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TAXONOMY AND PERCEPTION IN VEGETATION ANALYSIS

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Abstract. This paper discusses the idea that perceptions of the vegetation are affected by the taxonomic system on the basis of which plant populations are identified. It is argued that the best taxonomic system is not necessarily species-based, and that the traditional belief that a common taxonomic platform can be found for vegetation analysis is not realistic. The question of taxonomic choice is raised and resolved through simple reasoning as follows. Examples from the Brazilian Caatinga, Argentine Chaco, and Canadian Sub-Boreal Forest clarify both concepts and techniques.

Introduction

Vegetation analysis begins with definitions of the "unit vegetation", a stand, and "unit vegetation component". This task requires areal dissections of the landscape and taxonomic dissections of the plant multitude. Area dependence (scale effect) is well understood (see Mueller-Dombois and Ellenberg 1974:33, Kershaw 1964:26, Greig-Smith 1983:19, Juhász-Nagy and Podani 1983, Podani 1982, 1984, Kenkel 1984:54, Kenkel, Juhász-Nagy and Podani 1989, Orlóci and Pillar 1989), but not so well taxonomy dependence (context). The latter is the topic which we subject to analytical scrutiny.

The individual plant, the fundamental community component is the sole corporeal object in the vegetation that responds to and survives environmental adversity, reproduces its kind, and perpetuates its community. Taxonomy enters the analytical process when the focus shifts from the plant to the population of plants which have to be identified. The number of taxonomic systems available for this task is limitless, some species-based, others species-free.

We observe that the dominant taxonomic system in vegetation study is species-based. Notwithstanding this fact, we believe that the collective experience indicates that greater ecological utility may issue from alternative taxonomies that de-emphasize inheritance and emphasis characteristics that enable the plant individual to survival under the environmental extremes of its site. Alternative taxonomies may be based on plant life-form (Raunkiaer 1904, Mueller-Dombois and Ellenberg 1974), growth-form (Grisebach 1872, Warming 1909, Dansereau 1957:148, Barkman 1988, Halloy 1990), phenological type (Barkman 1988), and other indicator traits. To aid the choice, Pillar (1992) suggests objective evaluation functions and ordering (ranking) algorithms within the framework of generalized character set analysis (Orlóci 1991a). We discuss these in detail.

Relevé: crisp or fuzzy

The description of the vegetation stand is referred to as a "relevé". This is usually a data vector (*e.g.*, Braun-Blanquet 1928), but it can be a score matrix (Orlóci 1991a). The relevé reflects choices, mostly the taxonomic system and area size/shape of the vegetation stand. One consequence of these is a normally ill-defined, fuzzy relevé (Orlóci 1988a,b, 1991, Roberts 1989, Feoli and Orlóci 1991:ix, Pillar and Orlóci 1991). The ways relevé fuzziness is treated is a point of concern in some analyses, albeit most often fuzziness is ignored by phytosociologists by pretending that their relevés are in fact crisp.

An area where the analytical methods have made provision for fuzziness is vegetation typification. Briefly stated, a fuzzy classification operates under the assumption that a vegetation stand can be a member in more than one, or possibly in all vegetation types, although with different degrees of membership (Feoli and Zuccarello 1986, 1988). It is interesting to note that recognition of fuzziness necessarily emphasizes compositional continuity among stands. This is understandable, since fuzziness mitigates the absences of a taxon by the presence of other similar taxa in the relevé (Pillar and Orlóci 1991). Importantly, the fuzzy approach to classification clearly demonstrates that incorporation of the notion of continuity is compatible with the idea of classification.

Characters, taxonomies

It is important to realize that the character state is a property of the individual organism, but character variation is a population level property. In well known taxa such as in most of the species, information about population level variation in the key characters can be obtained from published sources, but is not be guaranteed. In the interest of accuracy direct observation of the plants in the survey site is required. If done, the observations may point up the need for redefinition of the primary taxa. The resulting taxonomy is analytical and secondary. Obviously, an analytical redefinition of the taxonomy has its limits. For example, it is impossible to fragment analytically the primary taxa if the records are population level descriptions. Redefinition by pooling primary taxa is always a possibility.

