COENOSES 6 (2): 79-89, 1991

MULTIVARIATE PLEXUS CONCEPT IN THE STUDY OF COMPLEX ECOLOGICAL DATA: AN APPLICATION TO THE ANALYSIS OF BIRD-HABITAT RELATIONSHIPS

C. Moskát, Ecological Research Group, Hungarian Natural History Museum, Budapest, Baross u. 13, H-1088, Hungary

Keywords: Bird-habitat relationships, Community structure, Multivariate analysis, Non-metric multidimensional scaling, Ordination, Plexus diagram, Vegetation structure

Abstract. The 'multivariate plexus concept' is an extension and generalization of Whittaker's species-environmental plexus applied in plant ecology. It is used in the analysis of complex multiway ecological data by a multistep procedure (eigenvector ordinations of two-way submatrices of data, rank correlations, non-metric multidimensional scaling, plexus diagram). The method was applied to four-way bird-habitat data collected in a Central-European oak forest. The integrated vegetation-bird plexus diagram showed significant relationships between several bird species and vegetation components, but the general physiognomic character of the forest had no relevant effect on bird species at the scale of the study. Using plexus diagram it was possible to detect strong negative effects between vegetation components and bird species; there are not usually revealed by the well-known ordination techniques.

Introduction

Multivariate statistical methods are frequently used to analyze ecological data, but the usefulness of results depends on the suitability of techniques to the aim of the particular study, the distributional properties of the data, that is, the question of robustness of the method, and the adequacy of sample size. Sometimes it is very difficult to avoid the second problem which may lead to misinterpretable artifacts in the results. There are many types of distributions of ecological data, and of species responses along ecological gradients (Austin 1979, 1985). For these reasons, ecological data rarely fit perfectly the requirements of specific multivariate techniques. However, well planned analyses can accomplish an exploration of the main structural relationships (Greig-Smith 1980) and hypothesis generation (Whittaker 1987). Under special circumstances, they can also be applied to testing hypotheses, through consistency of the results with known facts or with the outcomes of repeated field surveys/experiments, and through traditional means when the statistical distribution of the raw data is known and appropriate for the method applied (Orlóci 1978).

Finding robust techniques in community ordination is a current problem in numerical ecology (Kenkel and Orlóci 1986). Detrended correspondence analysis (DCA; Hill and Gauch 1980) has been claimed to be effective in revealing relatively long ecological gradients in sites x species type community data, but this claim was refuted (Kenkel and Orlóci 1986). Furthermore, environmental interpretation is a subsequent task (Gauch 1982a). Recently, modifications of non-metric multidimensional scaling (NM-MDS) have attracted considerable attention (Kenkel and Orlóci 1986, Bradfield and Kenkel 1987, Faith et al. 1987, Minchin 1987, Whittaker 1987), because of the fewer assumptions regarding the input variables than in the linear metric techniques. Ecological data are usually complex, containing different types of variables measured on the same sites. Water quality and phytoplankton data, inorganic sediment components and benthic invertebrates data, plant species distribution and environmental factors, bird abundances and habitat structure variables are examples. In the case of such complex measurements composed of two or more subsets of variables, the well-known multivariate techniques can rarely be applied directly to all of the variables. This makes it more difficult to interpret the results.

In this paper I extend Whittaker's (1987) vegetation-environement plexus concept for general ecological application. I propose to call this the *multivariate plexus concept* to indicate that it is based on multivariate analysis, like the eigenvector ordination techniques and non-metric multidimensional scaling. Since some of the methods in the multivariate plexus procedure can be chosen to suit the aims of the study, this concept gives a flexible framework for ecological analyses. Its special advantage is that the simultaneous analysis of different types of ecological measurements becomes possible; moreover, the analyses result in an easily interpreted graphical representation of the variable structure.

I demonstrate the utility of the multivariate plexus concept through an analysis of bird-habitat data. Birds presumably respond to both the physiognomical structure and the floristic composition of vegetation

(Wiens and Rotenberry 1981, Rotenberry 1985). The present study investigates the effect of the vegetation features (called components) on the abundance of individual bird species in oak forest. The multivariate plexus procedure maps the physiognomic and floristic components into a low-dimensional space together with the bird species and it demonstrates graphically the degree of their interrelationships. Issuing from the example, I describe ten characteristic features of the analysis.

Study area and variables measured

The study sites are in 80-90 year-old oak forest in the Pilis Mountains, Hungary (47°43'; 18°54') as it existed early April and mid-June in 1986. The forest is mainly composed of *Quercus petraea* and *Q. cerris*. The ground has a high grass cover and several species of shrubs are present (see the detailed list of tree and shrub species below). The sites occupy a south-east facing slope, 500 to 650 m a.s.l.

Fifteen discrete sampling sites were marked out for the breeding bird censuses. A sampling unit covered about 3.14 ha, and had circular shape with 100 m radius. So the total area sampled was about 47.1 ha. The usual territory mapping method (Robbins 1970, Pinowski and Williamson 1974) was combined with the circular plot method to identify territories and parts of territories at the edges of the sampling circles (Moskát 1990). Censuses were based on nine 10-minute visits at every site. The number of breeding pairs was used as an index of abundance.

Vegetation measurements were collected in a total of 75 subsamples, 5 subsamples in every sampling circle. A subsample unit covered about 0.03 ha, using a circle with 10 m radius. The placement of these units on the sampling circle was similar to that proposed by James and Shugart (1970) and represented by Noon (1981): one subsample unit in the center of the sample and four other subsamples around it, about 50 m apart from the centre.

Vegetation variables were separated into two categories: physiognomical characteristics of the habitat and floristic composition. The basic physiognomy variables were measured in a similar manner as proposed by James and Shugart (1970), but some additional variables were also measured. All of the vegetation variables were measured by T. Székely.

