

A MULTIVARIATE APPROACH TO THE ANALYSIS OF BIOTOPE STRUCTURE WITH SPECIAL REFERENCE TO THEIR AVIFAUNA IN PRESPA REGION, NORTHWESTERN GREECE: DATABASE AND PROCEDURES

By P. PETRAKIS⁽¹⁾

Introduction

There is no doubt that vegetation complexity is a major regulating factor of the structure of avian and other animal communities (MACARTHUR et al., 1962; MURDOCH et al., 1972. BLONDEL et al., 1973; WIENS, 1973, 1974; WILLSON, 1974; ROTH, 1976; ROTENBERRY and WIENS, 1980; CODY, 1981, 1983; SIEGFRIED and CROWE, 1983; PETRAKIS et al. 1986; MACNALLY and DOOLAN, 1986; PETRAKIS et al., 1987). Also it is obvious that this complexity can be decomposed in the two traditional Euclidean directions, namely vertical and horizontal, though other non Euclidean directions could be reasonably and appreciably participate into the decomposition, such as short termed temporal variations caused from plant phenological patterns (PETRAKIS et al., 1987).

What is not so obvious, is the initial particular favour of ecologists to measure in detail the vertical component of the vegetation complexity and neglect the other, though this frequently happened with a simultaneous recognition of its significance (MACARTHUR et al., 1962). Only recently, some attempts have been made towards the incorporation of the second diversity component in the sampling design and in the subsequent theoretical framework (ROTENBERRY and WIENS, 1980; PRODON and LEBRETON, 1981; SIEGFRIED and CROWE, 1983; BLONDEL et. al., 1984; PETRAKIS et. al., 1987) especially when convergencies of avifaunas in continental level are of interest (CODY, 1983). But all these attempts are yet unstandardized and a consistent body of theory, relating bird species diversity to horizontal heterogeneity (or habitat patchiness), is permanently lacking (but see PRODON and LEBRETON, 1981).

In this study we describe a set of biotopes in Prespa basin by summarizing biotope measured variables into major vegetation gradients both in horizontal and vertical direction. We attempt to find gradients in bird species biotope preferences and then to search for those features of biotopes that best account for these

(1) Oxya, Aghios Germanos 530 77, Prespa, GREECE.

gradients. Also we search for major vegetation gradients that account for individual bird species preferences.

The innovations of this work do not lie in the elaboration of any new ecostatistical technique, but in a new synthetic procedure of already existing methods of data exploration and analysis that works in the broader context of animal biotope interactions and that can affect existing theories (GREIG-SMITH, 1986).

Sampling Procedures

Study area.

The area - Prespa basin, National Park - from which the data for this study were collected, is located in the northwestern part of Greek peninsula. In this basin there are two lakes that give the whole area a unique character of high esthetic and scientific value. The altitude (852 m a.s.l., lake level) the diversified geomorphological configuration and the geographic isolation of the area, together with the low levels of human impact, made possible the existence of a rich flora and fauna and particularly high β -diversity. The entire set of mediterranean plant communities can be found in this area and the transitions from one to another varies from abrupt ecotonic transitions to very smooth changes by the reciprocal replacement of many woody species (e.g. *Fagus sylvatica* - *Quercus cerris* transitions), (Petrakis, in prep.). On the other hand, in the area, is very well illustrated the bifid adaptative feature of some mediterranean shrubs to cope successfully not only with drought conditions, but also with low temperature regimes of timberline.

Biotopes sampled for this study were subjectively selected to cover all types that occur in the non wetland environment of Prespa basin.

1. «Ostria» is an *Ostria carpinifolia* dominated site nearby Latsista bay with some other companion woody species such as *Fraxinus ornus* and *Cornus mas* in a lesser degree.

2. «Cerro» is located above Karyes village on Bella Voda mountain and is *Quercus cerris* dominated with some participation of *Jupinerus oxycedrus*.

3. «Oxya» is a *F. sylvatica* and *F. moesiaca* dominated forest with sparse occurrence of *J. oxycedrus* in the openings. It is located above Cerro on the Bella Voda mountain.

4. «Koula» is an open shrubland dominated by *J. oxycedrus* and *J. foetidissima* tree-shrubs and locally with sparse occurrences of *Q. macedonica*.

5. «Karyes» is a more or less open wood, dominated by *Q. cerris*, *J. oxycedrus*, *Q. robur* and *Q. petraea*. It is not included in this analysis because our samples are not representative enough for this type of transition from Oak wood to *Juniperus* open shrubland.

6. «Latsista» is an open degraded shrubland dominated by *J. oxycedrus*

and *J. foetidissima* with local occurrences of *Prunus webbii* and *Prunus Mahaleb*. It is located nearby Latsista bay, against «Ostria».

7. «Aghioneri» is a mixed deciduous forest located on Sfika mountain and is characterized by local codominance of *F. sylvatica* with a complex of other deciduous trees (*Acer spp.*, *Cornus mas*, *Quercus spp.*, *Ostria carpinifolia*, *Fraxinus ornus*). It is the richest biotope in phanerophytic vegetation. In Table I, some other features of these biotopes can be seen.

Bird populations

Bird species abundances were monitored for 3 years and cover the annual cycle of populations movements. In this study only the measurements in late spring and summer are taken into account.

All bird species that occur in the terrestrial biotopes of the study area are included and no distinctions, such as resident or migrant species, were made although they are discussed externally to the analyses.

Vegetation texture and structure

Vegetation was sampled in a stratified randomized unaligned scheme (QUENOUILLE, 1949; GREIG-SMITH, 1983). In each biotope the same transect, that

TABLE I

Biotopes sampled for this study

Code Name	Mean Altitude masl	Slope degrees	Length of transect in meters	Impact index	
				timbering	grazing
1 <i>Ostria</i>	935	42	600	1	1
2 <i>Cerro</i>	1350	40	1400	5	0
3 <i>Oxya</i>	1650	42	1050	7	0
4 <i>Koula</i>	935	37	1400	2	10
6 <i>Latsista</i>	880	40	600	1	10
7 <i>Aghioneri</i>	1300	40	1300	10	5

Impact index has been arbitrarily divided in a range (0,10). The upper value 10 corresponds to a biotope showing the largest observed impact. Two kinds of impact are recognized and treated differently.

TABLE II

Horizontal variables measured

- T *Fagus sylvatica* (incl. *F.moesiaca*)
 R *Ostrya carpinifolia* (incl. *Carpinus betulus L.C.orientalis*)
 E *Quercus cerris* (incl. *Q.frainetto, petraea, robur*)
 E *Acer spp.* (incl. *A.campestre, monspessulanum, obtusatum, pseudoplatanus*)
 S *Juniperus oxycedrus*
J.foetidissima
Fraxinus ornus
 - *Cornus mas* (incl. *C.sanguinea*)
Rosa spp. (incl. *canina, nitidula, caesia*)
Fragaria vesca
Micromeria juliana
Ononis sp.
 S *Crataegus monogyna*
 H *Rubi Corylifolii* (hybrids between *R.caesius* and other *Rubus spp.*)
 R *Colutea arborescens*
 U Leguminous shrubs (incl. *Astragalus vesicaria, Cytisus villosus C.scoparii*)
 B *Prunus webbii*
 S *P.mahaleb*
Sorbus sp.
Asparagus aphyllus

Hoa (True or False)

Hob (True or False)

Hoc (True or False)

NGR (Number of homogenous Groups)

RHL (Ratio of Highest to Lowest dissimilarity value determined by cluster analysis)

***** Trees and shrubs performances were input as the three factors dominance ratio

***** Factors were coverage density and frequency.

Vertical variables measured

Total hits at 0-10 cm

Total hits at 10-100 cm

Total hits at 1-3 m

Total hits at 3-5 m

Total hits at 5-8 m

Total hits at 8-15 m

Total hits at >15 m

Hoa (True or False)

Hob (True or False)

RHL (as in the previous set)

NGR (as in the previous set)

had been used for bird populations monitoring, was followed and with the aid of pseudorandom numbers we positioned a set of plots on both sides of the transect line. All plots were inside the band in which birds were monitored and all plots that had been predicted by random numbers were sampled irrespective of the geomorphology of the location. Each plot was marked by a 10×10 m colored band with direction parallel to the transect axis.

Within each plot, two sets of variables were measured. Horizontal and vertical ones (Table II). Horizontal variables, actually plant importances and substrate parameters, were estimated by photoestimating techniques similar to those already discussed in PETRAKIS et al. (1987) and in the context of Numata's three-factors dominance ratio (NUMATA, 1979).

A telephoto technique has been used to measure vegetation profiles, similar to that used by WARREN-WILSON (1965) and MACARTHUR and HORN (1969), with a focusing screen marked by 16 randomly placed points. The camera was placed on a tripod, 50 cm above ground and optical field depths allowed the counting of hits with plant parts, at those strata which are illustrated in Table II. Stratal measurements below 100 cm were taken with a stiff thin metal wire (4 mm diameter) which was placed vertically with the aid of a spirit level. Ten places, regularly located on the median of the plot, were used and for each stratum 160 points were handled as point quadrats. If some leaves, especially at lower levels (< 5 m) were hidden by lower leaves, the responsible branch was pushed and in two cases were cut to allow the resume of the measurement.

In biotope description, this method has been proved accurate and rapid enough, since it is not intended to be used for leaf-area-index estimations (ABER, 1979). If such measurements will be decided in the future, probably in other projects, these measurements need to be enriched by leaf litter collections. In addition to cope with difficulties in this camera point-quadrat technique when applied to *J. oxycedrus* and *J. foetidissima* stands, we combined it with metal wire measurements.

It is worth mentioning that all plots were in the same basin and no geographical barrier was interfered. This was to remove any biogeographical interference on the observed patterns.

Analytical procedure and discussion

I approached the problem through a methodology based on the intrinsic quadripartite nature of the subject. In the sequel I discuss the pros and cons of our methodology and I try to justify its relevance in the study of mediterranean type ecosystems.

Variables and scales

I have designed the sampling scheme by restricting the geographic scale of the study - in a few squared kilometers. This excludes the geographical component.

I have constructed two separate variable sets for horizontal and vertical description of the biotopes and I analyzed separately the impact of each one in the preference of bird species. This is not to say that I have excluded any type of interaction between the two directions, this can not be stated on biological grounds. Any methodological scheme that can do that is a priori unreliable since the main gradients in a series of successional stages (parasuccessional stages included) can be sufficiently described both in vertical and horizontal direction (WHITTAKER, 1975). A replacement of *F. sylvatica* by *J. oxycedrus* can be equally well reflected on both vertical and horizontal structure of the biotope.

In this context I have not included, in our variable sets, the structural variables such as the «coefficient of variation» of ROTENBERRY and WIENS (1980). This was because I have evidence that they are affected undetectably by the scale or scales of the pattern. There is a long tradition in plant ecology, to approach the detection of scales of pattern of plant species and of environmental parameters by plotting a variable (heterogeneity) measure versus the cumulative area in which it is performed. The scale of pattern is then estimated from the abscissas of the peaks of the previous curve (see for example KERSHAW, 1973; GREIG-SMITH, 1983, 1986). Although this method of pattern analysis possess some conditional pitfalls (PIELOU, 1977), in many cases has been proved workable and revealing. Any heterogeneity measure thereof is scale dependent and by no means it can be standardized since it is not monotonic.

In addition to the coefficient of variation of the already measured variables, the utility of an «heterogeneity index» can be criticized on the same grounds, and according to ROTENBERRY and WIENS (1980) terminology «a variability measure to approximate the scale of a localized activity of an individual bird» can be safely used only after its interaction with the variability measure(s) at upper levels of scale has been proved insignificant. For birds in Prespa basin this is not seem to be the case, since the majority of them used a vegetation phase for shelter and another vegetation phase for foraging activities and is not uncommon to use other phases for mating activities and nesting. This would be the case for some insects with very narrow preference spectrum, as is the case of *Holcogaster exilis* (Heteroptera, Pentatomidae) which usually uses only one tree or shrub of *J. oxycedrus* in Prespa or *J. phoenicea* in southern Greece throughout its life cycle (PETRAKIS et. al., 1987; PETRAKIS and DROSOPoulos, in press.). It is a pity that this phenomenon has not been taken into account in many studies (e.g. for insects MACNALLY and DOOLAN, 1986; but see CORNELL, 1985).

