

## SOME ASPECTS OF CLASSIFICATION AND ORDINATION OF VEGETATION DATA IN PERSPECTIVE

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**Abstract.** A discussion on the complementarity of classification and ordination methods in vegetation ecology is given. The need to work with different vegetation spaces and hierarchical processes is stressed.

### Introduction

Paraphrasing Stebbins (1969) in his "Comments on the Search for a Perfect System", it looks to me that, similar to what others discussed about the species concept, many epigones of the Braun-Blanquet school prefer to believe that the associations are discrete entities, created by God in a particular form, and that the only task of vegetation science is to discover, define and classify these God-given associations. But as Darwin started to question the "Linnean dictum" and his followers have often posed the question in the form of absolute alternatives, it happened that Negri's (Negri, 1914) and Gleason's (Gleason, 1917) epigones took exception with respect to Clements and Braun-Blanquet views. Continuing with the analogy and using the structure of another Stebbins's sentences the question: "are the associations completely objective entities, which exist in nature in only one form, which we must discover, recognize and describe?" or "are they purely man-made artefacts, having no real existence except in the mind of the syntaxonomist?" can be raised. I conclude as Stebbins has done for the species concept, that neither of these extreme points of view is acceptable. Plant associations have a basis in nature but this basis is not so rigid that we can recognize them in only one way. Before leaving Stebbins with his nice novel about King Linnus XIV and his fair daughter, I would like to say that I got the impression that many Negri-Gleason epigones are, more or less consciously feeling that "vegetation is an entity changing in a continuous way along gradients, gradients were created by God in particular form, and that the only task of vegetation science is to discover, define and describe these God-given gradients!". I have been convinced that they in fact think in this way by reading recent papers where the new unity for measuring the vegetation

changes along gradients, the "GLEASON", has been proposed and used. If the authors were of Italian origin, I should have proposed that they would call the unit "NEGRI".

I do not want to initiate another round of discussions on the continuity and discontinuity of vegetation, which I personally consider closed by the illuminating paper of Lieth (1968). I would certainly like to conclude based on other papers (cited in Orłóci, 1978; van der Maarel, 1979; Feoli, Lagonegro & Zampar, 1982) that: "God created simultaneously vegetation types and vegetation gradients in order to make simpler the life for some ecologists and more complicated for others...".

In my opinion, multivariate analysis of vegetation data has future in vegetation science only if the complementary functions of classification and ordination are fully understood and the exercise is directed to study both vegetation types and gradients. This is the main topic I intend to address in my introduction to this meeting.

### **Vegetation data and vegetation spaces**

The vegetation is a multi-variable which can be measured in space and time in many ways. The individual components of this medium can be chosen from among a great number which are biologically relevant. As a consequence, different "schools" of vegetation study evolved (see Whittaker, 1973). Notwithstanding efforts of integration, which have always been active, confusing and rather unpolite discussions still persist. However it is only human to try to inflict one's own ideas on one's neighbour. Fortunately it is also human to expect that the neighbour will react in some specific way.

The quality of the components chosen to describe the vegetation, in trying to understand existing patterns and processes, determines different types of vegetation data, and consequently, different types of spaces in which the vegetation states find their position. Each vegetation state is a vector of  $m$  components, the scores of which are coordinates of the state in the space. The  $m$  components define the dimensionality of this space. Three main types of spaces can be distinguished: extrinsic, intrinsic and semiextrinsic.

Extrinsic spaces are generated by the abiotic variables. They are used for the so called direct ordinations of vegetation (direct gradient analysis, see Whittaker, 1967). Semiextrinsic (or mixed) spaces are generated by biotic and abiotic variables, while intrinsic spaces by biotic variables.

Intrinsic spaces are used for ordinations in the indirect gradient analysis (see Whittaker, 1973). Since the biotic variables could be of several different types, the intrinsic spaces may be classified in several ways:

- Taxonomic spaces. These are obtained when the vegetation is described by taxonomic characters (species or genera or families etc., see van der Maarel, 1972). Such spaces, consequently, have different hierarchical meanings. The Braun-Blanquet approach is working with the space originated by species, which is the space at the lowest hierarchical level.

