Bird community changes in different-aged oak forest stands in the Buda-hills (Hungary)

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Bird community parameters were analysed in six stages of oak forest succession from brushwood to climax. Bird data were collected in the breeding season with the modified I.P.A. method, which gives density estimations for 100 m radius circles. Community diversity, expressed in relative density and rarefaction species number was greatest in the fourth stage of succession, in 61-80 year old forest stands. Open forest birds and hole-nesters reach their maximum densities here. A sharp difference was found between the community structure of the initial, open brushwood and the older, closed forest stages. This pattern emerged both from comparisons of the whole community and of different ecological groups of birds based on primary feeding, nesting and migratory habits. Different speciation and adaptation mechanisms in the open and closed habitats are supposed to be responsible for this difference. No clear pattern emerged from the analysis of the degree of specialisation within families.

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1. Introduction

Succession is the process whereby plant and animal communities succeed each other in time. Secondary succession takes place where some vegetation has existed before but has been removed. The earlier vegetation might be removed by either a natural (e.g., fire, wind, snow) or human action (clear-cutting). The study of secondary succession may follow two general methods. One of them is long-term, as is to examine the development of vegetation at the same place for a long time (direct method). The other is short-term, when we suppose that communities of different composition or age are members of a successional process and study them separately in the same year or within a few years (indirect method). Both of the methods are widespread among studies of animal communities.

Several hypotheses suggest that vegetation has the most significant role in forming bird community structure, through either its physiognomy (MacArthur 1964, MacArthur & MacArthur 1961, MacArthur et al.

1962) or its floristics (Rotenberry 1985). Whether general characteristics of succession such as an increase in diversity, density, stability and specialisation stated by Margalef (1968) and Odum (1969) can apply to birds or not is not yet unequivocal. In addition there is a strong bias in bird community studies towards north-temperate forests, so the possibilty of making generalisations from the results is rather restricted.

This paper analyses the bird community structure of a typical central-european oak forest secondary succession. To avoid biases caused by small study area size and subjectively chosen successional stages, I divided the whole successional sere into 20-year intervals and applied a method which enabled me to survey comparatively large areas. The method and number of study plots were chosen so that the results could be comparable to those previously obtained in a nearby beech sere (Moskát 1988, Moskát & Székely 1989). The multivariate analysis of the vegetational and bird species composition of the two series will be the topic of another paper (Moskát & Waliczky MS).

Tab. 1. Vegetation variables of the successional stages.

Variable	Successional stages					
	A	B	C	D	E	F
Grass cover (%)	21	66	66	71	60	36
Shrub cover (%)	82	11	39	23	41	65
Canopy cover (%)	0	78	74	71	71	71
Tree height (m)	0.00	11.50	14.30	16.70	15.50	17.50
Shrub height (m)	2.49	1.39	1.30	1.55	2.57	2.98
Tree distance (m)	0.00	1.37	2.06	2.76	2.36	2.52
Shrub distance (m)	0.45	1.04	0.51	0.83	1.39	1.06
DBH (cm)	4.00	13.70	17.30	25.70	26.00	30.50
Number of tree species	4	3	6	8	3	8

Here I will discuss only the patterns of bird community parameters (species numbers, composition and density).

2. Study area

The study area is situated in the Buda-hills near Budapest, North-central Hungary (47°35' N, 18°90' E). The hills lie between 215-529 m a.s.l. Average yearly precipitation is 650 mm, average temperature is 8.7°C (Pécsi 1958).

Different-aged oak forests were chosen to represent the whole spectrum of secondary succession from the brushwood stage to the climax. The study plots were later grouped into six evenly aged stages, each with a 20-year interval. These stages can be characterized as follows:

Stage A: brushwood stage (<20 years old). Very dense, shrub-like stands of primarily Sessile Oak (*Quercus petraea*). The percent coverage of several shrub species, mainly Dog Rose (*Rosa canina*), Common Hawthorn (*Crataegus monogyna*), Common Pivet (*Ligustrum vulgare*), Wart-cress (*Euonymus verrucosus*) is very high in these stands.

Stage B: young forest stage (21-40 years old). These are homogenous, dense, closed-canopy Sessile Oak-Turkey Oak (*Quercus cerris*) stands. Canopy cover is highest, shrub cover is lowest here.

Stage C: thinwood stage (41-60 years old). These forests are almost homo-genous plantations of Sessile or Turkey Oaks, with scattered Wild Cherry (*Prunus avium*), Field Maple (*Acer campestre*) and Flowering Ash (*Fraxinus ornus*) trees. More open stands with moderate shrub cover consisted of mainly low (<1m) shrubs.