The inclusion of a variable together with its variance (irrespective of the scale) in a multivariable analysis - say Principal component analysis - in many cases violates the model of the method (MORRISON, 1984) and severely reduces the discriminative power of the variables (HOPE, 1969). In addition it entails difficulties in the interpretation of the results in ecological grounds (ORLOCI, 1974).

I was not surprised when ROTENBERRY and WIENS (1980) revealed a strong correlation of many structural variables with the first principal axis of the ordination of steppe biotopes in a space created by vertical and horizontal variables. This fact may imply a scale effect on the analysis, since it is known that the more homogenous a data collection becomes, the more its first eigenvalue increases (FEOLI, 1977). Homogeneity may be attained since variability measures are entered into the matrix to be analyzed. By constructing two different sets of variables and keeping them separated throughout the analysis, I have avoided any type of interaction of vertical with horizontal diversity and I have made possible a differential assessment of the power of each variable type to affect bird community structure. The only dependence between vertical and horizontal variable sets, is the biological one. For example, the biotopes at Koula and Latsista, since they are dominated by *J. oxycedrus* and *J. foetidissima*, their vertical structure is expected to be very simple, actually a mediterranean two phase strubland. Another approach would be a stepwise multiple linear regression which estimates the partial contribution of each variable after the effect of the others has been subtracted (MORRISON, 1984). The only restriction here is the linearity and the sufficiently large sample size, which are not fulfilled in this type of studies.

In the horizontal variable set I have included, phanerophytic plant taxa groups, on the basis of structural and textural features. Each group has been characterized by its three-factors dominance ratio (NUMATA, 1979) and factors were considered its coverage, density and foliage volume (PETRAKIS et. al., 1987). Dominance ratios were expressed in the octave scale (WHITTAKER, 1975). This scale is logarithmic with 16 possible values, the first being unmeasurable - veil line below 0.004% level - and can approximate natural processes, while linearizes the data in a satisfactory degree (GAUCH, 1982). I have not used the traditional techniques of ornithologists such as those used by WILLSON (1974), BLONDEL and CAVILLIER (1977) or that of ROTENBERRY and WIENS (1980), because with these methods the mediterranean character of some habitats would not be satisfactorily represented and this character is above all to be maintained in this study. A low bush such as a three years old root sprout of *J. oxycedrus* is treated differently than an *Ononis* sp. bush with our method, because these two species show different successional courses and present different opportunities for birds to exploit. *J. oxycedrus* is active throughout the year by producing fruits in predictable rates and seasons and by attracting large insect populations exhibiting new nitrogen rich leaf tissues in a large part of the year (PETRAKIS et. al., 1987; PETRAKIS, in prep.). *Ononis* sp. bush, has a phenological pattern restricted in late spring and early summer and has a low fruit production consumed mainly by its insect visitors and residents (frugivorous Coleoptera and Heteroptera). On the other hand, by selecting ecophysiological similar plant taxa as horizontal variables, I gain much more information on bird preferences, not only spatial but also temporal since these groups show a consistently similar phenological pattern.

The mediterranean character of some biotopes is of great importance in this study because it is a generating factor of particularly high β -diversities. The coexistence of open mediterranean type biotopes with more evolved successional forest stages of medio European character has permitted the coexistence and evolution of animal taxa of a wide spectrum of zoogeographical categories (see for birds BLONDEL 1984; for Hemiptera in general PETRAKIS et. al., 1986; and for Pentatomoidea: Hemiptera PETRAKIS and DROSOPOULOS, in prep.). An exclusion of plant taxa from the horizontal variable table would have underestimated this very fact. A more coarse grouping has only been done on the therophytes, hemicryptophytes, cryptophytes and low chamaephytes which have been assigned into two variables, namely annual and perennial herbs. Grasses have been allotted into two separate variables because they are substantially different in their habit, their insect visitors, their phenologies and their seed production from all other herbs.

The biological meaning of the logical horizontal variables, Hoa, Hob, Hoc is discussed below, while NGR and RHL measure the dissimilarity values (sum of squares) as it was calculated by cluster analysis of the plots, measured within each biotope. The number of homogenous groups gives a scale independent measure of biotope heterogeneity. It measures the number of different plot «types» that exist within each biotope. The level of cluster recognition (stopping level) was subjectively taken. I stopped at that level at which I could not find any ecological explanation significant enough to cause any further splitting.

The ratio of highest/lowest dissimilarity value is dependent on the clustering strategy and the heterogeneity (distance) measure that has been used. In this study, the selected strategy was the minimization of the within-group sum of squares –Orloci's optimal agglomeration (ORLOCI, 1978)– and heterogeneity measure was the euclidean distance. Since the sum of squares is dependent on the order of and the dispersion of values in the similarity matrix, we used this ratio to cope with different biotope sizes. Only in this way the size of the biotope has been entered in the analysis (formation scale effect) and it is believed to be standardized. Highest value is the within biotope sum of squares and lowest value is the sum of squares at the level of subjectively accepted groups.

Profile analysis

A second step of our methodology is a reductionistic series of stages, through which I summarize the variation in a set of plots within each biotope into two vectors, characterizing the biotope in a vertical and in a horizontal sense respectively. Although several multivariate techniques pertain to the subject, we have used the profile analysis (MORRISON, 1984). This is a technique that belongs in the broad family of multivariate analysis of variance methods.

In profile analysis, horizontal variables are entered in three well discriminated

ecophysiognomic groups: the tree-shrub group, the herb group and the substrate group (see Table II for this grouping). There are ecological reasons to believe that the last two groups contain no significantly additional information than the first group and the profiles of their mean responses are parallel to the mean responses of the variables in the first group (Fig. 1). In case they do contain additional information, the logical variable Hoa is set equal to 0 (the numeric analog of «false»). If profiles are parallel then Hoa is set equal to 1 (the numeric analog of «true»). These parallelisms are ecologically justified in many biotopes.

At Ostria biotope, of which the profiles are depicted in Fig. 1, substrate variables exhibit parallel profiles with trees-shrubs and in this way they do not contain any additional information for the description of the biotope. They can be considered conditionally redundant and their inclusion in further analyses would obscure any clear correlation of bird preferences with biotope descriptive variables or it would generate non-existent spurious correlation (SCOTT, 1979).

At Koula, the two vegetation phases –shrubs and therophytes– are competitive and reciprocally excluded. In this biotope high performance of *J. oxycedrus* and *J. foetidissima* means low performance of the therophytic stratum. This is of direct relevance in bird species preference since the places for foraging and for shelter are different in each phase. At the biotope in Oxya, it is meaningless to expect high herb performances and thin litter depths where *F. sylvatica* is highly performed. The low penetration of light and the reductive conditions of the upper soil make the microenvironment adverse for herbs and decrease the decomposition rates of litter. Profile analysis provides an objective criterion to test if these scenarios are significantly true.

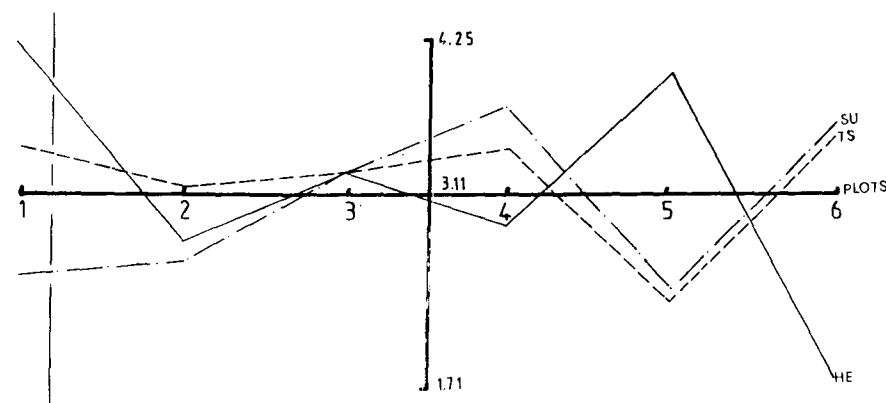


Fig. 1. The profile of the three groups of horizontal variables in a set of six plots within the biotope at Ostria. SU = substrate variables, TS = tree-shrub variables, HE = herb variables. Hypotheses testing for this biotope indicated that H0a, H0b, H0c accepted (see text for details).

In addition profile analysis provides the possibility of statistical tests of stratal parallelisms and equality of group levels. The later was entered in the analysis through the logical variable *Hob*. Its range is as usually, 1 for equal group levels and 0 for different group levels. The ecological meaning attached to this variable is the same as in the previous *Ho* variable. The *Hob* variable amplifies the biological meaning of *Ho*. *Hoc* logical variable is the result of the test of equal contributions of various plots in the configuration of the profile and in this sense it is used as a purely qualitative scale independent heterogeneity measure.

Profile analysis has been used as a tool for the simultaneous rowwise and columnwise reduction of the original biotope data matrices and in this sense the method was preferred from other reductionistic techniques, such as the heuristic method of variable ranking on the basis of its variance, published by JANCEY (1977). In contrast to Jancey's variable reduction, profile analysis leaves a trace to indicate the reasons of the reduction. That trace is deposited in *Ho*, *Hob* and *Hoc* logical variables.

Diversity analysis

Quite often in this type of studies, where the variability of a biotope is of prime interest, diversity indices are traditionally used (HILL, 1973). The approach of some ecologists to incorporate both the vertical and horizontal diversity of a biotope into a single ecologically meaningful index, can be criticized from the view point that information loss is monotonously increased, if multidimensional structures are projected into spaces of lower dimensionality (ORLOCI, 1984). This loss is maximized if the projection is done into unidimensional space, as is the case of a diversity index. On the other hand, indices do not bear any information; they do measure the amount of information content in a data collection but they do not incorporate this information.

I have used for each biotope, the vertical diversity profile of RENYI (1961) diversity index family approach (Fig. 2a-2f) to detect how the various aspects of diversity—Richness, Uncertainty, Dominance—are reflected at various heights within each biotope (PIELOU, 1977; PATIL and TAILLIE, 1979). It has been emphasized in the past (HILL, 1973), that much more insight in the data structure is gained, when the profiles of the diversity aspects are observed rather than simple values. In Fig. 2a-2f the vertical diversity profile of each biotope is depicted for each stratum. Horizontal axes can be considered as conceptual linear transitions from the left extreme (richness) to the right one (dominance) through the middle (uncertainty). All intermediate values can not be translated into human languages. Many aspects of the vertical complexity of each biotope can be revealed, while the intersections of the profiles are indicating of the fact that the rank of each stratum on a diversity criterion may change when several aspects of the diversity are considered.

Figs. 2. Vertical diversity profiles of studied biotopes. Abscisa includes aspects ranging from Richness to Dominance through Uncertainty. The curves correspond to height classes (see Table II for explanation to symbols of height classes). The construction of the curves has been done by twenty values of the parameter alpha in the Renyi diversity index family.