It is interesting that plant taxa are defined by characters, but the description of a vegetation stand may not use the defining characters of the taxa, only the taxon labels, such as the species names. This type of condensation of information leads in the vector type relevé to depravation by lack of detail. A more informative description will score the character states such as in the score matrix relevé.

There are the unit characters at one extreme (Sneath and Sokal 1973:72). These cannot be further reduced into more elementary characters. Reducibility is very much the property of complex characters, such as plant life-form. The latter is in fact so complex that it requires an elaborate scheme to identify its component states.

It is important to note that characters while different, may represent the same evolutionary answer to adaptation under the same selective force. This possibility has been recognized early by Warming (1909:3), who mentions hereditary constraints (phylogenetic constraints in Givnish 1987) which made it possible

> "... for different species, in their evolution under the influence of identical factors, to achieve the same object by the most diverse methods."

These constraints can account for the high diversity of plant forms found in the community under the same environmental conditions. This idea is very important to justify substitutions of some characters by others in the taxonomic scheme by which phytosociologists describe the vegetation.

Taxonomic systems are distinguished by the defining character sets and the rules of operation by way of which the system dissects the plant multitude. Highly relevant commentaries on this are found in Mayr (1942:119), Walters (1963), Davis and Heywood (1963:89), Sokal and Crovello (1970), Michener (1970), Stace (1989:11) and Stuessy (1990:51). We recognize a basic dichotomy in the taxonomic systems: species-free or species-based. "Species-free" implies "character-based" in the sense of the early tradition of vegetation description. These often involve the notion of character "functionality", which we realize is a valid notion, albeit controversial because its operationality requires identification of traits that are instrumental in an individual plant's survival in its environment (Mayr 1961, 1982:67-9, Wilkins 1968, Peters 1976, Harper 1982, Rosenberg 1985:37). Such traits forming one group are set aside from others that do not play a direct role in the survival of the individual plant, but are essential in the transmission of genetic information between generations. The latter are the defining characters in "species-based" taxonomy.

A characters role need not be connoted *a priori* and taxon recognition may be reduced to perception of totality, a Gestalt (Heywood 1973, Lausi and Nimis 1985). Gestalt has played an important part in plant classifications. Most recently Barkman (1988) suggested a taxonomy in which the taxa are perceived mentally and then a search for characters begin that distinguish the taxa. Exact opposites of this are systems which have no preconceived plant types, only combinations of character states that define potential taxa (Dansereau 1951, Orlóci and Orlóci 1985, Lausi and Nimis 1985, Orlóci, Feoli, Lausi and Nimis 1986, Orlóci 1991a). In these the characters have to be selected before the taxa are recognized. As regards the character selection problem in a general context, we refer to Cain and Harrison (1958) for interesting definitions, to Sneath and Sokal (1973) and Key (1967) for a discussion of homology, and to Williams, Dale and MacNaughton-Smith (1963), Sokal and Rohlf (1970) and Orlóci (1978) for character (or species) choice and weighting.

Species-free taxonomies

With focus on plant characters other than those that are instrumental in heredity by facilitation of the passage of genetic information between generations, different taxonomic systems have been conceived (Adamson 1939, Lacza and Fekete 1969, Fekete and Lacza 1970, Shimwell 1971:63, Barkman 1988, Orlóci 1991a). We give brief characterization of some of these in groups that identify the character type and/or the character arrangements:

The early plant taxonomic systems of vegetation description were mainly physiognomic (Humboldt 1806, Kerner 1863, Grisebach 1872) or had a physiognomic component (De Candolle 1818). These did not involve considerations of character functionality, unlike Warming's early system (1884), the first of a series (Drude 1887, 1896, Warming 1895, 1909, Raunkiaer 1904, 1907, 1908) based on plant function, the so called epharmonic component of physiognomy (Du Rietz 1931:14). From this group, Raunkiaer's (1907) life-form classification gained broadest acceptance (Braun-Blanquet 1928:287, Adamson 1939, Cain 1950, Gimingham 1951, Mueller-Dombois and Ellenberg 1974:449), despite the initial criticisms (*e.g.*, Drude 1913).