Stage D: high forest (61-80 years old). This includes the most open stands with low srub cover and lowest tree density. Tree species besides the two oaks are Field Maple, Wild Service Tree (*Sorbus torminalis*) and European Ash (*Fraxinus excelsior*).

Stage E: preclimax stage (81-100 years old).

Stage F: climax stage (>100 years old, mostly between 101-120 years). The older stands are similar in appearence, though the oldest ones have higher shrub cover and taller shrubs in average. In these stands there are a few montane tree species like Beech (*Fagus sylvatica*), Sycamore (*Acer pseudoplatanus*), Norway Maple (*Acer platanoides*) and European Ash.

The physiognomical parameters of each successional stage can be consulted on Tab. 1, number of study plots and size of study area on Tab. 2.

3. Material and Methods

3.1. Bird data

Tab. 2. Main bird community parameters of the six phases of secondary oak succession. S : species number; Sr : rarefaction species number; N : total number of individuals in each phase; D : density (pairs/10 ha); n : number of study plots; A : study area (total coverage of study plots) (ha).

Phase	S	Sr	N	D	n	A
A	19	19.0	129	46.36	9	28.26
B	24	21.2	185	45.32	13	40.82
C	29	22.2	454	60.24	24	75.36
D	28	24.1	510	70.62	23	72.22
E	24	24.0	175	61.92	9	28.26
F	26	23.1	279	63.47	14	43.96

Bird density estimations were made in the spring of 1988 on each of the 92 plots. The method applied was the modified I.P.A. method (Moskát 1987). This is a point-count survey with a fixed, 100 m radius. All birds detected - heard or seen - have to be recorded within a 10 minute interval in each plot. The count has to be done twice in the breeding season at the same place, preferably once in April and once in May. This aims to survey the whole bird community, the early as well as late breeders. For every species recorded the higher estimate has to be accepted. Compared to the territory-mapping method this census gives an approximately 71% efficiency (Moskát 1987) in estimating bird densities on a community basis.

For the sake of censusing on exactly the same plots, big, yellow numbers were painted on selected trees, marking the centres of plots. The painting work and selection of study plots was carried out in early spring, in February-March.

3.2. Vegetation data

The physiognomical variables recorded were as follows: grass cover, shrub cover, canopy cover, tree height, shrub height, tree distance, shrub distance, diameter of breast height (DBH), number of tree species. Grass, shrub and canopy cover were estimated by eye on each plot. Data on tree height, DBH and number of tree species were collected from the data bank of the Forestry Commission. Shrub height, tree distance and shrub distance were measured on at least twenty shrub and tree individuals around each plot center and later averaged.

3.3. Statistical analysis

Tab. 3. Species which have the highest dominance in different phases of oak succession (numeric dominance is over 10 percent of the whole community).

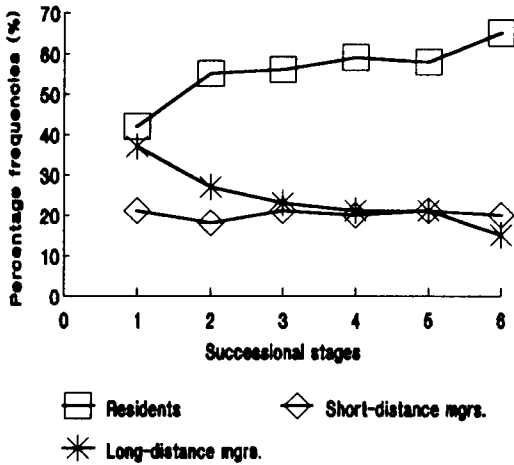| Species	Dominance (%) in stage					
	A	B	C	D	E	F
Sylvia atricapilla	15		11			
Phylloscopus collybita	15					
Luscinia megarchynchos	13					
Fringilla coelebs		13	11	11		
Emberzia citrinella		11	13			
Parus major					11	13
Sitta europea					10	
Sturnus vulgaris						14

Fig. 1. The contribution of residents, short-distance migrants and long-distance migrants to the whole community in the successional stages in terms of species richness.

