 2,05 ha)
- pravidelné snímkovanie v priesečníkoch štvorcovej siete – 1 plocha/ ha
- náhodné snímkovanie v celej rezervácii
- floristické a štrukturálne premenné

# Príklad použitia mapovacej metódy



# Príklad snímkovej a druhovej mapy



# Vegetačná charakteristika plochy

## (Národná prírodná rezervácia Šrámková)

Metóda kruhových plôch s polomerom 11,3 m (n = 51; celková plocha snímkovania 2,05 ha)

| SPECIES                    | Abundancia (n) | Dominancia (%) | Hustota (ex./ha) | Výška (m) | n (Výška) |
|----------------------------|----------------|----------------|------------------|-----------|-----------|
| <i>Fagus sylvatica</i>     | 403            | 43,43          | 196,98           | 17,57     | 142       |
| <i>Abies alba</i>          | 157            | 16,92          | 76,74            | 25,02     | 46        |
| <i>Corylus avellana</i>    | 92             | 9,91           | 44,97            | 4,91      | 30        |
| <i>Acer pseudoplatanus</i> | 54             | 5,82           | 26,39            | 20,51     | 18        |
| <i>Picea abies</i>         | 44             | 4,74           | 21,51            | 25,42     | 19        |
| <i>Sorbus aucuparia</i>    | 23             | 2,48           | 11,24            | 11,86     | 11        |
| <i>Ulmus glabra</i>        | 11             | 1,19           | 5,38             | 9,77      | 9         |
| <i>Acer platanoides</i>    | 5              | 0,54           | 2,44             | 0,00      | 0         |
| <i>Salix caprea</i>        | 1              | 0,11           | 0,49             | 0,00      | 0         |
| <i>Tilia cordata</i>       | 1              | 0,11           | 0,49             | 0,00      | 0         |
| Štompy                     | 137            | 14,76          | 66,96            | 8,96      | 95        |
| <b>TOTAL</b>               | <b>928</b>     | <b>100,00</b>  | <b>452,60</b>    | —         | —         |

# Metodika výskumu

## 3. Potravné pozorovania vtákov (štruktúra gíld, stromové preferencie, potravná ekológia vtákov)

- náhodné bodové pozorovania vtákov pri kŕmení
- druhá polovica mája až koniec júla
- klasifikácia potravného správania podľa schémy Remsena a Robinsona (1990, Studies in Avian Biology 13)
- redukcia kategórií útokov: zberanie (gleaning), trepotanie (hovering), chytanie (sallying) a d'ubanie (pecking)
- štandardizované formuláre – 39 premenných
- pohlavie (1 premenná), čas (1), výška kŕmenia (3), smer pohybu (2), potravné substráty (16), potravné stratégie (4) v kombinácii s morfológickými orgánmi rastlín (3)
- 4214 potravných pozorovaní 41 druhov vtákov v 1997-2000

# Štruktúra a diverzita ornitocenózy

Biologia, Bratislava, 59/2: 219–231, 2004

## Structure of the breeding bird assemblage of a primeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts

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KORŇAN, M. Structure of the breeding bird assemblage of a primeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts. *Biologia, Bratislava*, 59: 219–231, 2004; ISSN 0006-3088.

The structure of a breeding bird assemblage of a primeval beech-fir forest in the Malá Fatra Mts, the Western Carpathians was studied in the period 1997–2001. A 27.5 ha (500 × 550 m) forest interior study plot was established for bird censusing. Population abundances were estimated by means of an improved version of the mapping method from April to mid-July. Altogether, 57 bird species (52 breeders) were recorded within the reserve during the 5-year period. Of these, 48 species bred in the study plot reaching a mean density of  $58.17 \pm 3.60$  pairs/10 ha (CV = 6.18%). The year assemblage densities varied between 52.15–61.20 BP/10 ha. The Shannon diversity index ( $H'$ ) varied between 4.10–4.36 bites. The evenness index ( $J'$ ) reached values between 0.78–0.82. The year rarefaction estimates [ $E(S_{100\text{pairs}})$ ] were 22.77–25.16 species. The year rarefaction estimates on area [ $E(S_{100\text{ha}})$ ] varied between 19.46–21.30 species. Bird species diversity was comparable to other mixed primeval stands in the Western Carpathians e.g. Dobroč and Hadin reserves. In total, seven species were characterized as dominant ( $\geq 5\%$ ): *Pringilla coelebs*, *Erithacus rubecula*, *Sylvia atricapilla*, *Parus ater*, *Phylloscopus collybita*, *Regulus regulus*, and *Prunella modularis*. The species structure and relative abundance of the bird assemblage showed high temporal stability. Major differences were found in assemblage composition in comparison to the past survey in the reserve. A serious need for reevaluation and new rigorously designed quantitative inventory surveys of the Slovak reserve network is stressed.

Key words: bird community, primeval beech-fir forest, mapping method, population density, rarefaction, the Šrámková National Nature Reserve, Slovakia.

### Introduction

Natural old growth forests represent the unique remains of original ecosystems and usually function as core areas in most ecological networks. They are identified as areas of high nature conser-

vation value from the landscape ecology aspect. In Slovakia most primeval forests create a backbone of the existing nature reserve system and in the near future will be transformed into special areas of conservation (SAC) or special protection areas (SPA) meeting the criteria of NATURA

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

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### Abstract

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

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

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

### Introduction

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

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# Štruktúra ornitocenózy v NPR Šrámková

| SPECIES                              | ABUNDANCIA   |              |               |              |              | DENSITA      | DOMINANCIA    | SD          | CV          |
|--------------------------------------|--------------|--------------|---------------|--------------|--------------|--------------|---------------|-------------|-------------|
|                                      | 1997         | 1998         | 1999          | 2000         | 2001         | (páry/10 ha) | (%)           |             | (%)         |
| <i>Fringilla coelebs</i>             | 25.7         | 25.6         | 34.3          | 35.7         | 34.5         | 11.33        | 19.47         | 1.84        | 16.23       |
| <i>Erithacus rubecula</i>            | 10.7         | 14.5         | 15.6          | 16.2         | 11.2         | 4.96         | 8.52          | 0.92        | 18.59       |
| <i>Sylvia atricapilla</i>            | 8.7          | 7.6          | 12.4          | 15.9         | 14.0         | 4.26         | 7.32          | 1.28        | 29.93       |
| <i>Parus ater</i>                    | 13.5         | 15.3         | 7.0           | 8.8          | 10.0         | 3.97         | 6.82          | 1.24        | 31.24       |
| <i>Phylloscopus collybita</i>        | 7.1          | 9.8          | 10.3          | 11.5         | 10.6         | 3.59         | 6.16          | 0.60        | 16.86       |
| <i>Regulus regulus</i>               | 8.0          | 11.1         | 9.3           | 9.7          | 9.3          | 3.45         | 5.92          | 0.40        | 11.71       |
| <i>Prunella modularis</i>            | 6.7          | 8.8          | 7.5           | 9.0          | 9.5          | 3.02         | 5.19          | 0.42        | 13.97       |
| <i>Ficedula albicollis</i>           | 7.5          | 6.9          | 5.3           | 6.3          | 6.0          | 2.33         | 4.00          | 0.31        | 13.17       |
| <i>Certhia familiaris</i>            | 6.4          | 4.9          | 5.7           | 7.8          | 7.0          | 2.31         | 3.97          | 0.41        | 17.67       |
| <i>Columba palumbus</i>              | 6.9          | 7.0          | 7.3           | 6.5          | 2.0          | 2.16         | 3.71          | 0.81        | 37.39       |
| <i>Troglodytes troglodytes</i>       | 4.5          | 5.9          | 5.0           | 6.0          | 6.4          | 2.02         | 3.47          | 0.28        | 14.08       |
| <i>Columba oenas</i>                 | 5.3          | 3.0          | 3.5           | 5.0          | 11.0         | 2.02         | 3.47          | 1.16        | 57.42       |
| <i>Turdus merula</i>                 | 4.5          | 4.5          | 3.5           | 3.6          | 6.2          | 1.62         | 2.79          | 0.39        | 24.28       |
| <i>Turdus philomelos</i>             | 1.8          | 5.5          | 3.2           | 4.8          | 4.7          | 1.45         | 2.50          | 0.54        | 37.21       |
| <i>Phylloscopus sibilatrix</i>       | 4.7          | 4.0          | 4.3           | 1.0          | 4.5          | 1.35         | 2.31          | 0.56        | 41.39       |
| <i>Sitta europaea</i>                | 1.8          | 4.0          | 2.8           | 4.0          | 5.6          | 1.32         | 2.27          | 0.52        | 39.32       |
| <i>Pyrrhula pyrrhula</i>             | 3.3          | 4.5          | 2.0           | 1.0          | 1.0          | 0.86         | 1.47          | 0.55        | 64.58       |
| <i>Muscicapa striata</i>             | 3.0          | 3.0          | 3.8           | 0.0          | 0.5          | 0.75         | 1.29          | 0.62        | 82.21       |
| <i>Ficedula parva</i>                | 3.5          | 1.0          | 1.5           | 2.5          | 1.5          | 0.73         | 1.25          | 0.36        | 50.00       |
| <i>Coccothraustes coccothraustes</i> | 2.0          | 1.0          | 3.0           | 2.0          | 0.5          | 0.62         | 1.06          | 0.35        | 57.33       |
| <b>TOTAL</b>                         | <b>143.4</b> | <b>162.1</b> | <b>159.55</b> | <b>168.3</b> | <b>166.5</b> | <b>58.17</b> | <b>100.00</b> | <b>3.60</b> | <b>6.18</b> |

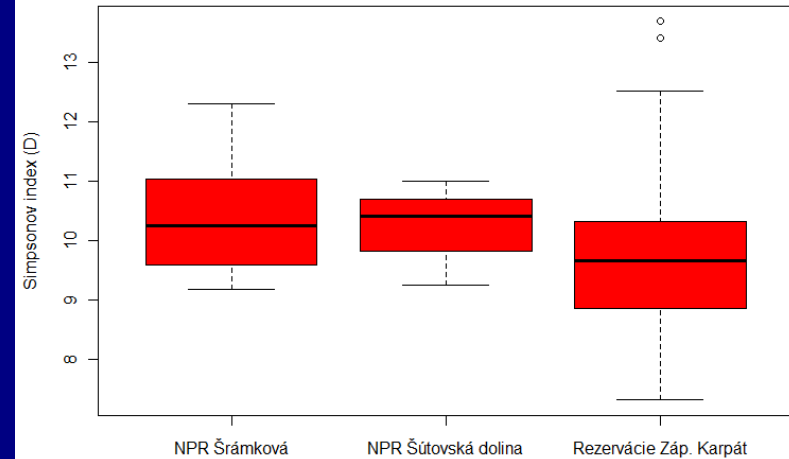
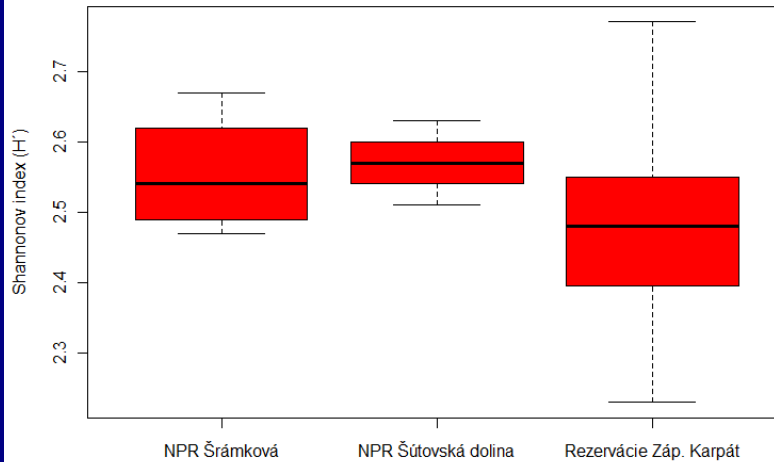
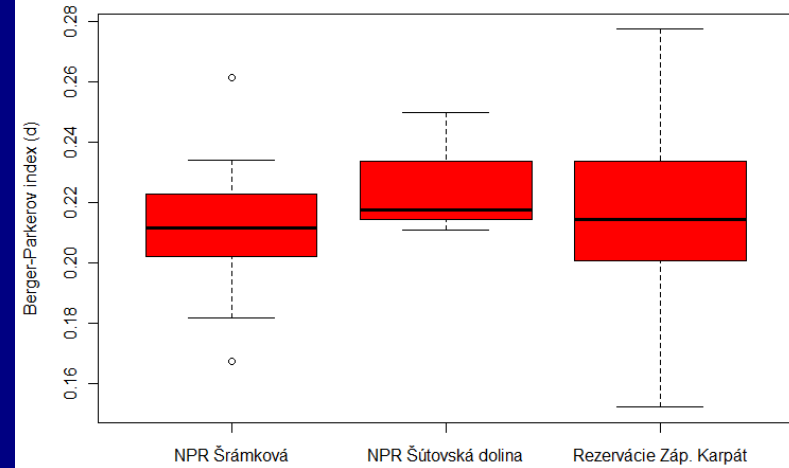
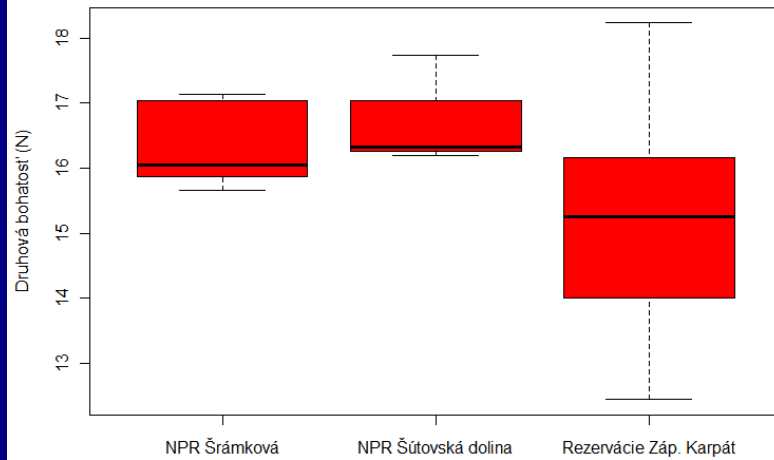
# Štruktúra ornitocenózy v NPR Šútovská dolina

| Druh                                     | Početnosť |       |       | Hustota (páry/10 ha) |       |       |       | Dominancia (%) |       |       |       | SD   | CV<br>(%) |
|------------------------------------------|-----------|-------|-------|----------------------|-------|-------|-------|----------------|-------|-------|-------|------|-----------|
|                                          | 2000      | 2001  | 2002  | 2000                 | 2001  | 2002  |       | 2000           | 2001  | 2002  |       |      |           |
| 1. <i>Fringilla coelebs</i>              | 22,6      | 28,6  | 32,4  | 11,30                | 14,30 | 16,20 | 13,93 | 25,28          | 23,29 | 28,62 | 25,73 | 2,69 | 10,47     |
| 2. <i>Erithacus rubecula</i>             | 7,6       | 13,4  | 9,4   | 3,80                 | 6,70  | 4,70  | 5,07  | 8,50           | 10,91 | 8,30  | 9,24  | 1,45 | 15,72     |
| 3. <i>Sylvia atricapilla</i>             | 7,6       | 8,2   | 8,4   | 3,80                 | 4,10  | 4,20  | 4,03  | 8,50           | 6,68  | 7,42  | 7,53  | 0,92 | 12,17     |
| 4. <i>Parus ater</i>                     | 7,6       | 8,6   | 7,9   | 3,80                 | 4,30  | 3,95  | 4,02  | 8,50           | 7,00  | 6,98  | 7,49  | 0,87 | 11,63     |
| 5. <i>Regulus regulus</i>                | 5,6       | 7,5   | 5,3   | 2,80                 | 3,75  | 2,65  | 3,07  | 6,26           | 6,11  | 4,68  | 5,68  | 0,87 | 15,33     |
| 6. <i>Certhia familiaris</i>             | 6,2       | 4,7   | 6,0   | 3,10                 | 2,35  | 3,00  | 2,82  | 6,94           | 3,83  | 5,30  | 5,35  | 1,55 | 29,03     |
| 7. <i>Ficedula albicollis</i>            | 4,0       | 6,2   | 5,5   | 2,00                 | 3,10  | 2,75  | 2,62  | 4,47           | 5,05  | 4,86  | 4,79  | 0,29 | 6,11      |
| 8. <i>Troglodytes troglodytes</i>        | 4,0       | 6,7   | 5,0   | 2,00                 | 3,35  | 2,50  | 2,62  | 4,47           | 5,46  | 4,42  | 4,78  | 0,58 | 12,21     |
| 9. <i>Prunella modularis</i>             | 4,4       | 5,3   | 5,5   | 2,20                 | 2,65  | 2,75  | 2,53  | 4,92           | 4,32  | 4,86  | 4,70  | 0,33 | 7,09      |
| 10. <i>Phylloscopus collybita</i>        | 3,0       | 4,5   | 5,8   | 1,50                 | 2,25  | 2,90  | 2,22  | 3,36           | 3,66  | 5,12  | 4,05  | 0,94 | 23,33     |
| 11. <i>Phylloscopus sibilatrix</i>       | 4,2       | 4,0   | 4,0   | 2,10                 | 2,00  | 2,00  | 2,03  | 4,70           | 3,26  | 3,53  | 3,83  | 0,76 | 19,97     |
| 12. <i>Sitta europaea</i>                | 2,6       | 4,8   | 2,0   | 1,30                 | 2,40  | 1,00  | 1,57  | 2,91           | 3,91  | 1,77  | 2,86  | 1,07 | 37,46     |
| 13. <i>Turdus merula</i>                 | 1,0       | 2,8   | 2,8   | 0,50                 | 1,40  | 1,40  | 1,10  | 1,12           | 2,28  | 2,47  | 1,96  | 0,73 | 37,44     |
| 14. <i>Turdus philomelos</i>             | 2,0       | 1,5   | 2,0   | 1,00                 | 0,75  | 1,00  | 0,92  | 2,24           | 1,22  | 1,77  | 1,74  | 0,51 | 29,18     |
| 15. <i>Ficedula parva</i>                | –         | 1,5   | 2,7   | 0,00                 | 0,75  | 1,35  | 0,70  | 0,00           | 1,22  | 2,39  | 1,20  | 1,19 | 99,21     |
| 16. <i>Pyrrhula pyrrhula</i>             | 1,0       | 2,0   | 1,0   | 0,50                 | 1,00  | 0,50  | 0,67  | 1,12           | 1,63  | 0,88  | 1,21  | 0,38 | 31,48     |
| 17. <i>Coccothraustes coccothraustes</i> | 2,0       | 1,0   | 1,0   | 1,00                 | 0,50  | 0,50  | 0,67  | 2,24           | 0,81  | 0,88  | 1,31  | 0,80 | 61,17     |
| Celkovo                                  | 89,4      | 122,8 | 113,2 | 44,70                | 61,40 | 56,60 | 54,23 | 100,0          | 100,0 | 100,0 | 100,0 | 8,60 | 15,85     |

# Porovnanie diverzity rezervácií

|                                             | NPR Šrámková | NPR Šútovská dolina |
|---------------------------------------------|--------------|---------------------|
| Obdobie výskumu                             | 1997–2006    | 2000–2002           |
| Veľkosť sčítacej plochy                     | 27,5 ha      | 20 ha               |
| Celkový počet hniezdičov                    | 53           | 49                  |
| Priemerný počet hniezdičov                  | 39           | 41,3                |
| Priemerná celková hustota                   | 59,5         | 54,2                |
| Druhovú bohatosť–zriedňovanie 30 párov      | 16,27        | 16,75               |
| Shannov index–zriedňovanie 30 párov         | 2,56         | 2,57                |
| Simpsonov index–zriedňovanie 30 párov       | 10,45        | 10,22               |
| Berger-Parkerov index–zriedňovanie 30 párov | 0,21         | 0,23                |
| Rozdiely medzi ročnými vzorkami plochy      | NS           | NS                  |
| Rozdiely medzi plochami                     | NS           | NS                  |

# Porovnanie diverzity zmiešaných pralesov



# Štruktúra potravných gíld a ich konvergencia

Biologia, Bratislava, 58(2): 275–285, 2003

## The effect of habitat structure on guild patterns and the foraging strategies of insectivorous birds in forests

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In order to investigate the role of habitat heterogeneity on the foraging ecology of birds and overall guild patterns, two structurally different forest habitats were studied. The first represented a heterogeneous old-growth forest in the Malá Fatra Mts, while the second a structurally homogeneous spruce sylviculture in the Javorinky Mts, Slovakia. The observed guild structure patterns and the organization of foraging niches are significantly different. The cluster analysis of Euclidean distances revealed four main guilds in the primeval forest comprising 23 bird species: foliage gleaners, bark foragers, aerial foragers, and ground foragers, while in the sylviculture only three guilds consisting of 11 species: foliage gleaners, ground foragers, and bark foragers were detected. Foraging niche breadth indices revealed that species occurring at both study sites had significantly broader niches in the old-growth forest. Possible causes of the absence of the aerial foragers in the structurally homogeneous habitat, and the effects of habitat deterioration on bird foraging ecology, and consequently on settlement patterns, are discussed.