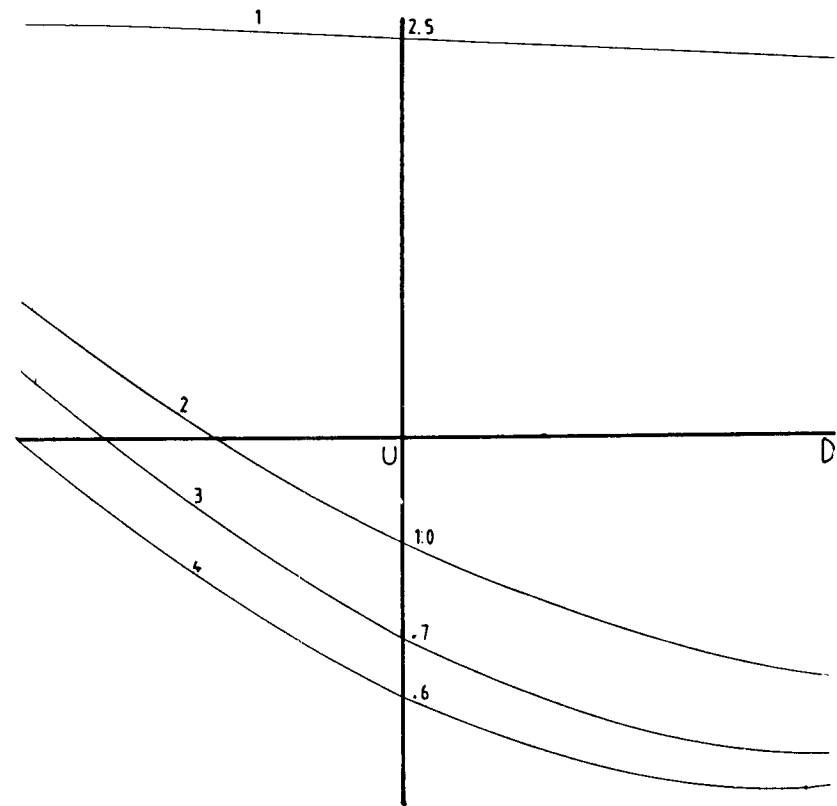


Figura 2a: Koulá

In these diversity profiles the vertical complexity is revealed again to follow the successional status of each biotope. Koulá (Fig. 2a) and Latsista (Fig. 2b) show simple profiles with the first stratum positioned well above the others.

Oxya (Fig. 2e) is also similar in appearance. Here the ranking of the strata reflects their rank in height, but with the first stratum not very well differentiated from the others. All these biotopes can be considered as stable self-maintained successional stages, similar to the absorbing successional stages, in terms of VAN HULST (1978, 1979). The first two biotopes belong to formations widespread in mediterranean degraded areas, which continue to receive human impact and

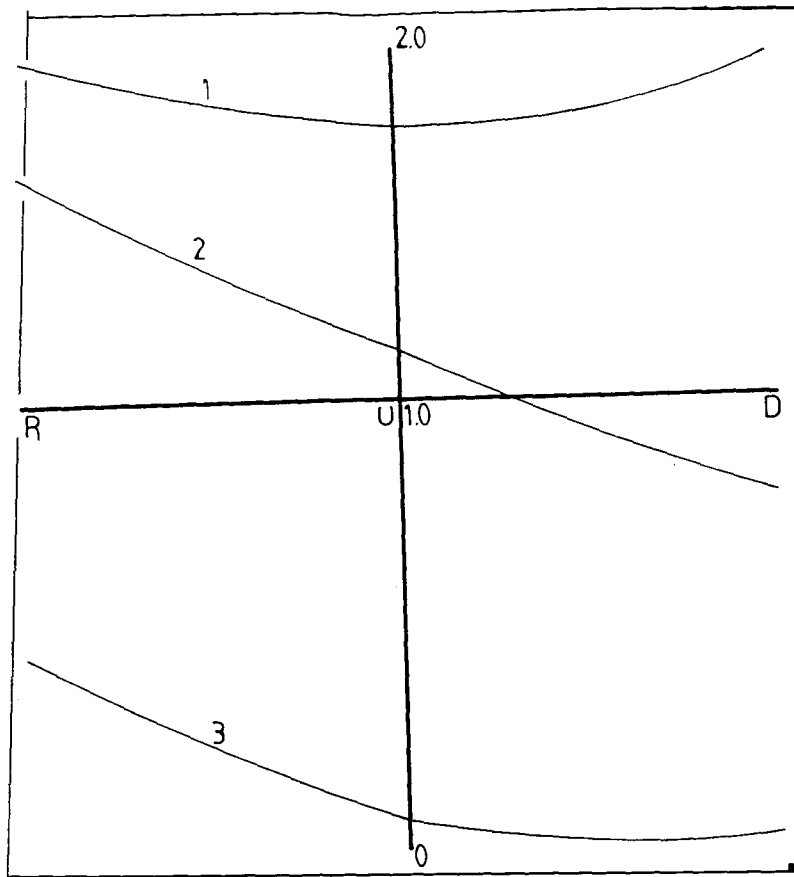


Figura 2b: Latsista

support a rich herb stratum with dominant life form the therophytic one. Therophytes here are temporally and spatially intermingled with spiny low bushes, cryptophytes and hemicryptophytes. *Oxya* is considered as climax stage for medio-European territories and the evenness of the diversity curves reflects this fact.

The other biotopes show complex diversity profiles with rank reversals and intersections. This is indicating that the ecological role of each stratum is not stabilized or successional processes are in progress. In *Cerro* (Fig. 2c) the most diverse, in an uncertainty dominance sense, is the second stratum, while the most rich is the third one. The substantially higher position of the second stratum is explained by the presence of well developed low shrubs which are intermingled with the lower branches of the dominant trees species *Q. cerris*. These cooccurrences of shrubs and tree branches, create many partitions of the Euclidean space and make possible the existence of many shelters and foraging opportunities.

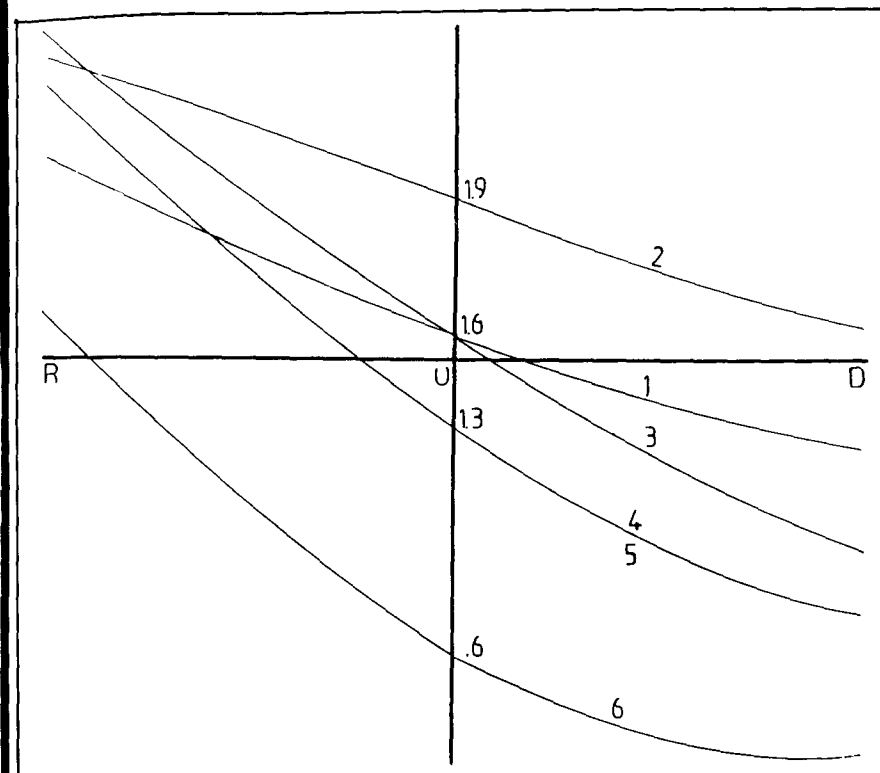


Figura 2c: Cerro

The allocated phenologies of these trees and shrubs cause an extension of the resource spectrum in time but in the same position.

In *Aghioneri* (Fig. 2b) the same situation holds, but here the intermingling is among treelets and saplings of many codominant deciduous tree species in all plots where *F. sylvatica* does not reach high dominance, while the herb stratum is quite developed and rich to raise the first stratum at the highest position of the diversity profile. The «regularity» that can be observed in the ranking of the last four strata, as far as the dominance sense of diversity is of concern, can be explained by the local dominance of *F. sylvatica*. Beech is dominant in shady places where streams in March-April snow melting, carry large quantities of leaf litter creating thus unfavorable conditions for other trees and herbs. *Aghioneri* is considered as occupied by two different climax communities that coexist in a very narrow area.

Ostria (Fig. 2f) is a peculiar biotope with all strata more or less equally rich and a reversal at the fifth stratum. *O. carpinifolia* is adapted to withstand

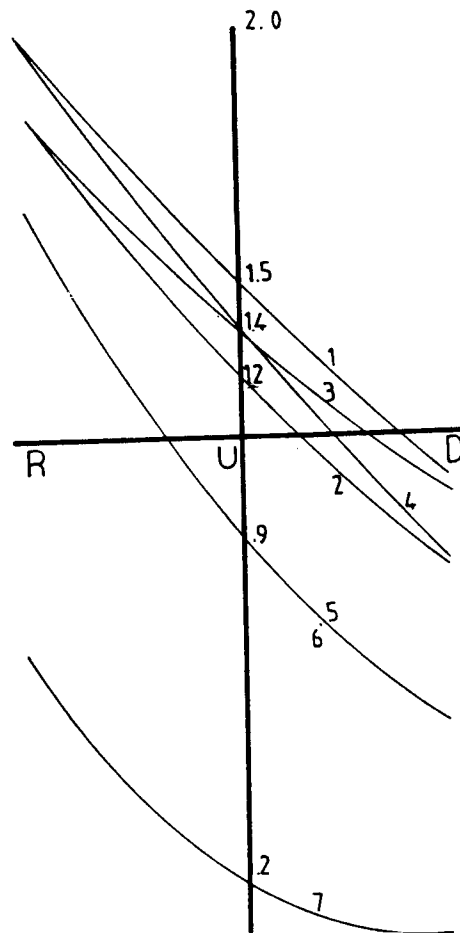


Figura 2d: Aghioneri

some human impact and is particularly well responded in branch cutting management. New robust straight branches emerge very soon after this treatment and reach the top layer of the vegetation. This most probably caused the decrease of the diversity at the third and fourth layer, because these branches are effective competitors and dominate in these strata after some years the cutting has stopped. *Ostria* has been used in this way. Local bean culturers have used the branches of this plant to support *Phaseolus vulgaris* plants (the area is famous for the quality of beans it produces). On the other hand, local people have from old times appreciated the importance of *O. carpinifolia* trees and had never applied any catastrophic management (Petrakis and Catsadorakis pers. observ.).

In Fig. 3 the diversity profiles of all biotopes measured in bird variable space are presented, to make possible direct comparisons of birds diversities with biotope as presented until this point of the study. *Latsista* is the least diverse biotope

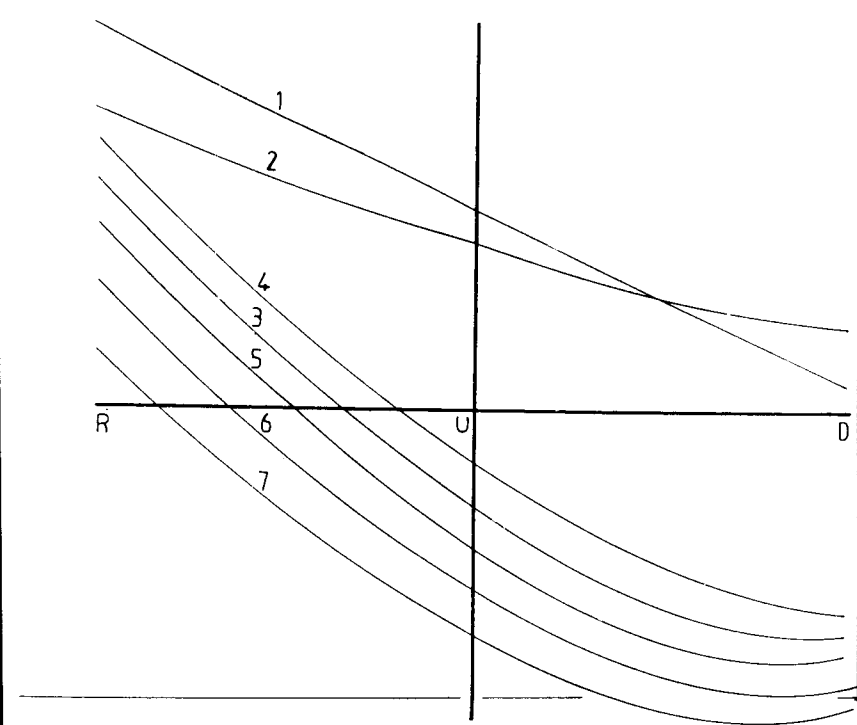


Figura 2e: Oxya

in all aspects and follows *Cerro*. Among the remaining four biotopes *Aghioneri* is the most diverse and the other three exhibit intersected profiles. It is readily shown that there is no any sweeping rule to account for all aspects of bird species diversity. Bird richness is a very poor diversity aspect and for this the description of bird preferences in a qualitative manner (presence - absence) or logical manner (PETRAKIS, 1988) can be severely criticized (e.g. PRODON and LEBRETON, 1981). In addition, discussions on avifauna - habitat affinities in mediterranean successional sceneries, must be supported by very detailed measures of vegetation structure such as those used in this study (contra PRODON and LEBRETON, 1981). Sampling intensity in these studies is affected strictly by the topological spread of successional stages and may broadly vary in successional studies, but the variable set has to be independently constructed in a detailed scheme so that many competition cases in vegetation strata to be accounted by this. Our variable set is specifically devised to serve both, faunistic orientation biotope descriptions and pure vegetation successional studies.

