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Ecological Succession of Breeding Bird Communities in Deciduous and Coniferous Forests in the Sopron Mountains, Hungary

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Abstract – The relationship between breeding bird communities and different phases of secondary succession of deciduous (sessile oak – *Quercus petraea*) and coniferous (spruce – *Picea abies*) forests in the Sopron Mountains was studied. The bird censi have been carried out in 5 different successional stages using the "double-visit fixed-radius point count technique". A total of 38 bird species were encountered. There are typical bird communities to order to different stages of forest succession, containing unique bird species or species appearing predominantly in that successional stage. The study has shown structural changes in breeding bird communities during the succession. Bird species richness, density and diversity showed the same trends. Their numerical values were the lowest in the clear-cut areas with young (1-2 year old) plantations, and the highest in the mature stands. After a starting increase (shrub stage) there is a slight decline (10-12 year old stands) because of the canopy closure of the young trees. Further decrease can be observed in the low pole stands, as these habitats are no longer appropriate for species nesting in shrubs and not yet suitable for the hole-nesting ones. Species richness, density and diversity were lower in early pole and older spruce stands than in the corresponding oak stands.

bird communities / succession / vegetation structure / habitat / clear-cut

Kivonat – Fészkelő madárközösségek szukcessziójának vizsgálata a Soproni-hegység lomb- és fenyő állományaiban. A Soproni-hegységben kocsánytalan tölgyes és lúcfenyves másodlagos szukcessziójának madártani vonatkozásait vizsgáltam. A vizsgálatokhoz a vegetáció 5 különböző fejlődési stádiumát különítettem el. A fészkelő madárközösségek felvételéhez a kétszeri pontszámlálás (fix sugárral) madárszámlálási módszert alkalmaztam. A felvételek során összesen 38 faj fordult elő. A szukcesszió különböző stádiumaihoz jellemző, sajátos összetételű madárközösségek rendelhetők sokszor olyan stenök fajokkal, amelyek kizárólag vagy dominánsan csak az adott stádiumban fordulnak elő. Az erdei szukcesszió során a madárközösségek is szerkezeti változásokon mennek keresztül. A fajszám, denzitás és diverzitás hasonló trendet mutattak. Értékük legkisebb a tarvágást követő 1-2 éves felújítások esetében és legnagyobb az idős állományokban. A kezdeti emelkedés után (bokros, cserjés stádium) kisebb csökkenés mutatkozik (10-12 éves fiatalos), ami a nagyobb záródásnak tudható be. További csökkenés tapasztalható a rudas korú állományokban, mivel a nyíltabb területekre, bokrosokra jellemző énekesmadaraknak már nem, az odúlakóknak pedig még nem megfelelő ez a habitat. A kocsánytalan tölgyes illetve lúcfenyves fiatalosok madárközösségeinek fajgazdagsága, denztitása és diverzitása közel azonos volt. Jelentős eltérés mutatkozott azonban rudas és idősebb állományok esetében. Az elegyetlen lúcfenyvesek fajszám, denzitás és diverzitás tekintetében is szegényebb képet mutattak.

madárközösségek / szukcesszió / vegetáció-szerkezet / habitat / tarvágás

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1 INTRODUCTION

Several studies have shown that vegetation structure, its complexity and spatial dispersion are the primary determining factors in bird community composition (MacArthur – MacArthur 1961, Cody 1974, Wilson 1974, Blicke 1982), while other studies have pointed out that floristic composition of vegetation also plays an important role (Wiens – Rotenberry 1981, Ralph 1985, Moskát 1988a, Whelan 2000). The consecutive phases of a forest succession might provide habitats of different structure and often different plant species composition. These progressional changes can cause significant changes in the associated bird communities. The pattern and process of ecological bird community succession related to forest succession have been well studied and documented, mainly during the last few decades (Jones 1972, Shugart – James 1973, Glowacinski 1975, 1981, May 1982, Helle 1985, Moskát – Székely 1989, Bezzel 1990, Helle – Mönkkönen 1990, Schwab – Sinclair 1994, Rumble – Gobeille 1998, Lang et al. 2003).

The aim of this study is was determine the relationship between bird community composition, species richness, density, diversity and secondary succession of a deciduous and a coniferous forest in the Sopron Mountains. Further investigations were related to the comparison of structural properties of bird communities between these two forest types.