Key words: foraging behaviour, habitat selection, guild structure, resource partitioning, primeval forest, habitat degradation, Štráňová NNR.

## Introduction

The relationship between animal communities and habitats has held an important place in community ecology studies for several decades. According to optimization thinking it is assumed that traits of species have evolved to be adaptive to maximize evolutionary success (BROOKS & MCLENNAN, 1991; PRICE et al. 1997). Based on this assumption, one may expect species-specific preferences for a particular habitat type as a consequence of an historical relationship between species and their environment. The patterns of bird habitat relationships have been well documented to maximize evolutionary success (BROOKS & MCLENNAN, 1991; PRICE et al. 1997). Based on this assumption, one may expect species-specific preferences for a particular habitat type as a consequence of an historical relationship between species and their environment. The patterns of bird habitat relationships have been well documented

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DOI: 10.1556/ComEc.8.2007.2.1



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

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**Keywords:** A posteriori approach, Bootstrap testing, Cluster analysis, Generalist species, Guild concepts, Ordination, Specialist species, Štráňová National Nature Reserve.

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

**Nomenclature:** Marhold and Hindák (1998) for plants and Snow and Perrins (1998) for birds.

## Introduction

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

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

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

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DOI: 10.1556/ComEc.14.2013.1.10



## 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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**Keywords:** Bird community structure, Bondi State Forest, Bootstrap testing, Cluster analysis, Foraging guilds, Hubbard Brook Experimental Forest, Intercontinental guild comparisons, Ordination, Resource partitioning, Štráňová National Nature Reserve.

**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 ordinations. 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).

**Abbreviation:** BMDS – 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 Schlüter 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 (Loren 1992), birds (Lesler and Winiker 2001; Korňan-Nieveland and Lesler 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; Nee 1985; Wiens 1991a; Lee et al. 2007; Gido et al. 2009). However, in some cases the detected patterns were ambiguous and interpretation depended on the

# Konvergenia gíld a metodické postupy

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## Konvergenia štruktúry potravných gíld ornitocenóz medzi lesmi dvoch zoogeografických oblastí

*Convergence in foraging guild structure of bird assemblages between forests in two zoogeographic regions*

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*We compared the foraging guild structure of bird assemblages between two model plots in two zoogeographic regions. The research was conducted in a beech-maple-birch forest with admixture of spruce in the Hubbard Brook Experimental Forest in USA (Nearctic region) and beech-fir forest in the Štránková National Nature Reserve in Slovakia (Palearctic region). Foraging guild structure was determined from observed frequencies of foraging substrates used by individual species. Data matrices 22 species × 35 variables (Nearctic) and 26 species × 47 variables (Palearctic) were constructed from the database of foraging observations. Multivariate numerical procedures such as bootstrapped cluster analysis (UPGMA) and correspondence analysis (CA) were applied for determination and interpretation of the foraging guild structure. Four guild categories (litter and trunk foragers, two distinct guilds of foliage gleaners and one significantly different dendrogram branch were determined in the bird assemblage of Nearctic forest (critical threshold level  $\alpha = 0.1$ ). Six guild categories (litter foragers, herb foragers, trunk foragers, foliage gleaners, flycatchers, and stream foragers) and one independent dendrogram branch were detected in the bird assemblage in the Palearctic forest. Presence of three analogous guild categories connected to foraging in/on litter/ground, on trunk and on leaves implies convergence in evolution of bird assemblages. Similar basic division of guilds has been described in the eucalypt forests in the Australian region indicating rough patterns of convergent evolution in the structure of forest bird assemblages on the global scale, perhaps related to similarities in the physical structure and types of food resources of these geographically distinct forests.*

## Úvod

Konvergenia je chápaná ako fenomén, keď v ekologicky podobných podmienkach na rôznych kontinentoch alebo oblastiach s izolovaným vývojom dochádza k vzniku podobných ekologických adaptácií alebo štruktúr na rôznych úrovniach organizácie ekologických systémov. Myšlienka, že druhy s rozdielnou fylogenezou, ktoré obývajú podobné niky

v podobných environmentálnych podmienkach na rôznych kontinentoch, konvergujú v morfológických, etologických a ekologických znakoch, je pomerne stará. Ešte Darwin (1859) in Wiens 1989, 1991) poukázal na podobnosť v morfológii a etológii medzi morskými druhmi vtákov čeľade Pelecanoididae, ktoré obývajú južnú hemisféru, a alkami čeľade Alcidae severnej hemisféry. Od toho času bola konvergenia dokumentovaná na mnohých druhoch

Oecologia  
Moriána 2002,  
11, 82 - 93

## Porovnanie a priori a a posteriori prístupov pri analýze potravných gíld vo vtáčích spoločenstvách: modelový príklad

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**Abstract.** Two fundamental approaches of guild structure analyses – a priori and a posteriori have not been empirically compared within the framework of a model study at one site up to now. This is the first attempt to describe, compare, and analyze the main differences between the two approaches using the example of bird assemblages. The study was conducted in a primeval beech-fir forest in the Štránková National Nature Reserve. Population densities of breeding birds were estimated using an improved version of the mapping method in a 27.5 ha (500 × 550 m) study plot. An a priori foraging guild analysis was based on the foraging characteristics of birds from previous studies. In total, 10 types of guilds were defined for a priori assemblage analysis: stream foragers, ground foragers, foliage gleaners, bark foragers, air-space foragers, and plant eaters. An a priori data matrix (25 × 10, 57 × 10) was prepared for comparative analyses. Bird species were divided into guild categories before the field observations of foraging birds started. The a posteriori classification was based on extensive field survey of the study plot. Foraging observations were collected from the middle of May until the end of July in 1997–99. In total, 2 921 random point observations of foraging birds were recorded on the data sheets with a standardized set of variables indicating species, sex, day time, duration, foraging height, direction of foraging movement, substrate type, and foraging strategy. Only 25 bird species were subjected to further statistical analyses based on the criterion  $\geq 40$  observations per species. Multivariate statistical procedures such as hierarchical cluster analysis and correspondence analysis were applied to the classification of guild patterns. The observed pattern consists of 7 types of guilds: ground foragers, stream foragers, bark peckers, bark gleaners, foliage gleaners, air-space foragers, and sky foragers. Comparing the same set 25 bird species, a priori approach detected only 6 guild types and incorrectly classified 5 species (20 %). Only 5 types of identical a priori guilds (71.4 %) were detected in the emerged a posteriori pattern. Incorrect classification was mainly caused by the lack of previous information on foraging ecology and niche requirement of species. It is summarized that when correctly applied and based on reliable

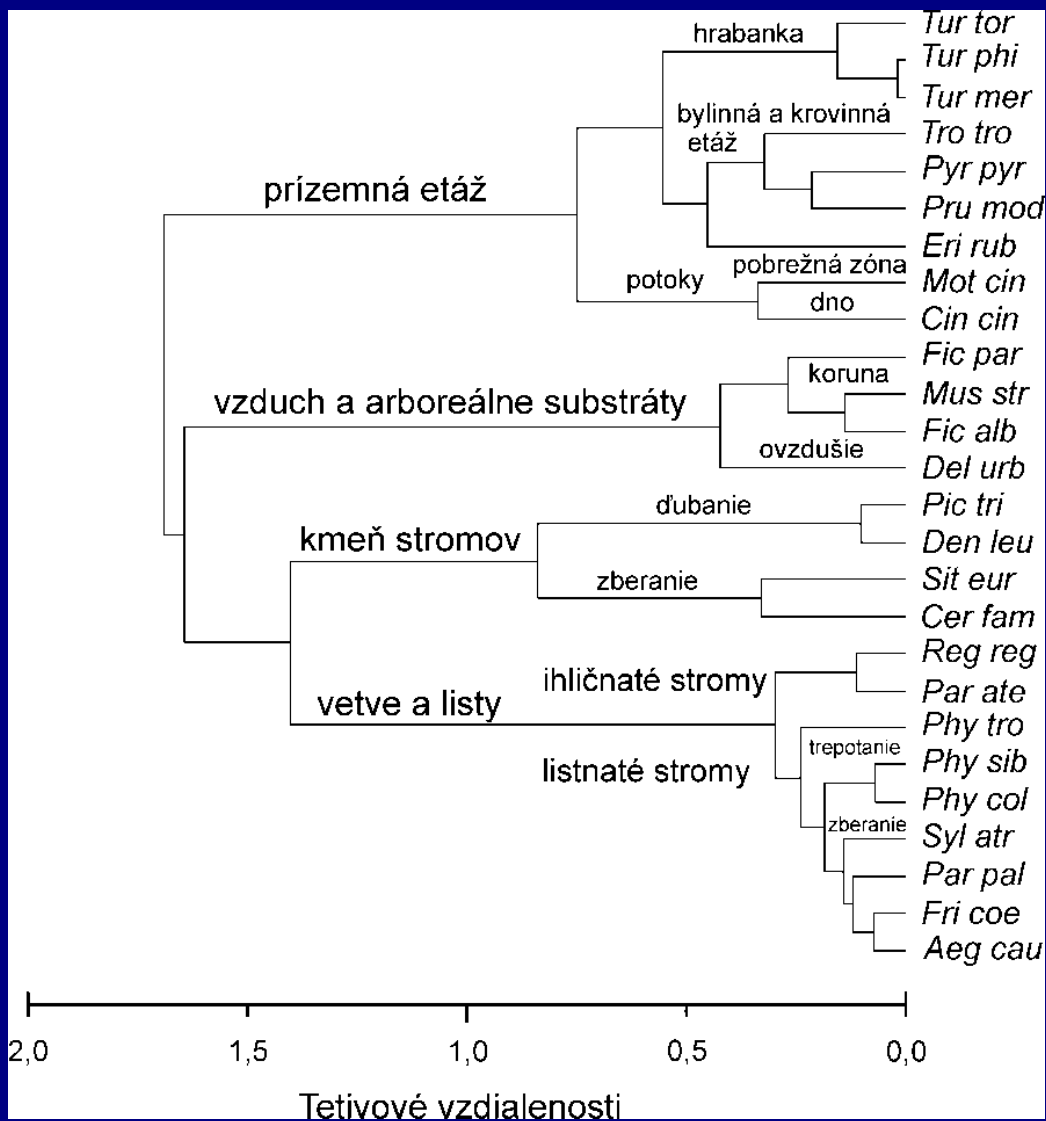
information from past studies, a priori approach is a fast, cheap, and powerful tool for basic functional analyses in wildlife management. In contrast, a posteriori approach is very time consuming and requires large sample sizes of foraging observations. Only 40–60 % of species meets satisfactory sample size for further statistical analyses. In addition to practical application for wildlife management and landscape planning, such study may be used for testing hypothesis in theoretical ecology. Further recommendations and improvements based on the experience in the field with data analyses, and general methodology are given.

**Key words:** birds, community ecology, guilds, resource partitioning, Štránková National Nature Reserve, the Malá Fatra Mts.

## Úvod

Gíldová príslušnosť druhov v spoločenstvách a charakteristika vlastností spoločenstiev vyjadrená na základe štruktúry gíld sa stala v posledných desaťročiach základom mnohých ekologických štúdií. Mac Nally (1994) konštatuje, že determinácia gíld je pre ekologov výhodná minimálne z dvoch dôvodov: (1) uľahčuje analýzu a interpretáciu ekosystémov a spoločenstiev, ktoré sú vo všeobecnosti ťažko analyzovateľné, (2) gíldy sú chápané ako "prírodné ekologické jednotky", ktoré sú akýmsi stavebným základom spoločenstiev a v takom zmysle reprezentujú daný typ spoločenstva. Jakšič (1981) konštatuje, že na objektívnu analýzu spoločenstva alebo ekosystému je potrebné analyzovať všetky druhy, ktoré patria do danej gíldy. Jakšič tiež navrhuje, že je potrebné rozlišovať medzi "skutočnými" gíldami spoločenstva založenými na reálnom využívaní zdrojov spoločenstva druhmi z rôznych systematických skupín a taxonomickými gíldami vzniknutými (spoločenstiev v zmysle taxonómie). Na rozdiel od pôvodnej definície gíld v zmysle Roota (1967), kde jedným z hlavných kritérií pri definícii gíld bolo využívanie zdrojov "podobným spôsobom" (in similar manner), MacMahon et al. (1981) a Jakšič (1981) sa odklákajú od tejto koncepcie a navrhujú, že hlavným kritériom pri klasifikácii druhu do gíldy by mal byť vplyv využívania zdroja organizmom na samotný zdroj v ekosystéme. Autori diskutujú: "...nie je podstatné či organizmus využíva listy na hnašedny materiál, potravu, alebo substrát, na ktorom môžu rásť huby, ktoré sú následne konzumované; v konceptom dôsledku listy sú spozorované a druhy, ktoré ich využívajú patria do jednej gíldy." Z metodického hľadiska existujú dva principiálne odlišné postupy ako vyjadriť štruktúru gíld v spoločenstvách: a priori a a posteriori postup (pozri Wiens 1989, Šimberloff and Dayan 1991).

# Štruktúra potravných gíld: Rootovský prístup



Hierarchická klasifikácia s bootstrapom

Algoritmus Sampler (Pillar 1999)

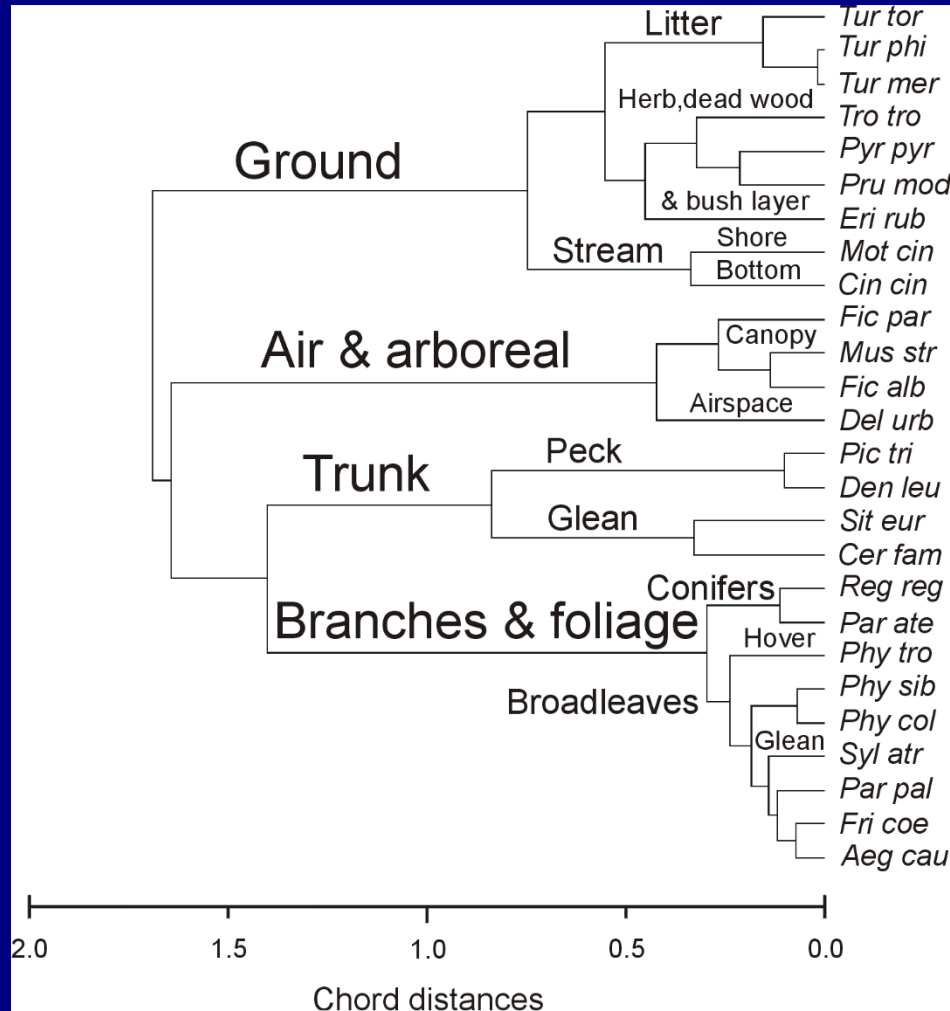
Možnosť testovania významných rozdielov medzi zhlukmi na jednotlivých úrovniach zhlukovania

**Celkovo rozlíšených 6 a 9 typov potravných gíld:**

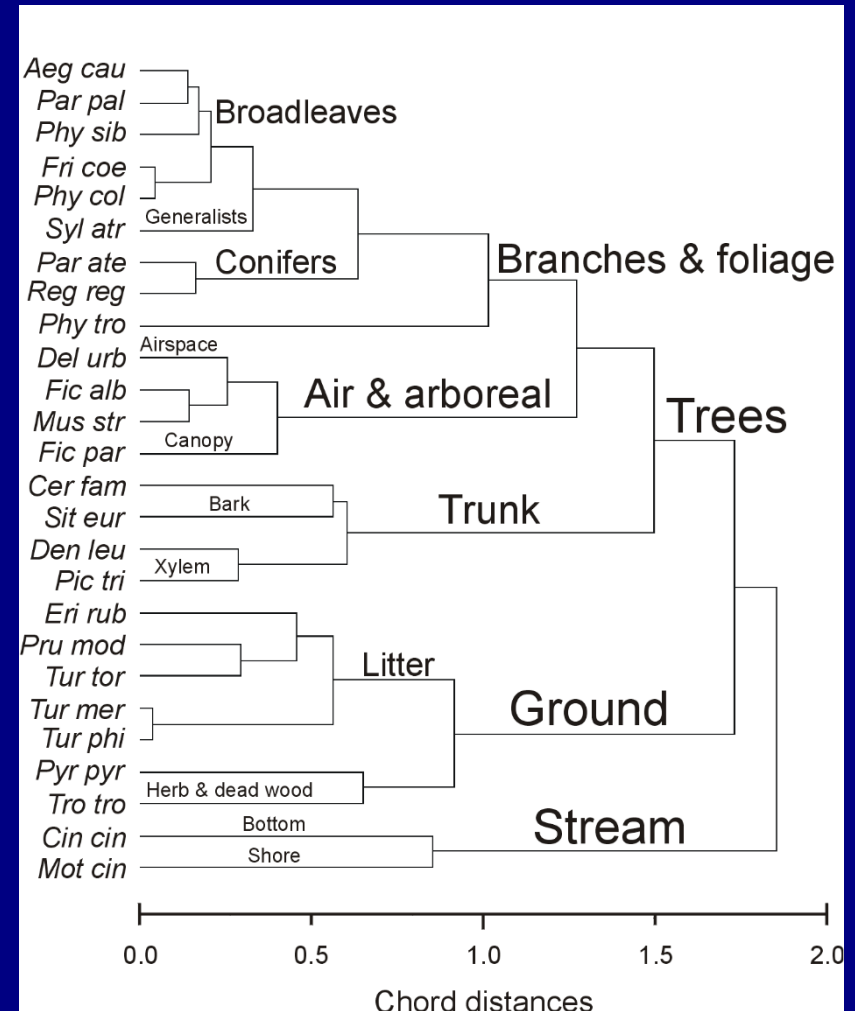
1. zberači na zemi
2. evertebratófágy viazané na toky
3. evertebratófágy vo vzduchu
4. d'atle
5. zberači na kmeni
6. zberači z listov