In *Aghioneri* all the existing communities can be thought as «climaxes», in the sense that they are self-perpetuated and stable enough, but the term is

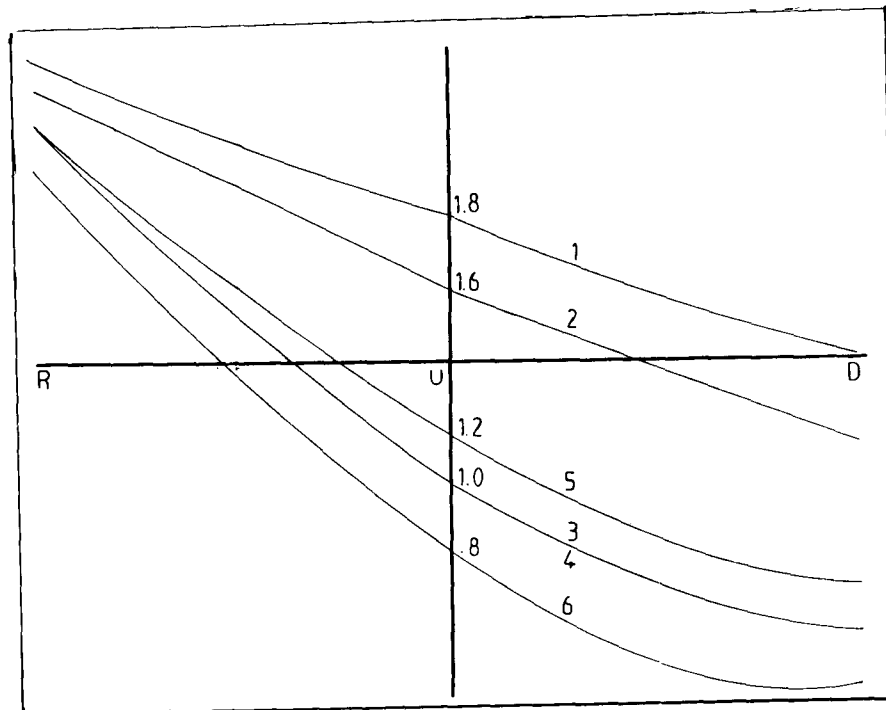


Figura 2f: Ostria

used here to denote more evolved communities. We used this term to substitute the «absorbing stage» of VAN HULST (1978, 1979) and these four biotopes can be characterized in this way.

The dominance aspect of the bird diversity, approximates more closely our conception of variability and contrasts PRODON and LEBRETON's (1981) approach. Only detailed quantitative data for bird populations can allow such a biotope ranking. Also we disagree with the predictions of these authors on the temporal evolution of vegetation layers. They have predicted that «each vegetation layer becomes more and more dense until a maximum is reached, it then thins out in response to the increasing competition of the upper layer». This predictions were made in the context of the monoclimate theory (cf WHITTAKER, 1975), while in Prespa this is not the case. In particular at Aghioneri, several communities—identified by cluster analyses in this and in other studies—can be readily observed to occur in the same hectare independently of the substrate —e.g. *F. sylvatica* and mixed deciduous— being in competitive replacement.

The biotope at Ostria has a very extraordinary bird diversity profile. It is the richest in bird species but it is the poorest —among the four most diverse biotopes— in the dominance sense. Many birds were found in this biotope but

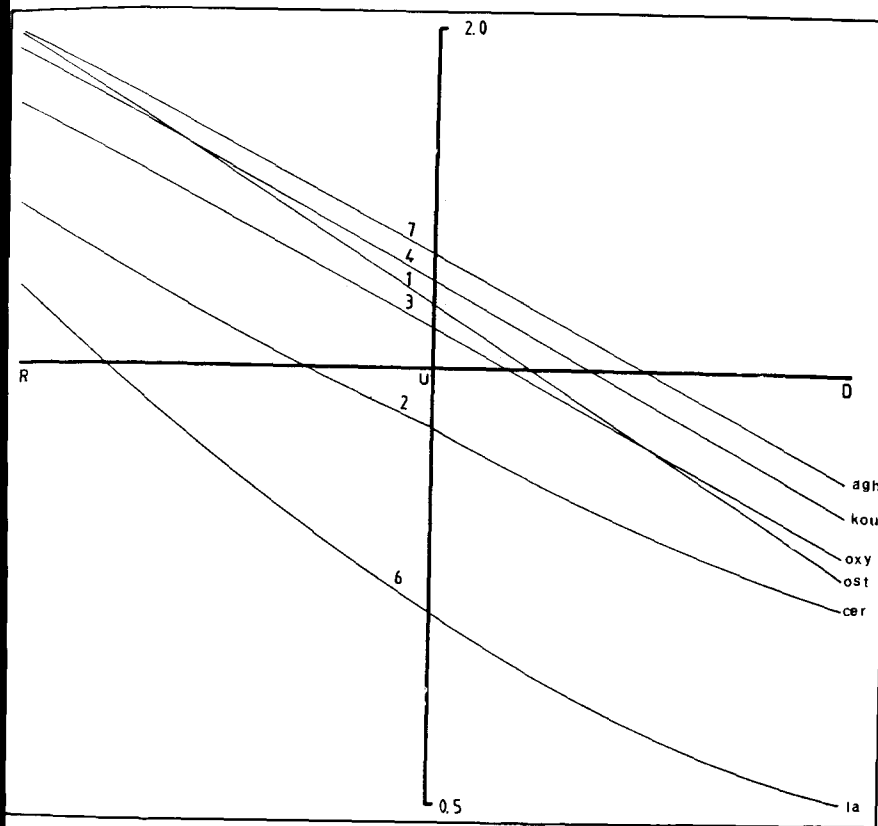


Fig. 3. Biotope diversity profiles as measured in bird variables space. Each curve corresponds to one biotope. Biotope labels are the first three letters of their name. The numbers on each curve are the codes of the biotopes (see Table I).

few of them reached dominance above the level of a simple presence. The biotope at Oxya is the lowest—in the group of the four diverse biotopes—with respect to the richness and uncertainty aspect of the diversity. This means that in this self-maintained successional stage, there are fewer species but they are more or less abundant (habitat restricted or faithful). More overall faithfulness was thus revealed for this biotope, though smaller than Aghioneri and Koula.

The comparison of Koula and Aghioneri reveals an important feature of the Prespa basin. Koula is a representative mediterranean type biotope and Aghioneri is a mixed deciduous forest of medio-European character and both have comparable avifaunal diversities, the later being more complex in vertical structure.

Verticality is proved insufficient to explain the high diversity in Koula and horizontality is necessary to be taken into account together with phenological spreads of plant constituents, as mentioned above.

Phenological spreads contribute significantly to habitat availability and predictability, a fact that in general enhances diversity (CODY, 1983). Also the constancy of available avian resources in Koula seems to compensate for low structural diversity and in this way it permits a finer partitioning of the total avian niche space. This satisfactorily explains the equality of richnesses at Koula and Aghioneri and the divergencies in other aspects of the diversity (see also SIEGFRIED and GROWE, 1983). Another property of the mediterranean type open shrubland at Koula contributes to high richness. The ecological action of the two strata as different synousia (SCHMIDA and WHITTAKER, 1981; WESTMAN, 1983) provides birds a variety of resources horizontally arranged and temporally varied, which are reflected in avifaunal qualitative synthesis. Latsista seems to be an exception but this must be sought in other reasons. One possible reason might be the recent perturbation of the successional sequence –a fire event– that produced this stage. Other reasons might be the small area it occupies –species area effect– and the isolation of the area since it is surrounded by *O. carpinifolia* and *Q. cerris* forests. My findings are opposed to the findings of WIENS (1984), who found no reflection of habitat temporal change to the avian community and not even to a single bird species.

These diversity profiles are external explanators of patterns revealed in subsequent analyses.

Vegetation and avian species ordinations

In the third step of our analysis, before attempt any correlation between bird species densities and biotope describing variables, we ordinated biotopes in three spaces. A bird density space, a vertical variables space and a horizontal variables space. Also we have ordinated bird species in a biotope space. These ordinations were used as a tool for the detection and identification of major gradients (if any) amongst bird species and biotopes separately. The collapson of the multidimensionality of the data set formed up to here has been used in the sense of direct gradient analysis (WHITTAKER, 1975 and references therein) and has been proved very efficient in noise reduction when animal – habitat relations are sought (ROTEBERRY and WIENS, 1980; PRODON and LEBRETON, 1981; CODY 1983; PETRAKIS et al. 1986, 1987; MACNALLY and DOOLAN 1986). This reduction of dimensionality will be used later for direct correlations of avifaunal and habitat major trends. The adopted ordination technique was the reciprocal averaging or reciprocal ordering (ORLOCI, 1978).

In Fig. 4, bird species are shown in the first two principal axes of a biotope space. It can be easily observed the existence of four distinct clusters located on

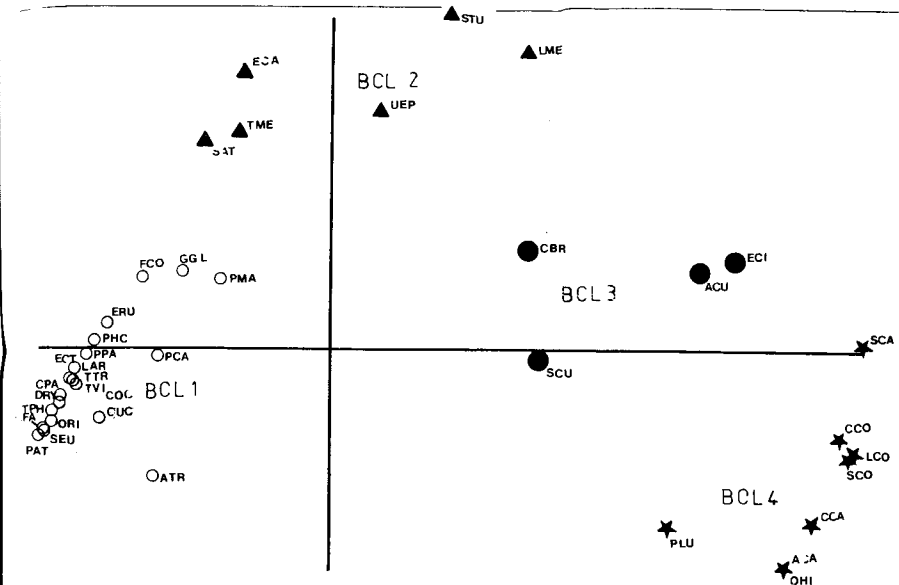


Fig. 4. Ordination scattergram of bird species in a biotope space. Four clusters are recognized and labeled by BCL 1,2,3,4 respectively. Scaling of the axes is proportional to the percentage of the variation explained by each axis. The three letter code for bird species is explained in Table V (see text for discussion). Horizontal axis is the first principal axis and the vertical is the second.

the principal plane. The first axis accounts for 50% of total trended variation and the second axis accounts for 20%. The superiority of the first axis is a general phenomenon which arises in this ordination technique which emphasizes the first axis (GAUCH, 1982) and for this the results in axes above the first must be very carefully interpreted. In addition the interpretation of axes above the second has very little to do with ecological reality (but see PRODON and LEBRETON, 1981). The above explainable percentage is unexpectedly high for quantitative data on bird abundances and possibly this is ought to prior reduction of the raw data by profile analysis. The problem of data linearity and continuity has been confronted both in the stage of the data collection (octave scale) and in the stage of previous analysis (profile analysis). Reciprocal averaging has been proved superior to principal component analysis (GAUCH et. al., 1977; ORLOCI, 1978; GEIG-SMITH, 1983) and for a set of other properties useful in this study. The diagonalization of the analyzed matrix is an aspect of reciprocal averaging which makes the method valuable in the serial pattern seeking approach adopted here. The quadratic distortion and the scale contraction (GAUCH, 1982), was not a

problem in this study because of the provisions taken prior to analysis on ecological grounds, but in other data sets it may render axes meaningless (Petrakis unpubl.)