- Cytogenetic spaces. These are obtained when the species are described by their degree of polyploidy (Pignatti, 1960) or number of chromosomes with satellites, and so on.

- Structural spaces. These are specific to vegetation descriptions by such structural characteristics as life forms, growth forms, types of leaves, etc. Barkman (1979) uses structure as distinct from texture, which he defines as "the qualitative and quantitative composition of the vegetation as to different morphological elements... regardless of their spatial arrangement". To him, structure is the spatial arrangement (horizontal and vertical) of the morphological elements. This distinction is certainly useful, however, here, I prefer to consider the space originated by textural characters also as a structural space, because the biological parameters used in both cases could be the same.

- Anatomic spaces. These are obtained by using as descriptors anatomic characters, such as those describing the tissue structure (e.g. number of vessels, dimension of vessels, thickness of tissues, etc.), which are related to adaptation. However it appears to me useful to distinguish the anatomic space from structural spaces since I do not see now evident relationship between the anatomy of the plants and the visible structure of the vegetation.

- Functional, physiological spaces. These are obtained by using functional descriptors of the species, such as type of photosynthesis, type of response to stress, type of phenology, etc.

- Biochemical spaces. These are defined by using biochemical characteristics of the species (pigments, oils, vitamins, alkaloids, tannins, etc.).

- Chorological spaces. These are obtained when chorological characters are used.

- Syntaxonomical spaces. These are obtained when the syntaxonomic units are used rather than species as the basis of analysis.

- Sociological spaces. These are obtained when sociological species groups (see Doing, 1969) obtained on local data sets rather than single species are the units (e.g. Feoli & Orlóci, 1979).

Other spaces could be easily mentioned, e.g. evolutive, reproductive, regenerative etc. All of them can be used to describe and interpret vegetation patterns and processes in quantitative ways being the basis on which multivariate methods can be applied.

The taxonomic spaces of higher hierarchical meaning than the species space, cytogenetic space, structural space, anatomic space, functional space, biochemical space, chorological space, syntaxonomical space and sociological space, etc., can be obtained by multiplying the design matrix of species descriptions ( $k, m$ ) by the matrix of species-vegetation states ( $m, n$ ).  $K$  is the number of character states used to describe the species. A species may be described by a different number of them. Each species will be described by only one in case of taxonomic or sociologic spaces and by one or more in the other cases.

Since all other spaces can be obtained by the space defined by the species, this space can be designated as the basic space. If a matrix multiplication is used, the

axes of the higher hierarchical spaces are all linear combination of variables of the spaces of lower hierarchical level. All these different spaces can be the basis of measuring in an objective way, convergences and divergences of vegetation states in different ecosystems or different phytogeographic areas (see Cody & Mooney, 1978) or in time (see van der Maarel & Werger, 1978). If a suitable function is found the difference between the similarity of two vegetation states in different spaces could be interpreted as a measure of convergence or divergence. Researches in this area have yet to be addressed.

### Hierarchical processes, similarity, convergence and divergence

All the spaces described before may be obtained directly by multiplying the matrix 'character states-species' by the matrix 'species-relevés'. However there are other spaces which cannot be originated by a simple multiplication or a series of successive multiplications of matrices. These spaces can be called 'conditioned spaces'. Some examples will clarify the matter and explain the definition.