# Porovnanie dvoch gildových koncepcií

Rootovská koncepcia  
6 a 9 signifikantných gíld



MacMahonovská koncepcia  
7 signifikantných gíld



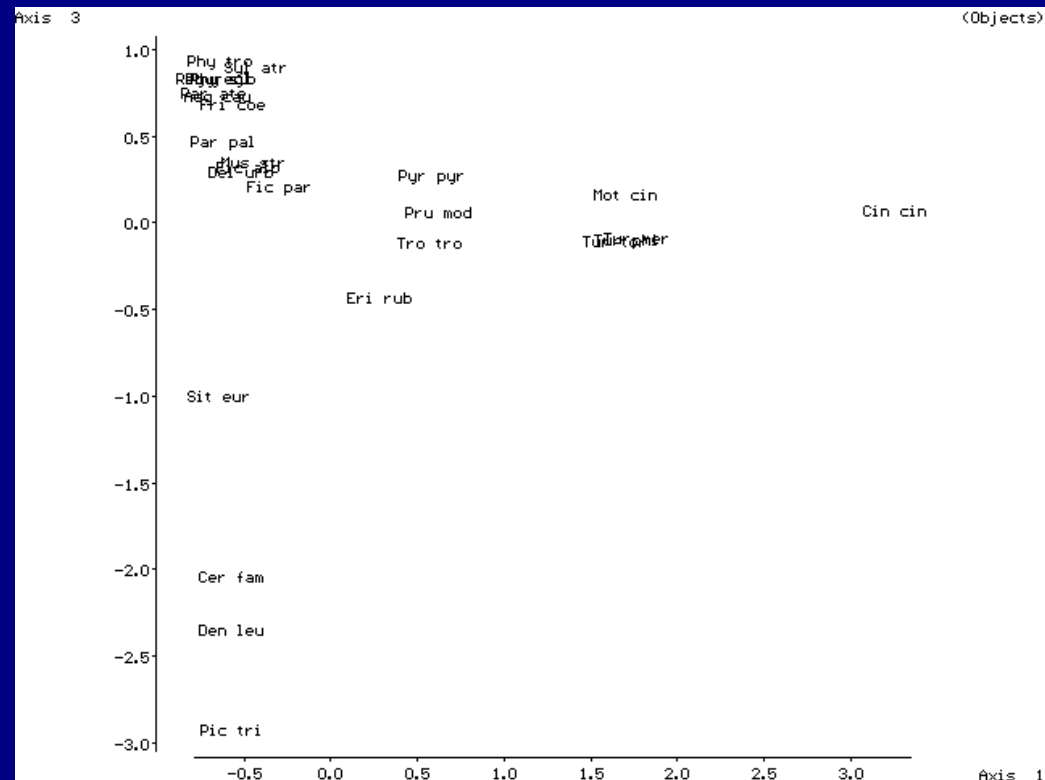
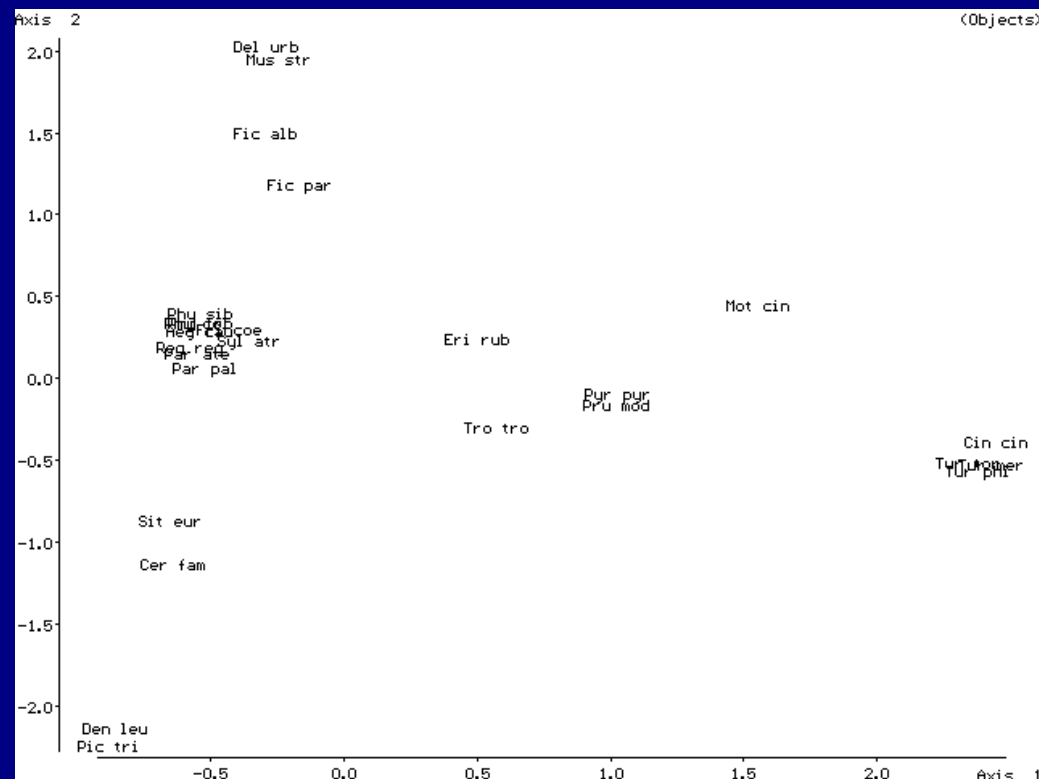
# Porovnanie dvoch gildových koncepcií

Ordinačný diagram korešpondenčnej analýzy (CA): identická interpretácia faktorov

1. faktor (os): gradient výškového rozloženia potravných substrátov: vertikálna štruktúra habitatu)
2. faktor (os): gradient priestorovej morfológie stromu: kmeň-vetva-vetvička-list

Rootovská koncepcia

MacMahonovská koncepcia



# Konvergencia potravných gíld: medzikontinentálne porovnanie podľa Rootovskej koncepcie

Bootstrapová zhuková analýza (UPGMA) (Bootstrapped cluster analysis)

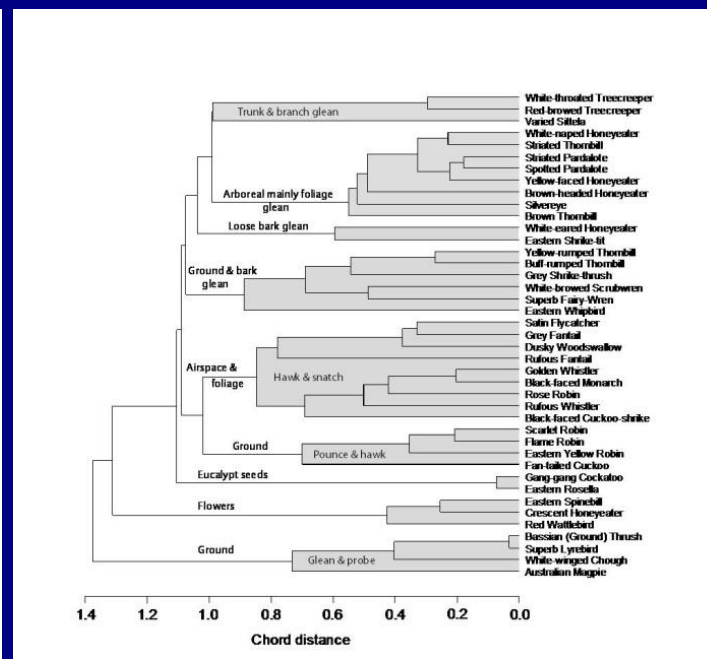
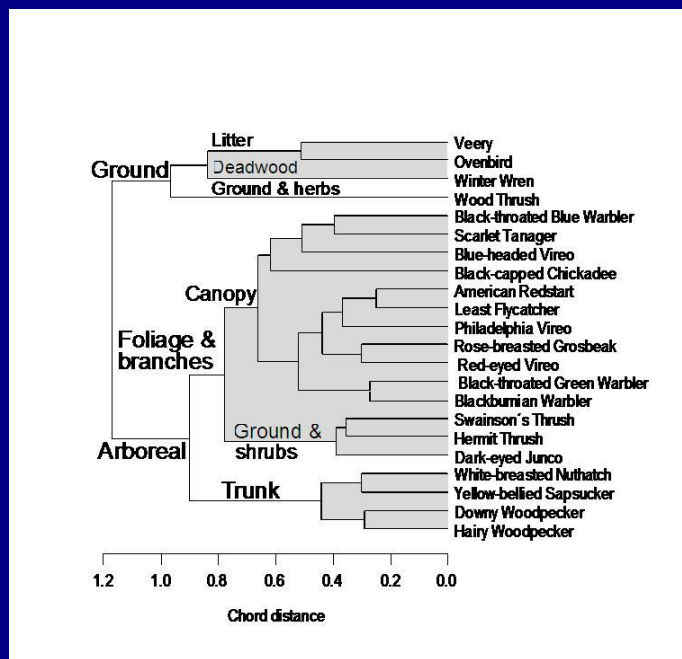
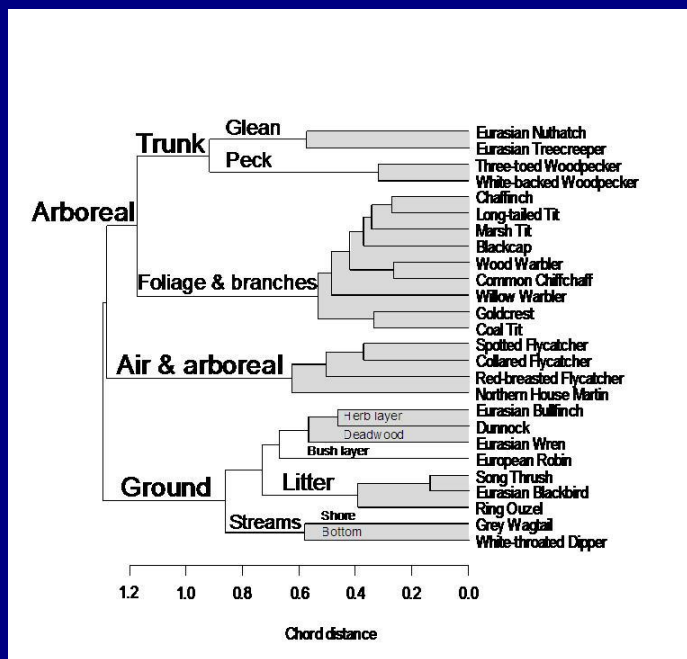
Analogická základná štruktúra potravných gíld medzi kontinentmi:

1. konzumenti na listoch,
2. konzumenti na kmeni,
3. konzumenti na zemi a hrabanke.

Európa  
NPR Šrámková

Severná Amerika  
Hubbard Brook Forest

Austrália  
Bondi State Forest



# Konvergencia potravných gíld: medzikontinentálne porovnanie podľa Rootovskej koncepcie

Bootstrapová hlavná analýza súradníc (BPCoA) (Bootstrapped Principal Coordinate Analysis)

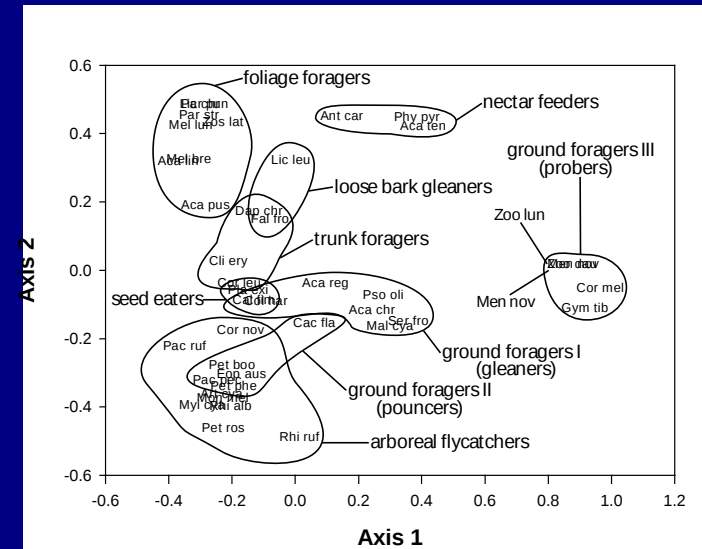
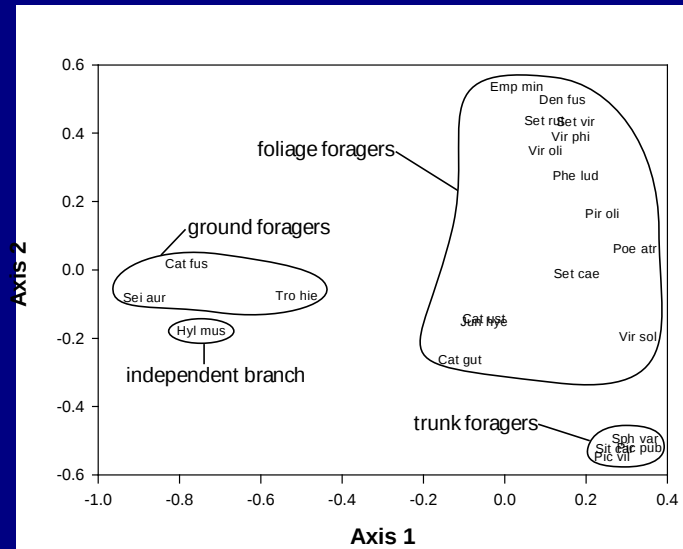
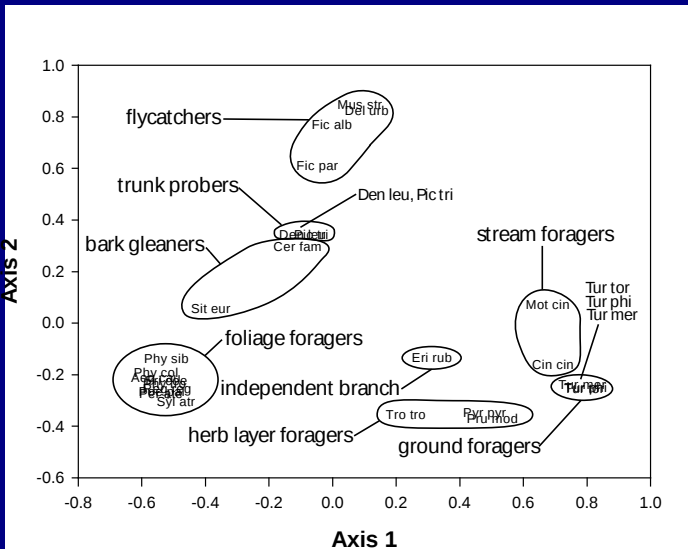
Analogické faktory radiácie druhov do potravných gíld medzi kontinentmi:

1. faktor (os): gradient výškového rozloženia potravných substrátov: vertikálna štruktúra habitatu)
2. faktor (os): gradient priestorovej morfológie stromu: kmeň-vetva-vetvička-list

Európa  
NPR Šrámková

Severná Amerika  
Hubbard Brook Forest

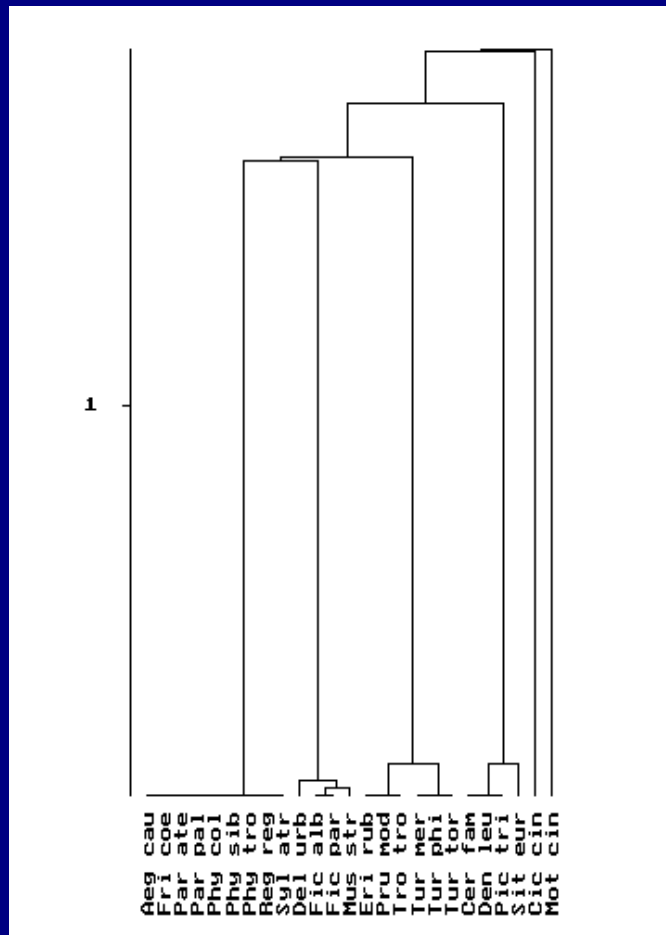
Austrália  
Bondi State Forest



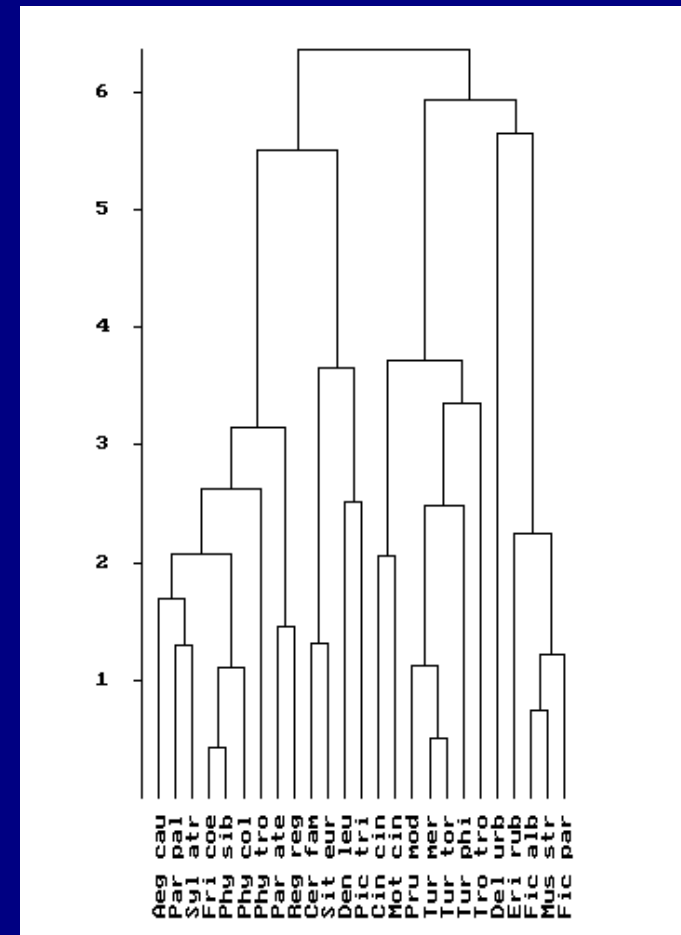
# Porovnanie apriórnych a posteriórnych postupov determinácie gíld

Zhluková analýza Euklidovských vzdialeností, metóda nevážených priemerov (UPGMA)

*A priori* prístup (25 druhov)



*A posteriori* prístup (25 druhov)



