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# Bird-vegetation relationships along ecological gradients: ordination and plexus analysis

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Breeding birds were counted and vegetation structure was recorded along two seres of forest succession, in beech forest (*Aconito-Fagetum*) and oak forest (*Quercetum petraeae-cerris)* in Central-Europe. Bird-vegetation relationships were analyzed by two multivariate techniques: canonical correspondence analysis (CCA) and multivariate plexus analysis (MPA). The two methods revealed different aspects of bird-vegetation relationships. CCA demonstrated the dynamical aspect of changes in community structure. In both habitats it revealed two gradients which are important in bird-vegetation relationships. The first axis was interpreted as the successional gradient and the second axis as the closeness-openness gradient. Results of MPA revealed the association structure between individual bird species and vegetation components. Multiple regression analysis showed that MPA is sensitive to the detection of both the linear and the non-linear features of bird-vegetation relationships. CCA and MPA gave some new insights into bird-vegetation relationships across the forest succession. They are not alternatives of each other, they revealed different aspects of the relationships.

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## 1. Introduction

Many studies have shown strong associations between vegetation physiognomy and avian community structure (e.g., MacArthur & MacArthur 1961, MacArthur et al. 1966, Cody 1974, Willson 1974, Rotenberry & Wiens 1980, James & Wamer 1982), although floristical composition of vegetation may also be relevant (e.g., Tomoff 1974, Wiens & Rotenberry 1981, Rotenberry 1985, Moskát 1988). Although multivariate statistical analyses are frequently applied in these studies (see review in Wiens 1989), the analysis of bird-vegetation relationships suffers from methodological problems (Moskát 1991). The [site x birds x vegetation] -type data matrices cannot be analyzed directly by standard ordination techniques. Methodological problems increase when the ecological data relate to long ecological gradients, such as in a successional sere (Gauch 1982).

The present paper demonstrates the usefulness of two new techniques, which can be recommended for such type of analyses, namely the canonical correspondence analysis (CCA) (ter Braak 1986, 1987a), and the multivariate plexus technique (MPA) (Whittaker 1987, Moskát 1991). The application of these multivariate statistical methods gives more insight into bird-vegetation relationships.

## 2. Study area, successional categories

The study was conducted in two successional seres of Central-European deciduous forests in Hungary. In 1985 an area of managed beech forests (*Aconito-Fagetum*) was studied in the Bükk Mountains (Bükk National Park, 48°06'N, 20°35'E). The area is situated about 600-750 m a.s.l. Six stages of forest regeneration were distinguished:

B1: Clear-cut area (0-1 years old).

B2: Younger shrubby phase (2-5 years old).

B3: Older shrubby phase (5-10 years old).

B4: Young forest (brushwood) (10-20 years old).

B5: Preclimax stage (50-60 years old).

B6: Climax stage (90-110 years old).

See more details of habitat description in Moskát & Székely (1989).

A sere of oak forest (*Quercetum-petraeae cerris*) was studied in the Buda Hills, near the capital Budapest (47°35'N, 18°90'E) in 1988. Oak forests occupy lower zones in Central-Europe than the beech forests. This study area is situated about 240-450 m a.s.l. Six stages of forest regeneration were also distinguished:

O1: Younger shrubby phase (<20 years old).

O2: Older shrubby phase (21-40 years old).

O3: Young forest (brushwood) (41-60 years old).

O4: Middle-aged forest (61-80 years old).

O5: Preclimax stage (81-100 years old).

O6: Climax stage (100 years old).

See more details on vegetation physiognomy and floristical composition in Waliczky (1991).

Different stages of growth were not equally available in the two seres. Young stages of growth were much more strongly represented in the beech than the oak sere.

## 3. Methods

### 3.1. Bird censuses

A double-visit fixed radius point count technique was applied (Moskát 1987) for counting woodpeckers, pigeons, and passerine bird species. This technique is a variant of the French IPA technique (Blondel et al. 1981). In early mornings birds were counted for 10 minutes on circles with 100 m radius around each site, while the census-taker was standing at the centre of the sampling circle. The first counts were carried out in April, the second in May for both seres. The greater value of the two counts was chosen as a representative value, as in the IPA technique. Relative density of breeding pairs was calculated by relating the number of singing males and/or observed pairs to the area of the sampling circle. The results can be regarded as abundance indices for the sites. The accuracy of this technique was over 70%, as tested against the territory mapping method in a climax beech forest (Moskát 1987).

In the beech forest sere 83 sites were located; 9, 13, 11, 11, 16, and 23 in the six successional stages denoted by B1 to B6, respectively. In the oak forest sere 92 sites were selected; 9, 13, 24, 23, 9, and 14 in the six stages abbreviated by O1 to O6. A sampling circle at a site covered about 3.14 ha, so sampling areas varied between 28.26 ha and 75.36 ha in stages. For this reason the rarefaction method (Heck et al. 1975, James & Rathbun 1981) was required for the comparison

of bird communities between stages.

### 3.2. Vegetation measurements

Vegetation physiognomy data were collected on 20-25 points within the circles used for bird counts. The average of these measurements was used to represent a site. The basic variables were chosen after James & Shugart (1970), and they were estimated visually.

The vegetation variables measured were grass cover (%), bush cover (%), canopy cover (%), average tree height (m), average bush height (m), average minimal stem distance (m), average minimal bush distance (m), number of tree species, dominance of the most dominant tree species, beech or oak (%), average diameter at breast height (cm).