Because of the negative affect of different-sized study plots on diversity calculations (Wiens 1989), a rarefaction method was applied to estimate expected species number on plots of equal size (James & Rathbun 1981). This method has advantages over diversity indices (Wiens 1989) and gives a more accurate picture of community heterogeneity over different areas. The program RAREFACTION (Ludwig & Reynolds 1988) was applied for performing calculations. The formula is that of Hurlbert (1971):

$$E\left(S_n\right) = \sum_{i=1}^{S}\left\{1 - \left[\left(\begin{array}{c}N - n_i\\n\end{array}\right) / \left(\begin{array}{c}N\\n\end{array}\right)\right]\right\}$$

where n_i is the number of individuals of the ith species, N is the total number of individuals and S is the species number when the sample contains n individuals .

For measuring similarity between bird communities in different successional stages the Sörensen's similarity index was used:

$$C = 2 j / (a + b)$$

where j : number of species common to the two samples; a, b : total number of species in samples a and b.

4. Results

4.1.General community parameters

The absolute number of species is highest in stage C; the total number of individuals, average density per 10 ha and rarefaction species number is highest in stage D (Tab. 2.). The lowest number of species and individuals was found in stage A, the lowest density in stage B (Tab. 2).

The dominant species (over 10% of the total number of individuals) of each successional phase and their numerical dominance values can be consulted on Tab. 3. Species, which are dominant in more than one phase are Blackcap (*Sylvia atricapilla*), Chaffinch (*Fringilla coelebs*), Yellowhammer (*Emberiza citrinella*) and Great Tit (*Parus major*).

4.2. Community similarity

Tab. 4. shows that community similarity is

Tab. 4. Sörensen's similarity indices for the comparison of bird communities in different succesional stages in oak secondary succesion.

	A	B	C	D	E	F
A	1.000	0.500	0.531	0.500	0.500	0.435
B		1.000	0.830	0.808	0.833	0.760
C			1.000	0.912	0.830	0.764
D				1.000	0.885	0.852
E					1.000	0.880
F						1.000

Tab. 5. Grouping of bird species in each successional phase according to their primary nesting habits. Species numbers, numeric dominance in parentheses (percentage).

Breeding habit	A	B	C	D	E	F
Ground-nester	5 (26)	6 (25)	7 (24)	6 (22)	5 (21)	5 (19)
Shrub-nester	9 (47)	4 (17)	5 (17)	4 (14)	3 (12)	3 (12)
Canopy-nester	3 (16)	4 (17)	4 (14)	4 (14)	5 (21)	5 (19)
Hole-nester	2 (11)	10 (41)	13 (45)	14 (50)	11 (46)	13 (50)

lowest between stage A and all of the other stages, especially stage F. Other stages show a high similarity to each other in terms of species; the indices are lower for B-F and C-F comparisons.

4.3. Ecological groups

Grouping the species in each seral community according to their primary nesting habits we see that ground-nesters and foliage-nesters have similar ratios in every stage. Shrub-nesting species predominate in stage A then fall sharply and remain in a fairly constant ratio in closed-canopy stands. For the hole-nesters the situation is reversed, they have the lowest contribution to the whole community in stage A and predominate in all of the stages from B to F (Tab. 5).

For the groups using similar feeding places the ground-feeding group has the highest contribution to total species number in stage A then stabilizes at a lower level from stage B on. The foliage-gleaners have a fairly constant ratio in the whole sere. There are no bark-foragers in the initial stage, from B on their ratio is very similar to those of ground-foragers (Tab. 6).

4.4. Migratory status

Rarefaction species numbers were estimated on 27.1 ha (the area of the smallest number of study plots in a stage) according to their status of being sedentary, short-distance migrant or long-distance migrant. Short-distance migrants have a low and stable ratio in the whole sere (Fig. 1). On the same figure long-distance migrants and sedentary species show a reversed ratio: starting from almost the same position the former increases, the latter decreases in the course of succession.

For densities of the same groups we see very similar results with the difference that long-distance migrants have the lowest ratios in every stage and the short-distance migrant group has intermediate position (Fig. 2).

4.5. Specialization in genus and families

The highest species/genus ratio was calculated for stage C, and the highest species/family and genus/family ratios were found in stage A. In each case stage D has the lowest indices (Tab. 7).

5. Discussion

5.1. General community parameters

Tab. 6. Grouping of bird species in different stages of forest succession according to their primary feeding habits. Species numbers, numeric dominance in parentheses (percentage).