# Porovnanie apriórnych a posteriórnych postupov determinácie gíld

| SPÔSOB DETERMINÁCIE GÍLD                                                 | APRIORI  | POSTERIORI |
|--------------------------------------------------------------------------|----------|------------|
| Celkový počet gíld v zoskupení                                           | 10       | 7          |
| Počet typov gíld pri klasifikácii rovnakých druhov (25 pre oba prístupy) | 6        | 7 (5)      |
| Počet rovnakých typov gíld                                               | 5/6      | 5/7        |
| Percento posteriori gíld z celkového počtu apriori gíld                  | 83,33 %  | —          |
| Percento apriori gíld z celkového počtu posteriori gíld                  | —        | 71,43 %    |
| Celkový počet analyzovaných druhov zoskupenia                            | 57       | 25         |
| Percento z celkového počtu zistených druhov                              | 100,00 % | 43,86 %    |
| Celkový počet analyzovaných hniezdičov v 27,5 ha kvadráte                | 47       | 24         |
| Percento z celkového počtu hniezdičov v 27,5 ha kvadráte                 | 100,00 % | 51,06 %    |
| Počet rozdielne klasifikovaných druhov pri porovnaní 25 druhov           | 5        | 5          |
| Percento rozdielne klasifikovaných druhov/ celá vzorka 25 druhov         | 20,00 %  | 20,00 %    |

# Zhodnotenie posteriórneho prístupu

Posteriórny prístup: hĺbkové hodnotenie podobnosti využívania potravných substrátov alebo potravy v zmysle Hutchinsonovej multidimenzionálnej niky, **reálne pozorovania alebo analýza potravy**

**Možnosti:** hodnotenie gildovej príslušnosti

- analýza reálneho využívania potravných substrátov

- analýza šírky ník

- analýza prekryvu ník

- analýza vegetačných (napr. stromových) preferencií

- analýza podobnosti potravného správania v zmysle útočných stratégií

**Nevýhody:** dostatočná vzorka len pre najbežnejšie a nápadné druhy

- v našom prípade 25 z 57 druhov (44 %) ornitocenózy

- nedostatočná rozlišovacia schopnosť a problémy klasifikácie

- niektorých druhov (napr. gilda fytofágov)

- subjektivita výberu premenných pri substrátových gíld, nie pri potrave

# Zhodnotenie apriórneho prístupu

Apriórny prístup: vychádza z publikovaných údajov pričom gildové kategórie sú subjektívne a je použiteľný len pre hrubé a rýchle klasifikovanie druhov do gíld

**Výhody:**

1. aplikovateľný pre všetky druhy ornitocenózy
2. pomerne rýchlo realizovateľný
3. nevyžaduje žiadny zber údajov
4. nevyžaduje žiadnu štatistickú analýzu

**Nevýhody:**

1. silne subjektívny (umelé kategórie gíld)
2. u druhov, o ktorých nie sú známe informácie ohľadne potravnej ekológie (napr. niektoré tropické druhy) môže byť zavádzajúci
3. slabá rozlišovacia schopnosť pre detailnejšie štúdium medzidruhovej konkurencie, využívania potravných ník a rozdeľovanie zdrojov

# Štruktúra potravných gíld v prírodnom a hospodárskom lese (Adamík et al. 2003. Biologia)

- študijné plochy: NPR Šrámková a smrekový hospodársky les v LHC Hliník (okres Bytča, Horné Považie)
- porovnanie šírky potravných ník podľa Shannovho indexu (5 druhov)

| ŠÍRKA NIKY (H')      | <i>Phylloscopus collybita</i> | <i>Certhia familiaris</i> | <i>Erithacus rubecula</i> | <i>Fringilla coelebs</i> | <i>Regulus regulus</i> |
|----------------------|-------------------------------|---------------------------|---------------------------|--------------------------|------------------------|
| NPR Šrámková         | 3,36                          | 3,15                      | 4,29                      | 3,64                     | 2,85                   |
| Smreková monokultúra | 2,15                          | 2,31                      | 1,00                      | 2,26                     | 2,23                   |

Všetky párové porovnania boli signifikantne rozdielne, Studentov t-test  $P < 0,001$

# Dynamika populácií, gíld a ornitocenózy

Ornis Fennica 90:151–177. 2013

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

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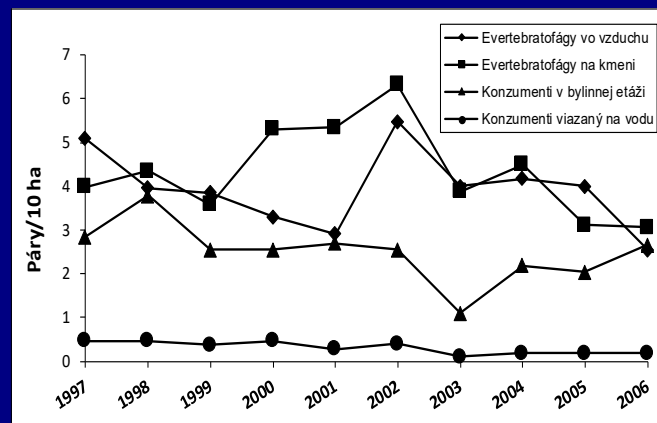
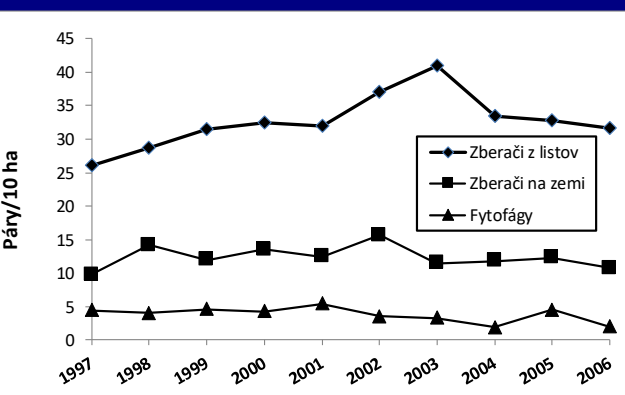
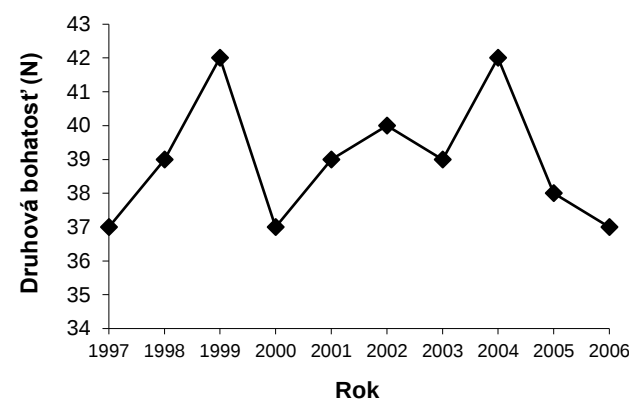
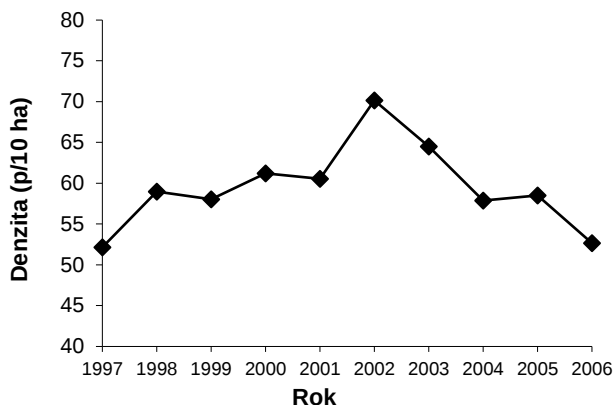
Received 30 October 2012, accepted 11 February 2013

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

### 1. Introduction

The first community concepts proposed by Clements (1916, 1936) and Gleason (1917, 1926) offered sharply differing views on organization and functioning of communities. Clements understood community as a discrete and integrated unit of taxa, a superorganism, repeatable in space and

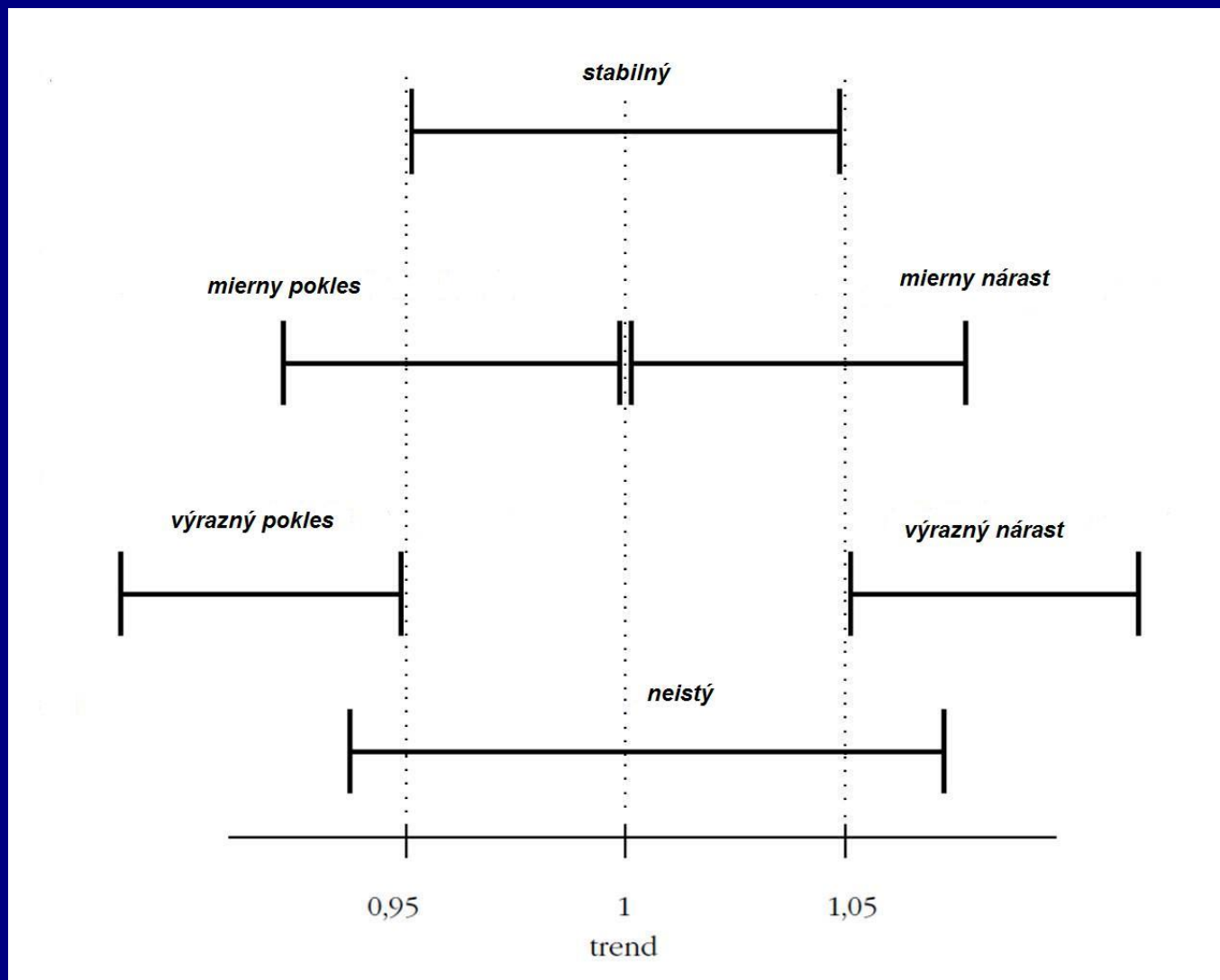
time and possessing fundamental properties analogous to those of an individual organism. Various species were thought to coexist because of similar requirements for habitat and resources and to develop together along a deterministic path of succession, leading eventually to stable climax communities (Underwood 1986). These processes were sometimes considered akin to the onto-



# Variabilita populačných hustôt

| DRUH                                 | Dominancia    | Hustota (p/ 10 ha) |      |        | CF   | PV    |
|--------------------------------------|---------------|--------------------|------|--------|------|-------|
|                                      | $\bar{x}$ (%) | $\bar{x}$          | SD   | CV (%) |      |       |
| <i>Fringilla coelebs</i>             | 21,92         | 13,03              | 2,41 | 18,47  | 1,22 | 0,192 |
| <i>Erithacus rubecula</i>            | 8,60          | 5,11               | 1,00 | 19,59  | 1,22 | 0,199 |
| <i>Sylvia atricapilla</i>            | 7,20          | 4,28               | 1,00 | 23,47  | 1,28 | 0,241 |
| <i>Periparus ater</i>                | 7,08          | 4,21               | 1,10 | 26,01  | 1,31 | 0,256 |
| <i>Regulus regulus</i>               | 5,92          | 3,52               | 0,43 | 12,33  | 1,13 | 0,133 |
| <i>Phylloscopus collybita</i>        | 5,87          | 3,49               | 0,54 | 15,46  | 1,18 | 0,165 |
| <i>Prunella modularis</i>            | 5,23          | 3,11               | 0,47 | 15,05  | 1,16 | 0,154 |
| <i>Ficedula albicollis</i>           | 4,39          | 2,61               | 0,72 | 27,56  | 1,31 | 0,263 |
| <i>Certhia familiaris</i>            | 3,84          | 2,28               | 0,57 | 24,86  | 1,30 | 0,250 |
| <i>Troglodytes troglodytes</i>       | 3,06          | 1,82               | 0,44 | 24,27  | 1,39 | 0,225 |
| <i>Columba oenas</i>                 | 2,87          | 1,71               | 1,10 | 64,21  | 2,03 | 0,510 |
| <i>Columba palumbus</i>              | 2,79          | 1,66               | 0,78 | 47,29  | 1,66 | 0,409 |
| <i>Turdus merula</i>                 | 2,74          | 1,63               | 0,38 | 23,36  | 1,27 | 0,233 |
| <i>Turdus philomelos</i>             | 2,45          | 1,46               | 0,39 | 26,79  | 1,38 | 0,267 |
| <i>Phylloscopus sibilatrix</i>       | 2,36          | 1,40               | 0,75 | 53,21  | 3,24 | 0,470 |
| <i>Sitta europaea</i>                | 2,09          | 1,24               | 0,58 | 46,78  | 1,63 | 0,404 |
| <i>Ficedula parva</i>                | 1,18          | 0,70               | 0,43 | 61,65  | 1,89 | 0,469 |
| <i>Pyrrhula pyrrhula</i>             | 1,13          | 0,67               | 0,44 | 65,73  | 1,79 | 0,427 |
| <i>Poecile palustris</i>             | 1,11          | 0,66               | 0,26 | 39,28  | 1,53 | 0,350 |
| <i>Muscicapa striata</i>             | 1,00          | 0,59               | 0,54 | 91,73  | 3,07 | 0,601 |
| <i>Coccothraustes coccothraustes</i> | 0,84          | 0,50               | 0,33 | 66,13  | 2,08 | 0,490 |
| <i>Phylloscopus trochilus</i>        | 0,79          | 0,47               | 0,28 | 60,65  | 2,07 | 0,482 |

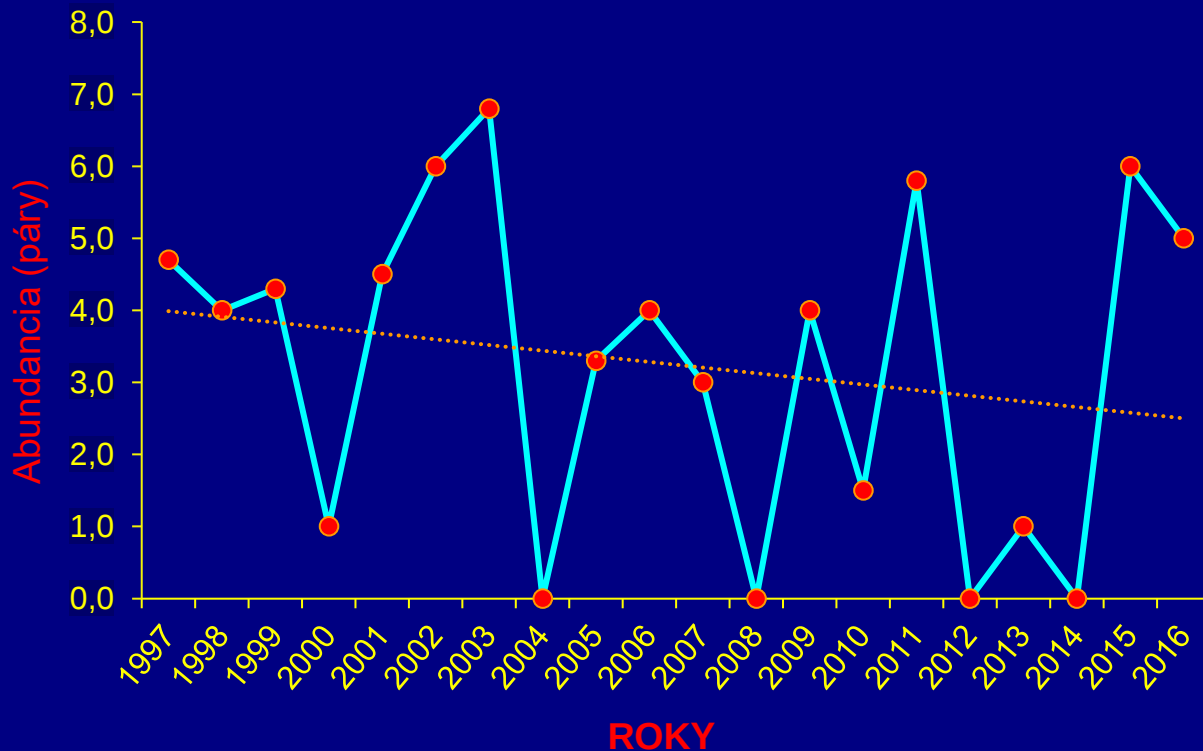
# Klasifikácia populačných trendov



| Druh                        | Smerník ± SE | Hodnota<br>t-testu | P       | Spodný 95 % interval<br>spoľahlivosti | Horný 95 % interval<br>spoľahlivosti | Klasifikácia trendu |
|-----------------------------|--------------|--------------------|---------|---------------------------------------|--------------------------------------|---------------------|
| Druhovú bohatosť            | 0.00 ± 0.22  | 0.00               | 1.0000  | −0.51                                 | 0.51                                 | neistý              |
| Celková hustota             | 0.10 ± 0.62  | 0.17               | 0.8697  | −1.32                                 | 1.53                                 | neistý              |
| <b>Potravné gildy</b>       |              |                    |         |                                       |                                      |                     |
| Konzumenti vo vzduchu       | −0.10 ± 0.10 | −1.01              | 0.3434  | −0.33                                 | 0.13                                 | neistý              |
| Konzumenti na listoch       | 0.73 ± 0.40  | 1.80               | 0.1099* | −0.18*                                | 1.38*                                | neistý              |
| Konzumenti v bylinnej etáži | −0.12 ± 0.07 | −1.86              | 0.0919* | −0.21*                                | 0.01*                                | neistý              |
| Konzumenti v hrabanke       | −0.05 ± 0.20 | −0.24              | 0.8182  | −0.50                                 | 0.41                                 | neistý              |
| Fytofágy                    | −0.23 ± 0.11 | −2.15              | 0.0634  | −0.47                                 | 0.02                                 | neistý              |
| Konzumenti na kmeni         | −0.10 ± 0.12 | −0.81              | 0.4417  | −0.37                                 | 0.18                                 | neistý              |
| <b>Hniezdne gildy</b>       |              |                    |         |                                       |                                      |                     |
| Krovinové hniezdiče         | −0.07 ± 0.21 | −0.33              | 0.7475  | −0.54                                 | 0.41                                 | neistý              |
| Korunové hniezdiče          | 0.38 ± 0.25  | 1.55               | 0.1602  | −0.19                                 | 0.96                                 | neistý              |
| Hniezdiče na zemi           | −0.11 ± 0.17 | −0.64              | 0.5426  | −0.51                                 | 0.29                                 | neistý              |
| Dutinové hniezdiče          | −0.11 ± 0.23 | −0.48              | 0.6431  | −0.64                                 | 0.42                                 | neistý              |
| <b>Migračné skupiny</b>     |              |                    |         |                                       |                                      |                     |
| Migranti mierneho pásma     | 0.24 ± 0.48  | 0.51               | 0.6245  | −0.86                                 | 1.34                                 | neistý              |
| Tropický migranti           | −0.11 ± 0.16 | −0.70              | 0.5056  | −0.49                                 | 0.26                                 | neistý              |
| Stále druhy                 | −0.02 ± 0.21 | −0.11              | 0.9158  | −0.50                                 | 0.46                                 | neistý              |