### 3.3. Statistical analyses

#### 3.3.1. Canonical correspondence analysis

Canonical correspondence analysis (CCA) is a statistical method to relate community composition to known variation in the environment (ter Braak 1986). This technique combines the algorithm of correspondence analysis on [species x site] data, and a weighted multiple regression analysis on environmental data. We applied CCA to reveal bird-habitat relationships relating the [bird abundance x site] data matrix to the [vegetation physiognomy x site] matrix. We carried out CCA by the computer program CANOCO (ter Braak 1987b).

#### 3.3.2. Multivariate plexus analysis

The plexus technique is useful to produce a graph representation of plant species associations according to their ecological similarities (Whittaker 1967, McIntosh 1978). Matthews (1978) tried to combine this technique with numerical ordinations, drawing a plexus graph on an ordination diagram obtained by non-metric multidimensional scaling, based on species correlations. Whittaker replaced the correlation coefficient by the more robust rank correlation, and analyzed detrended correspondence analysis (DCA) components of vegetation together with environmental variables (Whittaker 1987). Whittaker's plexus analysis identifies the vegetation-environment complex in four stages: (1) DCA for vegetation variables, (2) rank correlation for vegetation components and environmental variables, (3) ordination of rank correlations by non-metric multidimensional scaling, (4) drawing the plexus graph on the ordination diagram. This technique seems to be suitable for the analysis of complex ecological data ('multiway data matrices'), and can be generalized into the multivariate plexus concept (Moskát 1991). We can substitute DCA in Whittaker's version of the method by any other eigenvector ordination technique (e.g., principal component analysis, principal coordinate analysis, correspondence analysis), so it is possible to choose the best technique for the statistical features of the data set.

We derived vegetation components by correspondence analysis (CA, also called 'reciprocal averaging') (Hill 1973). We selected only the first two components for the subsequent steps, because the interpretation of results is more difficult at higher dimensions (Gauch 1982). For correspondence analysis the computer program CANOCO was applied (ter Braak 1987b).

Vegetation components and bird spe-

Tab. 1. Number of species (S), expected number of species on 28 ha, counted by the rarefaction method (R), and densities (D) (pairs/10 ha).

| Category | S | R | D |
|---|---|---|---|
| Beech sere | | | |
| B1 | 12 | 12.00 | 14.51 |
| B2 | 19 | 17.77 | 33.32 |
| B3 | 19 | 17.86 | 32.43 |
| B4 | 19 | 17.53 | 26.35 |
| B5 | 23 | 20.63 | 35.63 |
| B6 | 29 | 26.04 | 50.68 |
| Oak sere | | | |
| O1 | 20 | 20.00 | 46.35 |
| O2 | 24 | 21.27 | 45.32 |
| O3 | 29 | 21.67 | 59.31 |
| O4 | 28 | 24.11 | 70.61 |
| O5 | 24 | 24.00 | 61.92 |
| O6 | 25 | 22.51 | 63.24 |

cies abundance values were pooled into a common data matrix, then Kendall's rank correlation coefficients ($\tau$) were computed between all of the elements. For computation of Kendall's tau the program package SPSS/PC+ was applied (Norusis 1986). Following the transformation of the rank correlations ($\tau$) into the (1–abs($\tau$)) dissimilarities, non-metric multidimensional scaling (NM-MDS) was applied. It was carried out according to the suggestions by Orlóci and Kenkel (1985), applying their computer program MDS.

#### 3.3.3. Multiple regression analysis

Multivariate plexus analysis is a suitable technique to detect both the linear and the non-linear relationships between individual bird species and vegetation components. For detecting the relationships in detail we applied stepwise linear regression analysis, using the program package SPSS/PC+ (Norusis 1986). Following Meents et al. (1983) the correspondence analysis component scores for the first and the second components were transformed by squaring and cubing. We ran the program on the set of the original linear and the transformed polynomial CA components as the independent variables, and on the abundance of individual bird species as the dependent variable.

#### 3.3.4. Cluster analysis

We classified bird community data derived from both of the seres by agglomerative cluster analysis. The analysis was performed by the group average technique from similarities calculated according to the Czekanowski's formula. The computer program NCLAS2 was applied from the program package SYNTAX-III (Podani 1988).

## 4. Results

### 4.1. General characteristics of the bird communities

Overall, 40 woodpecker, pigeon, and passerine bird species were recorded in the beech sere, and 40 species in the oak sere. Species richness and density increased with successional stages in the beech sere, whereas the pattern was slightly different in the oak sere where it showed peak at about the fourth stage (Tab. 1). The Tree Pipit (*Anthus trivialis*), the Greenfinch (*Carduelis chloris*), and the Yellowhammer (*Emberiza citrinella*) were the most abundant species (>10%) in the B1 stage, the Barred Warbler (*Sylvia nisoria*) and the Yellow-