2 MATERIAL AND METHODS

2.1 Study area

This study is based on the breeding bird data of two successional series in managed deciduous (*Quercus petraea* – sessile oak) and managed coniferous (*Picea abies* – spruce) forests in the Sopron Mountains (N 47º 39-40’, E 16º 26-34’). The elevation of the area ranges from 450 to 550 m above sea level. Five different phases of secondary forest succession have been investigated for both forest types.

Succession stages in deciduous (sessile oak) forest

I_D: Recently clear-cut area – 1-2 year old afforestation. The area is planted with young trees of up to 50 cm height. The cover of herb layer is 80-90%, including species e.g. *Calamagrostis epigeios, Euphorbia amygdaloides, Carex digitata, Cirsium vulgare, Dactilis glomerata.*

II_D: 4-7 year old afforestation – medium-dense shrub stage. Apart from the young trees, additional shrubs could also be found (Rubus fruticosus, Rosa canina). Height: up to 1,5 m. The cover of small trees and shrubs is 65-75%. Species in the herbaceous vegetation are e.g. *Deschampsia flexuosa, Carex digitata, Poa nemoralis.*

III_D: 10-12 year old, dense stand – the cover of young trees is 80-85%. Height: 2-6 m.

IV_D: Low pole stage – height of the trees 10-14 m. Canopy is closed, the cover is 80-90%. The ground vegetation includes species e.g. *Galium odoratum, Brachypodium sylvaticum, Geum urbanum, Deschampsia flexuosa.*

V_D: “climax” forest – old sessile oak stands, height: 20-34 m. Apart from the main tree species *Quercus petraea*, scattered trees of *Carpinus betulus* and *Fagus sylvatica* can be found too. Cover is about 80-85%. Species in the herbaceous vegetation are e.g. *Carex sylvatica, Festuca drymeia, Brachypodium sylvaticum, Hieracium sylvaticum.*

Succession stages in coniferous (spruce) forest

I_C: clear-cut area – 1-2 year old afforestation. Height of the young plantation is up to 60 cm. The cover of herbaceous layer is 75-90%, including species e.g. *Calamagrostis epigeios, Stenactis annua, Deschampsia flexuosa.*

II_C: 4-6 year old spruce afforestation – medium-dense shrub stage. Additional shrubs (*Rubus fruticosus, Rosa canina*) can also be found. Height: up to 1.8 m. Tree and shrub coverage is 65-70%. Species in the ground vegetation are e.g. *Deschampsia flexuosa, Calamagrostis epigeios, Festuca drymeia.*

III_C: 10-12-year-old, dense stand – the cover of young trees is 85-90%. Height: 3-6 m. The common shrub *Rubus fruticosus* also appears among trees. Ground vegetation cover is not significant, species are e.g. *Deschampsia flexuosa, Stenactis annua.*

IV_C: Low pole stand – height of the trees 11-14 m. Canopy is closed, cover is 85-95%. Shrub layer is completely missing, herbaceous vegetation is not significant.

V_C: "climax" forest – old spruce stands. The cover is 75-85%, height: 24-32 m. Shrubs like *Rubus fruticosus* are also present. Species in the herbaceous vegetation are e.g. *Deschampsia flexuosa, Hieracium lachenalii, Luzula albida.*

These succession stages roughly correspond to the ones marked A, B, C, D and F as determined by Moskát – Székely (1989) in a beech forest.

2.2 Bird census

Bird censi were carried out twice during the breeding season (once in April and once in late May 2002) using the "double-visit fixed-radius point count technique" (Moskát 1986) which is a modified version of the French IPA point count method (Blondel et al. 1970). Observations took place in early mornings (about 4.00-9.00 am) inside a circle with fixed distance radius (100 m) around the sample points. With the use of fixed radius the relative density values of breeding pairs can be calculated easier than using the species-specific coefficients of detectability described in the original technique. 61 sampling points were set out with a total sampling area of about 192 ha. At each survey station singing males and observed pairs were recorded during the 20 min. count period. The method used was suitable for recording pigeon- (*Columbiformes*), nightjar- (*Caprimulgiformes*), woodpecker- (*Piciformes*) and passerine bird (*Passeriformes*) species only.