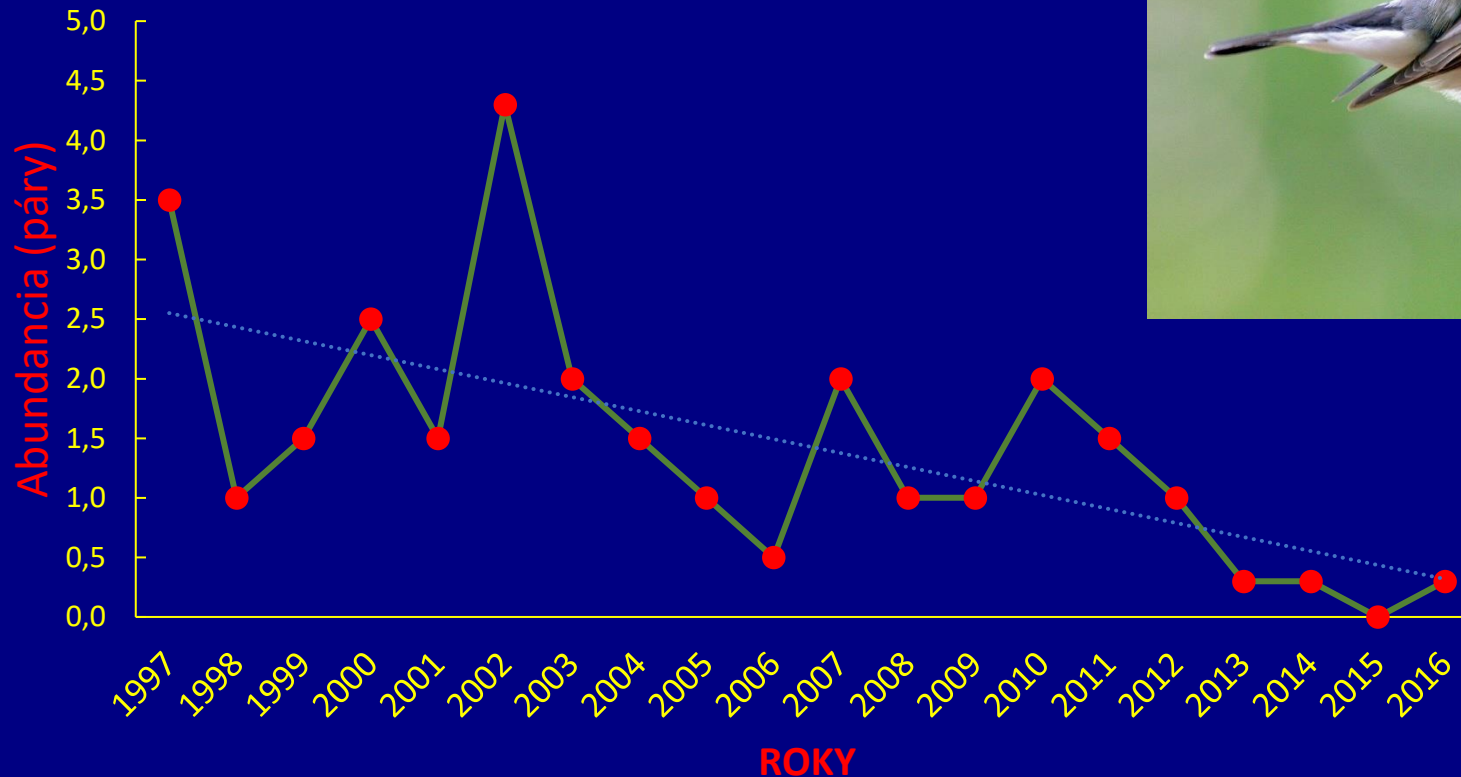
# Dynamika kolibiarika sykavého (*Phylloscopus sibilatrix*): 20-ročné výsledky

Neistý trend (2007-16);  $b = 0,20$ ;  $P = 0,494$   
95% interval spoľahlivosti: -15 až 28 %



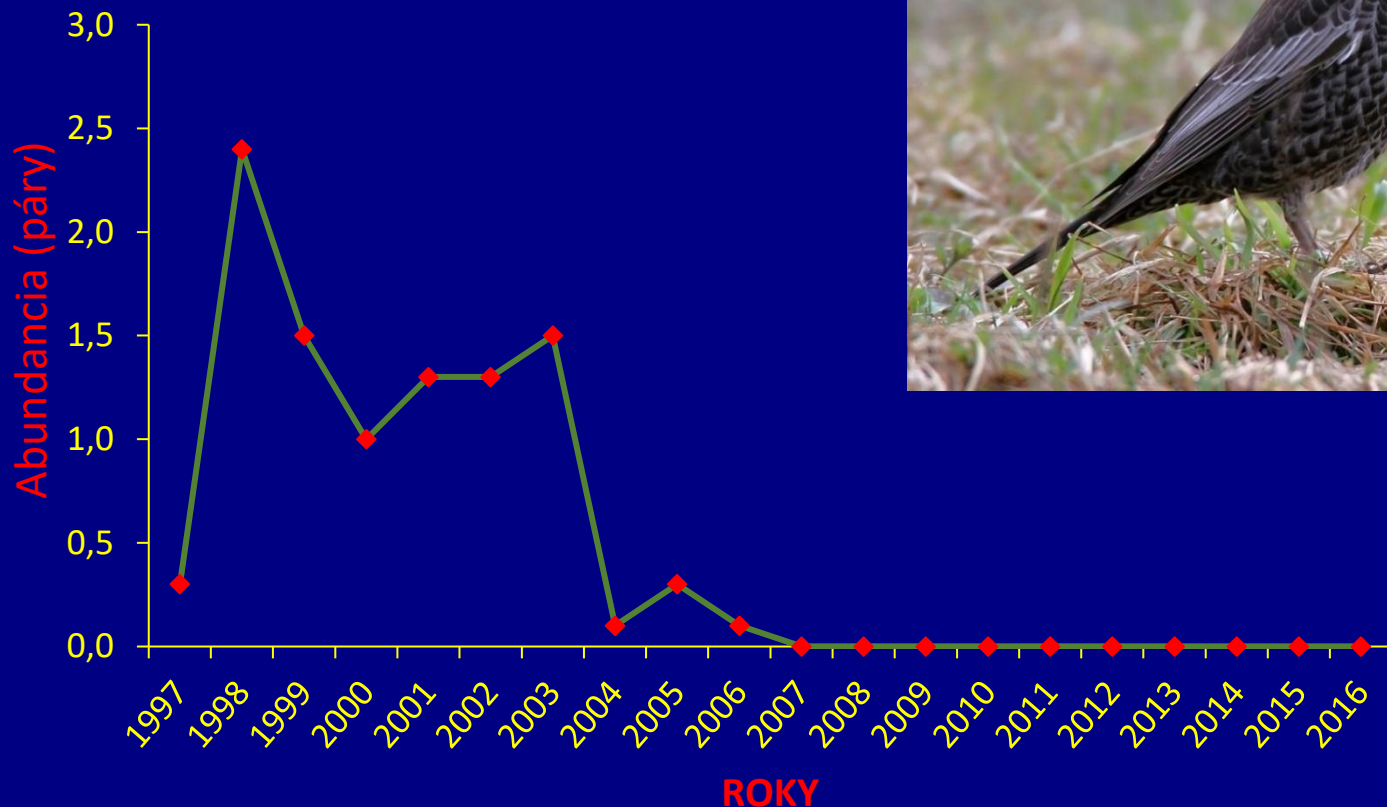
# Dynamika muchárika malého (*Ficedula parva*): 20-ročné výsledky

Mierny pokles (2007-16);  $b = -0,20$ ;  $P = 0,005$   
95% interval spoľahlivosti: -4 až -16%



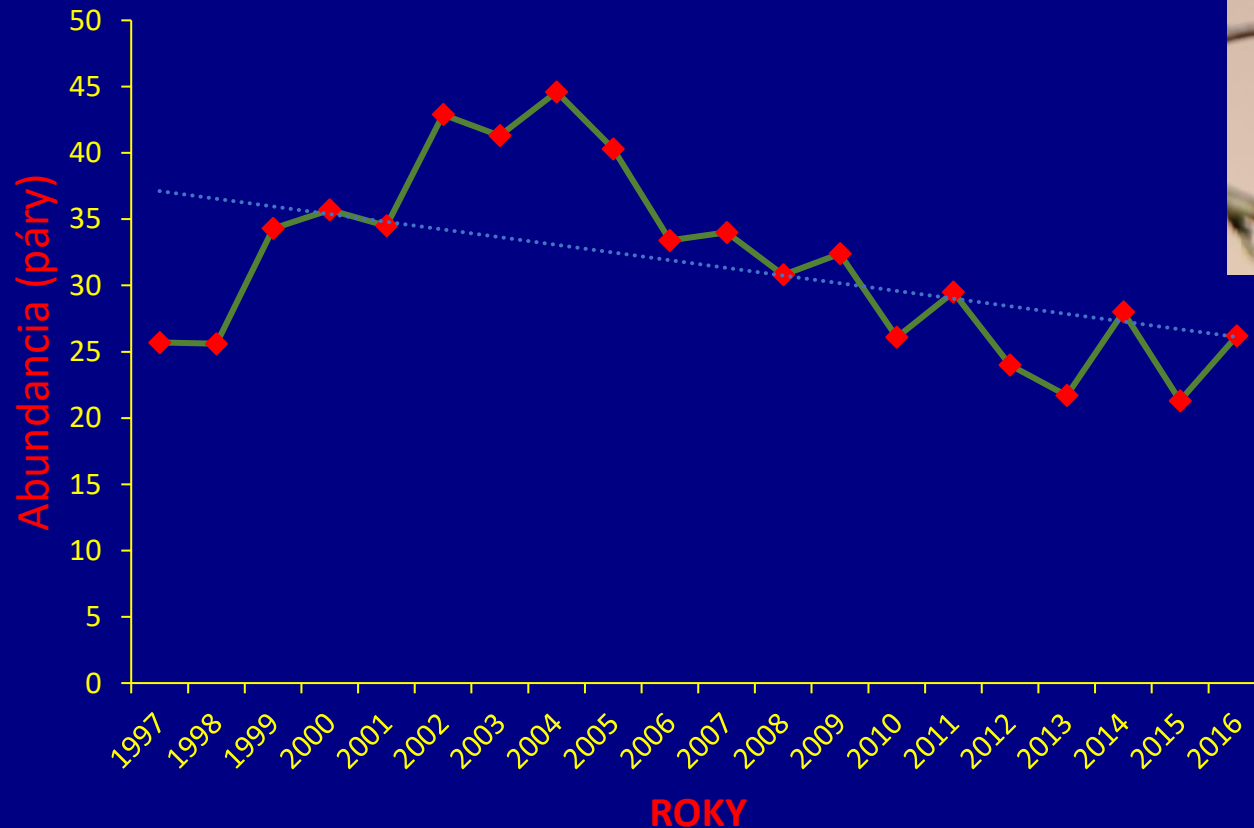
# Dynamika drozda kolohrivého (*Turdus torquatus*): 20-ročné výsledky

Výrazný pokles (2007-16)  
Pravdepodobne nehniedzdič, len 3 pozorovania pri hľadaní potravy



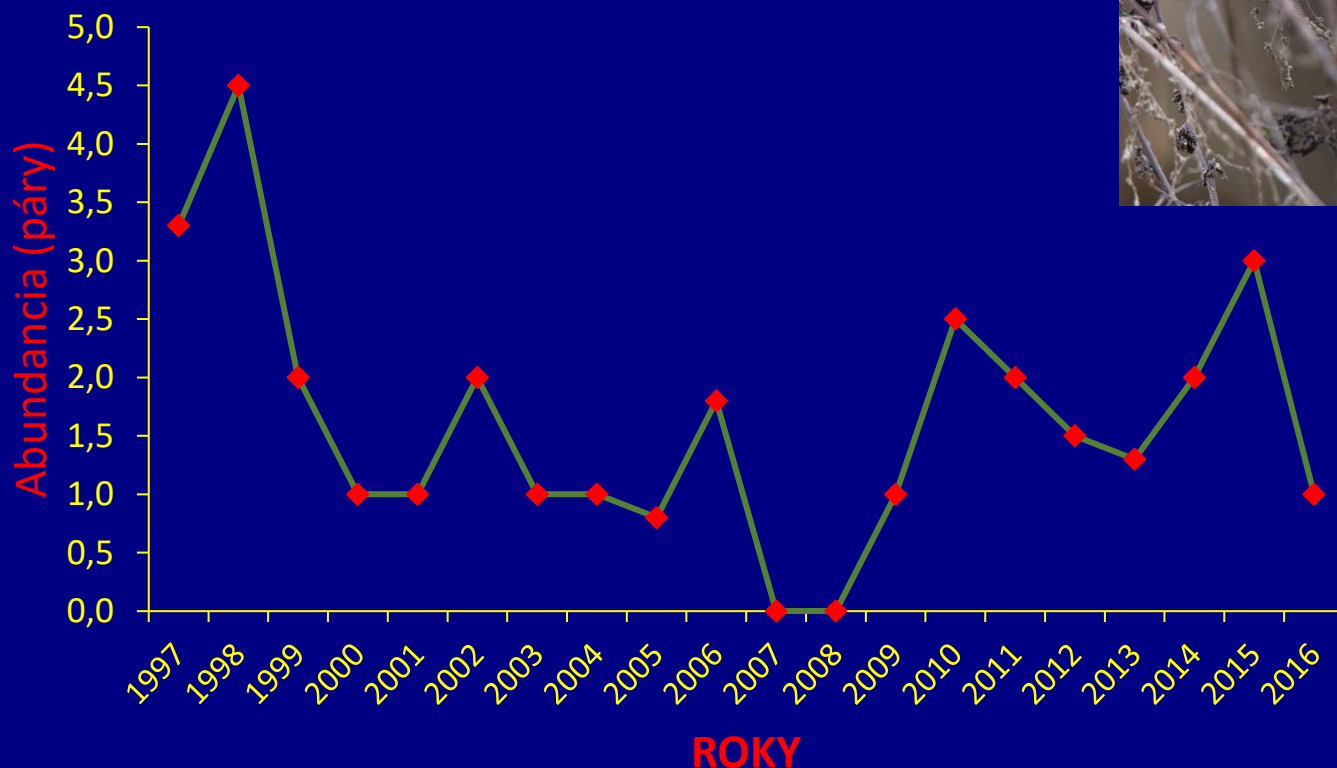
# Dynamika pinky obyčajnej (*Fringilla coelebs*): 20-ročné výsledky

Mierny pokles (2007-16);  $b = -1,08$ ;  $P = 0,012$   
95% interval spoľahlivosti: -1 až -5%



# Dynamika hýľa obyčajného (*Pyrrhula pyrrhula*): 20-ročné výsledky

Mierny nárast (2007-16);  $b = 0,21$ ;  $P = 0,035$   
95% interval spoľahlivosti: 1 až 27%



# Dynamika orieška obyčajného (*Troglodytes troglodytes*): 20-ročné výsledky

Neistý trend (2007-16);  $b = -0,13$ ;  $P = 0,507$   
95% interval spoľahlivosti:  $-9$  až  $5$  %



# Rozdeľovanie zdrojov a stromové preferencie

Oecologia  
Montana 2000,  
9, 36–43

## Interspecific foraging substrate preferences among flycatchers in a primeval mixed forest (Štrámková 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 Štrámková 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. rubra* 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 alpine 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*, *Empidonax rubecula*, *Ficedula albicollis*, *Ficedula parva*, *Monticola 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 Schotter 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, Schotter 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, Faure and Auger 1993, Richter, Oppiger, 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 Štrámková 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

Ornis Fennica 81:13–22, 2004

## Foraging ecology of two bark foraging passerine birds in an old-growth temperate forest

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This study deals with the foraging ecology of two bark foraging birds Nuthatch (*Sitta europaea*) and Eurasian Treecreeper (*Certhia familiaris*) in an old-growth temperate montane forest (Malá Fatra Mts., Western Carpathians, Slovakia). Tree species preferences and foraging behaviour were studied during four breeding periods. Both species showed similar annual dynamics in tree species preference; Beech (*Fagus sylvatica*) was avoided whereas Norway Spruce (*Picea abies*) and Sycamore (*Acer pseudoplatanus*) were preferred. Both bird species showed clear year-to-year variation in foraging patterns on Beech, but not for other tree species. In all three tree species the trunk itself and the larger branches were the most preferred foraging substrates. The Treecreeper over-utilized the trunks of Beech, Spruce and Fir (*Abies alba*) but no such differences between Treecreeper and Nuthatch were found for either Sycamore or snags. Overall, Nuthatch tends to be a broad-niched forager employing a greater variety of foraging techniques (mainly the glean and probe strategy) than Treecreeper (mostly glean and occasionally flutter chase). According to the results of this study, single-year studies might give an inaccurate picture of tree species preference by bark foraging bird species. Tree species composition may play an important role in habitat quality for both Nuthatch and Treecreeper and have implications for forest management.



### 1. Introduction

The abundance, distribution and availability of food resources are believed to be the principle factors influencing habitat suitability for birds (Cody 1974, Martin 1987) with several recent studies supporting this view (Strong & Sherry 2000, Johnson & Sherry 2001, Fayt 2003). There are inherent methodological difficulties associated with quantifying food resources, evaluating food availability and prey selection (e.g. Cooper & Whitmore 1990, Johnson 2000). Studying foraging behav-

iour has become widely accepted in both management studies and applications (e.g. Steeger & Hitchcock 1998, Gabbe *et al.* 2002) as an alternative whereby differences in microhabitat use and foraging behaviour are thought to reflect differences in the use of the food resources themselves (MacArthur 1958).

Several studies have pointed to the strong foraging preferences of some bird species for particular tree species (Holmes & Robinson 1981, Parrish 1995, Gabbe *et al.* 2002, Adamík *et al.* 2003). Apart from the theoretical considerations of such

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Taylor & Francis  
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## Tree species preferences of foraging insectivorous birds in a primeval mountain mixed forest: implications for management

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**ABSTRACT** Bird-plant species associations can be an important component of habitat selection in forest birds. We assessed tree species preferences of foraging insectivorous birds in a primeval beech-fir forest in north-west Slovakia, hypothesizing that bird population densities are negatively associated with foraging specialization. We sampled foraging behaviour by random point observations from mid-May until the end of July during 1997–2003. Significant preference or avoidance patterns were found in 16 of 17 bird species. Based on the tree preference index, we distinguished four main foraging specializations: generalists, deciduous specialists, coniferous specialists, and dead wood specialists. Many bird species showed strong preferences for such rare and uncommon tree species as wych elm (*Ulmus glabrus*), sycamore (*Acer pseudoplatanus*), and Norway spruce (*Picea abies*). European beech (*Fagus sylvatica*), hazel (*Corylus avellana*), and rowan (*Sorbus aucuparia*) were generally avoided. Birds with low densities tended to be more selective, but that effect was not statistically significant. Population variability was not significantly associated with foraging specialization. We hypothesize that impoverishment of tree species diversity within forest stands could lead to less diverse bird assemblages composed of species specialized on those tree species remaining and of generalist foragers able to adapt to a wide range of foraging substrates.