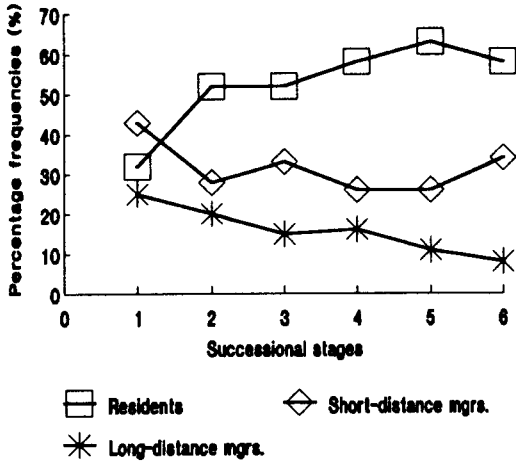| Feeding on	A	B	C	D	E	F
Ground	10 (53)	6 (25)	9 (31)	9 (32)	7 (29)	7 (27)
Foliage	9 (47)	12 (50)	14 (48)	11 (39)	10 (42)	11 (42)
Bark	0 (0)	6 (25)	6 (21)	8 (29)	7 (29)	8 (31)

Fig. 2. The ratio of the three different group of birds based on migratiory status in each of the successional stages measured in abundances.

Absolute species number was found to be highest in stage C (see results). The area is greatest here, so it may come from the species-area relationship proposed by Preston (1960, 1962). This predicts that the greater the area the higher the species number it supports. This bias in species numbers towards the larger areas can be eliminated by the application of the rarefaction method (James & Rathbun 1981). According to successional theory (Odum 1969) community diversity and stability increases during succession. For birds this is supported by a wealth of studies (e.g., Kendeigh 1948, Odum 1950, Johnston & Odum 1956, Karr 1968, Shugart & James 1973, Glowacynski 1975). However, this increase is not monotonic in every case. Smith & MacMahon (1981), for example, found that diversity peaked in the preclimax forest. According to the data of May (1982) in North America and Bejcek & Stastny (1984), Glowacynski & Weiner

(1983) and Moskát & Székely (1986) in Europe diversity and density show a two-peaked distribution in the course of succession. In Europe the decrease takes place between 30-40 years of age which is in agreement with my density data but not with the rarefaction species number. Moskát & Székely (1986) explained it as a consequence of a lack of both hole-nesters and shrub-nesters in these communities. The absence of high trees and a significant shrub level is also true for our study forests of this age.

My results that both density and rarefaction species number have their peaks in stage D do not fit the above-mentioned patterns. Several common species reach their maximum density here, namely Great, Middle and Lesser Spotted Wood-peckers (*Dendrocopos major, D. medius and D. minor*), Tree Pipit (*Anthus trivialis*), Collared Flycatcher (*Ficedula albicollis*), Chaffinch and Golden Oriole (*Oriolus oriolus*). In the habitat selection of these species either old trees or open-ness seem to play a significant role. The vegetational physiognomy of this stage satisfies these requirements as both canopy and shrub cover are low here. This follows from the forest management practice of selective thinning which creates a situation uncommon in natural succession. However, there are no great differences between rarefaction species numbers of the five closed forest stages.

This similarity of the later stages is expressed in the similarity indices, too. The same applies to ecological groups of birds. All these suggest that there is a sharp difference between shrub-like and closed-canopy forests. Analysing bird community data from successional seres of different localities over Europe Blondel & Farré (1988) found that the initial, open stages

Tab. 7. Degree of specialization in bird communities of different phases of forest succession in terms of species/genus, species/family and genus/family ratios.

Ratio	A	B	C	D	E	F
Species/genus	1.357	1.500	1.526	1.400	1.333	1.368
Species/family	2.111	2.000	2.070	2.153	1.714	1.857
Genus/family	1.555	1.333	1.357	1.538	1.286	1.357

differed much while old stages converged to each other. They explained this on historical grounds, namely, that the similarity of the european forest faunas is pronounced because these habitats were not fragmented during the Pleistocene. On the other hand, speciation in open and semi-open habitats were helped by the fragmentation of such habitats in the same time period. This hypothesis is also helpful when explaining the sharp demarcation found between bird communities of the initial stage A and closed forest stages in our study.

5.2. Migratory status

The ratio of long-distance migrants is highest in the initial brushwood phase and decreases towards the climax while that of the sedentary species show an opposite trend. This is true for both the species number and density. The difference between these ratios in the initial and later stages is statistically significant (Mann-Whitney U-test, p<0.05). The same pattern has been obtained by many researchers for european forest successions (Bilcke 1984, Helle & Fuller 1988, Mönkkönen & Helle 1989), while a reversed ratio of tropical migrants were found in North American successions (MacArthur 1959).