Let us consider a relevé with six species:  $a$  (2),  $b$  (1),  $c$  (3),  $d$  (4),  $e$  (5),  $f$  (2). In the brackets are the species scores. Such relevé has six non-zero coordinates in the basic space. If  $a$  and  $b$  belong to genus  $k$ ,  $c$ ,  $d$ ,  $e$  to genus  $l$ , and  $f$  to genus  $p$ , then the relevé will have three non-zero coordinates in the space of genera, i.e.  $k$  (3),  $l$  (12) and  $p$  (2). If  $k$  and  $p$  belong to family  $t$  and  $l$  belong to family  $z$ , then the relevé will have two non-zero coordinates in the space of families, i.e.  $t$  (5),  $z$  (12). The definition of the spaces follows a hierarchical process of combining the basic axes. In the case of taxonomic spaces the hierarchical process is unequivocally defined by taxonomy and all of them can be obtained by successive matrix multiplication, however in other cases many different hierarchical processes may be defined by different ways of hierarchical combination of the basic axes. A relation of order (see the set theory) may be arbitrarily established in a set of characters. A relation of order establishes automatically a hierarchy. If the following is the chosen hierarchy of a set of characters:

species < leaf type < growth form < life form

than the matrix describing the species (numbers identify character states):

species	leaf type	growth form	life form	scores
a	1	1	2	2
b	2	1	3	1
c	1	2	1	3
d	2	1	1	4
e	1	1	3	5
f	1	3	2	2

is rearranged according to the established hierarchy in the following way:

species	< leaf type	< growth form	< life form	scores
c	1	2	1	3
d	2	1	1	4
a	1	1	2	2
f	1	3	2	2
b	2	1	3	1
e	1	1	3	5

In this case the hierarchical process of combining the basic axes produce two conditioned spaces, the space of leaf types (leaf types / growth forms, life forms) and the space of growth forms (growth forms / life forms). The coordinates of the relevé in the conditioned spaces are the following: (leaf types / growth forms, life forms): 1, 2, 1, 1, 2, 1 (the same as in the basic space); (growth forms / life forms): 3, 4, 2, 2, 6.

If the hierarchy is the following:

species < growth form < life form < leaf type

than the table should be rearranged in the following way:

species	< growth form	< life form	< leaf type	scores
a	1	2	1	2
f	3	2	1	2
e	1	3	1	5
c	2	1	1	3
b	1	3	2	1
d	1	1	2	4

In this case the coordinates in the conditioned spaces are the following: (growth forms / life forms, leaf types) same as in the basic space; (life forms / leaf type): 4, 3, 1, 3, 1. It is evident that the coordinates in the conditioned life form space are different than in the non-conditioned life form space, where they are 7, 4, 6.

Similarity between relevés can be computed in the different spaces. When it is computed in a series of spaces originated according to some hierarchical process, than the convergence of vegetation states or types can be measured. Such convergence may be structural, chemical, cytogenetical, anatomical, etc. The measure of convergence makes sense only in a process. As we can say that the trajectories of two moving points are converging if the points tend to have the same coordinates in a given space, so we can say that two vegetation types or states are converging if their similarity is increasing from the basic space to spaces of higher hierarchical meaning. In vegetation study the measure of convergence is meaningful in all the described spaces in function of time (i.e. convergence during succession) or

in a hierarchical process of space generation. This last aspect is particularly suitable to explore the possibilities of comparing vegetation types at a world scale level (see Lieth, 1968; Box, 1981).

Divergence is the contrary of convergence. We can say that two vegetation states or types are diverging if their similarity is decreasing as a function of time or of the change of the meaning of the space. It is obvious that in the last case divergence should be registered only in limited circumstances as a consequence of the fact that two relevés should not be more different as they are in the basic space. For the study of convergence and divergence suitable measures of similarity should be tested or developed. They should be formulated in such a way to be comparable when applied to different spaces.

### **Vegetation states and vegetation types**

When the vegetation of a given area is under study, it is divided into smaller or larger "portions" (vegetation stands).