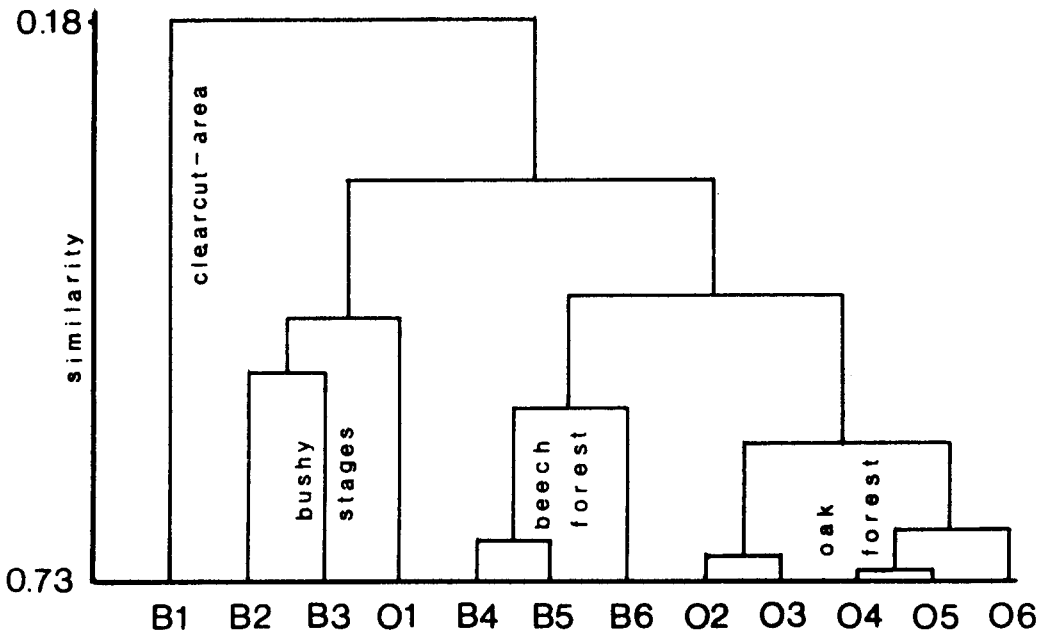


Fig. 1. Dendrogram of bird communities with respect to seral stages in a beech and oak sere, derived by agglomerative cluster analysis (Czekanowski's index, group average fusion strategy).

hammer in stage B2. In all of the other four stages of the beech sere the Robin (*Erithacus rubecula*) and the Chaffinch (*Fringilla coelebs*) were the most dominant species, while in stage B3 the following three species also showed dominance value greater than 10%: Blackbird (*Turdus merula*), Blackcap (*Sylvia atricapilla*), and Chiffchaff (*Phylloscopus collybita*). The oak sere can be characterized by the following species: Blackcap, Chiffchaff, and Nightingale (*Luscinia megarchynchos*) in the O1 stage, Chaffinch and Yellowhammer in the O2 stage, Yellowhammer, Blackcap, and Chaffinch in the O3 stage, Chaffinch in the O4 stage, Great Tit (*Parus major*) and Nuthatch (*Sitta europaea*) in the stage O5, Starling (*Sturnus vulgaris*) and Great Tit (*Parus major*) in the stage O6. Generally, the bird communities in the young stages were very similar in the two seres, but less so between the mature and the climax stands (Fig. 1). A more detailed discussion of bird community structures of these seres can be found in Moskát & Székely (1989), and in Waliczky (1991).

### 4.2. Ordination of the bird-vegetation data by canonical correspondence analysis

Fig. 2 shows the ordination diagram of the beech forest sere. We interpreted the first axis as the successional gradient, and the second axis was identified as a closeness-openness gradient. This interpretation was supported by the correlation values between these axes and the vegetation variables, and by the values

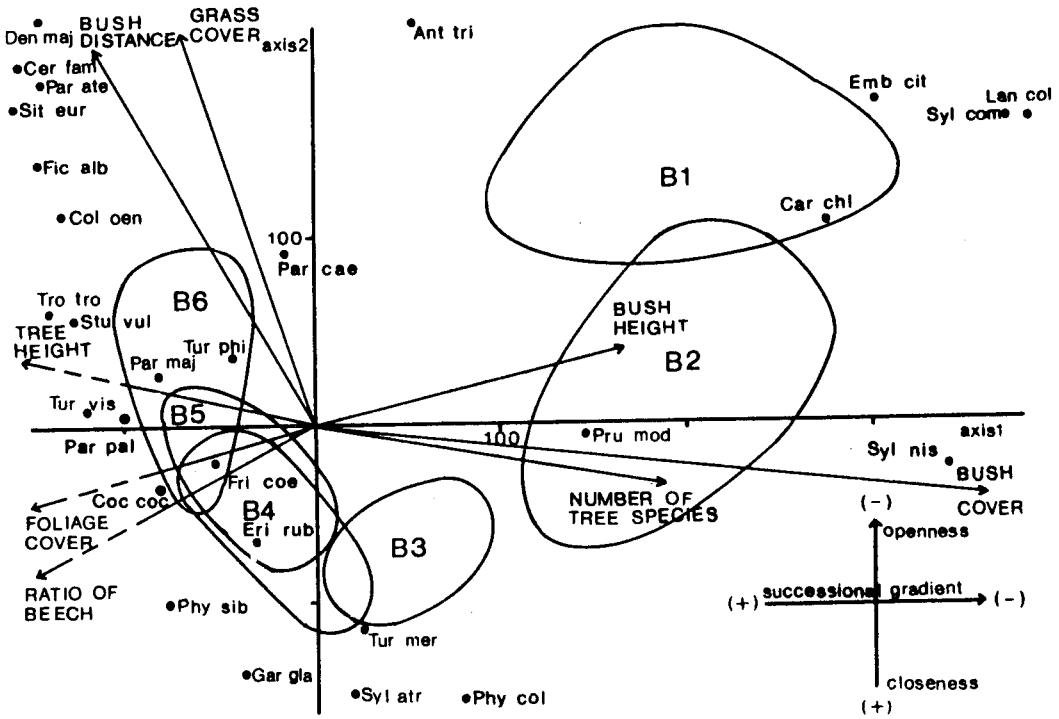


Fig. 2. Bird distribution in a successional sere of beech forests: CCA ordination diagram with bird species (.) and site scores (only contour-line of site points are presented).

of standardized regression/canonical coefficients and interset correlations.