The *physiognomy variables* included:

GHE - grass height (cm)

SHE - shrub height (m)

THE - tree foliage height (m)

NT1 - number of thunks of living trees between 0 and 10 cm at breast height

NT2 - number of trunks of living trees between 10 and 20 cm at breast height

NT3 - number of trunks of living trees greater than 20 cm at breast height

VV1 - vegetation volume between 0 and 4 m (%)

VV2 - vegetation volume between 4 and 8 m (%)

VV3 - vegetation volume between 8 and 12 m (%)

VV4 - vegetation volume between 12 and 16 m (%)

VV5 - vegetation volume between 16 and 29 m (%)

GLC - grass layer cover (%)

SLC - shrub layer cover (%)

TFC - tree foliage cover (%)

STD - the average of the 5 shortest tree-trunk distances in the case of 5 randomly selected trees

SSD - the average of 5 shortest shrub distances in the case of 5 randomly selected shrubs

An additional variable, VDI, was computed from variables VV1 to VV5, and was used instead of them. This variable expresses the vertical heterogeneity of the habitat according to the Shannon formula using the natural logarithm.

The *floristic variables* included measures of the percentage contribution of tree species to the tree foliage cover and the same for shrub species contributions to shrub foliage cover. The following tree species were included: *Quercus petraea, Q. cerris, Tilia platyphyllos, Carpinus betulus, Fagus silvatica*. The list of shrubs found is: *Rubus* spp., *Quercus* spp., *Tilia platyphyllos, Rosa* spp., *Fraxinus ornus, Crataegus* spp., *Carpinus betulus, Corylus avellana, Ligustrum*

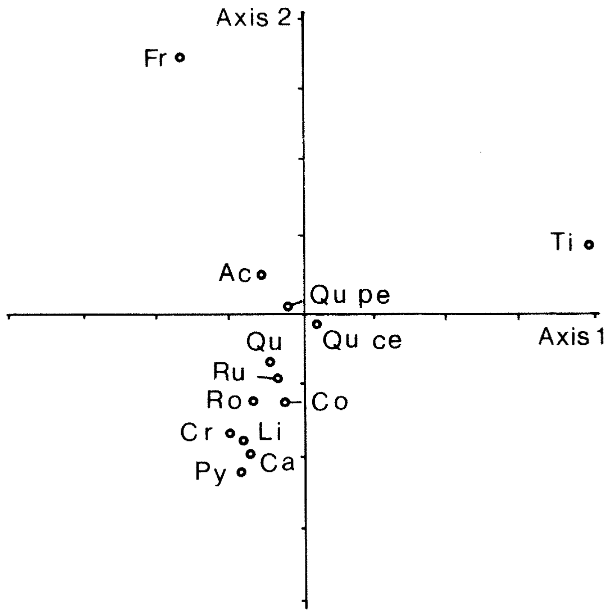

Fig. 1. Ordination diagram of shrub and tree species obtained by correspondence analysis. The analysis did not include rare species. Legends, Trees: Qu pe - *Quercus petraea*; Qu ce - *Q. cerris*; Shrubs: Ru - *Rubus* spp.; Qu - *Quercus* spp.; Ti - *Tilia platyphyllos*; Ro - *Rosa* spp.; Fr - *Fraxinus ornus*; Cr - *Crataegus* spp.; Ca - *Carpinus betulus*; Li - *Ligustrum vulgare*; Co - *Cornus mas*; Ac - *Acer campestre*; Py - *Pyrus pyraster*.

vulgare, Clematis vitalba, Cornus mas, Prunus spinoza, Acer campestre, A. pseudo-platanus, Cerasus avium, Ribes uva-crispa, Sorbus torminalis, Fagus silvatica, and *Pyrus pyraster*. The rare species were omitted from the analysis. The caption to Fig. 1 gives a list of plant species.

Variables showing non-normal distributions were transformed (Dunn 1981, Johnson 1981), using the arcsine transformation.

General concepts to analyze multiway data

The measurements are arranged in a four-way data matrix (sites x vegetation physiognomy x vegetation floristic x birds). Only multivariate analyses can reveal structural relationships in such a complex data set. Since multivariate techniques can usually handle only two-way data matrices (Gauch 1982a), matching the results of vegetation analyses to bird abundances is a primary technical problem. One solution could be the application of canonical correlation analysis (CCA), which can handle 2 two-way matrices (e.g., sites x vegetation and sites x birds). This technique, however can be addressed only to strictly linear relationships (Gauch and Wentworth 1976). Another possibility is to calculate the correlation coefficients for bird species and vegetation components (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). Because birds may respond to habitat features in a non-linear fasion (Meents et al. 1983, Rotenberry 1986), rank correlation is advisable. Multiple linear regression models like regression on correspondence analysis factors (Prodon and Lebreton 1981) or regression on principal components (Moskát 1988), are suitable for summarizing linear relationships between birds and vegetation. There have been some attempts to express bird-habitat measurements directly in a two-way data matrix of a vegetation x birds form (James 1971, Whitmore 1975). This procedure usually counts the averages for vegetation variables for each species, and therefore obscures important details for species having a wide habitat breadth. Plotting the mean position of a species by averaging the sample scores where it occurs is also possible (Smith et al. 1987). However, this technique while eluding the problem of analyzing a three-way data matrix, since the ordination is only based on sites x vegetation data, can handle only the presence/absence of birds and can show only the mean positions of species.

In plant ecology there is a similar problem: how to match vegetation components to environmental data. Adopting the species-plexus idea (Whittaker 1967, McIntosh 1978, Matthews 1978), Whittaker (1987) developed a four-stage computational procedure for analyzing vegetation-environment relationships. In the first step, he ordinated vegetation data by DCA, summarizing the structure of the data set. The next stage was to compute correlation coefficients between environmental variables and the DCA sample scores. Kendall's rank correlation was used. After that, an NM-MDS was carried out on this correlation matrix, ordinating the vegetation DCA axis and environmental variables into a common space. Since NM-MDS does not contain restrictive assumptions on the distributions of input variables, it is suitable for analyzing a rank correlation matrix. The last step was the construction of an integrated plexus for the ordinated variables. By this procedure it was very easy to demonstrate vegetation-environment relationships. This plexus technique seemed to be superior over the previous approaches.

The multivariate plexus concept

The plexus concept is concerned with graph representation of variables in a space of low dimensionality. For showing the interrelationships between the variables different lines can be applied, e.g., continuous line between points for strong relationships, and dotted line for weak relationships.

Following the Whittaker plexus model, based on multivariate ordination techniques (see above and Whittaker 1987), I attempted to map bird-habitat relationships in a common coordinate system. The main purposes of this procedure is

1) to simplify the structure with negligible losses of information;

2) to reduce noise in the raw data; and

3) to reveal the main structural relationships and to draw the simplified complex structure in an easily-interpretable form.