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**KEYWORDS**  
Beech; foraging; habitat selection; foraging niche; forest birds; trophic interactions; old-growth forest; Štrámková National Nature Reserve

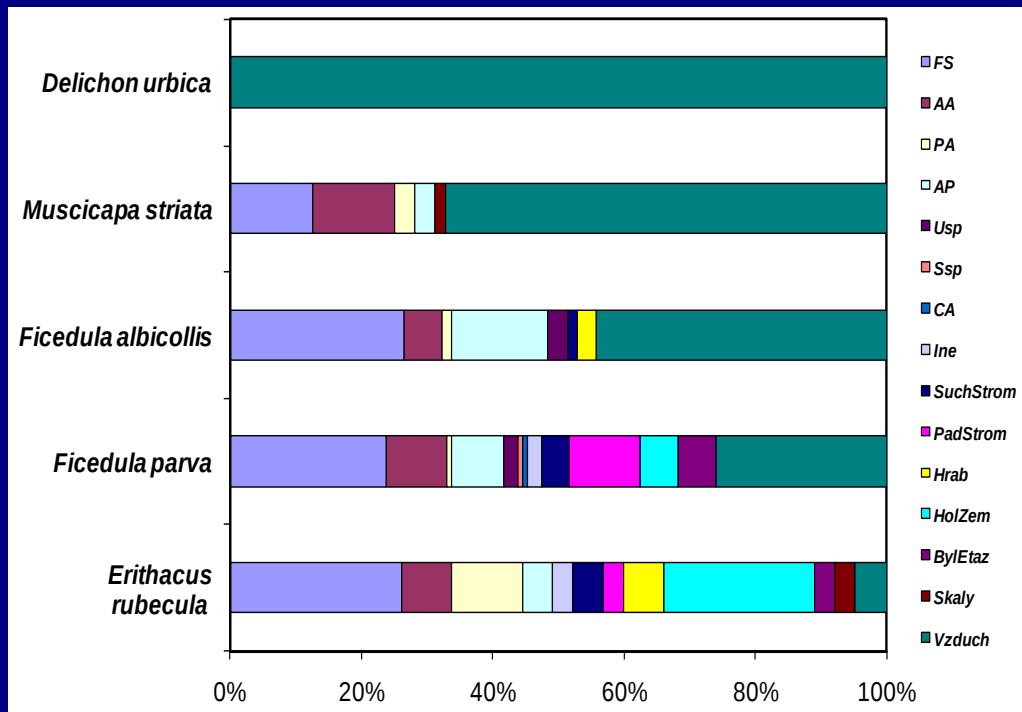
### Introduction

Habitat selection by birds is likely to be a multistep process wherein both vegetation structure and species composition (floristics) are key determinants. Such other factors as predation pressure (Fontaine & Martin 2006) and conspecific (Betts *et al.* 2008; Fletcher 2009) and heterospecific attraction (Mönkkönen *et al.* 1990; Sebastián-González *et al.* 2010) have also been shown to play roles in some systems. The seminal work by MacArthur and MacArthur (1961) highlighted the role of vegetation structure, but an accumulating number of studies have provided evidence also for the importance of floristic composition (e.g. Wiens 1989; Lee & Rotenberry 2005). The results of these studies indicate that the diversity and abundance of forest bird species positively correlate with tree species diversity (Peck 1989; Lee & Rotenberry 2005). Tree species host variable insect assemblages and possess different structural properties (e.g. leaf shape, petiole length, branching patterns, and bark structure), which can account for the co-evolved foraging preference exhibited by many bird species in a variety of forest types (Francis 1978; Holmes & Robinson 1981; Robinson & Holmes 1984; Peck 1989; Gabbe *et al.* 2002; Adamík & Korňan 2004; Böhm & Kalko 2009; Beltrán & Wunderle 2013). Bird species preferences for foraging in particular tree species have been shown to be strongest in habitat specialists or in those species which occur in low densities (Holmes & Robinson 1981; Gabbe *et al.* 2002). Although birds were found to prefer tree species with high arthropod biomass

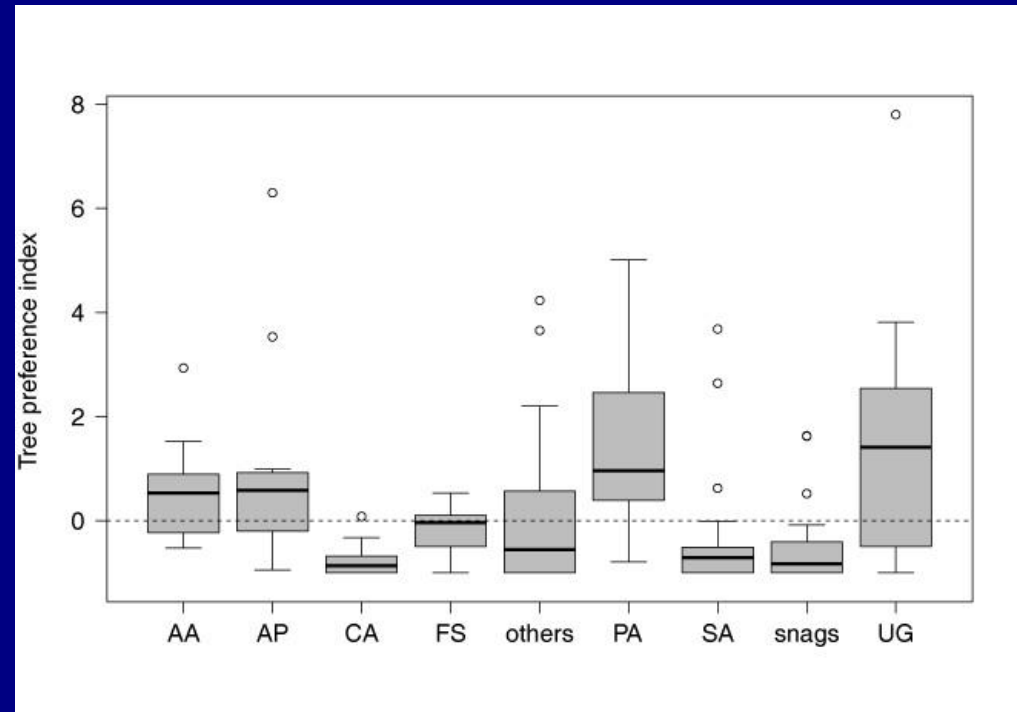
Díaz *et al.* 1998; Beltrán & Wunderle 2013), this is not always the case (Abbott & Van Heurck 1985; Holmes & Schultz 1988; Unno 2002). Among the main reasons that bark foraging on trees does not necessarily track arthropod biomass are innate or learned preferences, morphological constraints of birds, and food accessibility due to foliage structure or prey behaviour (Hildén 1965; Holmes & Schultz 1988; Whelan 1989, 2001; Leisler & Winkler 1991; Davis & Stamps 2004). Experimental studies in avian evaluating tree species choice among birds often have found strong preferences for particular tree species. Most authors identified these preferences to be driven intrinsically (Partridge 1974; Emilen & Dekong 1981; Grünberger & Leisler 1990; Parrish 1995; Adamík & Bureš 2007). This means that they are either innate, genetically determined for a given habitat (Partridge 1974; Grünberger & Leisler 1990), or a consequence of learning and imprinting (i.e. the individual's experience with natal habitat during an ontogenetically sensitive period leads to imprinted preferences for its natal habitat) (Davis & Stamps 2004; Slegvad & Wiebe 2007). Tree preferences must therefore be considered when assessing bird-habitat interactions, especially in the context of sustainable forest management. The key argument here is that forestry practices favouring certain tree species at the expense of others are likely to impact bird species, too, and especially those with specific habitat requirements (Holmes & Schultz 1988; Gabbe *et al.* 2002). The fundamental assumption is that removing preferred tree species or snags could significantly impoverish

# Rozdeľovanie zdrojov a stromové preferencie

Využívanie potravných substrátov v gilde evertibratófágov vo vzduchu (mucháriky)



Preferencie kŕmenia na stromoch u 17 insektivorných druhoch vtákov



# Potravná selektivita (úroveň špecializácie) a populačné hustoty

Existuje súvislosť medzi potravnou špecializáciou v zmysle selektivity využívania stromov a populačnými hustotami?

**Predpoklad:** Úzko špecializované druhy, ktoré preferujú isté druhy stromov by mali mať nižšie populačné hustoty v ornitocenóze ako generalisti, ktorý sú potravné euryekný.

Podpora: Holmes & Robinson 1981. *Oecologia* 48: 31–35.

korelácia medzi indexom preferencie stromov a priemernými hustotami silne negatívna ( $\rho = -0,789$ ;  $P < 0,01$ )

Gabbe et al. 2002. *Conservation Biology* 16: 462–470.

korelácia medzi indexom preferencie stromov a priemernými hustotami okrajovo signifikantná ( $\rho = -0,533$ ;  $P = 0,061$ )

Korňan & Adamík 2017. *Scandinavian Journal of Forest Research* 32: 671–678.

korelácia medzi indexom preferencie stromov a priemernými hustotami negatívna ale nesignifikantná na úrovni ornitocenózy ( $\rho = -0,28$ ;  $P = 0,1339$ ) aj gíld

# Populačná stabilita a potravná selektivita (špecializácia)

Hypotéza Korňana & Adamíka 2017. Scandinavian Journal of Forest Research 32: 671–678.: Existuje súvislosť medzi populačnou stabilitou a potravnou špecializáciou v zmysle stromových preferencií.

Predpoklad: Úzko špecializované druhy, ktoré preferujú isté druhy stromov by mali mať nižšiu populačnú stabilitu z dôvodu väčšej fluktuácie zdrojov v ornitocenóze ako generalisti, ktorý sú schopný viac flexibilne prepínať medzi druhmi stromov lepšími potravnými adaptáciami.

Podpora hypotéza sa nepotvrdila: korelácia medzi indexom preferencie stromov a indexom populačnej variability (PV) na úrovni ornitocenózy ( $\rho = 0,12$ ;  $P = 0,684$ ) aj gildi zberačov z listov ( $\rho = 0,23$ ;  $P = 0,7379$ ) boli nesignifikantne pozitívne.

# Kompenzačná dynamika, druhové asociácie a koncepcie organizácie spoločenstiev

Myšlienka medzidruhovej konkurencie (kompetície): Darwin, Gleason, Voltera, Hutchinson, MacArthur a Diamond.

Šachovnicová distribúcia (checkerboard distribution) resp. komplementárna distribúcia (complementary distribution).

Diamondove (1975, s. 344) pravidlo organizácie spoločenstiev: „Niektoré páry druhov nikdy nekoexistujú, buď navzájom alebo ako súčasť väčšej kombinácie.“

Priestorová segregácia druhov alebo časová segregácia sa dá chápať ako negatívna asociácia druhov t.j. jeden druh priestorovo alebo časovo vylučuje alebo limituje druhý, tak, že ich interakcie spôsobujú zníženie populačných hustôt jedného alebo druhého.

Štatistické predpoklady pre šachovnicovú distribúciu: Indexy pozorovaného „šachovnicového skóre (C-skóre)“ alebo „šachovnicového indexu“ by mali byť signifikantne vyššie ako hodnota generovaná nulovým modelom.

| Študijná plocha                      | Lokalita                       | Typ biotopu                                          | Časové rozpätie(roky) | Veľkosť plochy (ha) |
|--------------------------------------|--------------------------------|------------------------------------------------------|-----------------------|---------------------|
| Národná prírodná rezervácia Šrámková | Európa, Slovensko              | bukovo-jedľový prales                                | 1997-2006 (10)        | 27,5                |
| Białowiežský národný park, plocha CM | Európa, Poľsko                 | dubovo-lipovo-hrabový prales                         | 1975-2014 (40)        | 24                  |
| Białowiežský národný park, plocha K  | Európa, Poľsko                 | riečny jelšovo-jaseňovo-smrekový prales              | 1975-2014 (40)        | 33                  |
| Białowiežský národný park, plocha L  | Európa, Poľsko                 | jelšový slatinný prales                              | 1976-2014 (37)        | 25                  |
| Białowiežský národný park, plocha MS | Európa, Poľsko                 | dubovo-lipovo-hrabový prales                         | 1975-2014 (40)        | 30                  |
| Białowiežský národný park, plocha NE | Európa, Poľsko                 | smrekovo-borovicovo-brezový prales                   | 1975-2014 (40)        | 25                  |
| Białowiežský národný park, plocha NW | Európa, Poľsko                 | smrekovo-borovicovo-brezový prales                   | 1975-2014 (40)        | 25                  |
| Białowiežský národný park, plocha W  | Európa, Poľsko                 | dubovo-lipovo-hrabový prales                         | 1975-2014 (40)        | 25.5                |
| Słowacki park, Mesto Wrocław         | Európa, Poľsko                 | mestský park                                         | 1970-1999 (29)        | 7-7,5               |
| Pohorie Gaisatjakke and Valle        | Európa, Švédsko                | subalpínsky brezový prales                           | 1963-1999 (37)        | 36,2-62,2           |
| Estenstadský les                     | Európa, Nórsko                 | druhotný smrekový les                                | 1960-1972 (12)        | 100                 |
| Finsefetene sedimentačná rovina      | Európa, Nórsko                 | bariny, vodné plochy, náplavové duny                 | 1967-1984 (18)        | 100                 |
| Údolie vtáčie spevu                  | Európa, Švédsko                | izolovaný druhotný dubovo-jaseňový les               | 1953-2009 (57)        | 13                  |
| Národný park Dalby Söderskog         | Európa, Švédsko                | druhotný jaseňovo-brestovo-dubovo-bukový les         | 1980-1993 (13)        | 37                  |
| Ammarnäs región, plocha K1           | Európa, Švédsko                | alpínske suché vresovisko a močiar                   | 1964-1983 (20)        | 100                 |
| Ammarnäs región, plocha K2           | Európa, Švédsko                | alpínske suché vresovisko a močiar                   | 1964-1983 (20)        | 100                 |
| Les Bookham Common                   | Európa, Anglicko               | izolovaný druhotný dubový les                        | 1950-1975 (25)        | 16,19               |
| Experimentálny les Hubbard Brook     | Severná Amerika, New Hampshire | druhotný bukovo-javorovo-brezový les                 | 1969-2013 (45)        | 10                  |
| Les Williama Trelease                | Severná Amerika, Illinois      | izolovaný primárny javorovo-brestovcovo-jaseňový les | 1927-1976 (44)        | 24                  |

# Analýza druhových asociací pomocí nulových modelů: tři hierarchické úrovně



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Basic and Applied Ecology 31 (2018) 72–81

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## Pairwise null model analyses of temporal patterns of bird assemblages contradict the assumptions of competition theory

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### Abstract

Compensatory dynamics assume inverse patterns of population dynamics of species with similar ecological resource requirements (temporal segregation). The objective of this study was to test this hypothesis on temporal samples (10–57 years) of 19 breeding bird assemblages of various habitats. We used presence/absence null model (SIM2) in combination with the C-score and Sørensen indices. The C-score index estimates the average number of checkerboards for two species, while the Sørensen index measures the qualitative similarity of co-occurrence between two species in a time series. We used pairwise null model analysis to select significant species pairs based on three selection criteria: the standard confidence interval criterion, conservative empirical Bayes mean based criterion and confidence limit based criterion. Altogether, 21 402 species pairs were analysed. The SIM2 algorithm detected from 157 to 7 segregated pairs depending on the selection criterion. The number of significant negative pairs with possible biological significance (foraging guild membership, predator–prey interactions) was far lower and represented approximately 0.0–0.3% (4–65) of pairs in a matrix. Indeed, the number of detected negative associations depended on the selection criterion. Moreover, the number of segregated pairs was negatively related to the area of the census plots and fill of the species matrix. Our results underline the minor importance of interspecific competitive interactions in temporal patterns of bird assemblages. Instead, we suggest that stochastic factors, climate or heterospecific social information may lead to more or less synchronous dynamics of bird pairs.

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**Keywords:** Bird community; Co-occurrence; Compensatory dynamics; Species associations; Null model analyses; Pairwise analyses; Empirical Bayes approach; Presence/absence matrices

### Introduction

Testing community assembly patterns has become one of the major tasks in community ecology in the past decades (Weiher & Keddy 1999). The most influential assembly rule

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## ORIGINAL RESEARCH

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## Null model analyses of temporal patterns of bird assemblages and their foraging guilds revealed the predominance of positive and random associations

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### Abstract

Patterns of species associations have been commonly used to infer interactions among species. If species positively co-occur, they may form predominantly neutral assemblages, and such patterns suggest a relatively weak role for compensatory dynamics. The main objective of this study was to test this prediction on temporal samples of bird assemblages ( $n = 19$ , 10–57 years) by the presence/absence and quantitative null models on assemblage and guild levels. These null model outcomes were further analyzed to evaluate the effects of various data set characteristics on the outcomes of the null models. The analysis of two binary null models in combination with three association indices revealed 20% with significant aggregations, 61% with random associations, and only 19% with significant segregations ( $n = 95$  simulations). The results of the quantitative null model simulations detected more none-random associations: 61% aggregations, 6% random associations, and 33% segregations ( $n = 114$  simulations). Similarly, quantitative analyses on guild levels showed 58% aggregations, 20% segregations, and 22% random associations ( $n = 450$  simulations). Bayesian GLMs detected that the outcomes of the binary and quantitative null models applied to the assemblage analyses were significantly related to census plot size, whereas the outcomes of the quantitative analyses were also related to the mean population densities of species in the data matrices. In guild-level analyses, only 9% of the GLMs showed a significant influence of matrix properties (plot size, matrix size, species richness, and mean species population densities) on the null model outcomes. The results did not show the prevalence of negative associations that would have supported compensatory dynamics. Instead, we assume that a similar response of the majority of species to climate-driven and stochastic factors may be responsible for the revealed predominance of positive associations.

### KEYWORDS

birds, community ecology, compensatory dynamics, co-occurrence indices, effects of matrix properties, species association

[Correction added on 16 July 2019, after first online publication: The supporting information was previously incorrect and files are now presented correctly in this version.]

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www.ecoevol.org | 8541

# Analýza druhových asociácií pomocou nulových modelov

**Gotelli & Graves (1996. Null models in ecology)** definovali analýzu nulovými modelmi ako štatistický vzorec generujúci model založený na randomizácii (Monte Carlo prístup) ekologických údajov alebo náhodnom prevzorkovaní z poznanej alebo špecifikovanej distribúcie.