In order to make the interpretation of the ordination diagram easier, we did not draw the exact positions of individual site scores. Only the contour lines for the clouds of the points for each of the seral stages were drawn. Positions of the seral stages on the ordination diagram show a sequence from stage B1 to B6. Variability of stages B1 and B2 is much greater than that of the older stages. Stages from B3 to B6 show a partial overlap with their neighbours representing the continuity of stages. Contour maps of the stages are positioned on an arch, indicating the well-known arch effect (Hill & Gauch 1980), which reveals important non-linear characteristics of the data set (Wartenberg et al. 1987). In the case of the beech forest sere, the arch effect has drawn attention to a slight relationship between the two ends of the sere. Open patches within the climax stage make possible territory establishment for the Tree Pipit. The Yellowhammer is also known to be a similar species in habitat selection along a beech forest sere (Moskát & Székely 1989), but its density is much greater in the youngest stage than in the old one, therefore CCA placed it far from the Tree Pipit.

Positions of the bird species on the ordination diagram with respect to the contour maps of the stages reveal the association between individual species and successional stages. CCA placed habitat specialists for the young stages (e.g., Red-backed Shrike *Lanius collurio*, and

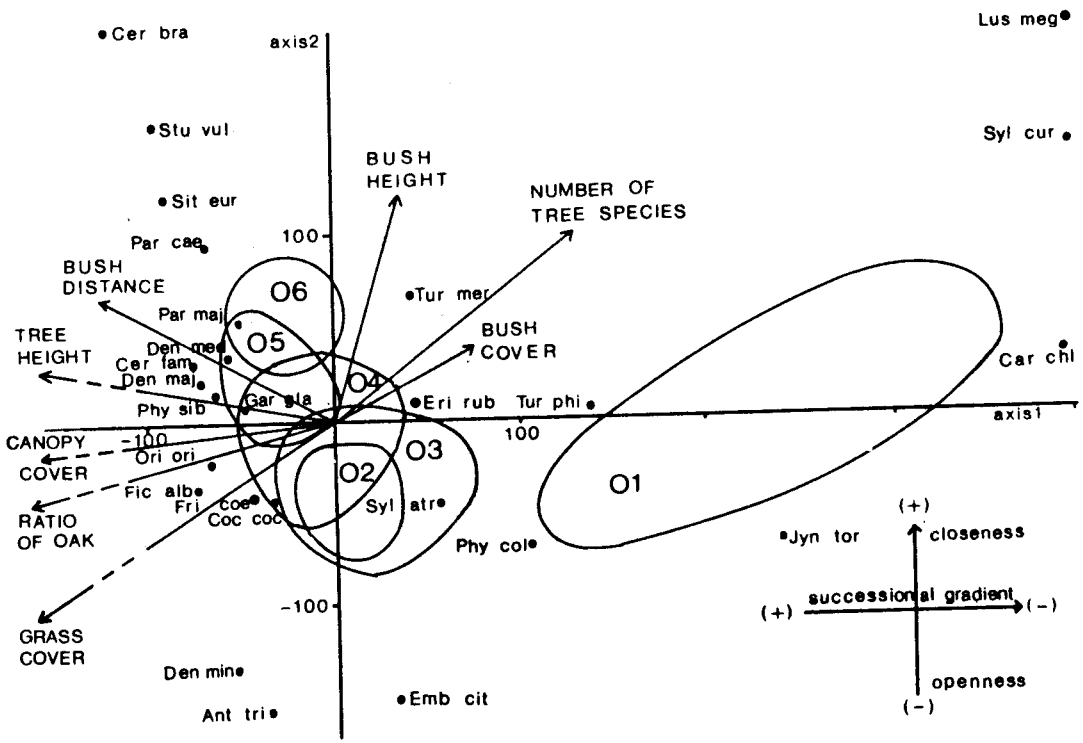


Fig. 3. Bird distribution in a successional sere of oak forests: CCA ordination diagram with bird species (.) and site scores (only contour-line of site points are presented).

Whitethroat (*Sylvia communis*) on the upper right corner of the diagram. In the inner parts of the sere there are habitat generalist species (e.g., Blackcap, Robin, Blackbird), and there are older stage specialists around the older stages (e.g., Mistle Thrush *Turdus viscivorus*, Great Tit). Some climax specialist species (Stock Dove *Columba oenas*, Great Spotted Woodpecker *Dendrocopos major*, Collared Flycatcher *Ficedula albicollis*, Nuthatch, Tree Creeper *Certhia familiaris*) are placed to the upper left corner of the diagram. The Coal Tit (*Parus ater*) was also put into this group. Although this species can be found in pine and coniferous forest stands at great variability in age in Central-Europe, in the beech sere it is restricted to the climax stage.

In CCA vegetation variables are presented by arrows, where close angle with any of the axes show close relation between the variable and the axis. The length of the arrows represents the relative importance of the vegetation variable among the vegetation characteristics.