The analyses (e.g., PCA, CA, DCA) selected for ordination of a given data set should conform to the aims of the study and the distributions of variables. In the case of bulky and complex data sets of two or more subsets of variables, it is advisable to reduce the subsets separately, substituting a small number of components for the original variables. This manoeuvre also reduces the noise in data (Gauch 1982b). Such reductions may however not be useful when variables are logically or statistically (linearly) independent or their analysis gives too many, uninterpretable components. For revealing interrelationships between components and raw variables an NM-MDS based on a rank correlation input matrix is suitable.

In the present study, three different types of data were recorded: vegetation physiognomy, vegetation floristics, and bird abundances. Handling physiognomy and floristic data separately is a usual procedure in ecology, although a synthesis is desirable (Beard 1978). Several studies have already proved the existance of relationships between vegetation components and bird communities (see reviews in Farina 1985, Cody 1985, Wiens 1989). Following this approach, in the first step

I derive vegetation components and then attempt to establish their relations to bird species.

Application of the multivariate plexus concept

The main steps are as follows:

1) principal component analysis to reduce the physiognomy data set;

2) correspondence analysis to simplify the floristic data set;

3) evalutation of the relation between vegetation (physiognomy and floristic) components and bird abundances by Kendall's rank correlation coefficients; and

4) an ordination of the vegetation components and bird species by non-metric multidimensional scaling into a common space of reduced dimensionality.

The coice of PCA is justifiable, considering relatively short ecological gradients (Gauch 1982a, Pielou 1984, Austin 1985). This PCA starts from the correlation matrix. There are several methods for selecting the minimum number of components that explain a large proportion of the original variance. Here components having an eigenvalue greater than 1.0 are deemed to be important (Harman 1976). To confirm the usability of this selection, a "scree-test" (Cattel 1965) was also applied. This technique plots the eigenvalues against the number of components in their order of extraction. The point at which the curve begins to straighten is considered as the decision criterion for the necessary number of components. Following PCA, the VARIMAX orthogonal rotation technique was applied to construct a new, more easily interpretable pattern of component loadings. For computation of PCA, the SPSS/PC+ program package (Norusis 1986b) was applied.

The floristic data collected at each of the 75 subsamples contain many zero values, which causes distortions in PCA (Swan 1970). To avoid these, the classical CA was chosen to reveal the structure of floristic data. CA is a similar method to PCA, but while PCA allocates the points in a Euclidean space, CA uses chi-square distances instead of the Euclidean distances. For this reason, CA is less sensitive to the double-zeros (Legendre and Legendre 1983). Program DECORANA (Hill 1979) was applied and only the first two axes were used for representation of the floristic data. Vegetation component scores were computed for each of the 75 subsample sites. A sample site was characterized by the mean value of its subsamples.

Kendall's rank correlation coefficient was used for a direct measurement of bird-habitat relations. Coefficients were computed between all possible pairwise combinations of vegetation components and bird species abundances using the SPSS/PC+ program package (Norusis 1986a). As the NM-MDS program applied needs a distance matrix for input, complements of the rank correlations were computed, $c_{ij} = 1 - \text{abs}(\tau_{ij})$, where c is the complement coefficient, τ is Kendall's rank correlation coefficient, i, j are variable indices.

The ordination of vegetation physiognomic and floristic components together with bird abundances was carried out by NM-MDS. This technique rearranges points in a reduced dimensionality space with the provision that the rank order of the new between-point distances must agree with the rank order of the original distsances as closely as possible (Davison 1983). In a detailed test of multivariate ordination techniques applied to simulated coenoplane data, NM-MDS with

Table 1. Kendall's rank correlation coefficients between bird species and vegetation components. (PH1, PH2, PH3: physiognomic components; FL1, FL2: floristic components).

bird species	PH1	PH2	PH3	FL1	FL2
Parus major	0.261	−0.391*	−0.130	0.339	0.156
Parus caeruleus	0.589**	−0.056	−0.234	0.411*	0.256
Sitta europaea	0.095	0.222	−0.095	0.180	0.392*
Turdus viscivorus	−0.412*	0.063	0.158	−0.348	−0.443*
Turdus philomelos	−0.184	0.381*	0.012	−0.258	0.283
Turdus merula	0.264	0.096	0.024	0.216	−0.096
Erithacus rubecula	0.415*	0.131	−0.065	0.306	0.131
Sylvia atricapilla	0.502**	−0.087	−0.262	0.415*	−0.022
Phylloscopus collybita	0.196	−0.087	−0.175	−0.022	−0.153
Phylloscopus sibilatrix	0.613**	0.204	0.113	0.454*	0.113
Muscicapa striata	0.213	−0.260	0.118	0.024	0.024
Ficedula albicollis	0.423*	0.054	−0.054	0.314	0.119
Anthus trivialis	−0.501**	−0.317	0.113	−0.358*	−0.481**
Sturnus vulgaris	0.087	0.000	−0.240	0.196	0.306
Coccothraustes coccothraustes	0.056	0.146	0.214	−0.146	−0.011
Fringilla coelebs	−0.282	0.136	0.282	−0.555**	−0.199
Emberiza citrinella	−0.498**	−0.074	−0.074	−0.392*	−0.498**

*PL .05, **PL .01.

Euclidean chord distance, and particularly with shortest path distance proved to be the best procedure for recovering the data structure (Kenkel and Orlóci 1986, Bradfield and Kenkel 1987). Sabo and Whittaker (1979) introduced NM-MDS into bird community ecology to reveal bird niches from complex ecological measurements.

In the present study, NM-MDS was carried out by the program "MDSCAL" published by Orlóci and Kenkel (1985). The analysis was started from the matrix of the complements of Kendall's rank correlation coefficients. The starting configuration of the variables was random, and the dimensionality of the final solution was specified to be 2. For the calculation of the innerpoint distances the option "Euclidean chord" was selected.

Results

Thirty bird species were recorded during the surveys, but for the multivariate plexus-procedure rare species were omitted from the data set (see Table 1 for list of bird species).