## Dva základné typy nulových modelov:

Binárne – prezencia/absencia druhov

Kvantitatívne – abundancia druhov

## Tri hierarchické úrovne:

Druhové páry

Potravné gildy

Cela taxocenóza

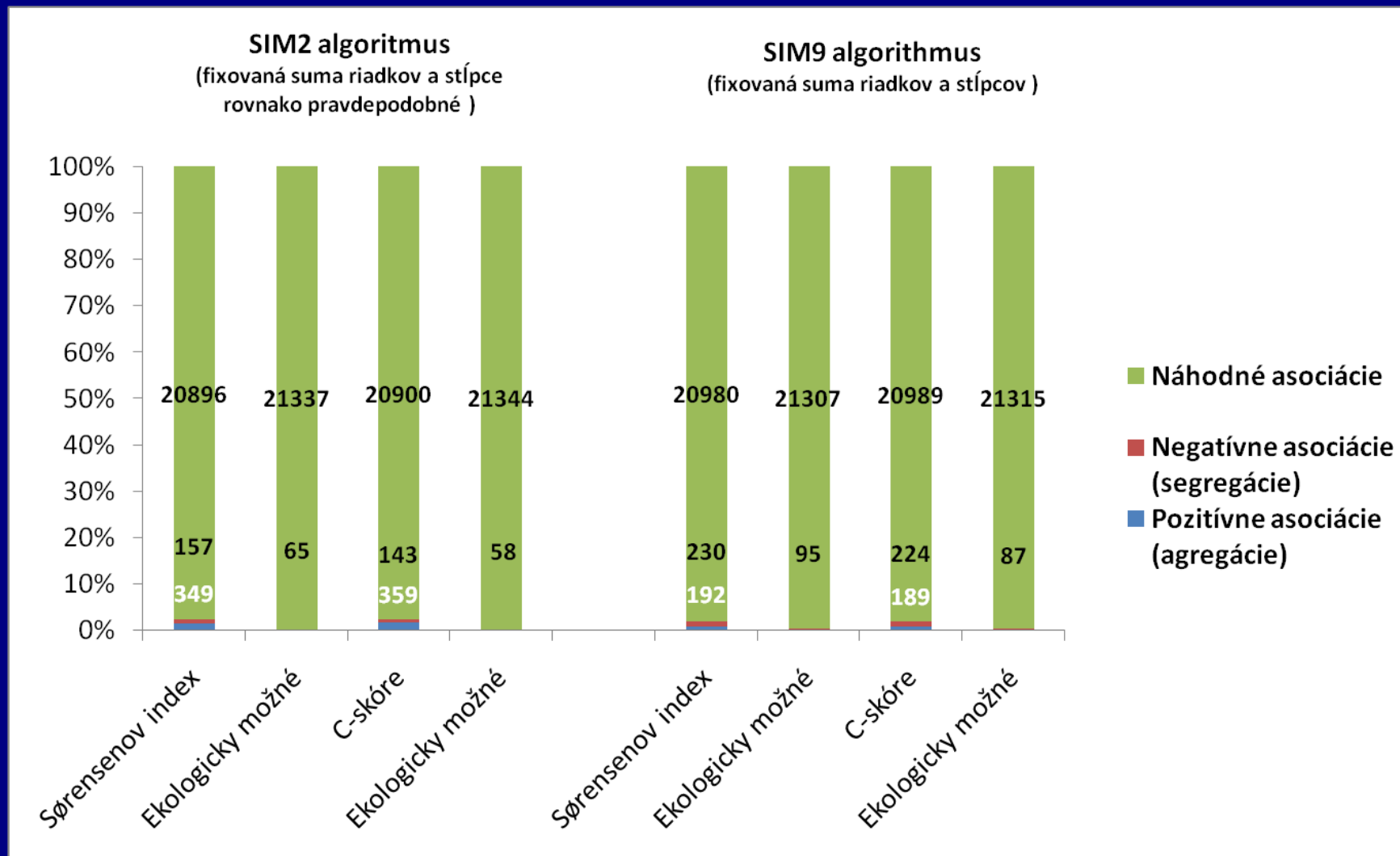
## Dva základné typy analýzy druhových asociácií pomocou nulových modelov:

Párový prístup (pairwise approach)

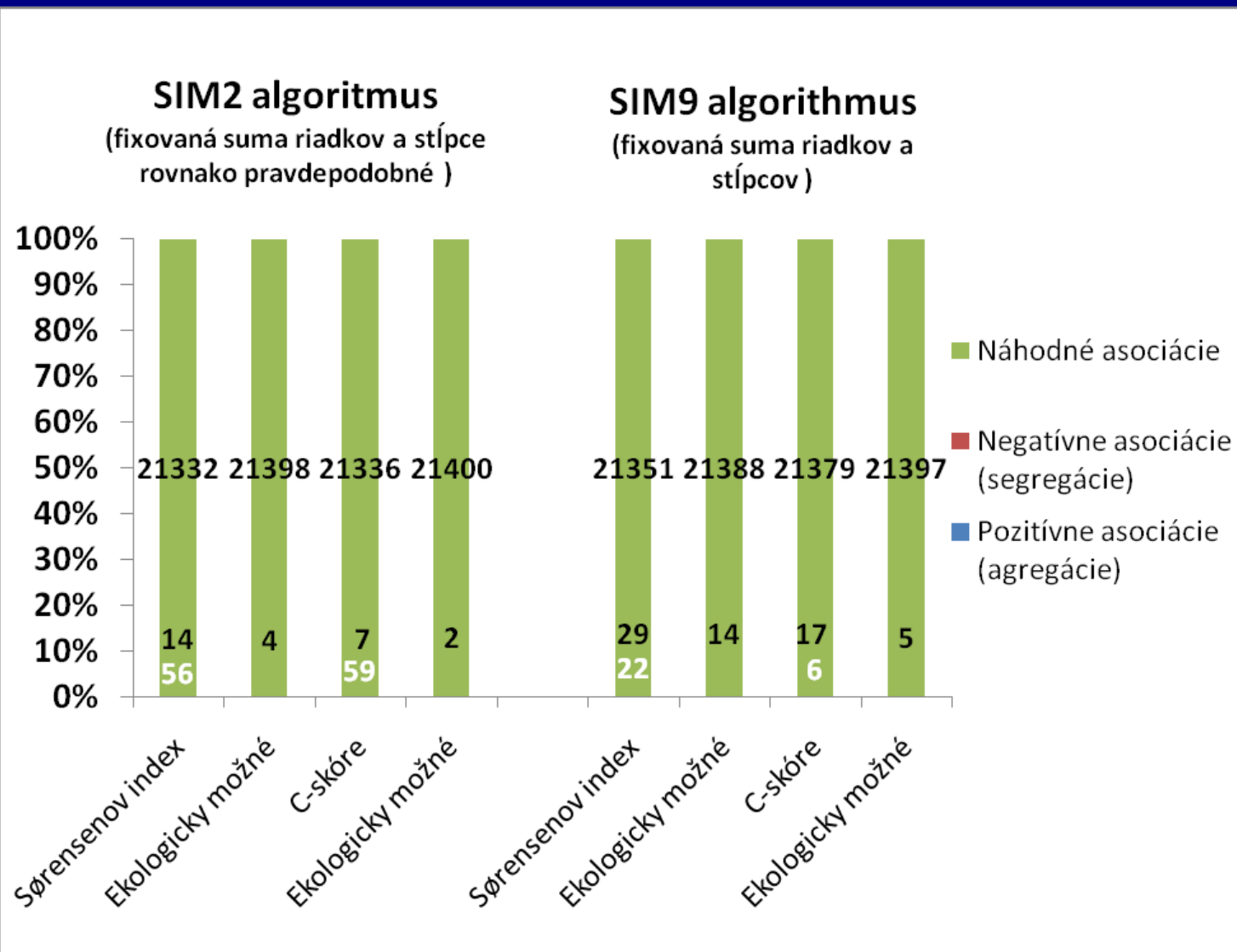
Prístup na úrovni celého spoločenstva alebo gíld (assemblage-wide or guild approach)

# Analýza druhových asociácií nulovými modelmi tradičným prístupom: úroveň druhových párov

Binárne (prezencia/absencia) nulové modely a asociačné indexy, tradičné IS



# Analýza druhových asociácií nulovými modelmi a Bayesov empirický prístup: úroveň druhových párov

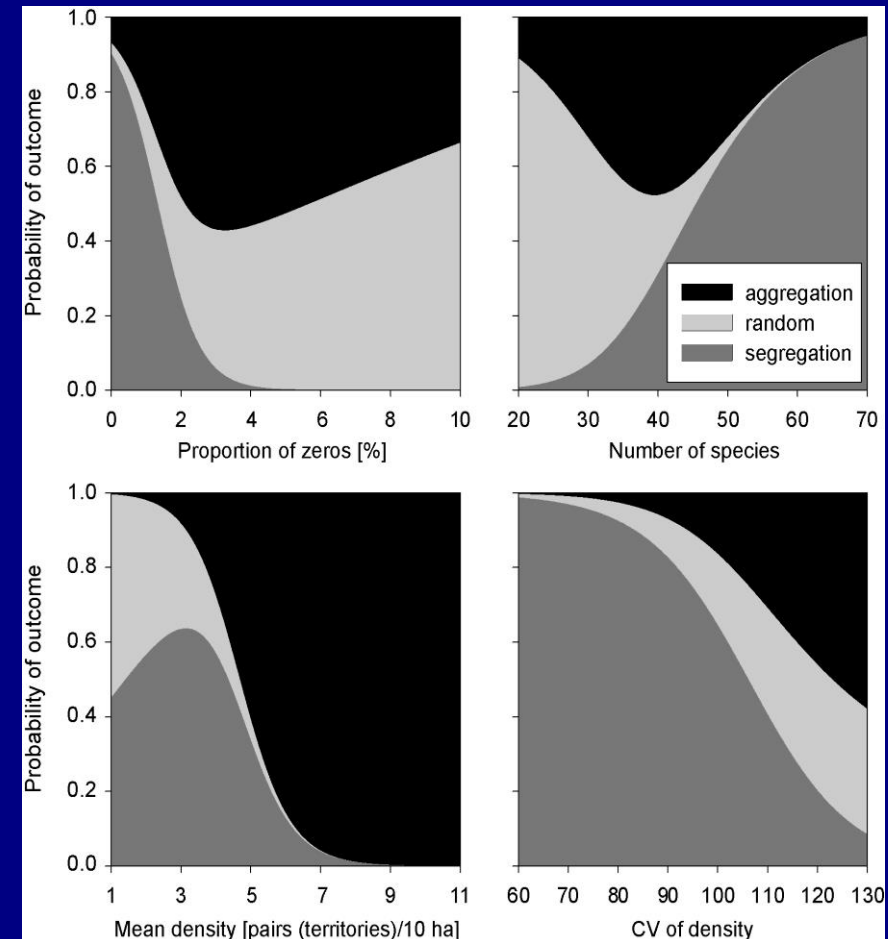
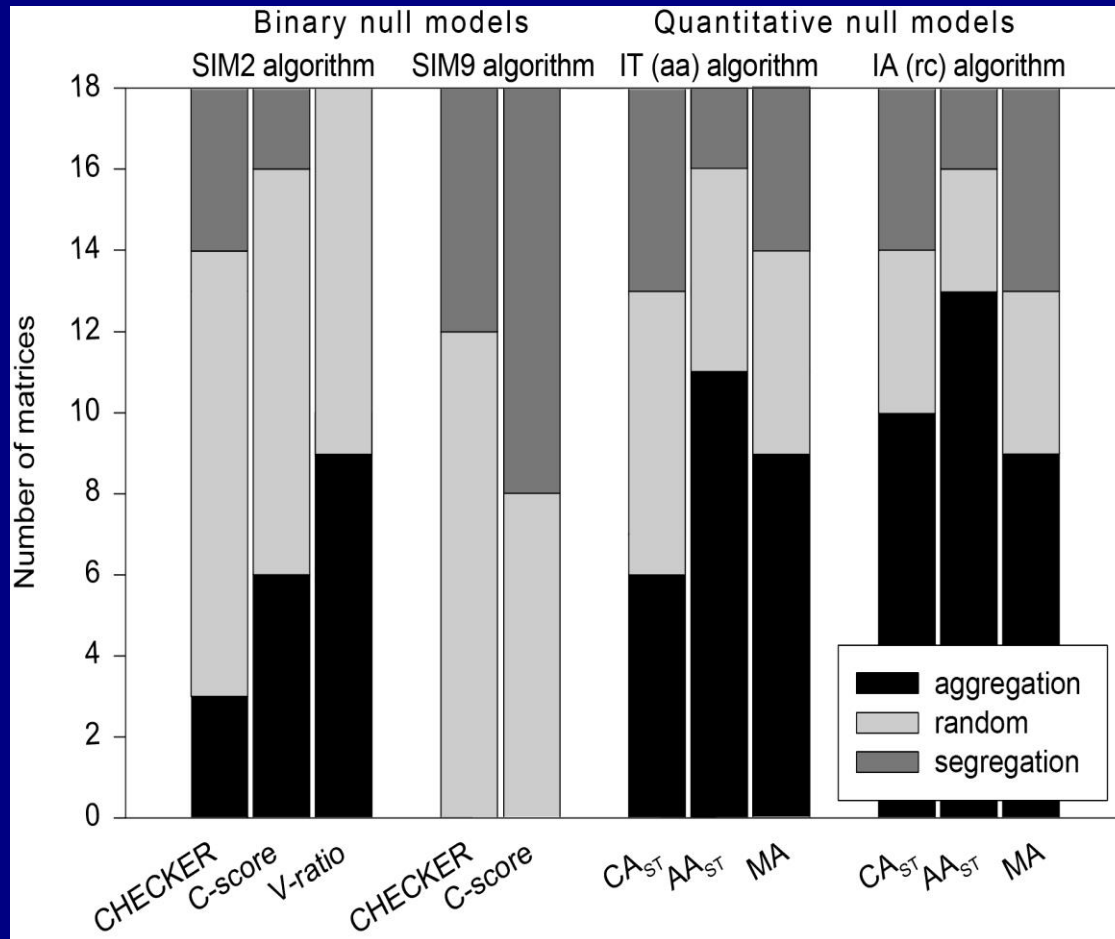


Binárne nulové modely a asociačné indexy

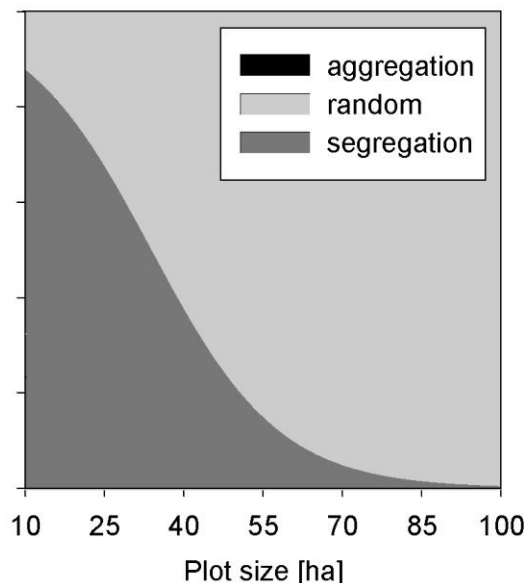
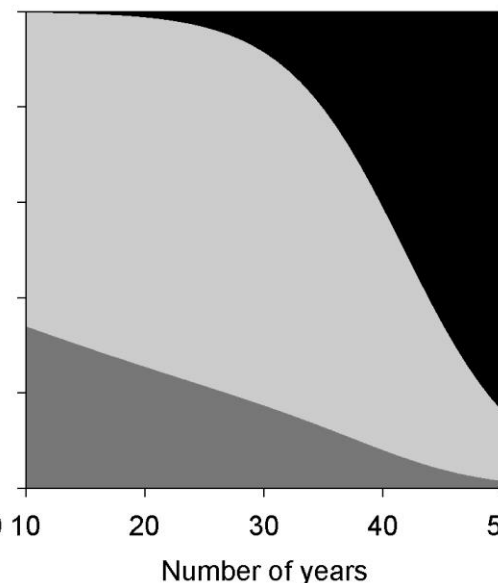
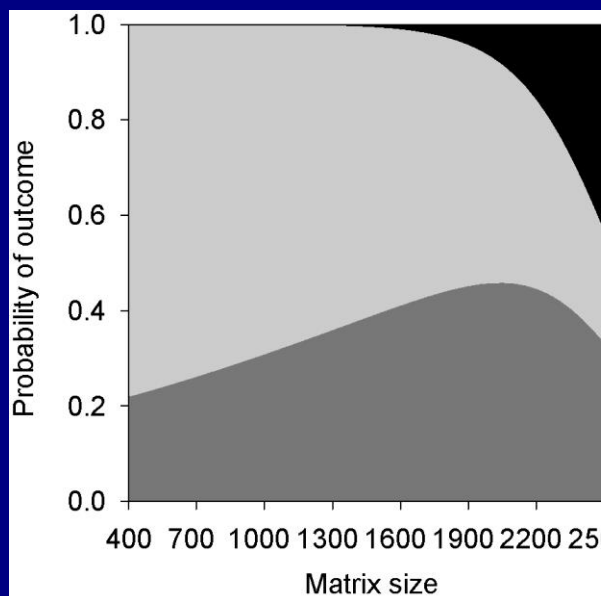
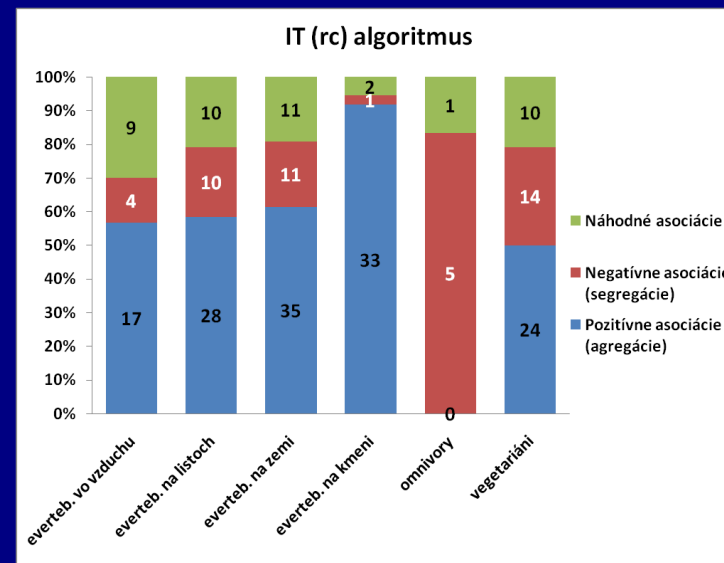
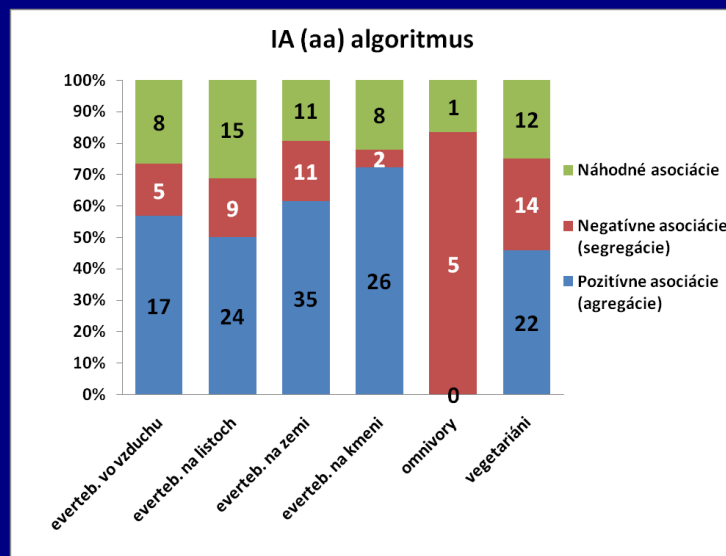
Baysove kritérium podľa intervalov spoľahlivosti

# Analýza druhových asociácií nulovými modelmi: úroveň zoskupenia

Binárne (prezencia/absencia) a kvantitatívne nulové modely a asociačné indexy



# Analýza druhových asociácií nulovými modelmi: úroveň gíld



# Aplikácie pre manažment lesov, vtákov a prírody

BIOLOGICKE LISTY 70 (3): 81–106, 2005

## Koncepcia štruktúralno-funkčnej organizácie spoločenstiev: gildy a funkčné skupiny

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## 1. Teória evolúcie a medzidruhovej konkurencie

Jedným zo základných pilierov modernej ekológie bolo vytvorenie modelu fungovania spoločenstiev a ekosystémov. Ako jeden z hlavných evolučných mechanizmov formujúcich a determinujúcich organizáciu a funkciu spoločenstiev a ekosystémov je chápaná medzidruhová konkurencia. Táto teória je založená na predpokladoch, že syntypické druhy obývajúce rovnaký ekologický priestor v rovnakom čase bojujú o prežitie – potrava a priestor. V širšom chápaní je to vlastne aplikácia Darwinovej (1859) teórie o pôvode druhov prirodzeným výberom. Darwinova teória je zameraná predovšetkým na vnútrodruhovou konkurenciu ako mechanizmus selekcie najkvalitnejších jedincov. Teória medzidruhovej konkurencie je aplikácia tohto princípu na vyššej hierarchickej úrovni (spoločenstvo, ekosystém), čím vlastne neší výber najvhodnejších druhov v daných ekologických podmienkach.