Arrows of the vegetation variables 'bush height', 'bush cover' and 'number of tree species' show close relation to the right side of the first ordination axis ('successional gradient'). In the beech forest sere bushes are represented only in the young stages, they are nearly absent from the older ones. The number of tree and bush species in the older stages is low. The variables 'tree height' and 'foliage cover' show close relation to the other side of the first ordination axis, representing the main physiognomical

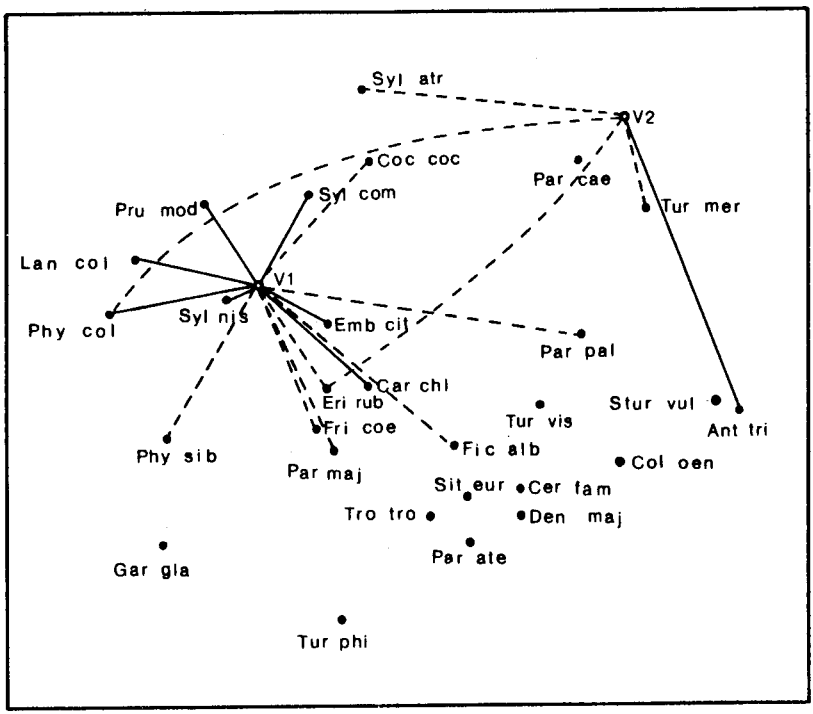


Fig. 4. Relationships between bird species and vegetation components in a successional sere of beech forests: plexus diagram with bird species (.) and vegetation components (V1, V2). (Only highly significant relationships are shown ($P<0.01$); straight line represents a positive (+) relationship, broken line means a negative (–) relationship; V1+: shrub character, V1–: old forest character/scarce shrub layer, V2+: openness, V2–: closeness).

characteristics of the older stages. The position of the variable 'percent of beech trees' along the left part of the successional gradient agrees with the floristical simplicity of the older stages. The vegetation variables 'grass cover' and 'bush distance' show relations with the second axis, which was identified as a closeness-openness gradient. Tree Pipit is positioned to the upper end of this axis, showing a close association with openness. Open areas are typical in the 'B1' stage, moreover small open patches can be found in the 'B6' stage. Stages in the middle of the sere, such as the 'brushwood' – like young forest are very closed, herefore they were placed to the lower part of this axis.

The ordination diagram of the oak sere (Fig. 3) revealed a very similar pattern to the beech one. Axis 1 is the successional gradient, axis 2 is the openness-closeness gradient, but the interpretation of the second axis is not as clear as in the case of the beech sere. Seral stages take place on an arch from stage 'O1' to 'O6'. There is a little difference in the structural characteristics between the stages of the oak and beech vegetation seres. The beech sere starts from the clear-cut area, while the oak one begins from the small bush stage, therefore stage 'B2' in the beech sere is approximately equal in structure to

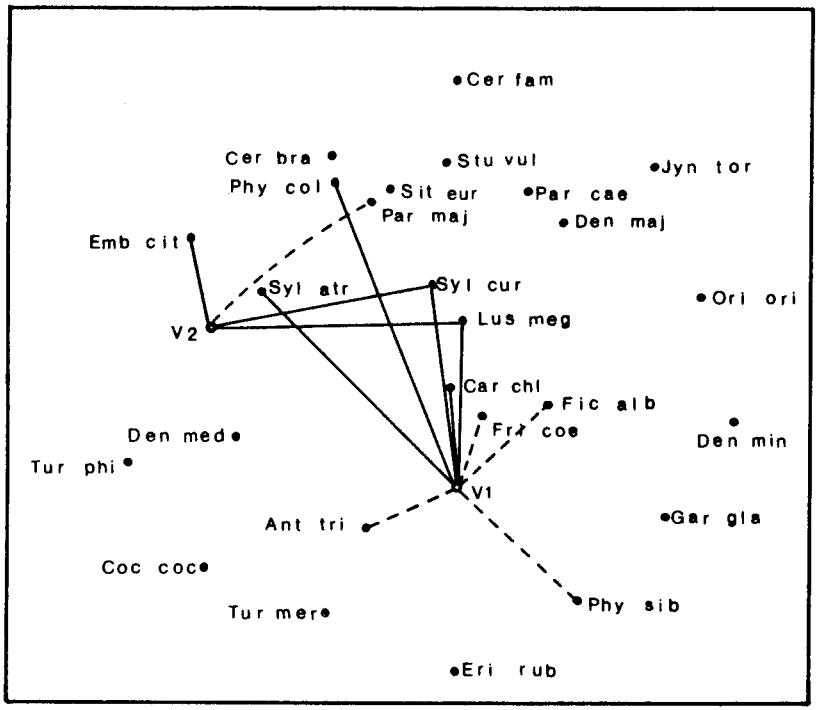


Fig. 5. Relationships between bird species and vegetation components in a successional sere of oak forests: plexus diagram with bird species (.) and vegetation components (V1,V2). (Only highly significant relationships are shown ($p<0.01$); straight line represents a positive (+) relationship, broken line a negative (–) relationship; V1+: shrub character, V1–: old forest character/scarce shrub layer, V2+: openness, V2–: closeness).

stage 'O1' in the oak sere. Stages 'O2' and 'O3' in the oak sere did not separate from each other in this analysis. In both of the seres variability of the older stages is much less than that of the young stages.