Vegetation physiognomy components were extracted by PCA. Four eigenvalues showed values larger than 1.0, accounting for 74.4% of the total variance. The contribution of the fourth eigenvector was only 8.8%, and the scree-test suggested the use of only the first 3 components. It is desirable to reduce the number of components to 2 or 3 if possible (Pielou 1984), so I selected the first three components to represent vegetation physiognomy. The structure of component loadings can be more easily interpreted after a VARIMAX orthogonal rotation, because this rotation technique attempts to increase high loadings on a component and reduce small loadings to zero, maximizing the variance of component loadings (Bennett and Bowers 1976). An orthogonal rotation does not change the sum of the variance explained by the selected components, but it distributes the variance more equally between them (Rummel 1970, Bennett and Bowers 1976). Component I (PH1) contains high loadings of the following variables: SHE, NT1, SLC, GLC (—) (Table 2). It portrays the shrub character of the habitat, also including the grass cover by negative sign. Component II (PH2) gathered the following variables: THE, NT3, TFC, STD (—). It contains the closed, old-forest characters. In component III (PH3), variables SSD, NT2, STD (—), GHE (—) show high loadings; it is interpretable as a closed, mature forest component.

For the analysis of bird-habitat relationships, component scores are needed for every subsample site. For this reason, it is desirable to spread the variance into components relatively evenly, because there is no possibility for weighting the components in the subsequent analysis. For this reason, component scores were computed after VARIMAX rotation.

Correspondence analysis computed on the basis of plant species cover values revealed two floristic components (Fig. 1). The first contained only the shrubs (or young trees) of *Tilia platyphyllos*. This species

Table 2. Rotated component matrix of vegetation physiognomy variables obtained by principal component analysis. Legend: STD - the average of 5 closest tree-trunk distances in the case of 5 randomly selected tress; SSD - the average of 5 closest shrub distances in the case of 5 randomly selected shrubs; GHE - grass layer height; SHE - shrub layer height; THE - the foliage height; NT1 - number of living tree trunks (n.l.t.t.) between 0 and 10 cm at breast height (b.h.); NT2 - n.l.t.t. between 10 and 20 cm at b.h.; NT3 - n.l.t.t. greater than 20 cm at b.h.; GLC - grass cover; SLC - shrub cover; TFC - tree foliage cover; VDI - vertical diversity based upon 5 categories of percentage vegetation volume.

Physiognomy variable	Component 1	Component 2	Component 3
STD	0.089	−0.604	−0.604
SSD	0.107	−0.077	0.795
GHE	−0.399	−0.148	−0.575
SHE	0.791	−0.063	0.295
THE	0.454	0.725	0.058
NT1	0.833	0.103	0.003
NT2	−0.056	0.305	0.554
NT3	−0.321	0.702	0.174
GLC	−0.688	−0.240	−0.318
SLC	0.869	−0.009	−0.207
TFC	0.172	0.749	0.040
VDI	0.574	0.634	0.191

occupies the wetter sites in the area, so it was positioned separately. Oak trees *(Quercus petraea* and *Q. cerris)* cluster around the origin because they are evenly dispersed over all the sites. The shrubs form of *Fraxinus ornus* occupie outher points far from the other species, indicating the sunny and warmer sites in the area. Shrubs form a linear cluster along the second axis almost at right angle to the first one. Since each of the first two eigenvalues showed much higher values than either the third or fourth ones computed by DECORANA (I = 0.364, II = 0.306, III = 0.179, IV = 0.159), there was no need to keep more than two axes. The usefulness of the results was confirmed by mapping the 75 subsamples into 2-dimensional CA-plane, with no outliers found. This result is not presented here.

Kendall's rank correlation coefficient measures the similarity between vegetation components and bird species (Table 1). Rank correlations between bird species are not presented, because they measure the similarity of their distribution between sites rather than the similarity of responses to vegetation characteristics. Bird species share the habitat vertically, so a simple value of their rank correlation has restricted meaning