2.3 Data analysis

Avian species richness was calculated for each successional stage. Due to different number of sampling points in the different stages, it was relevant to calculate the expected number of species on plots of equal sizes for each stage using rarefaction analyses to allow a more reliable comparison of bird communities. Rarefaction is a statistical method that estimates the number of species expected from a given sample of point counts based on multiple random sampling (James – Rathbun 1981, Moskát 1988b). The expected number of species [$E(S_n)$] in a random sample of n pairs drawn without replacement from N pairs is calculated by:

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]$$

S: total number of species.

Relative density-values of all species were calculated for each stage. Out of the results of two bird censi (carried out in April and May) the higher density values were chosen for each species.

Bird species diversity (*H*) was also computed for each stage of both sessile oak and spruce forests using the Shannon-Weaver formula.

To compare diversity values of two assemblages (H_1 and H_2) a *t* test was used to determine if they are significantly different (Hutcheson 1970).

Pielou's equitability index (*J*) was used to measure the evenness of species distribution within the community (Pielou 1966).

3 RESULTS

Table 1 shows the most important structural properties of breeding bird communities recorded.

Table 1. Structural properties of bird communities in different successional stages, by stand types

Successional stages	Species richness (*S*)	Expected number of species [$E(S_n)$]	Density (D) (pairs/10 ha)	Diversity (*H*)	Evenness (*J*)
I_D	8	7.14	8.92	1.87	0.90
I_C	8	6.44	7.42	1.94	0.93
II_D	16	13.28	26.28	2.42	0.87
II_C	14	13.12	23.32	2.43	0.92
III_D	14	12.04	22.96	2.27	0.86
III_C	12	10.51	19.84	2.20	0.89
IV_D	13	11.71	20.16	2.21	0.86
IV_C	8	8.00	10.37	1.88	0.90
V_D	24	22.58	36.29	2.89	0.91
V_C	19	16.74	29.94	2.72	0.92

Breeding bird species richness and its estimated values corrected for differences in plot size were significantly higher in mature forests than it is in young afforestations. Species richness has shown a rapid initial increase during the first two successional stages following clear-cutting. This first increase peaked in the 4-7 year old plantations of both deciduous and coniferous stands (stage II) The species of bird communities in these shrub stages often include species characteristic for open habitats, like the yellowhammer (*Emberiza citrinella*). There is a slight decrease in stages II_D and II_B mainly because of the closed canopy in these dense stands. Species like the tree pipit (*Anthus trivialis*) or the nightjar (*Caprimulgus europaeus*) can no longer find their optimal nesting habitats in these stands. Further decrease of bird species richness can be found in stage IV. This decrease is moderate in the case of the oak stands (IV_D) but very drastic in pure spruce stands (IV_C) where species richness dropped to the lowest observed level, except for clear-cut areas. Generally, habitats in these low pole stands are no longer appropriate for bird species nesting in shrubs such as the blackcap (*Sylvia atricapilla*) or the red-backed shrike (*Lanius collurio*), and not yet suitable for the hole-nesting ones like tits (*Paridae*) and woodpeckers (*Piciformes*). Species richness was the highest in both deciduous and coniferous mature stands (V_D and V_C). Some characteristic hole-nesting species appeared in this stage, such as the stock dove (*Columba oenas*), the great spotted woodpecker (*Dendrocopus major*), the great tit (*Parus major*), the collared flycatcher (*Ficedula albicollis*) and especially in old spruce stands the coal tit (*Parus ater*).

Table 2. Density values (pairs/10 ha) of bird species in different successional stages