Many species (e.g., Blackcap and Chaffinch) are placed around the middle of the sere on the diagram. Although the signs of the second axes on Fig. 2 and Fig. 3 are opposite, the axes represent nearly the same closeness-openness gradients for both of the seres. Along axis 2 on Fig. 3 species preferring openness (Tree Pipit and Yellowhammer) and closeness (Robin, Blackbird) are well separated. Species preferring the older stages are at the left side of axis 1. The Nuthatch, the Short-toed Tree Creeper (*Certhia brachydactyla*), and the Starling prefer old, closed stands.

Vegetation variables represented by arrows on the diagram show only a slightly different pattern from the beech sere. The variables 'bush height', 'bush cover' and 'number of species' show relations with both of the axes. 'Tree height', 'foliage cover' and 'percent of oak trees' are positioned to the left side of axis 1, which means a considerable role of these characters at the older stages. 'Grass cover' and 'bush distance' have only minor importance according to this analysis.

Tab. 2. Significant bird-vegetation relationships in the beech sere, according to Kendall's rank correlation and stepwise multiple regression. (Non-linearity was tested by using $x^2$ and $x^3$ transformations in the regression models.) (V1 and V2 are the vegetation components derived by correspondence analysis; significance levels: +/−: $p<0.1$, ++/−−: $p<0.05$, +++/−−−: $p<0.01$).

| | Kendall's tau ($\tau$) | | Stepwise multiple regression | | | | | |
|---|---|---|---|---|---|---|---|---|
| Bird species | $V_1$ | $V_2$ | $V_1$ | $V_2$ | $V_1^2$ | $V_2^2$ | $V_1^3$ | $V_2^3$ |
| *Columba oenas* | − | | | | | | | |
| *Dendrocopos major* | | | | | | | | |
| *Garrulus glandarius* | | −− | | | | | | |
| *Parus palustris* | −−− | | −−− | | | | | |
| *Parus ater* | | | | | | | | |
| *Parus caeruleus* | − | ++ | | | | | | |
| *Parus major* | −−− | | −−− | | | | | |
| *Sitta europaea* | −− | + | −−− | | | | | |
| *Certhia familiaris* | | | | | | | | |
| *Troglodytes troglodytes* | −− | | −−− | | | | | |
| *Erithacus rubecula* | −−− | −−− | −−− | | | −−− | | |
| *Turdus merula* | | −−− | | −−− | | | | |
| *Turdus philomelos* | | | | | | | | |
| *Turdus viscivorus* | −− | | | | | | | |
| *Sylvia nisoria* | +++ | −− | +++ | −− | +++ | | | |
| *Sylvia atricapilla* | | −−− | | −−− | | | | |
| *Sylvia communis* | +++ | ++ | +++ | | | | | |
| *Phylloscopus collybita* | +++ | −−− | +++ | −−− | −− | | | |
| *Phylloscopus sibilatrix* | −−− | | −−− | | | | | |
| *Ficedula albicollis* | −−− | | −−− | | | | | |
| *Prunella modularis* | +++ | | +++ | | | | | |
| *Anthus trivialis* | | +++ | | +++ | | | | |
| *Lanius collurio* | +++ | | | | | | +++ | |
| *Sturnus vulgaris* | −− | | | | | | | |
| *Fringilla coelebs* | −−− | | −−− | | | | +++ | |
| *Carduelis chloris* | +++ | | +++ | | | +++ | | |
| *Coccothraustes coccothraustes* | −−− | | −−− | | | | | |
| *Emberiza citrinella* | +++ | + | +++ | ++ | | | | |

Tab. 3. Significant bird-vegetation relationships in the oak sere, according to Kendall's rank correlation and stepwise multiple regression. (Non-linearity was tested by using $x^2$ and $x^3$ transformations in the regression models.) (V1 and V2 are the vegetation components derived by correspondence analysis; significance levels: +/–: $p<0.1$, ++/––: $p<0.05$, +++/–––: $p<0.01$).