These are the basis for the relevés which are the descriptions of the vegetation stands. Given a vegetation sample, i.e. a set of relevés, some basic questions ask for answers: Is the sample heterogeneous? If yes what are the ecological factors influencing the variation, and what of them are the most important in producing variations? These questions are always the basis of some hypothesis formulated by the researcher before the survey. Since the relevés are made at a certain time and a certain place, they describe states of vegetation in time and space. If the area of relevés is very small the state of only one or few individuals of the same or different species is described. If the area of relevés is very large the state of populations of many species could be described. The size of the area is related to the problem under study, however if the definition of vegetation communities is one of the aims of the research, the area should be large enough to represent a "unit of vegetation". In the Braun-Blanquet approach (see Westhoff & van der Maarel, 1973) the concrete unit is the phytocoenosis which is defined as a relatively homogeneous vegetation at a particular site. The weakness of the phytocoenosis concept is the subjective judgement of homogeneity. It appears to me that no operational solution is available to overcome this weakness other than to find ecological justifications for subdivisions or aggregations. The exercise should be considered as the search for definition of vegetation types, for which multivariate methods are suitable tools (Orlóci, 1978). In the Braun-Blanquet approach the sampling is preferential (Orlóci, 1978) and plot size should exceed the so called minimal area. The concept of minimal area may be useful to clarify the concept of phytocoenosis, however it is far to be used for making relevés of unknown vegetation. The minimal area was defined as the smallest area which should hold all the properties, morphological and functional of a phytocoenosis (see Moravec, 1973).

It follows therefore, that the minimal area is itself a property of the phytocoenosis. The definition of the minimal area of a phytocoenosis is not as obvious as it may appear from past uses. The basic problem relies on the fact that not all the species present in a phytocoenosis are typical of that phytocoenosis, because a

given phytocoenosis can contain species and therefore structural and functional characteristics more typical of other phytocoenoses. Dietvorst, van der Maarel & van der Putten (1982) use quantitative data and suggest to link the search with pattern and dominance-diversity studies. I believe that the real problem is the definition of the phytocoenosis before to look for the minimal area.

The argument is clearly circular, however I think the minimal area should be a useful parameter, as many others, to be defined only for well defined phytocoenoses. What means a well defined phytocoenosis? It means one which can be assigned to a plant community (vegetation type). If a typification is lacking the concept should have no relevance in vegetation study, in line with the conclusions of Goodall (1961). If the problem to find a suitable area to do relevés arises, how to define the vegetation types? In my opinion the problem to find a suitable area is occurring also in experimental ecology, when, for example, the interaction between different species is to be studied (see Harper, 1977). Actually the area for relevés is always a matter of subjectivity in all the approaches of vegetation study irrespective to the sampling designs. When in a paper it is declared that the relevés have been done according to the method of Braun-Blanquet, it actually means that the relevés have been done according to the author's pre-interpretation of the vegetation diversity (number of different vegetation types).

Thanks to ability of the human mind to perceive the phenetic diversity, this pre-interpretation is possible in many areas of the world, it is of course more difficult or impossible in tropical and equatorial forests, at least with the usual tools of a traditional european phytosociologist.

Given any set of relevés, numerical methods can be used to define sets of such relevés (classification) and to define the optimal classification in term of internal or external predictivity (predictivity analysis) (see Orlóci, 1978; Feoli, 1983; Popma et. Al., 1983; Feoli, Lagonegro & Orlóci, 1984). Only if a set has biotic and abiotic peculiar characteristics, i.e. characteristics significantly related to the set in terms of probability, then it should be considered a vegetation type.