Species	Succession stages									
	I_D	I_C	II_D	II_C	III_D	III_C	IV_D	IV_C	V_D	V_C
	Density (pairs/10 ha)									
Columba oenas L.	-	-	-	-	-	-	-	-	0.64	0.64
Columba palumbus L.	-	-	-	-	-	-	-	-	0.64	-
Caprimulgus europaeus L.	-	0.53	-	0.53	-	-	-	-	-	-
Jynx torquilla L.	-	-	-	-	-	-	-	-	0.64	-
Picus viridis L.	-	-	-	-	-	-	-	-	0.64	-
Dryocopus martius L.	-	-	-	-	-	-	-	-	0.64	-
Dendrocopos major L.	-	-	-	-	-	-	-	-	0.64	0.64
Anthus trivialis L.	1.27	1.06	0.80	2.12	-	-	-	-	1.27	-
Prunella modularis L.	0.64	1.06	3.18	2.12	3.18	1.36	0.53	0,80	0.64	0.64
Erithacus rubecula L.	1.27	1.06	1.99	1.59	4.24	1.82	4.25	0,80	4.45	1.91
Saxicola torquata L.	0.64	0.53	-	-	-	-	-	-	-	-
Turdus merula L.	-	-	2.39	3.18	2.47	3.64	1.06	0,80	1.27	1.91
Turdus philomelos Ch.L.Brehm	-	-	0.40	0.53	0.35	0.45	0.53	0,80	0.64	1.91
Locustella naevia Bodd.	-	0.53	0.40	0.53	-	-	-	-	-	-
Sylvia nisoria Bechst.	-	-	-	-	0.35	0.45	-	-	-	-
Sylvia curruca L.	-	0.53	0.80	0.53	0.71	0.91	-	-	-	-
Sylvia atricapilla L.	0.64	-	3.18	2.12	3.18	4.55	2.12	0,80	1.27	0.64
Phylloscopus sibilatrix Bechst.	-	-	0.40	-	0.35	-	1.06	-	1.91	1.91
Phylloscopus collybita Vieill.	-	-	2.79	2.12	2.83	3.03	2.65	2,39	1.91	1.27
Regulus regulus L.	-	-	-	-	-	-	-	-	-	1.27
Regulus ignicapillus Temm.	-	-	-	-	-	-	-	-	-	1.27
Ficedula albicollis Temm.	-	-	-	-	-	-	-	-	1.91	-
Aegithalos caudatus L.	-	-	0.40	-	-	-	-	-	-	-
Parus palustris L.	-	-	-	-	0.35	-	-	-	1.27	-
Parus ater L.	-	-	-	-	-	-	-	0.80	-	2.55
Parus caeruleus L.	-	-	-	-	-	-	0.53	-	1.27	1.91
Parus major L.	0.64	-	0.40	-	-	-	1.06	-	3.18	2.55
Sitta europea L.	-	-	-	-	-	-	-	-	1.27	0.64
Certhia brachydactyla Ch.L.Brehm	-	-	-	-	-	-	-	-	1.27	0.64
Lanius collurio L.	0.64	-	1.59	2.12	0.35	0.91	-	-	-	-
Garrulus glandarius L.	-	-	-	-	-	-	-	-	0.64	0.64
Sturnus vulgaris L.	-	-	-	-	-	-	-	-	0.64	-
Fringilla coelebs L.	-	-	1.59	0.53	3.18	1.36	4.78	3,18	6.37	5.73
Carduelis chloris L.	-	-	0.40	1.06	0.71	0.91	0.53	-	-	-
Carduelis carduelis L.	-	-	-	-	-	-	0.53	-	-	-
Loxia curvirostra L.	-	-	-	-	-	-	-	-	-	1.27
Coccothraustes coccothraustes L.	-	-	-	-	-	-	0.53	-	1.27	-
Emberiza citrinella L.	3.18	2.12	5.57	4.24	0.71	0.45	-	-	-	-
Total density:	8.92	7.42	26.2	23.3	22.9	19.8	20.1	10,3	36.2	29.9

Table 2 shows the pair density of each bird species encountered in different succession stages. Changes and trends in bird community density (*Figure 1*) paralleled the changes described for bird species richness. As for species richness, the increases from stage I to stage II and from stage IV to stage V were significant for both deciduous and coniferous forests, and so the drastic decrease from stage III_C to stage IV_C for the spruce stands.