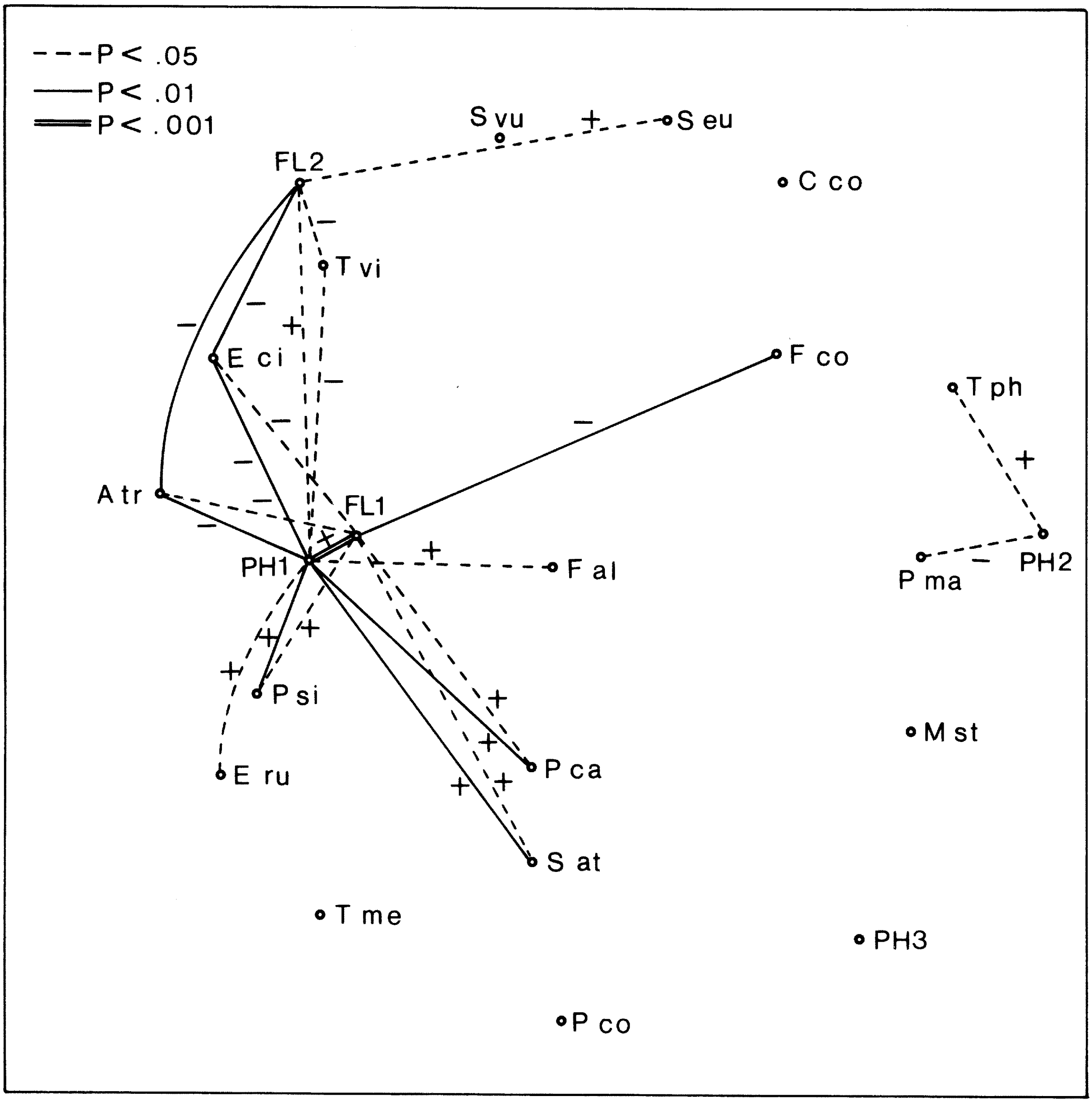

Fig. 2. Ordination diagram of vegetation components and bird species obtained by multivariate plexus analysis. Legend: PH1, PH2, PH3 - vegetation physiognomic components; FL1, FL2 - vegetation floristic components; P ma - *Parus major*, P ca - *P. caeruleus*, S eu - *Sitta europaea*, T vi - *Turdus viscivorus*, T ph - *T. philomelos*, T me - *T. merula*, E ru - *Erithacus rubecula*, S at - *Sylvia atricapilla*, P co - *Phylloscopus collybita*, P si - *Phylloscopus sibilatrix*, M st - *Muscicapa striata*, F al - *Ficedula albicollis*, A tr - *Anthus trivialis*, S vu - *Sturnus vulgaris*, C co - *Coccothraustes coccothraustes*, F co - *Fringilla coelebs*, E ci - *Emberiza citrinella*.

in a study focused on bird-habitat relationships.

The NM-MDS result was plotted into a 2-dimensional space, and all significant correlations between vegetation components and bird species were drawn in the plexus diagram (Fig. 2). Kendall's correlation is not a simple coefficient, but a test of association (Sokal and Rohlf 1981); the significance of its value was analyzed for every pair of variables.

The first floristic component (FL1, containing *Tilia platyphyllos*) shows highly significant correlation with the first physiognomic variable (PH1, shrub character, $\tau=0.600$, $p<.001$). This is understandable, since *Tilia* forms dense shrub patches in the area. There were no other significant correlations between vegetation components, only between PH1 and FL1 ($\tau=0.390$, $p<.05$). Several bird species showed significant ($p<.05$), or highly significant ($p<0.1$) correlation with PH1 (Table 1). Despite the high correlation between PH1 and FL1, the effect of these components on the bird component is somewhat different. That is, PH1 is a feature of several shrub species, not only of *Tilia*. *Anthus trivialis* has a similar connection with PH1 and FL2, and it also has a weak relation with FL1. *Turdus viscivorus* also represents the connection between PH1 and FL2. The PH1-FL1-FL2 complex of components seems to be affecting in a great part the composition of the bird community. PH2 does not show little positive relation with the bird community, but *Turdus philomelos* and *Parus major* have negative correlation with it. PH3 does not show significant relation with birds at all. PH2 is the common feature of the habitat, its effect can be found on every site. As it is a bulky feature, it does not have much role in the differentiation of the bird community at this level of scale. This role seems to be played by the PH1-FL1-FL2 vegetation complex. Some bird species *(Turdus philomelos, Phylloscopus collybita, Muscicapa striata,* and *Coccothraustes coccothraustes)* has no relation with the vegetation components. The selection of territory of these species is based on a random choice or affected by other non-vegetation features of the habitat.

The illustrated case shows important negative relationships between vegetation components and bird species. Interestingly, negative relationships often remain unrevealed in multivariate analyses and it is difficult generally to evaluate their importance. For example, in ordinations negatively correlated variables are generally placed far from each other, indistinguished from variables with no relevant interrelationships. Non-metric multivariate plexus analysis is helpful, since it represents interrelationships of both types: (1) There is a monotonic tendency to plot similar variables closer to each other than the less similar ones. (2) Significant positive and negative correlations are indicated. *Anthus trivialis* and *Emberiza citrinella* show very high negative relationships to the PH1-FL1-FL2 complex. Their preference for open patches has already been shown from seral stages of beech forest (Moskát and Székely 1989). In fact, these sepcies have bipolar habitat distributions along the successional gradient, selecting the young, open stages and the climax stage which contains open patches. Their distribution and abundance in the oak forest are inversely affected by the density of the shrub layer.

The success of an NM-MDS is measured by Kruskal's stress value (Kruskal 1964). In the present analysis, the stress (0.27) is much lower than in the random case (0.47). The acceptable level of stress depends on the number of variables analyzed and the number of the final dimensionality of the ordination. A very low stress value (about 0.01) could indicate a fully degenerate solution (Kruskal and Wish 1978, Dillon and Goldstein 1984). The solution would be a three-dimensional plexus diagram. A 2-dimensional final solution is advisable, even if the stress value is relatively high, to enhence interpretability. According to Coxon (1982), a high stress is acceptable when it is much lower than that of a random configuration.

NM-MDS programs sometimes cannot reveal the optimal solution, because of the problem of "local minima" (Davison 1983). In the case of high stress values, one may start the program with different starting configurations to find alternative solutions. In the present study, different initial configurations produced similar results, so the solution can be accepted as an optimal one for the task.