The first principal axis is strongly correlated to a transition from dense multistratal forests to open two phase semishrublands with herbaceous openings. First axis is considered as successional and in this sense it can be used later in subsequent analyses and discussions. The second axis is negatively correlated to RHL values (Table II), namely the within biotope horizontal heterogeneity. Also it is negatively correlated to *J. oxycedrus* and other shrubs with low branches and for this it represents a partition of lower vegetation in terms of *J. oxycedrus* (lowest end) and *O. carpiniifolia* (uppermost end).

The allotment of bird species into four clusters has been done objectively by using LEFKOVITCH (1976) algorithm and this classification is compatible with our knowledge on individual bird preferences. Ecological labels for these bird clusters are left to be defined later in the stage of correlations with major biotope gradients.

Another important pattern arises in this ordination (Fig. 4). Mediterranean and mixed origin birds, spread more extensively than those of medio-European category, which are located at the leftmost end of the first principal axis. This implies that birds of mediterranean distribution have a wider habitat range than those of medi-European distribution, a fact already suggested for mediterranean plants, within Prespa and in other mediterranean areas as well. In Prespa basin this is very intensively manifested especially in the case of *J. oxycedrus* and *Prunus webbii*, but it has also been observed in other continents with mediterranean climates (for California see WESTMAN, 1983; for Australia see SPECHT, 1969). In this study, both plants and birds which occupy biotopes of mediterranean character are widespread in the area and this has to do not only with their competitive ability, but also with their ability to tolerate human impact.

When biotopes are ordinated in a horizontal variable space by using the same technique, 58% of the total variation is accounted by the principal plane and it is partitioned in 34% for the first axis and 24% for the second. The first principal axis is strongly correlated to *J. oxycedrus* and for this it represents the major successional trend from open shrublands to dense woods. Secondary axis *a* expresses this trend perfectly and it is highly correlated to *J. oxycedrus* performance. Secondary axis *b* is interpreted as a combined effect of *Q. cerris* and leguminous understory shrubs.

In contrast to the not intense structure uncovered in the previous ordinations the ordination of biotopes in a vertical variable space accounts for 91% of the total trended variance. In the scattergram of this ordination the same successional trend is revealed again, though in reverse direction – an expected fact since high performance of *J. oxycedrus* entails poor stratification of the vegetation and *J. oxycedrus* is highly correlated to this axis. The second axis is internally correlated to the maximum number of hits at medium heights (third and second height class).

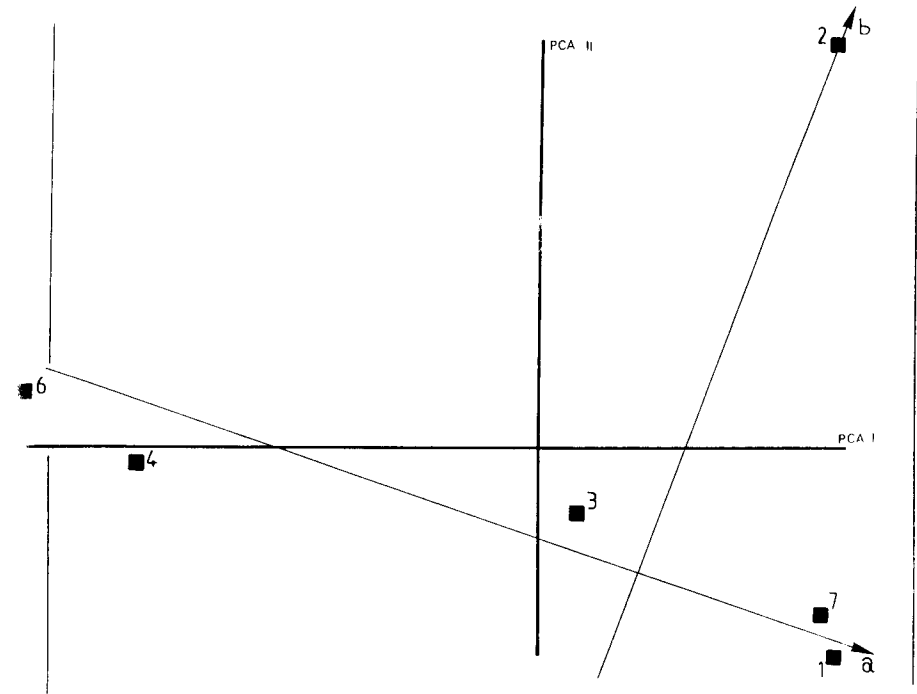


Fig. 5. Ordination scattergram of biotopes in a horizontal variable space. Axes are scaled proportionally to the percentage variance they explain. *a* and *b* are secondary axes (see text for the biological meaning attached to them). Biotope codes are explained in Table I.

This axis is also externally correlated to maximum richness at the third height class. These conditions are observed in *Cerro* and in *Ostria*. The principal function of this second axis is the discrimination it produces between biotopes similar in what has been already observed in the diversity profile of biotopes in terms of avian abundances. This axis is interpreted in this sense.

From the above, it is evident that the device of an index to incorporate both the vertical and horizontal heterogeneity is not only illusive but any inclusion of both types of variables in the same data matrix would produce spurious correlations. In Fig. 7 is presented an example of such a structure; in this scattergram both axes explain 25% of the total variation while the effects of the variable are completely interhooded.

Bird-biotope relationships

The fourth and concluding step of our analysis is a seeking procedure for relationships between birds distributional parameters and principal features of the

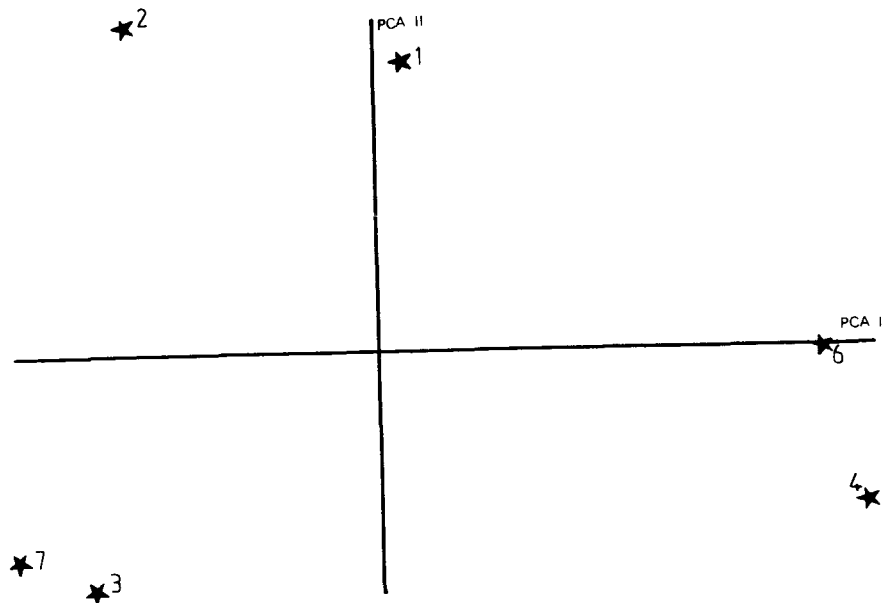


Fig. 6. Biotopes scattergram in an ordination in a vertical variables space. Axes are again proportionally scaled (see text for biological labels of these axes). Biotopes are coded as in Table I.

biotopes. Available methods for such an approach are few. The cross spectral analysis BOX and JENKINS, 1976), the multiple predictive analysis of ORLOCI (1978) and the multiple pattern analysis of Noy-Meir and ANDERSON (1971) have been used in the past with promising results. Canonical analysis is another powerful method, (GITTINS, 1979), that pertains to the subject and this method has been finally selected by us for many reasons the most important being:

1. There are no assumptions for continuity and commensurability of the variables entering into the analysis. So, several forms of specialization are allowed such as coded variables or principal scores of either or both sets of variables. In the case of bird cluster centroids, which are analyzed here (see results in Tables III and IV), this property is important since the various clusters are not present in commensurable abundances in the biotopes.

2. The model of canonical analysis can accommodate for a certain degree of nonlinearity in the data structure. This feature of the method has been amplified by linearizing manipulations prior to this analysis. Such manipulations are performed in the stage of data collection and in the entire third step of our methodology. In fact, reciprocal analysis is a linearizing manipulation since it

positions birds or biotopes in a diagonalized form which facilitates the major trends in the data to emerge by linear arrangement of the analyzed units.

3. The strategy of canonical correlation is quite similar to that of principal component analysis, at least as far as we are concerned with the geometric representation of the model. Principal component analysis translates and rotates the coordinate frame in order to reveal the axes of maximal variance in the point swarm. Canonical correlation rotates the coordinate frame in order to emphasize the covariance between two sets of variables and not the variance within a single set. This is done by finding linear transformations, namely the U and V canonical variates, for each set of variables, so that the correlations within and between these variables to be maximized. In this way the method is proved valuable for our analysis.

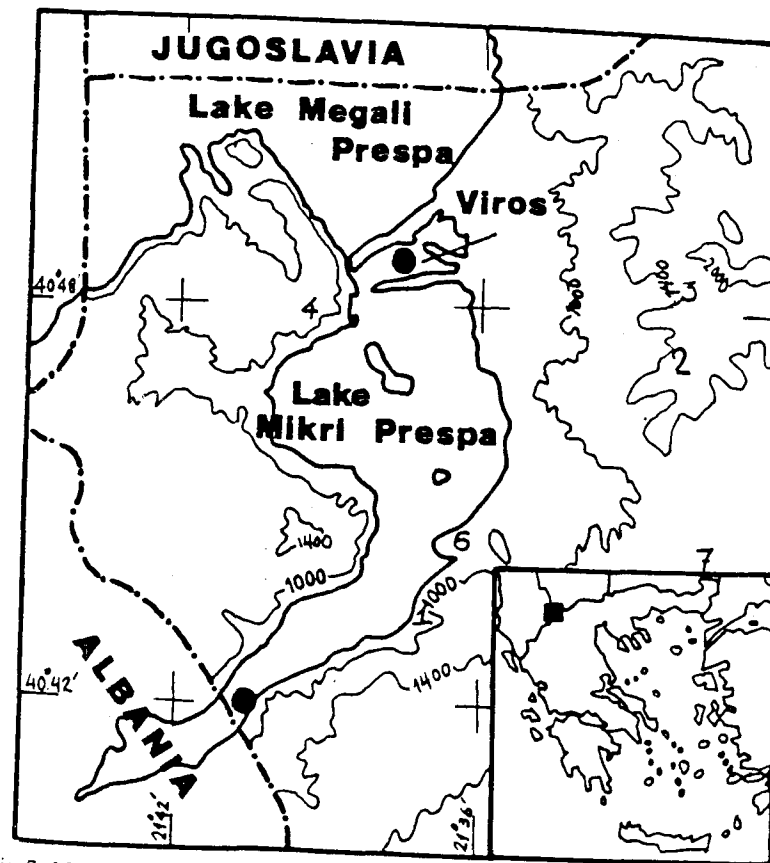


Fig. 7. Map of Prespa basin, showing the biotopes studied. Biotopes are labeled as in Table I.