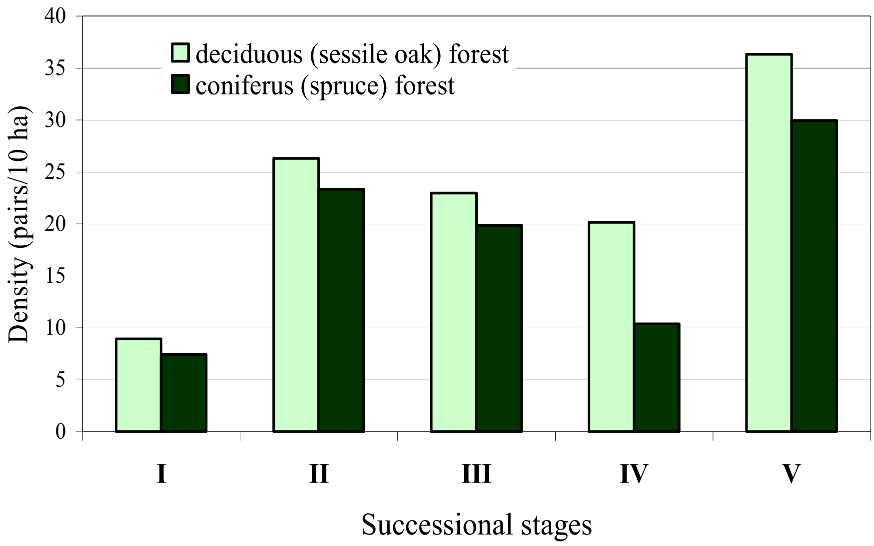

Figure 1. Changes of density during the succession

Bird community diversity shows a similar trend expressed in species richness and density. *Table 3* shows the results of *t* test based on Shannon indices. For what concernes stages I, II and III, there are no remarkable differences between diversity values of bird communities recorded in deciduous and coniferous afforestations (*t*-values are very low comparing diversity values of stages I_D and I_C; II_D and II_C; III_D and III_C). With reference to diversity values in stages IV and V, the differences between deciduous and coniferous stands are higher but not yet significant (P=0.05). Significant differences (above 5 percent probability level) can principally be observed comparing diversity values of stages I and II; I and V; III and V; IV and V. This phenomenon clearly shows that clearcut fields (stage I) and mature stands (stage V) represent two extremes.

Table 3. Results (t-values) of comparison of Shannon diversity (H) values. Significant differences are italicized (at P=0.05 level)

Succ. stages	I_D	I_C	II_D	II_C	III_D	III_C	IV_D	IV_C	V_D
I_C	0.268								
II_D	*2.255*	*2.191*							
II_C	*2.236*	*2.168*	0.005						
III_D	1.655	1.512	1.076	1.050					
III_C	1.318	1.131	1.419	1.390	0.459				
IV_D	1.289	1.101	1.200	1.182	0.350	0.050			
IV_C	0.058	0.204	*2.162*	*2.145*	1.567	1.236	1.211		
V_D	*4.004*	*4.148*	*2.970*	*2.897*	*3.994*	*4.070*	*3.604*	*3.902*	
V_C	*3.374*	*3.444*	1.942	1.890	*2.965*	*3.128*	*2.751*	*3.276*	0.990

Evenness values (Pielou's equitability index) haven't shown any trend during the succession. The relative high values in stages I_D, I_C and IV_C can be explained with the low number of species, with a relevant implication on the algorithm used.

Table 4 shows numerical dominance values of the most dominant bird species (Dominance % > 10%) in different successional stages. Bird species with a high dominance value in all stages could be found neither in deciduous, nor in coniferous successional series.

The most frequent species were the robin (*Erithacus rubecula*) appearing with high dominance in stages I_C, I_D, III_D and V_D (but recorded also in all other stages) and the chaffinch (*Fringilla coelebs*) appearing with high dominance in stages III_D, IV_D, IV_C, V_C and V_D (but recorded also in stages II_D, II_C and III_C with lower dominance). These species are generalists regarding forest succession.

Table 4. Dominance values (%) of the most dominant bird species (D%>10%) in successional stages, by stand types

Sessile oak stands		Spruce stands	
Succ. stages	Species – Dominance (%)	Succ. stages	Species – Dominance (%)
I_D	*Emberiza citrinella* – 35.71 *Erithacus rubecula* – 14.29 *Anthus trivialis* – 14.29	I_C	*Emberiza citrinella* – 28.57 *Erithacus rubecula* – 14.29 *Prunella modularis* – 14.29 *Anthus trivialis* – 14.29
II_D	*Emberiza citrinella* – 21.21 *Sylvia atricapilla* – 12.12 *Prunella modularis* – 12.12 *Phylloscopus collybita* – 10.60	II_C	*Emberiza citrinella* – 18.18 *Turdus merula* – 13.64
III_D	*Erithacus rubecula* – 18.46 *Sylvia atricapilla* – 13.85 *Prunella modularis* – 13.85 *Fringilla coelebs* – 13.85 *Phylloscopus collybita* – 12.31 *Turdus merula* – 10.77	III_C	*Sylvia atricapilla* – 22.73 *Turdus merula* – 18.18 *Phylloscopus collybita* – 13.64
IV_D	*Fringilla coelebs* – 23.68 *Phylloscopus collybita* – 13.16 *Sylvia atricapilla* – 10.53	IV_C	*Fringilla coelebs* – 30.77 *Phylloscopus collybita* – 23.08
V_D	*Fringilla coelebs* – 17.54 *Erithacus rubecula* – 12.28	V_C	*Fringilla coelebs* – 19.15