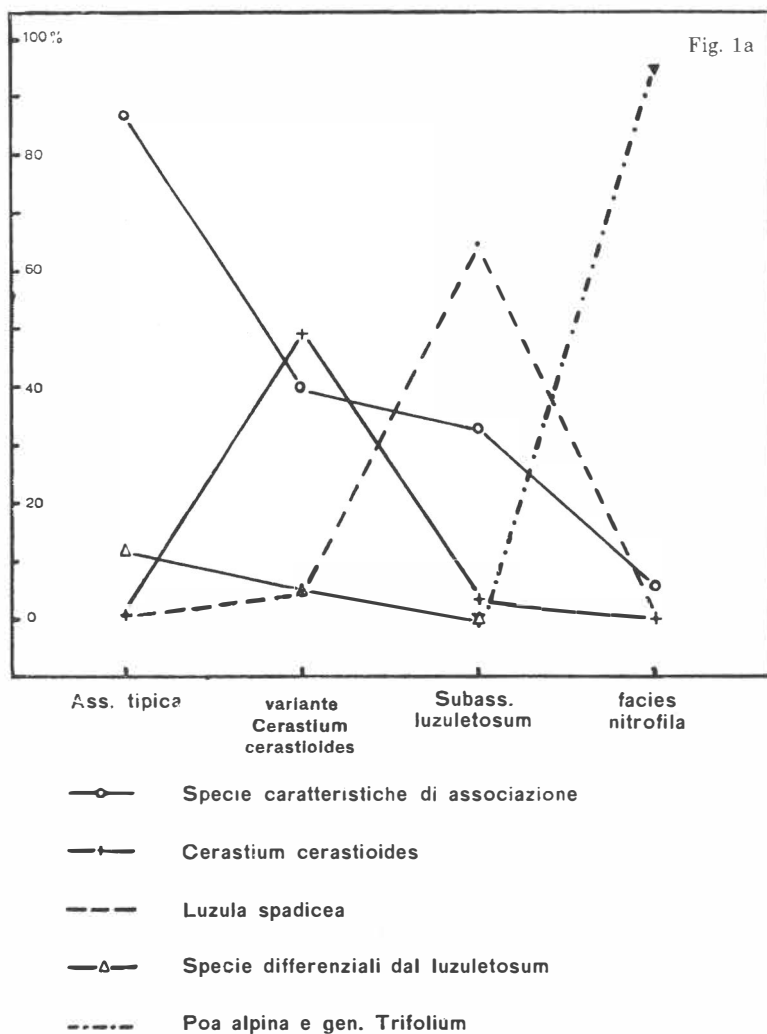
The classification of vegetation states, that can be done in all the mentioned spaces, is nothing less than a process partitioning the spaces. Classifications obtained in different spaces can be compared (congruence of classification, Sneath & Sokal, 1973), methods are largely available (see Orlóci, 1978; Feoli, 1983; Feoli, Lagonegro & Zampar, 1982; Feoli, Lagonegro & Orlóci, 1984). Different classifications may be produced with different hierarchical meaning and interesting different biological scales.

The vegetation study (vegetation science?) is an exercise involving complex systems which can be hierarchically or non-hierarchically classified in different ways, we should be open in this respect and try to explore as many ways as we can see. The vegetation types should be the basic units of vegetation study toward the auspicate development of a *comparative ecology* (see Intelcol Bulletin, 1983). They should be used to study in a more clear context ecosystem functions, infraspecific variations and spatial patterns. An example of the study of primary productivity in bentic ecosystems of the Gulf of Trieste, on the basis of previous defined types, is

offered by Lausi (1967). An example of infraspecific biochemical variation is given by Lokar et Al. (1984), while an example of pattern analysis by Juhasz Nagy & Podani (1983).

### Ordination versus classification?

The possibility to distinguish vegetation types in the different spaces is due to the fact that the different species have different ecological amplitude in respect to single ecological factors and respond to them in different ways. On the other hand the fact that the niches of the species (geometric niche, sensu Hutchinson, see Hurlbert, 1981) are overlapping, is responsible of the similarity between vegetation