Discussion

In many ecological studies, data describe gradients. In this sense one must make a clear distinction between data taken along a short ecological gradient and data over a long gradient. This distinction resolves some of the arguments on the usefulness of particular methods and makes it easier to choose the appropriate one. The applicability of the well-known ordination techniques to these basic types of ecological gradients is considered by Orlóci (1978, 1980) and also by Gauch (1982a). Although the applicability of NM-MDS to ordination of two-way matrices is not entirely clear, recent analyses (Kenkel and Orlóci 1986) suggest that it is applicable. NM-MDS can also be used after other ordinations to improve the results (Fasham 1977). Perhaps this approach could be a suitable technique in the first stage of the multivariate plexus analysis too, but one has to be very careful in using successive multivariate analyses with cumulative distortion. This problem is especially acute when the same type of analysis is applied, cumulating the same type of distortion. Further research is needed to understand the mechanisms of cumulative distortion. In the present study, NM-MDS was chosen for the final analysis because there seemed to be no other method that was suitably robust for the ordination of a rank correlation matrix.

The need to analyze species distribution and environmental data jointly has prompted the development of several combined methods in the last few years. Gauch and Stone (1979) and Sheard and Gale (1983) combined the analysis of plant species and environmental data. A similar analysis was done on bird-vegetation data by Prodon and Lebreton (1981). Each of these studies derived vegetation components by eigenvector ordination (PCA or CA) and then analyzed components by canonical correlation analysis (CCA). Gauch and Stone (1979) obtained better results by ordinating the vegetation and environmental data sets by CA separately than by using CCA. Sheard and Gale (1983), moreover, found this combined technique to perform better than when PCA or CCA was applied alone. As the robustness of CCA is low (Gauch and Wentworth 1976), its combination with PCA will be successful only if the PCA scores fit a multivariate normal distribution. So the applicability of this combined method is restricted to the fully linear special cases. Another similar approach was used by Carleton (1984), who applied a method called 'residual ordination analysis' (ROA) that is based on DCA and CCA. Because of the several linear assumptions of this technique, it was considered to be only a preliminary exploration technique.

Orlóci's (1981, 1991, Feoli and Orlóci 1985) technique of canonical contingency table analysis and Ter Braak's (1986, 1987) canonical correspondence analysis may be effective ways to interpret axes by environmental variables after an ordination of a sites x species data matrix. Ter Braak's method can handle three-way matrices. It can show sample sites and species as well as environmental variables in the same coordinate system; environmental variables appear vectors among the points. Each environmental variables is plotted regardless of importance, but the positions show the greatest association between the environmental vector and the points. Weaker, secondary relationships are not presented. These techniques allow to identify unidirectional effects of environmental variables on site and species variables. The applicability of these methods needs further studies in view to comparisons with the multivariate plexus method.

The dependency of bird communities on vegetation structure seems to be a scale-dependent process (Rotenberry 1985). On a larger, between habitat-type scale, bird community structure is associated with physiognomic components (MacArthur and MacArthur 1961, Willson 1974, Rotenberry and Wiens 1980); whereas on a smaller, within-habitat scale, bird community composition is often more closely associated with floristic components (Tomoff 1974, Wiens and Rotenberry 1981). The present study revealed strong associations between passerine birds and the PH1-FL1-FL2 complex. This result suggests that the key factors differentiating bird community structure cannot be the gross common characters of the habitat on a small scale, but on a large scale birds can relate to them by habitat selection. The PH1-FL1-FL2 complex contains only the bushy characters, both in a physiognomical and floristical sence.

Bird-vegetation analyses are usually restricted to consideration of linear relationships (but see: Meents et al. 1983, Best and Stauffer 1986). Rotenberry (1986) tested the applicability of response-surface analysis to predict bird abundances from shrub-steppe vegetation measurements. Although the applied method contained both linear and non-linear features, the predictability of densities was low because of the 'checkerboard effect' (Wiens 1981). Sometimes density is influenced by several factors, in addition to habitat structure, in which case density may be a misleading indicator of habitat quality (Van Horne 1983). According to the Fretwell-Lucas model (Fretwell and Lucas 1970), non-linearities in habitat-density relationships are most likely when the reproductive success of species is a function of habitat type, and the dynamics of habitat use is relevant (O'Connor 1986). Because of the great number of factors regulating the distribution and abundance of species, an ordination of characteristic vegetation variables together with birds is rarely appropriate for testing hypotheses (cf. Orlóci 1978). The importance of ordination (and generally multivariate) techniques in community ecology is to help hypothesis generation. Testing hypotheses is another task.

Conclusions

The multivariate plexus analysis involves a combination of techniques to ordinate complex ecological data, such as the eigenordination techniques in the following ways:

(1) It makes it possible to analyze multiway ecological data sets.

(2) It measures the between-variable (component or original variable) similarities in a non-linear fashion and ordinates them by a non-linear method.

(3) By drawing the plexus diagram, the relationships between the variables become easily recognizable.

(4) An eigenvector ordination technique can be chosen relatively freely in the first stage, this technique is suitable for the analysis of data collected either along a short or a long ecological gradient.

Generally the multivariate plexus concept, and especially its implementation in multivariate plexus analysis (MPA), a combination of eigenvector ordination and NM-MDS, has the following properties:

(1) *Integration.* MPA integrates the variables into a common space, regardless of their origin.

(2) *Simplification.* MPA projects the final configuration of variables in a reduced-dimensionality space. Two dimensions are suggested as a reasonable final solution.

(3) *Reduction of noise.* Eigenordinations in the first stage of MPA are efficient tools to reduce noise in ecological data (Gauch 1982b). But they have also a drawback nonlinear variation may count as noise.

(4) *Small degree of curvilinear distortion.* NM-MDS is a fairly robust technique (Prentice 1977, Minchin 1987), if coupled with an appropriate resemblance measure (Kenkel and Orlóci 1986), but eigenordinations in the first stage of MPA can produce some distortion.

(5) *Two basic scales of results.* NM-MDS ordinates the variables as points in ordination space, where the between-point distances have a rank-order relationship with the similarity of the original variables. Moreover, the plexus diagram displays the significance of the between-variable similarities.

(6) *Bipolar similarity feature.* Similarities are presented as negative or positive relationships. The

signs of the correlations between the variables do not affect the distances between the points in the final ordination.

(7) *Independent and dependent variables*. The plexus diagram reveals the fully independent variables and the dependent ones, but the analysis is likely to be insensitive to stronger cases of nonlinear dependence.