4 DISCUSSION

Successional trends in bird communities appeared to be determined by the development of vegetation patch types appropriate to specific bird-guilds. Species richness, bird density and diversity were the lowest in the earliest successional stage and the highest in the old stands. May (1982) found the same result in other studies of old-field forest succession. A sharp increase in the shrub stages (II) followed by declines in the dense thicket stages (III) and early pole stages (IV) are characteristic for successions of European forests (Glowacinski 1975, Moskát – Székely 1989, Helle 1985).

Each successional stage supported a characteristic community of breeding bird species. 53% of the observed species appeared in more than one successional stage. However, many species were still found in only one phase of secondary forest succession. In every successional stage a unique or predominant bird species characteristic for that successional stage could be identified.

The grasshopper warbler (*Locustella naevia*) was a very rare species in Hungary until the 1980's and appeared only in wet meadow habitats. Kárpáti (1982) reported for the first time that this species appeared as breeding bird species in a completely new habitat, in clear-cut areas and young afforestations in the Sopron Mts. The grasshopper warbler was recorded in stages I_C, II_D and II_C.

Another characteristic species in clear-cut areas is the nightjar. This ground-nesting species prefers the 1-7 year old afforestations (stages I and II) where the cover of the young trees is lower and the canopy is not yet closed, but it is completely absent in the dense thickets (stage III). Optimal habitats for the nightjar in the Sopron Mts. are young coniferous plantations and forest edges (Winkler 2001).

A hole-nesting species, the great tit was also surveyed in early successional stages (I_D and II_D). According to Krebs (1971), these are mostly young male birds not breeding in the actual breeding season. This phenomenon was also described by Moskát – Székely (1989).

The appearance of the dunnock (*Prunella modularis*) with relatively high and medium-high abundance in all successional stages was also an unusual phenomenon. All singing males of the dunnock were recorded during the first censi in April but one individual was counted also during late May censi. A theoretical explanation might be that these birds are not breeding but only staying in this area during their late springtime migration when the singing and territorial activity is already noteworthy. The breeding of the dunnock has been proved only once (a nest with 4 eggs has been found in a spruce plantation – stage II_C – during a survey).

Most of the spruce forests in the Sopron Mts. were damaged because of a heavy bark beetle gradation (*Ips typographus*). In the surveyed older stands (stage V_C) damaged trees with cracked barks provided optimal nesting places for the short-toed tree creeper (*Certhia brachydactyla*) and for the coal tit. In the less closed parts of these stands, the aggressively expanding shrub-vegetation (e.g. *Rubus fruticosus*) attracted the shrub-nesting species such as the blackcap (*Sylvia atricapilla*). This caused the relatively high species richness and diversity values in this stage.

5 CONCLUSIONS

The results of this study have shown that tree species (deciduous or coniferous) seems to be less important for bird community composition and has no particular effect on avian species richness, density and diversity in young afforestations. But the difference of the mentioned characteristics appear to be dramatic between the early pole sessile oak and the pure spruce forests (where their numerical values were almost as low as in the clearcut stage).

Avian assemblages are determined, to a degree, by vegetation and forest structure. Forest management has therefore a direct and strong effect on bird community composition, avian species richness, density and diversity. Late-successional forests are very important to several species of birds, especially to the cavity-nesting ones, and usually the avian diversity is the highest in these stands. On the other hand, the study has also shown that young clearcuts support vastly different bird communities and enrich the global avian diversity. But it has also been proved that most of the species of clear-cut areas also appear in small forest gaps caused by small-scale natural disturbance (Faccio 2003).

For what concernes the clearcutting system, another important factor related to avian diversity should be mentioned. The remnant (seed) trees play an important role not only in forest regeneration, they can also be considered as “ecological Noah’s arks” for birds, insects and other animals.

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