Uplatnilo takmer storočie od prvého vydania Darwinovho diela „Vznik druhov prirodzeným výberom alebo zachovanie vhodných druhov v boji o život“, keď bola prvýkrát oficiálne prijatá matematicky formulovaná teória viacrozmernej ekologickej niky (Hutchinson 1957, MacFadyen 1957), ktorá umožnila rigorózne štúdium ekologických nárokov druhov v závislosti od súboru faktorov prostredia. Týmto bol vytvorený prvý predpoklad na štúdium a testovanie medzidruhovej konkurencie na vyšších hierarchických úrovniach. Bol to veľký zlom a progresívny posun v histórii tohto vedného odboru, ktorý dramaticky

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## Hodnotenie vplyvu lesohospodárskeho využívania lesov na vtácie zoskupenia: literárna rešerš

*Evaluation of silviculture practices impact on forest bird assemblages: A review*

Martin KORŠAN

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*Intensive silviculture in the Slovak large-scale protected areas may seriously damage the original patterns of biodiversity, ecosystem structure, dynamics and stability. Our primary objective was to evaluate the current silvicultural practices and their effects on bird assemblages, based on previous studies. The second objective is to propose an optimal silvicultural strategy for re-establishing as close as possible the original landscape structure and biodiversity. Four basic forest thinning regimes (clear-felling, shelterwood cutting, group-felling, and selection cutting) are described and evaluated. Their impacts on forest interior structure, landscape patchiness, and forest temporal dynamics are discussed. Suitability of the thinning regimes is mainly evaluated based on the changes in species structure and density of avian assemblages during the forest development: from the establishment phase through pre-thicket, thicket to maturation phase. In general, clear-felling and selection cutting are two extremes of high forest management. Clear-felling is typical by creating small-sized forest patches of various ages, each consisting of even-aged trees. These patches represent all developmental stages of planted forest type. In contrast, selection cutting is based on removing individual trees, and it results in creating vertically very heterogeneous forests with well-developed all vegetation layers. The foliage profile of such a wood is extremely complex. Selection cutting in combination with group selection follows the natural dynamics of forest and leads to development of close-to-original bird assemblages, not just from aspect of species composition but also with similar population densities. Growing forest with native plant composition and plant species genotype managed by selection and group selection may be the first crucial step to sustainable forestry in our protected areas.*

## Úvod

Vo väčšine národných parkov Slovenska hospodárske lesy zaberajú hlavnú časť územia v porovnaní s lesmi v prírodných rezerváciách a lesmi osobitného určenia. Vzhľadom na zákonom stanovené pravidlo, že v teritóriu národných parkov sú priority ochrany prírody nadradené všetkým ostatným záujmom, je nutné pripraviť akceptovateľnú stratégiu manažmentu lesných celkov, ktorá by bola prijateľná predovšetkým pre potreby ochrany prírody a zachrán populácií ohrozených rastlín a živo-

číchov a taktiež zohľadňovala aj ekonomické záujmy lesného hospodárstva.

Cieľom tejto literárnej rešerše je pripraviť stručné hodnotenie poznatkov o vplyve jednotlivých bežne používaných spôsobov lesného hospodárstva na diverzitu a stabilitu vtáčích zoskupení. Vzhľadom na to, že na Slovensku sa doposiaľ nerealizovalo žiadne komplexnejšie štúdium, ktoré by dostatočne pokrývalo tým, bolo nutné vychádzať zo zahraničných monografií venovaných tejto téme, predovšetkým zo skúsenosti z Veľkej Británie, USA, Kanady a Fínska. Rešerš okrajovo zahŕňa aj výsledky

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## Vplyv výstavby lyžiarskych stredísk a zimnej rekreácie na vtáky: rešerš

*Effects of building ski resorts and winter recreation on birds: a review*

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*Abstract. Ski tourism negatively affects wildlife in mountain ecosystems. The Slovak society has nowadays faced a rapid increase in number of running ski resorts over whole country. Rigorously designed ornithological studies focused on effects of existing ski resorts on avifauna are lacking, consequently I tried to review existing knowledge on this topic from foreign countries; published primarily in database Web of Science. I focused on effects of resorts' construction and winter recreation on mortality, abundance, species richness, diversity, stress, home ranging behaviour, time budget and foraging ecology of birds. Electric and lift cable lines cause mortality of birds, especially gullsiforms, and can affect fluctuation patterns and viability of affected populations. Construction of ski slopes negatively affects species richness, diversity and abundance of original bird assemblages of forests and meadows. Edges of ski slopes with forests may cause negative edge effect causing decrease of species richness and diversity of bird assemblages. Winter ski tourism and flushing disturbance evoke high levels of stress hormones in tetrastids that may cause serious physiological symptoms. Presence of urban areas and new food sources provided by visitors for birds (alpine accent, choughs) in alpine areas may seriously change original home range size, seasonal home range dynamics, time budget activities, habitat selection and foraging ecology of affected populations. Effect of ski industry on birds in Central European countries was studied very insufficiently up to now. For most our regions, no sufficient information of the effects on bird assemblages, behaviour and physiology are available to identify the most affected bird populations. Majority of authors from foreign countries (mainly western Europe) concludes that ski resort areas represent suboptimal habitats for most wild birds and development of new ski resorts should be kept outside valuable natural areas.*

**Key words:** behaviour, birds, cable line mortality, diversity, environmental effects, species richness, stress

## Úvod

Popularizácia lyžovania, veľké investície do budovania a rekonštrukcie lyžiarskych stredísk a medzinárodné úspechy našich lyžiarov prispeli k veľkému záujmu verejnosti o tento šport na Slovensku. Druhou stránkou mince je vplyv budovania lyžiarskych stredísk na horské ekosystémy a ich jednotlivé spoločenstvá orga-

nizmov. Z dôvodu globálneho otepľovania sa predvída nižšie položených lyžiarskych stredísk stáva nerentabilná a investovať sa snažia strediská budovať v ťoraz vyšších polohách, pričom dochádza k deštrukcii biotopov, hlavne smrekového pásma, hornej hranice lesa, subalpínskeho pásma a alpského pásma. Tieto biotopy a ich fauna sú vážne ohrozené procesmi globálnej zmeny klímy (Flousek et al. 2015). Sato et al.

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# Neočakávané poznatky a pozorovania

## The first record of double breeding of red-breasted flycatcher (*Ficedula parva*) in the world?

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The red-breasted flycatcher (*Ficedula parva* Bechstein, 1794) is a polytypic species with Palearctic type of distribution that occurs from NW Europe through C and E Europe, Caucasus, Himalayas to E Siberia. It is a strictly migratory species wintering mainly in Tibet, India, Bangladesh, Burma, and Thailand. A typical forest species, it breeds in temperate, boreal but also montane forests (PEKLO, 1987; CRAMP & PERRINS, 1993; GLUTZ VON BLOTZHEIM & BAUER, 1993; FLADE, 1994; SNOW & PERRINS, 1998). On breeding grounds in the Western Carpathians (HUDEC et al., 1983; STASTNY et al., 1987; DANKO et al., 2002), it is strongly associated with the occurrence of beech (*Fagus sylvatica* L.) on macro habitat scale, however, on micro-habitat scale it is a generalist utilizing wide range of foraging substrates (KORŇAN, 2000).

High controversy on the number of breeding cycles this species can complete per season still persists in the world literature. CRAMP & PERRINS (1993) did not indicate the number of breeding cycles (breeding frequency) per year; they only concluded that little is known about fidelity of pair-bond within or between seasons (p. 32), and in the section "Breeding" there is stated "Normally one brood" (p. 38) without any further references or clarification. Later, SNOW & PERRINS (1998) again affirmed "Normally one brood" (p. 1355). PEKLO (1987) stated one, presumably two breeding cycles for the European subspecies *Ficedula parva parva* (p. 90), whereas for the Siberian race *Ficedula parva albicollis* only one breeding cycle (p. 98). For the European race, the author explained a second brood as a result of the first clutch destruction, but the possibility of two normal breeding cycles has not been mentioned. Similarly, GLUTZ VON BLOTZHEIM & BAUER (1993, p. 109) did not mention two breeding cycles per season. HUDEC et al. (1983, p. 723) pronounced only one regular brood and underlined the possibility of a second brood after clutch destruction.

The objectives of this paper were (i) to describe the first record of a probable double breeding of the red-breasted flycatcher, the nominate subspecies *F.*

*parva parva*, in the world, recorded in Slovakia and (ii) to clarify the open questions stated in the monographs of CRAMP & PERRINS (1993) regarding fidelity and pair bond within the breeding season.

Red-breasted flycatchers were regularly censused among other birds by intensive territory mapping technique in the Štrámková National Nature Reserve, the Malá Fatra Mts, NW Slovakia (49°11'22" N, 19°00'49" E), in the period 1997–2003 within a 27.5 ha study plot located in a primeval beech-fir forest (KORŇAN, 2004). During plot sampling, special attention has been paid to accurate territory definition to gain information on microhabitat requirements and foraging behavior. Totally, 17 breeding pairs having at least a portion of territory within the monitoring plot were detected during the study period. In 1997–2001, the species reached an average breeding population abundance of 2.00 pairs per study plot (SD<sub>1997–2001</sub> = 0.36) and a density of 0.73 pair/10 ha (KORŇAN, 2004).

Flycatchers usually arrived from wintering grounds at the end of April to the beginning of May and males started to defend their territories soon after arrival. Males arrived and started singing from the end of April to early May, usually between 29.IV.–12.V. Females were observed few days later, usually not later than a week. An exception in the arrival pattern was observed in 2000, when the first singing male was detected on 17.IV.2000.

During bird censusing on 13.VI.2000, an adult red-breasted flycatcher male and female were observed while feeding 4–5 fledged juveniles. After crossing the territory, both adults started to throat call typically used against intruders near the nesting area. After coming closer to the juveniles, both parents started to be very alert and frequently dive-attacked the intruder and, in the same time, they fed juveniles. Observing this behavior for 2–3 min, the adult male, just after feeding a juvenile, flew directly toward a hole with a nest on a close beech and sat on a branch. Afterwards, the male returned to feed juveniles. While checking the nest content, both parents returned back and dive

## Prvé dokázané hniezdenie sovy dlhochvostej (*Strix uralensis*) v Krivánskej Fatre (S Slovensko)

*The first documented breeding record of the Ural Owl (Strix uralensis) in Krivánska Fatra Mts. (N Slovakia)*

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Sova dlhochvostá (*Strix uralensis*) je najväčším

hniezdiacim druhom sovy typicky obývajúcim horské listnaté a zmiešané lesy. V našich podmienkach je glaciálnym reliktom so sibírskeho typom rozšírenia v Palearktiskej oblasti. U nás je centrum rozšírenia druhu východné Slovensko, kde jej areál začína od Východoslovenskej nížiny na juhu až po Laboreckú vrchovinu a Bukovské vrchy na severe, pričom do centrálnej časti areálu patria aj pohoria Slanské a Volovské vrchy, Vihorlat, Čergov a Ondavská vrchovina (Danko et al. 2002). Za západnú hranicu centrálnej časti areálu rozšírenia na Slovensku bola považovaná Popradská kotlina. Nepravdepodobne a sporadicky bola pozorovaná počas hniezdneho obdobia aj v iných častiach, napr. Muránskej planine, Poľane, Veporských vrchoch, Veľkej a Malej Fatre, Chočských vrchoch a Vtáčniku. V posledných rokoch bolo hniezdenie dokladované aj v Stražovských vrchoch, Vtáčniku, Tribeči, Lučanskej Fatre, Javorníkoch, Moravsko-Sliezskych Beskydách a Kysuckých Beskydách (Krištín et al. 2007). Na základe posledného mapovania sa predpokladá kontinuita hniezdny areál siahajúci z východného Slovenska až po Moravu. Krištín et al. (2007) odhadujú národnú populáciu na 1400–2500 párov. V centrálnej časti areálu na východnom Slovensku uvádzajú populačnú hustotu 1 pár/km<sup>2</sup> a vzácnosť až 3 páry/km<sup>2</sup>. Osobitnú pozornosť si zasluhuje jej rozšírenie na Orave v Skorúšických vrchoch, kde bežne hniezdi aj v smrečinách (Karaska et al. 1997). Najzápadnejšia hranica jej rozšírenia v bývalom Československu je na Šumave, kde boli v druhej polovici 90. rokov 20. stor. vypísané

umelo odchované jedince a zrejme tu dochádza k obojstranným preletom z Bavorského lesa v Nemecku (Kloubec 1997).

V oblasti Malej Fatre bol druh prvýkrát pozorovaný počas hniezdneho obdobia M. Majdom v r. 1992 (Danko 1994). Majda predpokladal možnosť hniezdenia na základe nálezov letky a kormidlového pera na obsadenom hniezde orla skalného (*Aquila chrysaetos*) v júli 1993 (Karaska et al. 1997). Tretí záznam z oblasti Krivánskej Fatre, k. ú. Pámnica – Lysica, hlásil J. Mášiar 2. 12. 1996 (Karaska et al. 1997). Prvé hniezdenie sovy z Malej Fatre opísal Šotnár (2008) z oblasti Vrického sedla (650 m n. m.), okres Prievidza, v Lučanskej Fatre. Sovy zahniezdili v položhnitom pahýži jedle v 50–80 ročnej smrekovej bučine v r. 2002. Tri mláďatá vyleteli z hniezda už 4. 5. Prvé hniezdenie v Krivánskej Fatre sa podarilo dokázať až v r. 2004 v NPR Štrámková v oravskej časti, k. ú. Kralčovo a Pámnica, kde bol zmapovaný tokajúci pár 20. 4. 2004 počas večerného a nočného sčítania vtákov (Korňan 2004). Biotop rezervácie predstavuje zachovalý fragment bukovo-jedľového pralesa. Dospelé jedince boli vizuálne aj akusticky pozorované. Samec sovy si typickým teritoriálnym hŕkaním obhajoval hniezdne teritórium v nadmorskej výške približne 825–900 m. Pri priblížení k suchému stojacemu kmeňu *Abies alba* agresívne klepal zobákom a nalietaval na pozorovateľa. Išlo pravdepodobne o hniezdny kmeň, ale hniezdo nebolo kontrolované z dôvodu vysokej rizikovosti kontroly tlejúceho kmeňa. Dňa 7. 6. 2004 približne o 9:03–9:08 SEČ boli pozorované 2–3 vyletvané mláďatá spolu s

# Návrh novej definície gildy

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## SHORT COMMUNICATIONS

### What are Ecological Guilds? Dilemma of Guild Concepts<sup>1</sup>

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Guilds can be considered basic structural units of ecological communities and ecosystems. The guild concept predicts temporally and spatially stable patterns of guild structure within communities based on (certain) assembly rules. This means that each community may have a specific set of species that are clustered into characteristic guilds based on species resource utilisation tactics. The temporal and seasonal variability of species resource utilisation also influences the dynamics and variability of species guild memberships, yet the basic guild structure is more or less constant (Jaksić et al., 1993; Mac Nally, 1994). In addition, basic guild structure may converge in evolutionary distinctive but ecologically similar ecosystems (Korňan et al., 2013). Since all structurally complex communities and ecosystems are, by definition, composed of guilds, the guild concept is one of the most significant outputs of thinking of structure in ecology in the past five decades. Application and utilization of guilds were widely discussed in plant (deKroon and Olff, 1995) and animal ecology (Austen et al., 1994; Precht, 1994; Zander, 2001; Blaum et al., 2011) and ecological management (Szaro, 1986; Croonquist and Brooks, 1991; Weller, 1995; Dearborn et al., 2001).

The guild concept was originally proposed by an American ecologist Richard Root (1967). Root in an autecological study of a bird, the Blue-gray Gnatcatcher (*Poliophtila caerulea*), defined guild as a group of species that exploit the same class of environmental resources in a similar way. The environmental resources can be viewed as food, shelter, habitat, or nest sites. Based on this definition, a guild groups together species without regard to taxonomic position that overlap significantly in their niche requirements. The guild has a position comparable in the classification of exploitation patterns to the genus in phylogenetic schemes (Root, 1967; p. 335). The original Rootian concept was reviewed and several authors

(MacMahon et al., 1981; Jaksić, 1981; Korňan and Adamík, 2007) suggest that “in similar way” should be excluded from the definition. The new definition means that guild members may be taxonomically very distinct. For instance, spiders, ants, frogs, birds, mammals can be all the members of an insectivorous guild regardless of their different foraging strategies. This contrasting view, propounded by MacMahon et al. (1981) is designed as a community approach to guild definition. In contrast, the Rootian concept is more appropriate for taxonomic assemblages such as spider assemblages, bird assemblages, etc. that can be described through similar foraging strategies. In addition, the MacMahonian concept is applicable to all organisms in a community, whereas the Rootian concept is only useful for animals that use certain types of feeding strategies (Korňan, 2005).

To clarify existing inconsistency in ecological terminology, Fauth et al. (1996) proposed to distinguish between terms “guild” and “ensemble”. They defined guild as a resource bounded group of species in a community in the original Root’s sense, whereas ensemble refers to assemblage guild that is phylogenetically bounded group of species that use similar set of resources within a community. They also proposed to use term “local guild” for species that share same resources and occur in the same community. After all, this terminology has not been widely accepted in ecological literature and vast majority of authors use the term guild to refer to both community and assemblage guilds.

Wilson (1999) proposed the concept of intrinsic guilds based on the assumption of competition theory. The concept assumes that species within a guild will tend to competitively exclude each other, and thus be mutually exclusive in their distribution. This in practice means that species from the same guild will not tend to co-occur to minimize interspecific competition. Intrinsic guilds are, therefore, sought using distributional data. The guild structure is tested by null

<sup>1</sup> The article is published in the original.

Rootovská (1967) koncepcia

MacMahonovská koncepcia (1981)

Wilsonova klasifikácia (1999)

Návrh novej definície: „Gilda je skupina druhov ktorá má signifikantný prekryv ník v zmysle Hutchinsonovej teórie mnohorozmernej niky.“

Druhy patriace do jednej gildy môžu byť chápané ako členovia jednotlivých signifikantných zhlukov (klastrov) v cenóze.

Predpoklad silnejších konkurenčných interakcií medzi členmi (druhmi) gildy.

# Závery

- Za 20-ročné obdobie výskumu: 56 hniezdičov v NPR, celkovo 61 druhov vtákov.
- Zistil sa pokles počas druhej dekády u *Ficedula parva*, *Fringilla coelebs* a pravdepodobne lokálne vymieranie u *Turdus torquatus*.
- Signifikantná ale rozdielna štruktúra spoločenstva do potranych gíld bola zistená na základe Rootovského a MacMahonovského prístupu.
- Konvergentný vývoj štruktúry gíld medzi evolučne rozdielnymi kontinentmi a faktory, ktoré tento vývoj mohli spôsobiť bol popísaný v zmysle Rootovskej koncepcie.
- Populácie 22 najpočetnejších druhov fluktovali na základe indexu „populačná variabilita“ v priemere  $0,33 \pm 0,14$  SD t.j. priemerný rozdiel medzi rokmi bol 33%.

# Závery

- Potvrdila sa potravná špecializácia u insektivorných druhov na špecialistov na listnaté stromy a ihličnaté stromy, mŕtve drevo a generalistov.
- Viaceré druhy vtákov majú výrazné potravné preferencie pri výbere stromov, čo môže súvisieť s dostupnosťou hmyzu a ekomorfologickými adaptáciami na architektúru koruny.
- Druhovo málo početné stromy boli ako brest horský a javor horský boli výrazne preferované potravné substráty. Potravnú preferenciu javorov potvrdili viaceré štúdie z Európy a Severnej Ameriky.
- Na základe meta-analýzy dlhodobých štúdií ornitocenóz, ktoré boli použité na testovanie druhových asociácií na úrovni ornitocenózy, gíld a druhových párov za zistila výrazná prevaha pozitívnych druhových asociácií.

# Závery

- Prevaha pozitívnych a náhodných asociácií nepodporuje primárny význam medzidruhovej konkurencie (kompenzačná dynamika) na organizáciu a dynamiku ornitocenóz.
- Z hľadiska ochrany biodiverzity vtákov (ornitocenóz) lesných biotopov je potrebné dbať na pôvodné druhové zloženie drevín medzi ktoré patria aj vzácne listnáče, ktoré sú vyhľadávané potravný substrát pre mnohé druhy.
- Ochudobnenie drevinového zloženia vedie k homogenizácii ornitocenóz (monokultúry), kde prevažujú euryekné druhy (potravný a substrátový generalisti) a je výrazne znížená ich diverzita.
- Publikácie v PDF: [www.ekoexpertizy.sk](http://www.ekoexpertizy.sk)

# Pod'akovanie

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