(8) *Cluster formation*. The plexus diagram of an ordination reveals clusters on different hierarchical levels, as the level of significance moves up or down. These clusters correspond to the structural similarities between the variables.

(9) *Connection between clusters*. The plexus diagram show between-cluster similarities (if any) by a direct link between clusters, or a weaker connection by links between clusters and an intermediate point.

(10) *Hypothesis generation*. MPA can be a much more effective tool for this purpose than any of the well-known ordination techniques, especially for complex data.

Acknowledgements. This paper was written during my stay at Colorado State University, Ft. Collins, supported by a grant from the MTA-Soros Foundation. I thank J.A. Wiens, L. Orlóci, B. Van Horne, and J. Podani for their helpful comments. I am grateful to T. Székely for technical help during the field work.

REFERENCES

AUSTIN, M.P. 1979. Current approaches to the non linearity problem in vegetation analysis. *In:* G.P. Patil and M.L. Rosenzweig (eds.), *Contemporary Quantitative Ecology and Related Ecometrics*. Statistical Ecology Seris, Vol. 12, pp. 197-210. International Cooperative Publishing House, Fairland, Maryland, U.S.A.

AUSTIN, M.P. 1985. Continuum concept, ordination methods, and niche theory. Ann. Rev. Ecol. Syst. 16: 39-61.

BEARD, J.S. 1978. The physiognomic approach. *In:* R.H. Whittaker (ed.), *Classification of Plant Communities*, pp. 33-64. Dr. W. Junk Publishers, The Hague.

BENNETT, S. and D. BOWERS. 1976. *An Introduction to Multivariate Techniques for Social and Behavioral Sciences*. John Wiley and Sons, New York.

BEST, L.B. and D.F. STAUFFER. 1986. Factors confounding evaluation of bird-habitat relationships. *In:* J. Vernep, M.L. Morrison and C.J. Ralph (eds.), *Wildlife 2000. Modeling Habitat Relationships of Terrestrial Vertebrates*, pp. 209-216. The University of Wisconsin Press, Madison, Wisconsin, U.S.A.

BRADFIELD, G.E. and N.C. KENKEL. 1987. Nonlinear ordination using flexible shortest path adjustment of ecological distances. Ecology 68: 750-753.

CARLETON, T.J. 1984. Residual ordination analysis: a method for exploring vegetation-environment relationships. Ecology 65: 469-477.

CATTEL, R.B. 1965. Factor analysis: An introduction to essentials. Biometrics 21: 190-215.

CODY, M.L. 1985. *Habitat Selection in Birds*. Academic Press, New York.

COXON, A.P.M. 1982. *The User's Guide to Multidimensional Scaling*. Heinemann, London, England.

DAVISON, M.L. 1983. *Multidimensional Scaling*. John Wiley and Sons, New York.

DILLON, W.R. and M. GOLDSTEIN. 1984. *Multivariate Analysis. Methods and Applications*. John Wiley and Sons, New York.

DUNN, J.E. 1981. Data-based transformations in multivariate analysis. *In:* D.E. Capen (ed.), *The Use of Multivariate Statistics in Studies of Wildlife Habitat*, pp. 93-102. U.S. Department of Agriculture, Forest Service, General Technical Report RM-87. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, U.S.A.

FAITH, D.P., P.R. MINCHIN and L. BELBIN. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

FARINA, A. 1985. Quantitative methods of habitat description in ornithological studies: a review. *In:* K. Taylor, R.J. Fuller and P.C. Lack, (eds.), *Bird Census and Atlas Studies: Proceedings VIII International Conference on Bird Census and Atlas work*, pp. 45-55. BTO, Tring.

FASHAM, M.J.R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines and coenoplanes. Ecology 58: 551-561.

FEOLI, E. and L. ORLÓCI. 1985. Species dispersion profiles of anthropogenic grasslands in the Italian Pre-Alps. Vegetatio 60: 113-118.

FRETWELL, S.D. and H.L. LUCAS, JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical developement. Acta Biotheor. 19: 16-36.

GAUCH, H.G., Jr. 1982a. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.

GAUCH, H.G., Jr. 1982b. Noise reduction by eigenvector ordinations. Ecology 63: 1643-1649.

GAUCH, H.G., Jr. and E.L. STONE. 1979. Vegetation and soil pattern in a mesophytic forest at Ithaca, New York. Am. Midl. Nat. 102: 332-345.

GAUCH, H.G., Jr. and T.R. WENTWORTH. 1976. Canonical correlation analysis as an ordination technique. Vegetatio 33: 17-22.

GREIG-SMITH, P. 1980. The developement of numerical classification and ordination. Vegetatio 42: 1-9.

HARMAN, H.H. 1976. *Modern Factor Analysis*. 3rd ed. The University of Chicago Press, Chicago.

HILL, M.O. 1979. DECORANA - *A* FORTRAN *Program for Detrended Correspondence Analysis and Reciprocal Averaging*. Ecology and Systematics, Cornell University, Ithaca, New York.

HILL, M.O. and H.G. GAUCH, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47-58.

JAMES, F.C. 1971. Ordination of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

JAMES, F.C. and H.H. SHUGART. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727-736.

JOHNSON, D.H. 1981. The use and misuse of statistics in wildlife habitat studies. *In:* D.E. Capen (ed.), *The Use of Multivariate Statistics in Studies of Wildlife Habitat*, pp. 11-19. U.S. Department of Agriculture, Forest Service, General Technical Report RM-87. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, U.S.A.

KENKEL, N.C. and L. ORLÓCI. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology 67: 919-928.

KRUSKAL, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29: 1-27.

KRUSKAL, J.B. and M. WISH. 1978. *Multidimensional Scaling.* Sage University Press Series on Quantitative Applications in the Social Sciences, 07-011. Sage Publications, Beverly Hills and London.

LEGENDRE, L. and P. LEGENDRE. 1983. *Numerical Ecology.* Developments in Environmental Modelling, 3. Elsevier Sci. Publ. Co., Amsterdam.

MACARTHUR, R.H. and J.W. MACARTHUR. 1961. On bird species diversity. Ecology 42: 594-598.

MATTHEWS, J.A. 1978. An application of non-metric multidimensional scaling to the construction of an improved species plexus. J. Ecol. 66: 157-173.