4. Our previous experience and familiarity with the method. We have used it to detect correlations between Hemiptera and visited plants in order to estimate degrees of specialization (PETRAKIS et. al. 1987; Petrakis in prep.). We are aware of some case studies in which the method failed to predict the appropriate patterns (e.g. BARKHAM and NORRIS, 1970), but we attribute the inefficiency of the method to its ability to reveal the most predictable criterion for the arrangement of data and not the most useful one (CRONBACH, 1971; GITTINS, 1979). The task of the unification of these criteria into one, lies entirely in the hands of the ecologists. Also some failures of the method have been observed in cases of data sets highly redundant. This last feature, not necessarily drawback, of the method has been taken into account in this study and for this we analyzed cluster centroids rather than individual birds principal scores. When many species exhibit similar preference spectrum then this tactic is appropriate. The dense packing of bird species in the leftmost end of the first principal axis of Fig. 4 introduces a high level of redundancy in the data set which, in geometric terms, makes difficult the handling of the two data swarms. The method in this cases is inactivated by nonsingularity of the correlation matrix (GITTINS, 1979) or it produces spurious results.

In Table II a summary of such an analysis of all plots can be easily seen. In the upper two panels, the first three columns include the intraset correlations, while the last three show the interset correlations. The first set includes the four bird species clusters centroids as original variables and U1, U2 are their canonical variates. The squares of the values below the canonical variable, show the percentage by the respective canonical variate. From these values it can be seen that U1 is primarily connected to BCL3 and BCL4. These clusters are not very apart in the scattergram of Fig. 4. and their position at the rightmost end of the first principal axis makes the ecological interpretation of U1 somewhat easy. We assign the label, transition from dense multistratal wood loving birds to open mediterranean biotope selectors. It can be observed also the compatibility of signs in U1 correlation coefficients with the position of the clusters on the first axis of Fig. 4. Canonical variate U2 has no direct connection with any principal axis but it can differentiate, by the sign of the correlation coefficient, the two kinds of birds. Those which occupy medio-European like biotopes, identified by the plus sign and those which occupy mediterranean type biotopes, identified by the minus sign. This is the ecological label of U2. In the hw (intraset communality) column the overall representativeness of the original variables in the set of canonical variates is measured. From the profile of the intraset communalities it is drawn the conclusion that birds of mediterranean distribution are best represented in the set of canonical variates.

Turning to the second set HOR1 and HOR2 of the ordination scores of biotopes in a horizontal variable space, it can be seen that the original variables

are better represented by their canonical variates. V1 canonical variate expresses a *J. oxycedrus* performance and in this sense it incorporates the major successional trend of the first principal axis of the ordination of biotopes in a horizontal variable space (Fig. 5). V2 canonical variate shows a sign discrimination between biotopes with tall vegetational configuration –plus signs– and biotope with low one –minus sign. It intensifies the successional line represented by the V1.

The redundancies (Table III) are important because they perform the basic task of this analysis. They express the power of a canonical variate to be predicted from the variables of the other set. In this respect they are more reliable in measuring the interrelations of the two data sets than the canonical correlation coefficients –lower panel. As has been stated by GITTINS (1979),

TABLE III

Canonical correlations between bird species clusters and biotopes horizontal principal scores (first two sets)

can-var	U1	U2	h ² w	V1	V2	h ² b
BCL 1	.179	.658	.465	.179	.639	.440
BCL 2	-.035	.522	.274	-.034	.507	.258
BCL 3	-.694	-.488	.720	-.693	-.474	.704
BCL 4	-.758	-.583	.914	-.757	-.566	.893
Variance extracted	.272	.303	.575	.272	.302	.574
Redundancies	.272	.302	.574	.272	.302	.575

can-var	V1	V2	h ² w	U1	U2	h ² b
HOR 1	.816	.598	1.000	.815	.581	1.000
HOR 2	.574	-.805	.978	.573	.556	.884
Variance extracted	.497	.487	.984	.497	.473	.971
Redundancies	.497	.473	.971	.497	.473	.971

canonical correlation	squared	cumulative %
.999	.996	50.6
.971	.942	98.3

* input values for bird clusters are the cluster centroids.

they have incorporated the ability of each variate to account for the original variables. Of ecological interest are of course the redundancies in the first set, but in studies where mutual interactions can be excluded –e.g. grazing animals and vegetation structure– both set redundancies are valuable. It can be seen that U1, U2 are poorly explained by the horizontal variables but if we consider both variables we see that an appreciable amount of the variance can be attributed to biotope horizontality (57.4%). The poor explainability of each canonical variate is due to that both variates represent the same successional trend though in a different way. The coefficient of canonical correlation is very high, but this must be not attributed only to ecological reasons.

The values in the left three column block (Table III) express the variance proportion of each variate of one set that can be predicted from the variate of the other set. Because of the proximity of the canonical correlations to unit, these correlations are not essentially different from those in the left three columns. In the interset correlations the communalities are of primary importance, since they show the ability of each bird canonical variate to be accounted by the variates of the other set. Running by eye the profile of interset communalities (hb) it is evident that the birds in the BCL3 and BCL4 are more effected by the horizontality of the biotopes as expressed in the underlying successional trend. BCL2 is very poorly explained by this trend while BCL1 is intermediate. This position of BCL4 is in contrast with the picture revealed in Fig. 4, but this is due to the inclusion of only the horizontal variables. Birds take into account much more many variables to select their biotope than those entered in this analysis and this fact indicates that horizontality is not important where vertical structure of the vegetation is quite diverse. Most probably, BCL4 birds prefer to partition the three dimensional Euclidean space, in the risk of increased competition rather than going in low stature vegetation where they are entirely restricted in two dimensions.

Another canonical analysis was applied on the same bird variables –clusters– but biotopes were measured in terms of the biotope scores on the first two principal axes of an ordination in a vertical variables space. The results are summarized in Table IV. The dimensionality is strictly one and the first dimension can be seen that explains 99.8% of the variation in U and V canonical variates. Redundancies are particularly high –80%– while the correlations of the original variables with the canonical variates show a remarkable pattern. BCL1 is highly negatively correlated to U1 while BCL3 and BCL4 are perfectly positively correlated to that variate. BCL2 is independent of U1 and can not be fully explained in the context of this canonical analysis. Its plus sign, however, may assign it the interpretations associated with the other BCL3 and BCL4 clusters but in a qualitative mode. The ecological meaning that can be assigned to U1 is straightforward. It is the discrimination axis on which birds can be located according to their preference in open and low configured vegetation types. As far as we restrict our interest

in the BCL3 and BCL4 bird species groups, this canonical variate perfectly predicts their variation (intra-set communalities are essentially unit).

Turning to the second set of vertical original variables, namely the principal scores of biotopes, it can be seen that V1 is essentially the first principal axis of Fig. 6 and for this it can be named as the previous detected successional trend. This may also explain the poor representation of the second axis in the V1 variate and finally the low correlation of BCL2 with U1. Birds in BCL2 are relatively abundant in Ostria and Cerro which are highly weighted in the second principal axis.

The interset correlation are again of directed interest. This means that interset correlations in the second panel of Table IV are lacking of any ecological interpretation. For Prespa this may be true in a certain extend, but we feel somewhat reserved to extrapolate it in other situations. Insectivorous birds in Schinias (Marathon, Attiki, Greece) exert an indirect effect on the herb stratum by regulating beetle and bug populations, an effect being important in the maintenance of composite herbs abundances (Petraakis, in prep.). If we take into account the possibility of viral infections of plants (CLARIDGE, 1987) by Hemiptera then the indirect effect of birds on the vegetation may not be negligible.

Inter-set correlations between variates in the first panel of Table IV amplify the pattern already detected up to here. The inter-set communalities (hb) show a pattern compatible to what has been already discussed above, namely, verticality is a good predictor of all bird classes except the BCL2. Using our knowledge on the behaviour of the members of BCL2 to explain its correlational pattern, we draw the inference that the only relationship yet detected is that with the V2 canonical variate of Table III –though moderate (0.522)– which means that their preferences are affected by the patchiness generated by the moderate presence of *J. oxycedrus* high performance of *O. carpinifolia* and of the understory shrubs of *Q. cerris* together with the low position of the branches of the oak trees. All these patterns have been revealed in the diversity analysis in biotopes where the BCL2 birds attain high abundances.

The trend seeking approach as presented up to here was based on the formation of four sharply bounded bird classes. This is primarily affected by the set of species that are analyzed. The most continuous the preferences spectrum the less sharp are the boundaries between clusters. In these situations the grouping is not ecologically justified (see for insects PETRAKIS et al., 1987). Then one has to analyze separately each biotope into two spaces. The first should be bird species space –original variables– and the second space should have two alternatives, namely vertical and horizontal variables –original variables. It must be appreciated that in a such a case the noise inherent in the data may obscure the correlational patterns since very much of the dimensionality of the canonical analysis will be consumed in identifying the trends between clusters. Also the sample size has to be quite large –much larger than the analyzed variables.

TABLE IV

Canonical correlations between bird species clusters and biotopes vertical principal scores (first two sets)

can-var	U1	U2	h ² w	V1	V2	h ² b
BCL 1	-.799	.016	.639	-.798	.001	.637
BCL 2	.203	-.258	.108	.203	.019	.041
BCL 3	.917	.292	.926	.916	.020	.839
BCL 4	.927	.531	1.000	.926	.037	.859
Variance extracted	.804	.400	.994	.803	.002	.805
Redundancies	.803	.211	.805	.803	.002	.805

can-var	V1	V2	h ² w	U1	U2	h ² b
VER 1	1.000	.015	1.000	.999	.001	.999
VER 2	-.008	.985	.970	-.008	.068	.005
Variance extracted	.500	.400	.900	.500	.400	.502
Redundancies	.499	.002	.502	.499	.002	.502

canonical correlation	squared	cumulative %
.999	.998	99.8
.069	.005	99.9

* input values for bird clusters are the cluster centroids in an ordination of birds in a biotope space.

Another non cluster procedure would be the consideration of the set of biotopes in two spaces generated by the biotope principal scores of an ordination of biotopes in a bird space and in a vertical or horizontal variable space. If clusters do ecologically exist within the data set, this approach will not differ than the one adopted here and in fact it can be used alternatively. The results of such an approach are presented in Table VI. Principal plane scores are denoted by B1 and B2 original variables and VER1 and VER2 respectively. The results of the first ordination are not shown. It can be seen that U1 canonical variate is perfectly correlated with B1 original variable and U2 with the other. In addition such an orthogonality already exists in the second variate set (V1, V2). Intraset communalities show that canonical variates are fully account for the total variation

TABLE V

Coded bird species studied in this work

Species name	Code
<i>Columba palumbus</i> (Wood Pigeon)	CPA
<i>Streptopelia turtur</i> (Turtle Dove)	STU
<i>Cuculus canorus</i> (Cuckoo)	CUC
<i>Upupa epops</i> (Hoopoe)	UEP
<i>Woodpeckers</i>	DRY
<i>Lullula arborea</i> (Woodlark)	ECT
<i>Anthus trivialis</i> (Tree Pipit)	ATR
<i>Lanius collurio</i> (Red backed Shrike)	LCO
<i>Sylvia communis</i> (Whitethroat)	SCO
<i>S.curruca</i> (Lesser Whitethroat)	SCU
<i>S.atricapilla</i> (Blackcap)	SAT
<i>S.cantillans</i> (Subalpine Warbler)	SCA
<i>Phylloscopus collybita</i> (Chiffchaff)	PHC
<i>Oenanthe hispanica</i> (Black-eared Wheatear)	ACA
<i>Erithacus rubecula</i> (Robin)	ERU
<i>Luscinia megarhynchos</i> (Nightingale)	LME
<i>Turdus merula</i> (Blackbird)	TME
<i>T.philomelos</i> (Song Trush)	TPH
<i>T.viscivorous</i> (Mistle Trush)	TVI
<i>Aegithalos caudatus</i> (Long-tailed Tit)	ACU
<i>Parus ater</i> (Coal Tit)	PAT
<i>P.major</i> (Great Tit)	PMA
<i>P.caeruleus</i> (Blue Tit)	PCA
<i>P.palustris</i> (Marsh Tit)	PPA
<i>P.lugubris</i> (Sombre Tit)	PLU
<i>Sitta europea</i> (Nuthatch)	SEU
<i>Certhia familiaris</i> (Tree creeper)	CFA
<i>C.brachydactyla</i> (Short-toed Tree creeper)	ORI
<i>Troglodytes troglodytes</i> (Wren)	TTR
<i>Emberiza cia</i> (Rock Bunting)	ECA
<i>E.citrinella</i> (Yellowhammer)	LAR