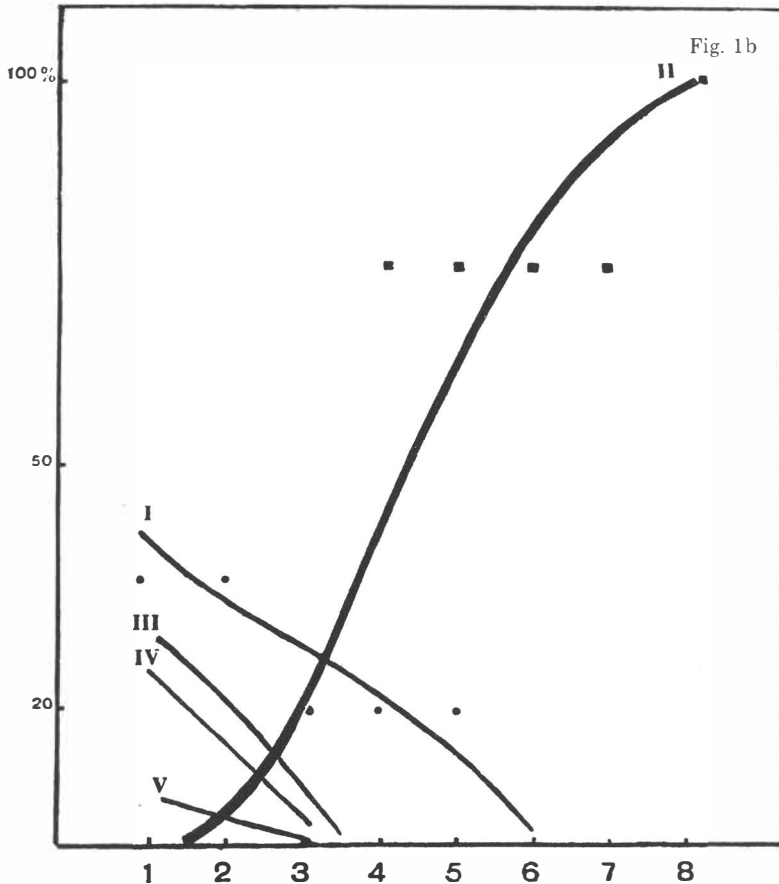


Fig. 1 — Species and groups of species responses to a gradient of nutrients (Fig. 1a) and to a gradient of soil texture (Fig. 1b). From Pirola (1959).

states and vegetation types ("continuum"). In a situation of similarity between vegetation states it necessarily could happen that many relevés can not be attributed significantly (by classification and identification methods, see Orlóci, 1978; Feoli, Lagonegro & Orlóci, 1984 and Goodall, 1968 for an alternative method based on probability) to one of the types, because of its intermediate position between two or more types in the space under study. This fact should not to be seen as a failure of classification or identification methods, but just a prove of the continuous data structure (see Orlóci, 1979) and therefore of gradual vegetation variation.

The ordination of vegetation was far to be only an exercise of north-american plant ecologists, examples can be found in the Braun-Blanquet's books and in many papers of european phytosociologists (eg. Pignatti, 1966). In the Braun-Blanquet approach it was given more emphasis to the study of total vegetation variation

rather than variation of response of single species. However the decomposition of variation in components related to single species or groups of species was focused several times.

An example, similar both to the coenocline representation of Whittaker (1967) for single species and that for species groups (Poldini & Feoli, 1976; Feoli & Lagonegro, 1982), is given in Fig. 1 from Pirola (1959).

In the study of vegetation it is quite difficult to meet a situation in which only one factor is varying when all the others remain relatively constant (Whittaker, 1967).

The simple example by Feoli Chiapella & Ganis (1980) proves in a relatively easy circumstance, the inadequacy, or better the inferiority of a direct gradient analysis in respect to the indirect method.

However if such a favourable situation is met, as it looks possible also from the paper of Austin et. al. (1984), the definition of vegetation types along the dominant gradient and within a well defined interval, can help to measure the so called *beta* diversity more correctly than it was done by Whittaker and his followers. Strictly speaking the diversity of a system is defined both by its richness, i.e. the number of its entities, and equitability or evenness, i.e. the way in which a certain quantity (number of individuals, biomass, cover, etc.) is distributed among the entities. It follows that it is conceptually weak to measure diversity by some way that does not take into account richness and evenness, at least if the *beta*, before the world diversity, would not have the property to change the meaning of diversity.