There are three hypotheses explaining these observations. MacArthur (1959) proposed that the proportion of migrants is highest in places where the change between winter and summer food supply is greatest. Alerstam & Enckell (1979) hypothesize that migrants are better competitors in open habitats because birds with simple niches can more easily fit into an existing community in their winter quarters. Finally, Bilcke (1984) assumes that the proportions of migrants in the breeding area is determined by the proportion and geographic distribution of the vegetation types in the winter quarters. This latter hypothesis was strongly supported by Mönkkönen & Helle's work (1989). They showed that the first two hypotheses failed to explain intercontinental differences while that of Bilcke's was successful in doing so. The proportion of forested land is highest in South America, lowest in Africa. The nesting habits of long-distance migrants follow this pattern: in North America they inhabit mainly forested habitats while in Europe they select open or brushy habitats more often. Though a rigorous test of this hypothesis is still needed, the arguments supporting it seem strong.

5.3. Specialization

The hypothesis that specialization as measured by species/genus, species/family or genus/family ratios increases during succession (Margalef 1968, Odum 1969) was not supported by our data. Because others reached the same conclusion (Glowacynski 1979, Helle 1985) either the method is wrong for measuring specialization or the hypothesis is false. A more promising method would be to actually measure diet or foraging microhabitat niche breadth of every species in the successive communities and calculate the actual ratio between specialists and generalists. Then we can conclude whether specialisation increases as succession progresses or not. In the absence of such data we cannot state that succession in our case would lead to greater specialization.

Összefoglalás

Madárközösség-változások különböző korú tölgyesekben a Budai-hegységben

Jelen dolgozat a tölgyerdei másodlagos szukcesszió hatását vizsgálja a madárközösségek szerkezetére. A vizsgálat a szukcesszió hat fázisát foglalja magában, a sűrűség fázistól a klimaxnak tekinthető öreg erdőkig. Az egyes madárfajok denzitásadatait az ún. módosított I.P.A. módszerrel becsültük, amely 100 m sugarú körökre szolgáltat adatokat. Összesen 92 mintavételi kör adatai szerepelnek az elemzésekben, ezek fázisonkénti megoszlása a sűrűségtől az öreg erdőig a következő:

9, 13, 24, 23, 9 és 14.

A legalacsonyabb fajszám a sűrűség fázisban, a legalacsonyabb denzitás a vékony rudas erdőben (B fázis) volt. Ez utóbbinak az oka valószínűleg a cserjeszint és az odúk szinte teljes hiánya ezekben az erdőkben. A legmagasabb denzitás és rarefaction-módszerrel számított fajszám a szálaserdőben (D fázis) mutatkozott, ami azzal magyarázható, hogy számos odúlakó faj (pl. harkályok, örvös légykapó) és nyílt, ligetes erdőket kedvelő faj (pl. erdei pityer) itt éri el a maximális denzitást. Ez a nyitott, kis cserjeszintű erdőszerkezettel hozható összefüggésbe, amit az erdőgazdálkodás a törzskiválasztó gyérítéssel és az ezzel járó munkálatok utóhatásaival hozott létre.

A teljes közösségek és a fészkelési, táplálkozási és vonulási szokásokon alapuló ökológiai csoportok összehasonlításakor egyaránt kifejezett a különbség a cserjeszintű, fiatalos fázis és a többi, záródott fázis között. Ez a hipotézisek szerint a kétféle élőhelyen különböző módon lezajlott fajképző folyamatok és alkalmazkodási mechanizmusok következménye lehet. Az európai madárközösségek szukcessziójában általános vonás, hogy a nyiltabb élőhelyektől a zártabbak felé haladva csökken a közösségekben a hosszútávú, trópusi vonulók aránya. Bilcke (1984) hipotézise szerint, amelyet Mönkkönen és Helle (1989) is megerősített, ennek magyarázata az, hogy az afrikai telelőterületen nagyobb arányban találhatók nyílt - szavannás, félsivatagi - élőhelyek.

Margalef (1968) és Odum (1969) hipotézisét, amely szerint a szukcesszió során a specializáció mértéke növekszik, a faj/nemzetség, faj/család, nemzetség/család arányszámok nem támasztották alá. Mivel más kutatók (pl. Helle 1985) is hasonló eredményeket kaptak, valószínű, hogy a módszer nem alkalmas a tényleges specializáció mértékének a megállapítására.

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