E.cirlus (Cirl Bunting)
Fringilla coelebs (Chaffinch)
Carduelis carduelis (Goldfinch)
C.chloris (Greenfinch)
Coccothraustes coccothraustes (Howfinch)
Acanthis cannabina (Linnet)
Oriolus oriolus (Golden Oriole)
Garrulus glandarius (Jay)

ECI
 FCO
 CCA
 CCO
 TVI
 OHI
 CBR
 GGL

TABLE VI

Canonical correlations between the first two sets of biotopes principal scores in a bird species space and a vertical variables space

can-var	U1	U2	h ² w	V1	V2	h ² b
B 1	.999	.038	.999	.972	.018	.945
B 2	-.113	-.962	.938	-.110	-.460	.224
Variance extracted	.505	.292	.797	.478	.276	.755
Redundancies	.478	.276	.755	.478	.276	.755
can-var	V1	V2	h ² w	U1	U2	h ² b
VER 1	1.000	.015	1.000	.973	.007	.947
VER 2	-.008	.985	.970	-.008	.471	.222
Variance extracted	.500	.498	.998	.478	.276	.587
Redundancies	.473	.114	.587	.478	.276	.587

canonical correlations	squared	cumulative %
.973	.946	62.9
.478	.229	78.1

of the original variables sets and U1, U2 canonical variates are explained in a 75.5% amount. These results are broadly the same as those detected in our analysis, though in a lesser extend, as it was expected for a non cluster approach.

Concluding thoughts

Habitat selection in birds is believed to be produced as a result of many causative factors (MACARTHUR et al., 1962; ROTENBERRY and WIENS, 1980; PRODON and LEBRETON, 1981; CODY, 1983; SIEGFRIED and CROWE, 1983; WIENS, 1984) that interact and show what ecologists measure as preference, namely the occurrence and abundance of a bird species in a specific biotope. Probing the features of the biotope that are responsible for such habitat selections, we have devised numerous variable sets that bestly account for all other unmeasurable parameters that cause the observed patterns. In this respect every variable set is good enough to describe a biotope configuration, unless it fails a posteriori to predict the observed preferences and the subsequently extracted niche relational patterns. It has been empirically proved that the ecological meaning of each variable strongly affects the analysis and the results, not necessary towards the desired direction (among others GAUCH, 1982). The more the ecological complexity in a measured variable the more it influences the analysis, since it incorporates many factors that contribute to the observed situation. In many cases it renders the dimensionality in the collected data impossible to be collapsed or if it is collapsed it produces spurious correlations (SCOTT, 1979). We tried to summarize the multifariousness of the data we gathered, by using objective methods, but our measured variables were very simple (Table I). This allowed us to take into account many more aspects of the biotope though at the expense of a large variable set. In mediterranean areas of the kind of Prespa basin, sclerophyllous elements compete with medioeuropean ones and the competition scenery is presented as a gradual transition though abrupt ecotones are not lacking. This unique opportunity to examine habitat selection by birds in an area where many other selections are offered, should take into account all biotope features. For instance, the herbs and forbs in a two phase mosaic of a sclerophyllous vegetation have to be treated differently than those in a closed deciduous forest. Our variables had to be fine enough to cope with these cases. The distinction between two different variable sets to measure the complexity of the biotopes was our first sampling approach. The other was the inclusion of species groups to measure the horizontality of a biotope. All these made the sampling effort quite large and this is a drawback of our approach. But it was necessary in the lack of other more quick methods.

Biotope heterogeneity is another point of conflict in many ecological discussions (HILL, 1973). In plant ecology heterogeneity in different scales, has been used as a method of detecting vegetation pattern (GREIG-SMITH, 1983; and references therein). Especially in mediterranean biotopes, the interaction of the different scales of vegetation, has been particularly emphasized (e.g. WESTMAN, 1983). We cope with the scaling problem by using reductionistic methods in a restricted geographic area. All reductions were done on variables and were based on ecological criteria.

Traces of variable eliminations were used as logical variables e.g. if herbs performed parallelly with trees then herbs were eliminated from further analyses but a logical variable was put to be equal to one, otherwise it was put equal to zero. On the other hand heterogeneity as far as it is semantically equivalent to diversity, has many aspects and in the range of biotopes of this work, all aspects are of equal concern. So the profiles of the diversity were considered and biotopes were ranked according to these profiles. In these profiles was proved that mediterranean biotopes may be of very low diversity (Latsista), or of very high one (Koula) in all the aspects of the term as far as we measure bird populations, although they proved structurally very simple in vertical direction. It was concluded that horizontality may be responsible for that and this was intensified by the formation of four bird classes in which the third and fourth class contained birds that prefer mediterranean type biotopes. These classes were identified in an ordination of bird species as measured in each biotope. The most apparent conclusion drawn from this ordination, was the spread of mediterranean habitat selectors over the principal plane of the ordination. The size of the clusters and the area they occupy on the plane give a measure of the average niche space of the constituent species. Mediterranean species show much larger niches than those in the medio-European cluster of closed forest selectors. Although niche patterns will be described elsewhere, we can infer that mediterranean occupators are eurydynamic as has been stated for plants (SPECHT, 1969), for Hemiptera insects (PETRAKIS et. al. 1986, 1987) and now for birds. Open biotopes offer a different partition of the total resource space on a more complicated mode. For instance, short term phenological patterns are more diverse in open biotopes than in closed forests and so they produce many opportunities for resource exploitation, both, directly seed and new leaf production and indirectly through supporting a rich insect fauna (SCHOWALTER, 1981). This findings are not restricted by the general opinion that mountainous mediterranean biotopes are more diverse as we proceed from the coasts to the inland (e.g. SIEGFRIED and CROWE, 1983) since this has been proved for all mediterranean biotopes at various distances from the sea.

The correlations of bird abundances with features of the biotopes were objectively analyzed by canonical analysis. Our salient findings show that verticality is a better predictor of habitat selection in birds but horizontality may be proved equally good for some classes of birds. In particular, mediterranean bird preferences may be equally well predicted by either horizontal or vertical features of the biotopes.

Another useful conclusion was the consistency of various successional stages with their avifaunal synthesis and abundance. Also canonical correlation analysis is proved valuable in defining principal axes as resource axes. In community niche pattern studies the identification of the principal axes is necessary if we are aiming to decompose the Hutchinsonian niche in more

simple identifiable dimensions.

The approach we have adopted is effective in ecological context, because of another facility it provides. It treats numerically the horizontality of the biotope by vegetation measurable units, namely plant species or plant species groups, and in this way it approaches in an integrated mode the biological meaning of environmental conditions (GOODALL, 1954; WHITTAKER, 1967; GOLF and COTTAM, 1967; GAUCH and WENTWORTH, 1976; GREIG-SMITH, 1983). This is an effective way to incorporate the bioclimatic status of an area, much better than compiling data of the directly measurable parameters - e.g. rainfall. In this sense our approach is more holistic, and for this it is valuable in studies of mediterranean ecosystems.

All data manipulation and data analyses has been done through the Mantela (tm) and Mantela-Multiva (tm) systems. These are the commercial versions of D APROPHECO database management system (PETRAKIS, 1988a, 1988b) enhanced with an environment for multivariate procedures written in Pascal procedural language.

Acknowledgements. Financial support for this study came from nowhere. Some algorithms were kindly offered by prof. Orloci, prof. Jancey and Dr. Wildi. Elias Katsis provided computer facilities in his software house, when needed. Thanks are extended to two anonymus reviewers, who suggested improvements on an early draft of this work.

Περίληψη

Η επιλογή βιότοπου στα πουλιά, πιστεύεται ότι προκαλείται από πολλούς παράγοντες (MACARTHUR et al., 1962; ROTENBERRY and WIENS, 1980; PRODON and LEBRETON, 1981; CODY, 1983; SIEGFRIED and CROWE, 1983; WIENS, 1984), που η αλληλεπίδρασή τους καταλήγει στη διαμόρφωση του μεγέθους εκείνου, που οι οικολόγοι ονομάζουν προτίμηση βιότοπου (biotope preference). Το οικολογικά μετρήσιμο αυτό μέγεθος εκφράζεται συνήθως από τον αριθμό των συμπτώσεων και την αφθονία ενός είδους πουλιού μέσα σε ένα συγκεκριμένο βιότοπο. Διερευνώντας τις παράμετρος του βιότοπου που ευθύνονται για τις προτιμήσεις των πουλιών, ορίσαμε ένα σύνολο παραμέτρων τέτοιων, ώστε να επιτρέπουν την έκφραση και άλλων μη μετρήσιμων παραμέτρων, που αναμένεται να επηρεάζουν τα παρατηρούμενα πρότυπα (patterns). Από αυτή την άποψη, κάθε σύνολο παραμέτρων είναι κατάλληλο για να περιγράψει τη διαμόρφωση ενός βιότοπου, εκτός εάν αποτύχει à posteriori να προβλέψει τις παρατηρούμενες προτιμήσεις βιοτόπων και τις επακόλουθες σχέσεις των niche. Έχει άλλωστε εμπειρικά αποδειχθεί, ότι η οικολογική σημασία μιας παραμέτρου επηρεάζει ισχυρά τόσο την ερμηνεία των αποτελεσμάτων όσο και αυτή την ίδια την πορεία της ανάλυσης (μεταξύ άλλων GAUCH, 1982). Όσο περισσότερη οικολογική πολυπλοκότητα ενέχεται σε μια μετρήσιμη παράμετρο, τόσο εντονότερα αυτή η παράμετρος θα επηρεάσει την

κής σύνθεσης με το διαδοχικό στάδιο της βλάστησης. Εξάλλου η κανονική ανάλυση συσχετίσεων αποδείχτηκε πολύ χρήσιμο εργαλείο στον επαναχαρακτηρισμό των βασικών αξόνων του προσανατολισμού (Principal Axes) μέσα στο χώρο αποθεμάτων.

Η προσέγγιση που μεθοδεύσαμε αποδειχεται αξιόλογη σε οικολογικά πλαίσια εξαιτίας μιας βασικής διευκόλυνσης που περιέχει. Χρησιμοποιεί αριθμητικά την οριζόντια δομή του βιότοπου σε φυτοοικολογικά μετρήσιμες και πλατιά αποδεκτές μονάδες, δηλαδή τα βιολογικά είδη ή τις ομάδες ειδών. Με αυτόν τον τρόπο προσεγγίζει με ολοκληρωμένο τρόπο τη βιολογική σημασία των περιβαλλοντικών συνθηκών (GOODALL, 1954; WHITTAKER, 1967; GOLF and COTTAM, 1967; GAUCH and WENTWORTH, 1976; GREIG-SMITH, 1983). Αυτή η προσέγγιση αποδειχεται ένας αποτελεσματικός τρόπος ενσωμάτωσης του βιοκλιματικού στάτους μιας περιοχής, πολύ ανώτερος από τη συλλογή και ανάλυση απευθείας μετρουμένων μετεωρολογικών παραμέτρων, όπως το ύψος βροχής κ.λπ. Μ' αυτήν την έννοια η προσέγγισή μας είναι πιο ολιστική και για αυτό σημαντική σε μελέτες μεσογειακών συστημάτων.