MCINTOSH, R.P. 1978. Matrix and plexus techniques. *In:* R.H. Whittaker (ed.), *Ordination of Plant Communities*, pp. 151-184. Dr. W. Junk Publishers, The Hague.

MEENTS, J.K., J. RICE, B.W. ANDERSON and R. OHMART. 1983. Nonlinear relationships between birds and vegetation. Ecology 64: 1022-1027.

MINCHIN P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89-107.

MOSKÁT, C. 1988. Breeding bird community and vegetation structure in a beech forest in the Pilis Mountains, N. Hungary. Aquila 95: 105-112.

MOSKÁT, C. 1990. A combined version of territory mapping and point count techniques. *In:* K. Stastny and V. Bejcek (eds.), *Bird Census and Atlas Studies*, Proc XIth Int. Conf. on Bird Census and Atlas Work, pp. 51-61. Prague.

MOSKÁT, C. and T. SZÉKELY. 1989. Habitat distribution of breeding birds in relation to forest succession. Fol. Zool. 38: 363-376.

NOON, B.R. 1981. Techniques for sampling avian habitats. *In:* D.E. Capen (ed.), *The use of multivariate statistics in studies of wildlife habitat*, pp. 42-52. U.S. Department of Agriculture, Forest Service, General Technical Report RM-87. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

NORUSIS, M.J. 1986a. SPSS/PC+ *for the* IBM PC/XT/AT. SPSS Incorporation, Chicago, Illinois.

NORUSIS, M.J. 1986b. SPSS/PC+ *advanced statistics for the* IBM PC/XT/AT. SPSS Incorporation, Chicago, Illinois..

NOY-MEIR, I. and M.P. AUSTIN. 1970. Principal component ordination and simulated vegetational data. Ecology 51: 551-552.

O'CONNOR, R.J. 1986. Dynamical aspects of avian habitat use. *In:* J. Verner, M.L. Morrison and C.J. Ralph (eds.), *Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates*, pp. 235-240. The University of Wisconsin Press, Madison, Wisconsin. U.S.A.

ORLÓCI, L. 1978. *Multivariate Analysis in Vegetation Research.* 2nd ed. Dr. W. Junk Publishers, The Hague.

ORLÓCI, L. 1980. Nonlinear data structures and their description. *In:* L. Orlóci, W. Stiteler and R. Rao (eds.), *Multivariate Methods in Ecological Work*, Statistical Ecology Series, Vol. 7, pp. 191-202. International Co-operative Publishing House, Fairland, Maryland, U.S.A.

ORLÓCI, L. 1981. Probing time series vegetation data for evidence of succession. Vegetatio 46: 31-35.

ORLÓCI, L. 1991. CONAPACK: *Program for Canonical Analysis of Classification tables.* Ecological Computations Series (ECS): Vol. 4. SPB Academic Publishing bv., The Hague.

ORLÓCI, L. and N.C. KENKEL. 1985. *Introduction to data analysis with examples from population and community ecology.* Statistical Ecology Monographs, Vol. 1. International Co-operative Publishing House, Burtonsville, Maryland, U.S.A.

PIELOU, E.C. 1984. *The Interpretation of Ecological Data.* John Wiley and Sons, New York.

PINOWSKI, J. and M. WILLIAMSON. 1974. Introductory information of the Fourth Meeting of the International Bird Census Committee. Acta Orn. 14: 152-164.

PRENTICE, I.C. 1977. Non-metric ordination methods in ecology. J. Ecol. 65: 85-94.

PRODON, R. and J-D. LEBRETON. 1981. Breeding avifauna of a mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modeling of the structure gradient. Oikos 37: 21-38.

ROBBINS, C.S. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. Audubon Field Notes 24: 722-726.

ROTENBERRY, J.T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecol. (Berl.) 67: 213-217.

ROTENBERRY, J.T. 1986. Habitat relationships of shrubsteppe birds: even "good" models cannot predict the future. *In:* J. Verner, M.L. Morrison and C.J. Ralph (eds.), *Wildlife 2000. Modeling Habitat Relationships of Terrestrial Vertebrates*, pp. 217-221. The University of Wisconsin Press, Madison, Wisconsin, U.S.A.

ROTENBERRY, J.T. and J.A. WIENS. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228-1250.

RUMMEL, R.J. 1970. *Applied Factor Analysis.* Northwestern University Press, Evanston.

SABO, S.R. and R.H. WHITTAKER. 1979. Bird niches in a subalpine forest: an indirect ordination. Proc. Natl. Acad. Sci., USA. 76: 1338-1342.

SHEARD, J.W. and D.W. GALE. 1983. Vegetation studies at Polar Bear Pass, Batharst Island, N.W.T.H. Vegetation-environment relationships. Can. J. Bot. 61: 1637-1646.

SMITH, K.W., B. AVERIS and J. MARTIN. 1987. The breeding bird community of oak plantations in the Forest of Dean, Southern England. Acta OEcol., OEcol. Gen. 8: 209-217.

SOKAL, R.R. and F.J. ROHLF. 1981. *Biometry.* 2nd edition. Freeman and Co., San Francisco.

SWAN, J.M.A. 1970. An examination of some ordination problems by use of simulated data. Ecology 51: 89-102.

TER BRAAK, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

TER BRAAK, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69-77.

TOMOFF, C.W. 1974. Avian species diversity in desert scrub. Ecology 55: 396-403.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893-901.

Whitmore, R.C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, Southwestern Utah. Wilson Bull. 87: 65-74.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207-264.

Whittaker, R.J. 1987. An application of detrended correspondence analysis and non-metric multidimensional scaling to the identification and analysis of environmental factor complexes and vegetation structure. J. Ecol. 75: 363-376.

Wiens, J.A. 1981. Scale problems in avian censusing. *In:* C.J. Ralph and J.M. Scott (eds.), *Estimating Numbers of Terrestrial Birds*, Studies in Avian Biology, No. 6, pp. 513-521. Cooper Ornithological Society, Lawrence, Kansas, U.S.A.

Wiens, J.A. 1989. *The Ecology of Bird Communities.* Vol. 1. + Vol. 2. Cambridge Univ. Press, Cambridge.

Wiens, J.A. and J.T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecol. Monogr. 51: 21-41.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55: 1017-1029.

Manuscript received: February 1991