| | Kendall's tau ($\tau$) | | Stepwise multiple regression | | | | | |
|---|---|---|---|---|---|---|---|---|
| Bird species | $V_1$ | $V_2$ | $V_1$ | $V_2$ | $V_1^2$ | $V_2^2$ | $V_1^3$ | $V_2^3$ |
| *Jynx torquilla* | ++ | | | –– | | | +++ | |
| *Dendrocopos major* | – | – | | | ––– | | | |
| *Dendrocopos medius* | – | – | | | | | | |
| *Dendrocopos minor* | | | | | | | | |
| *Oriolus oriolus* | | | | | | | | |
| *Garrulus glandarius* | –– | – | | | | | | |
| *Parus caeruleus* | | –– | | | ––– | | | |
| *Parus major* | | ––– | | | ––– | | | |
| *Sitta europaea* | | – | | | | | ––– | |
| *Certhia brachydactyla* | | | | | | | | |
| *Certhia familiaris* | | ++ | | | | | | |
| *Erithacus rubecula* | ++ | –– | | | | | | |
| *Luscinia megarchynchos* | +++ | +++ | | | | +++ | +++ | +++ |
| *Turdus merula* | ++ | | ++ | | | | | |
| *Turdus philomelos* | | | | | | | ++ | |
| *Sylvia atricapilla* | +++ | ++ | +++ | | | | | |
| *Sylvia curruca* | +++ | +++ | | | | | +++ | +++ |
| *Phylloscopus collybita* | +++ | + | +++ | | | ––– | | +++ |
| *Phylloscopus sibilatrix* | ––– | | | | | | ––– | |
| *Ficedula albicollis* | ––– | | ––– | | | | | |
| *Anthus trivialis* | ––– | ++ | ––– | +++ | | | | |
| *Sturnus vulgaris* | | – | ++ | | ––– | | | |
| *Fringilla coelebs* | ––– | | ––– | | | | | |
| *Carduelis chloris* | +++ | ++ | | | +++ | | | +++ |
| *Coccothraustes coccothraustes* | –– | | | | | | | |
| *Emberiza citrinella* | – | +++ | | +++ | | ––– | | |

### 4.3. Ordination of the bird-vegetation data by multivariate plexus analysis

MPA reveals both the positive and negative associations between individual bird species and vegetation components (Moskát 1991). The most important vegetation components (V1 and V2) were selected for further analysis of the CA results. In both of the seres the first component was identified as bush character with '+' sign, and on the other side of the axis ('–') as old forest character. The second vegetation component reflects to openness with '+' sign, and to closeness with '–' sign. These meanings of the components are similar to the interpretation of the CCA axes (see above). Tab. 2 and Tab. 3 exhibit the values of Kendall's rank correlation coefficients, measured between the vegetation components and individual bird species.

The plexus diagram for the beech sere is shown on Fig. 4. It revealed strong positive correlations between V1 and 7 bird species (Whitethroat, Chiffchaff, Dunnock *Prunella modularis*, Red-backed Shrike, Greenfinch, Yellowhammer, Barred Warbler *Sylvia nisoria*). All of them prefer bushy habitats, the earlier stages of the sere. The Yellowhammer prefers clearcut areas as well as short bushy stages, therefore it shows a very close '+' association with V1, which is the positive part of the successional gradient (axis 1). Close negative associations were found between V1 and 5 bird species (Great Tit, Wood Warbler *Phylloscopus sibilatrix*, Collared Flycatcher, Chaffinch, Hawfinch *Coccothraustes coccothraustes*). Each of them prefer old stages with tall trees. Preference of the Tree Pipit for open habitats is confirmed by its close '+' association with V2. The Blackcap, the Chiffchaff, and the Robin showed an affinity to close habitats according to their close '–' association with V2.

The plexus diagram for the oak sere indicates strong positive associations between the successional variable (V1) and 5 bird species (Fig. 5). The Nightingale, the Blackcap, the Lesser Whitethroat, the Chiffchaff, and the Greenfinch belong to this group, whereas 4 species (Wood Warbler, Tree Pipit, Collared Flycatcher, and Chaffinch) show negative relationships with V1. Three bird species show association with V2, which means the openness ('+') and closeness ('–') gradient. Whereas the Yellowhammer is placed near to V2, the Nightingale, and the Lesser Whitethroat have significant relations with V1 too, so they are placed at about half way between V1 and V2. The Great Tit is the only species, which shows great '–' association with V2, hence it prefers closed habitats.

Although plexus analysis is sensitive to both the linear and nonlinear cases of relationships between individual bird species and vegetation components we needed a further analysis by stepwise multiple regression to reveal the linear or nonlinear characteristics. We tested nonlinearity by using $x^2$ and $x^3$ transformations in the regression models (see above). In Tab. 2 and Tab. 3 we represent the significant relationships between birds and vegetation. In the beech sere 18 out of the 28 bird species exhibit linear relationships with at least one of the two vegetation components. These numbers in the oak sere are 9 and 26, respectively. About 55% of the linear relationships are negative. Six bird species showed nonlinear relationships with vegetation components in the beech sere, and 13 in the oak one. Taking into

account the most significant results ('+++' and '---'), there is a great agreement between them and the values of Kendall's rank correlation.

## 5. Discussion

### 5.1. Habitat selection of birds along forest successional gradients

If the gradient studied is long enough to contain habitats with rather sharply different physiognomic structure, as in our case, either CCA or plexus diagram can reveal broad affinities of bird species to certain characteristics of those habitats. In both seres CCA sharply distinguishes between the open grassy or brushy stages and the other, more closed forest stands. The initial phases are more diffusely distributed and heterogenous in themselves, whereas the older phases overlap widely. This indicates that the successional changes in bird communities are not gradual between the open brushwood and closed forest stages but that there is a sudden break in species habitat distribution: species with close affinities to trees (mainly hole-nesters) appear, while the densities of many shrub-nesting species fall to zero.

In the CCA space of the two successional seres the majority of species common to both forests show a very similar position according to the two axes. This suggests that, although the sample plots of the two seres differ greatly in species composition and densities, the structure of these forest types is similar and the individual habitat selection of common forest birds is much the same.

The plexus diagrams emphasize these general patterns. Interestingly, almost all of the species showing (+) and (–) connection with the first or the second vegetation components are open-nesting species (exceptions are Great Tit and Collared Flycatcher). This is partly explained by the fact that species selecting brushy or open habitats are exclusively open-nesters. For woodpeckers the diameter at breast height is the most important factor in their habitat selection.