Όλοι οι χειρισμοί και οι αναλύσεις δεδομένων, έγιναν με τη βοήθεια των συστημάτων MANTELA (Tm) και MANTELA-MULTIVA (Tm). Αυτά είναι οι εμπορικές εκδόσεις του συστήματος διαχείρισης δεδομένων DAPROPHCO (PETRAKIS, 1988a, 1988b) εμπλουτισμένο με περιβάλλον πολυπαραγοντικών αναλύσεων γραμμένων σε γλώσσα προγραμματισμού Pascal.

REFERENCES

- ABER J.D., 1979.— A method for estimating foliage - height profiles in broad - leaved forests. *J. Ecol.*, 67: 35-40
- BLONDEL J., 1984.— Avifaunes forestières méditerranéennes; histoire des peuplements. *Aves*, 21: 209-226
- BLONDEL J., C. FERRY and B. FROCHOT, 1973.— Avifaune et végétation: essai d'analyse de la diversité. *Alauda*, 41: 63-84
- BLONDEL J. & CUVILLIER R., 1977.— Une méthode simple et rapide pour décrire les habitats d'oiseaux: le stratiscope. *Oikos*, 29: 326-331
- BOX G.E.P. and G.M. JENKINS, 1976.— Time Series Analysis: Forecasting and Control. Holden-Day. San Francisco. USA
- CLARIDGE M.F., 1987.— Insect assemblages: Diversity, organization and evolution. In «Organization of Communities, Past and Present», G.H.R. Gee and P.S. Giller (eds). 27th Symp. British Ecol. Soc. 1986
- CODY M.L., 1981.— Habitat selection in birds: the roles of vegetation structure, competitors and productivity. *BioScience*, 31: 107-113
- CODY M.L. 1983.— Continental diversity patterns and convergent evolution in bird communities. In «Mediterranean Type Ecosystems: The Role of Nutrients», p.p. 357-402 (eds) F.J. Kruger, F.T. Mitchel and J.U. Jarvis.

- CRONBACH L.J. 1971.— Validity. In «Educational Measurement», (ed.) R.L. Thorndike. American Council on Education. Washington
- FEOLI E., 1977. On the resolving power of principal component analysis in plant community ordination. *Vegetatio* 33: 119-125
- GAUCH H.G. 1982.— Multivariate Analysis in Community Ecology., Cambridge Univ. Press., Cambridge, p.p. 298
- GAUCH H.G., and T.R. WENTWORTH, 1976. Canonical correlation analysis as an ordination technique. *Vegetatio*, 33: 17-22
- GAUCH H.G. R.H. WHITTAKER and T.R. WENTWORTH, 1977.— A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.*, 65: 157-174
- GITTINS R., 1979.— Ecological applications of canonical analysis. In «Multivariate Methods in Ecological Work» (eds) L. Orloci, C.R. Rao and W.M. Süteler, p.p. 309-5351CPH. Burtonsville. Md. USA
- GOFF F.G. and G. COTTAM, 1967.— Gradient analysis: the use of species and synthetic indices. *Ecology*, 48: 793-806
- GOODALL D.W., 1954.— Objective methods for the classification of vegetation. III. An essay in the use of factor analysis *Austr. J. of Botany*, 2: 304-24
- GREIG-SMITH P., 1983.— Quantitative Plant Ecology. 3rd ed. Blackwell, Oxford
- GREIG-SMITH P., 1986.— Chaos or order - organization. In «Community Ecology: Pattern and Process», (eds) J. Kikkawa and D.J. Anderson, p.p. 19-29 Blackwell, London, UK
- HILL M.O., 1973.— Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54: 427-32
- HULST R. VAN, 1978.— The dynamics of vegetation: Patterns of environmental and vegetational change. *Vegetatio*, 38: 65-75
- HULST R. VAN., 1979.— On the dynamics of vegetation: Markov chains as models of succession. *Vegetatio*, 40: 3-14
- JANCEY R.C., 1979.— Species ordering on a variance criterion. *Vegetation*, 39: 59-63
- KERSHAW K.A., 1973.— Quantitative and Dynamic Plant Ecology. 2nd ed. Edward Arnold, London, UK
- LEFKOVITCH L.P., 1976.— Hierarchical clustering from principal coordinates: an efficient method for small to very large numbers of objects. *Math. Biosci.*, 31: 157-174
- MACARTHUR R.H., J.W. MACARTHUR and J. PREER, 1962.— On bird species diversity: II Prediction of bird census from habitat measurements. *Am. Nat.*, 96: 167-174.
- MACARTHUR R.H. and H.S. HORN, 1969.— Foliage profile by vertical measurements. *Ecology*, 50: 802-805
- MAC NALLY R.C. & DOOLAN J.M., 1986.— An empirical approach to guild structure: habitat relationships in nine species of eastern-Australian cicadas. *Oikos*, 47: 33-46
- MURDOCH W.W., F.C. EVANS and C.H. PETERSON, 1972.— Diversity and pattern in plants and insects. *Ecology*, 53: 819-829
- MORRISON D.F., 1984.— Multivariate Statistical Methods. McGraw-Hill. Singapore.
- NOY-MEIR I. and D.J. ANDERSON, 1971.— Multiple pattern analysis or multiscale ordination: towards a vegetation hologram?. In «Statistical Ecology» vol. 3, (eds) G.P. Patil, E.C. Pielou and W.E. Waters. p.p. 207-225. The Pennsylvania State University Press. Pe. USA.

- NUMATA M., 1979.— The structure and succession of grassland vegetation. In M. Numata (ed.) "Ecology of Grasslands and Bamboolands in the World". Gustav Fisher Verlag, Jena., p.p. 182-96
- ORLOCI L., 1974.— On information flow in ordination. *Vegetatio*, 29: 11-16
- ORLOCI L., 1978.— Multivariate Analysis in Vegetation Research., 2nd ed. Junk, The Hague.
- PATIL G.P. and C. TAILLIE, 1979.— An overview of diversity. In "Ecological Diversity in Theory and Practice", (eds) J.F. Grassle, G.P. Patil, W. Smith and C. Taillie. p.p. 3-27 ICPH. Burtonsville. Md. USA.
- PETRAKIS P., 1988a.— DAPROPHECO: A specialized database system for integrated studies in plant-Hemiptera communities. *Coenoses* 3: 41-53
- PETRAKIS P., 1988b. MANTELA: Relational Database System (User guide). Ecologica Publ., Athens, Greece.
- PETRAKIS P., (in prep.) Hemiptera-Plant associations: plant phenologies and insect temporal assemblages.
- PETRAKIS P., TSELEPATIOTIS V. & DROSPOULOS S., 1986.— Structure organization and dynamics of Hemiptera-Plant communities of a mediterranean area: preliminaries and methodology. Proc. 2nd Int. Congr. Phynchota Balcan, Greece., 1986: 54-61
- PETRAKIS P., TSELEPATIOTIS V., DROSPOULOS S., 1988.— Auchenorrhyncha-host plants associations in east Mediterranean communities: a multivariate approach on structure and specificity. 6-th Auchenorrhyncha Meeting, Turin. Italy, p.p. 171-78
- PETRAKIS P. & DROSPOULOS S., 1989.— Greek Pentatomoidea: A biogeographic analysis with objective methods. I. Methods documentation and the database. 4th Con. Biog. & Ecol. of Greece, in press.
- PIELOU E.C., 1977.— Mathematical Ecology. Wiley, New York. USA.
- PRODON R. & LEBRETON J.D., 1981.— Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. *Oikos*, 37: 21-38
- ROTEBERRY J.T. & J.A. WIENS, 1980.— Habitat structure, patchiness and avian communities in north American steppe vegetation: a multivariate analysis. *Ecology*, 61: 1228-50
- ROTH R.R.,— 1976.— Spatial heterogeneity and bird species diversity. *Ecology*, 57: 773-782
- QUENOUILLE M.H., 1949.— Problems in plane sampling. *Ann. Math. Statist.*, 20: 355-375
- SCHOWALTER T.D., 1981.— Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession. *Oikos*, 37: 126-130
- SCOTT E.L., 1979.— Correlation and suggestions of causality: spurious correlation. In "Multivariate Methods in Ecological Work" (eds) L. Orloci, C.R. Rao and W.M. Stiteler, p.p. 237-251 ICPH. Burtonsville. Md. USA.
- SIEGFRIED W.R. & T.M. CROWE, 1983.— Distribution and species diversity of birds and plants in fynbos vegetation of mediterranean climate zone, South Africa. In "Mediterranean Type Ecosystems: The Role of Nutrients", p.p. 403-416 (eds) FJ Kruger, DT Mitchell and JUM Jarvis. Springer, Berlin. FDR
- SPECHT R.L., 1969.— A comparison of the sclerophyllous vegetation characteristic of mediterranean type climates in France, California and southern Australia. I. Structure morphology and succession. *Australian Journal of Botany*, 17: 277-292

- WARREN WILSON J., 1965.— Stand structure and light penetration I. Analysis by point quadrats. *J. of Applied Ecology*, 2: 383-390
- WESTMAN W.E., 1983.— Plant community structure - Spatial partitioning of resources. In "Mediterranean Type Ecosystems: The Role of Nutrients", p.p. 417-445, (eds) F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis.
- WIENS J.A., 1973.— Pattern and process in grassland bird communities. *Ecol. Monogr.*, 43: 237-270
- WIENS J.A., 1974.— Habitat heterogeneity and avian community structure in north American grasslands. *Am. Midl. Nat.*, 91: 195-213
- WIENS J.A., 1984.— On understanding a non-equilibrium world: myth and reality in community patterns and processes. In "Ecological Communities: Conceptual Issues and the Evidence", (eds) D.R. Strong, D. Simberloff, L.G. Abele and A.B. Thistle. Princeton Univ. Press., N. Jersey.
- WILLSON M.F., 1974.— Avian community organization and habitat structure. *Ecology*, 55: 1017-29
- WHITTAKER R.H., 1967.— Gradient analysis of vegetation. *Biol. Rev.*, 42: 207-264
- WHITTAKER R.H., 1975.— Communities and Ecosystems. MacMillan. New York, p.p. 387

ADDENDA

Acknowledgements. Data for birds were kindly provided by G. Catsadorakis who also have contributed to vegetation sampling. Thanks are also extended to Y. Petridis for various help at field work stages and to V. Tsigari for preparing the figures.

REFERENCES

- BARKHAM J.P. & J.M. NORRIS, 1970 — Multivariate procedures in an investigation of vegetation and soil relations of two beech wood lands, Costwold Hills, England. *Ecology*, 51: 630-639
- RENYI A., 1964 — On measures of entropy and information, In: *Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability* (Edit. J. Neyman, Univ. California Press, Berkeley, U.S.A.), pp. 547-561
- SCHMIDA A. & R.H. WHITTAKER, 1981 — Pattern and biological microsite effects in two shrub communities, southern California. *Ecology*, 62: 234-251

ERRATA

pages 72, 73, 81, 84, 90, 93, 98	read: PETRAKIS 1988	instead of	«PETRAKIS 1987»
page 67, line 31	read: measuring	instead of	«measured»
page 68, line 1	read: also	instead of	«also»
page 72, line 34	read: in prep.	instead of	«in press»
page 73, line 38	read: late	instead of	«ate»
page 76, line 13	read: (1979)	instead of	«(1977)»
page 76, line 22	read: 1974	instead of	«1984»
page 79, line 3	read: however	instead of	«but»
page 84, line 10	read: CROWE	instead of	«GROWE»
page 84, line 33	read: attempting	instead of	«attempt»
page 85, line 21	read: contraction	instead of	«contraction»
page 87, line 15	read: variables	instead of	«variable»
page 88, line 5	read: (BOX	instead of	«BOX»
page 91, line 12	read: As it has	instead of	«As has»
page 93, line 10	read: direct	instead of	«directed»
page 99, line 6-7	read: GOFF	instead of	«GOLF»
page 101, line 34	read: CROWE	instead of	«DROWE»
page 102, line 10	read: GOFF	instead of	«GOLF»