The measures of *beta* diversity suggested by Whittaker and followers (see Wilson & Mohler, 1983) are just measures of homogeneity or heterogeneity of vegetation along gradients. Rates of changes can be easily computed on the basis of any resemblance function judged suitable and the model presented in Fig. 2. A more appropriate measure for *beta* diversity should be based on the number of different vegetation types defined along the gradient (richness) and on the basis of the proportional extension of each type along the gradient (evenness). By this approach, if along a gradient, within a defined interval, there is only one type, the *beta* diversity is zero and the measurable diversity is only the *alfa* diversity.

The multivariate ordination methods, linear or non-linear (see Orłóci, 1978; 1979; Fewster & Orłóci, 1983) are mainly used to reduce the dimensionality of the spaces (all the mentioned spaces can be the objects of the reduction) with the aim to explore more easily the structure implicit in the data set, i.e. to detect the mutual position in the space of both vegetation states and vegetation descriptors. In the first case we are looking for similarity and trends of variation, in the second case for pattern of correlation between the descriptors. Both serve to discover the correlation between the intrinsic descriptors and the abiotic factors for causal analysis of vegetation variation (also in time, see van der Maarel & Werger, 1978) and for predictions (see Feoli, 1983).

The ordination methods impose an artificial order into the vegetation spaces by giving rise to ordination spaces (see Orłóci, 1974, for a description of information flow in ordination). The order imposed by the methods is more artificial as more the dimensions of the original spaces are reduced.

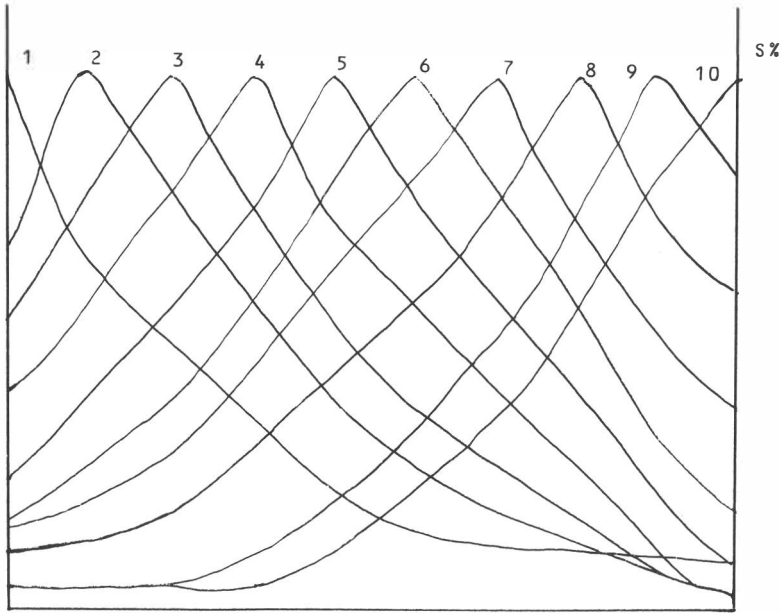


Fig. 2 — Curves of similarity of each relevé with all the other in an ordered sequence along a hypothetical gradient. The model can serve to quantify changes along gradients.

What is wrong by partitioning the ordination spaces according to some classification?

The operation allows one to analyse the spatial relationships between less entities than those original. Each of the new entity (set) is a cloud of points for which position and dispersion parameters could be computed (centroids, variances around the centroids) as well as some other shape parameters. Each point has now an extra set of new coordinates, i.e. those related to the centroid of the cloud to which it belongs and those related to the centroids of the other clouds. It is obvious that a great deal of informations has been introduced in the ordination space, these should be useful to understand the reticulate relationships between the vegetation types and between vegetation types and abiotic factors. The ordination spaces can be used in several ways to aid understanding. The superimposition of classifications (eg. Lausi & Feoli, 1977), minimum spanning trees, or values of other vegetation descriptors to detect isocoenes (Van der Maarel, 1969, 1972) are the most frequent. Ordination spaces can be presented also with the aim to reveal clusters as suggested by Andrews (see Everitt, 1978 and Mardia et. al., 1979) and they have been used explicitly for classification purposes (Parks, 1970; Noy Meir, 1973; Hill, Bunce & Shaw, 1975; Poldini & Feoli, 1976; Wildi, 1979), while some ordination methods as discriminant analysis (see Williams, 1983) and concentration analysis (Feoli & Orlóci, 1979) cannot be performed without previous classifications.