Our findings that the brushy phases differed much from closed stages in forest successions agrees with the hypothesis of Blondel & Farré (1988) and Blondel et al. (1988). They examined bird communities along forest successions from different geographical locations in Europe and found that there were sharp differences among communities of open and shrubby habitats but in a mature forest the phases converged on each other. They explained this pattern as a consequence of different speciation rates in homogeneous forest tracts and more patchily distributed open habitats in the Pleistocene. However, the early phases of several successional seres examined by them differed not only in location but in floristic composition as well, which has an impact on bird community structure (Rotenberry & Wiens 1980). Moreover, the physiognomical structure of vegetation was considered to be similar on the basis of vegetation height (in all four sites) and number of vegetational layers (in the two mediterranean sites only) alone, which is a rather poor measure of vegetational stratification in itself. On the other hand, oak forests are structurally similar all over Europe. Generally, initial phases differed relevantly, but the old forest avifauna tended to be similar. We consider the theory of Blondel & Farré (1988) and Blondel et al. (1988) to be relevant in explaining the overall simi-

larity of forest avifaunas throughout Europe. Speciation processes among birds inhabiting primarily broad-leaved forests (e.g., tits, woodpeckers) might have taken place largely within the biogeographical boundaries of Europe or, more broadly, in the Western Palearctic. On the other hand, birds of open and semi-open habitats in Europe might have evolved outside this region, especially in Africa (e.g., warblers, wheatears). This is, from our point of view, why the basic forest-dwelling species pool from which the actual community develops is so similar in different locations in Europe. For the bird communities of the second-growth habitats recent history, differential dispersal ability of species and chance effects may be more important.

### 5.2. Linear and nonlinear relationships

Investigations of nonlinear relationships between birds and vegetation are very scarce. Meents et al. (1983) analyzed relationships between birds and vegetation in the lower Colorado River valley, and found that about one-third of the cases showed a significant curvilinear response when there was no linear response at all. Best & Stauffer (1986) revealed nonlinear relationships between vertical vegetation density and habitat suitability indices for birds in riparian habitats of Iowa. They stated that commonly used statistical procedures in ecology were based upon assumption of linearity, but such relationships may be the exception rather than the rule. Our results also call attention to the importance of nonlinear features, besides the linear ones.

Technically, nonparametric statistical methods (e.g., Kendall's rank correlation) are robust and powerful tools for the detection of linear and nonlinear relationships together, but we need further analysis to reveal the characteristics of these relationships in detail. Following Meents et al. (1983) we squared and cubed variables to detect nonlinear features, but other type of nonlinearity may also occur.

### 5.3. CCA or MPA ?

Whereas multivariate plexus analysis revealed negative and positive associations between vegetation components and bird species abundances, canonical correspondence analysis placed sample sites and bird species into a common coordinate system. Although CCA suffers from linear distortion, it demonstrates the process of succession. MPA is the more robust procedure, because it uses non-metric multidimensional scaling for the main ordination, and it reveals both the linear and the nonlinear relationships as well.

Both CCA and MPA proved to be very helpful in understanding relationships between birds and vegetation components. These methods are not alternatives to each other, but reveal different aspects of bird-habitat relationships along a successional gradient. MPA showed close associations between elements, whereas CCA demonstrated the changes of community composition during the successional process.

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## Összefoglalás

**Madárközösség- és vegetáció–szerkezet kapcsolata ökológiai grádiens mentén: ordináció és plexus analízis**

Bükkös és tölgyes másodlagos szukcessziós sorozatában mértünk 10 vegetáció-szerkezeti változót és a madárfajok denzitásértékeit. A madárközösség- és vegetáció-szerkezet összefüggéseit sokváltozós analízisekkel elemeztük: a kanonikus korreszpondencia analízissel (CCA: ter Braak 1986) és a sokváltozós plexus analízissel (MPA: Whittaker 1987, Moskát 1991). Utóbbi nem-metrikus skálázáson alapuló többlépcsős módszer, melynél az egyes lépések az adattípushoz és a problémához viszonylag szabadon választhatók ("multivariate plexus concept", Moskát 1991). Módszertanilag mindkét eljárás rendkívül érdekes, mert megoldási lehetőséget kínál a [mintavételi hely x vegetçiós komponensek x madárdenzitások]-tipusú adatmátrixok közvetlen elemezhetőségének problémájára.

A két sokváltozós ordinációs eljárás a madárközösség- és vegetáció-szerkezet kapcsolatok különböző oldalát tárta fel. A CCA a szukcesszió során bekövetkező közösség-szerkezeti változások dinamikus jellegét hangsúlyozta. Az első ordinációs tengelyt a szukcessziós grádiensként azonosíthattuk, míg a második tengelyt egy nyitottsági–zártsági grádiensnek. Az MPA a vegetációs komponensek és a madárfajok közötti kapcsolatok finomabb részleteit tárta fel. A vegetációs komponensek speciális transzformációja után végrehajtott sokváltozós regresszióanalízissel kimutattuk, hogy az MPA egyaránt érzékeny a lineáris és a nem-lineáris kapcsolatokra. A CCA és az MPA új oldalát tárták fel a madárközösség- és vegetáció-szerkezet összefüggéseknek. A két eljárás nem tekinthető egymással alternatív módszernek, mivel az összefüggések más-más jellegét emelik ki.

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