Ordinations within defined vegetation types give informations about the variability of the types and of the species within the types. An example is given by Grabherr (1979).

Ordinations of vegetation types by their centroids or frequency vectors have been the subject of several studies (e.g. Lausi & Feoli, 1977; Komarkova, 1980; Feoli & Lagonegro, 1982; Torok & Podani, 1982). The ordinations may reveal many informations about the ecology of the species. By superimposing the scores of the species on the ordination diagrams detailed patterns of distributions and information about ecological optima within the sample can be obtained for all the species. This way of using ordinations has not been yet fully explored, however it is in line with the Westhoff's views (see van der Maarel & Werger, 1978b).

### Conclusions

I am not interested in answering a question whether vegetation study is a science or a pseudoscience, whether it is mature or non-mature; I think its role in understanding vegetation variation quite clear. Since vegetation is a complex system it is obvious that many approaches can be used to look into it, and that many different biological aspects can be considered as of relevance in understanding its functioning. Multivariate methods of classification and ordination are suitable tools to detect vegetation variation in respect of different biological phenomena. Classification is useful to detect vegetation diversity, ordination to detect vegetation order. We cannot speak about convergence between classification and ordination of vegetation (see Whittaker, 1972), they are just two complementary approaches that should not be bound respectively with the continuum or discontinuum ideologies. The methods can work in different vegetation spaces of biological relevance. The detection of vegetation order and vegetation diversity has nothing to do with problems related to holism or reductionsim (see Harper, 1982) (are they real problems?); diversity and order offer frames and patterns within which the total vegetation variation can be hierarchically decomposed. The decompositions may concern different phenomena down to the infraspecific variation of characters "unfortunately" (?) not used for taxonomic purposes (see again Harper, 1982) or used for very detailed taxonomic purposes (see Landolt, 1977) or for studying clinal variations (see Stebbins, 1973; Endler, 1977). The analysis of correlation between different characters useful to describe and explain variation in vegetation and the analysis of correlation patterns between such characters and environmental factors, can be a fruitful exercise directed to understanding problems related to the coexistence of different species in the same vegetation type, and the existence of a determinate structure of a vegetation type. Methods to measure such correlation can be based on both classification and ordination (see Feoli & Scimone, 1984, for a recent review in relation to the textural analysis of vegetation). Methods to measure redundancy (Orlóci, 1975; Rohlf, 1977; Feoli, Lagonegro & Orlóci, 1984) are particularly useful in decomposing total variation into the specific and common components.

An approach based on multivariate methods is clearly descriptive, but so open

that I can hardly see where it leads. Of course other approaches should be used in parallel, e.g. modelling (see Jeffers, 1982) and experimenting (see also Goodall, 1970). However, at least for me, it is difficult to make a clear separation between the descriptive approach and the experimental one, the description of the results being a necessary step after experimentation.

Description after experimentation should not be looked at in one way only; different hierarchical processes could be established also in describing experimental results!

There are many problems in describing vegetation (such problems actually render the topic interesting). The most important are related to sampling and the scale used (see Bouxin & Boulenge, 1983). Vegetation types can be defined at different scales, and they can be hierarchically arranged in various ways.

Syntaxonomy (in its broad sense, see Feoli, Lagonegro & Biondani, 1981, Maarel, van der, 1981), should be open in this respect. It should not claim to build up a general hierarchical system using only the species to characterize all the hierarchical levels (see Maarel, van der, 1972).

The introduction of multivariate methods into vegetation study offers now two new perspectives: a first related to different vegetational abstract spaces and a second related to hierarchical processes in arranging biological characters.

These should break barriers between different botanical approaches and should help the investigation into vegetation phenomena to become more consistent on the basis of underlying logical models.

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