Some systems are based on plant architecture, as Barkman (1988) put it "... free of hypotheses of environmental adaptation." Barkman excluded from consideration characters related to life strategy, life cycle, hibernation level, and size, consistency and inclination of leaves, and he named plant types after characteristic plant taxa (Piceids, Quercids, etc.) Systems more relevant to us, are the multicharacter systems, for which Du Rietz's (1931), is an early example, particularly the sequential and hierarchical systems of recent designs (Dansereau 1951, Knight 1965, Knight and Loucks 1969, Parsons 1976, Noble and Slatyer 1980, Box 1981, Feoli and Scimone 1984, Lausi and Nimis 1985, 1986, Gomez Sal *et al.* 1986, Grime, Hunt and Krzanowski 1987, Lausi, Nimis and Tretiach 1989, Halloy 1990, Guárdia and Ninot 1991a, and Cabido, Diaz and Acosta 1991). Our discussions are focused on the conditional (Feoli's 1984) or nested hierarchical systems (Orlóci and Orlóci 1985, Orlóci *et al.* 1986, Orlóci and Stofella 1986, Orlóci 1988a,b, Orlóci and Orlóci 1990, Orlóci 1991a). These define plant taxa as combinations of the states of several characters, known as character set types (CSTs, Orlóci 1991a) without the ambiguities of the earlier systems.

Species-based taxonomies

By the turn of the Century, taxonomy has seen great advances in thought and in the cataloguing of the World's flora. The explosion of taxonomic information has triggered a change of preference in phytosociological practice and wholesale adoption of species-based vegetation descriptions. Braun-Blanquet (1928:21) spoke for the majority of his contemporaries:

> "The Brussels [3rd International Botanical Congress] Congress (1910) *rightly* decided in favor of the species as the fundamental unit of the plant community."

He saw the 'life-form' classification of plants as the alternative, but found it wanting, because:

> "The concept of 'life-form' is indefinite, has not been adequately defined, and cannot be considered as a sufficient basis for a science of vegetation. Species, however, are groups of individuals with uniform inheritance and have been for many years the objects of careful investigation."

Although the 1910 Codgers did achieve a standardization of phytosociology, it also straitjacketed phytosociology. There always remained a small minority who saw utility in several parallel systems, as Du Rietz (1931:43) put it, based on "different points of view". Even Braun-Blanquet (1928:21, see also Salisbury 1940) suggested the possibility of using narrower taxonomic units below the specific level.

All along the ecological utility of the species concept has been questioned (Salisbury 1940, Constance 1953, Ehrlich and Holm 1962, McMillan 1969, Snaydon 1973, Grime 1979, Harper 1982, Ghiselin 1987). Basically, the species level was unacceptable to many, because it could not help to isolate important ecological indicators represented by specialized genotypes as explained in Harper (1982, Jancey and Wells 1987).

Species tend to be broad ecologically, yet they are limited geographically. This makes the species level unsuited for comparative vegetation analysis between geographic regions or between different habitats within the same geographic region. Under these conditions, species-based community comparison is scuttled by analytical indeterminacies owing to an unshared flora (Orlóci and Stofella 1986, Orlóci 1988a, 1991a).

As the species level proved inadequate, the use of higher level plant taxa that lump species has been suggested as a basis for vegetation analysis (Maarel 1972, Dale 1978). It is interesting to mention that Good (1974:55) considered the Cruciferae, Umbelliferae, Rosaceae, Rubiaceae and Euphorbiaceae as useful climatic indicators, and Dale and Clifford (1976) found little loss of interpretability when genus and subgenus levels were used instead of species in vegetation classifications. The positive experiences with supraspecific taxa notwithstanding, the use of these suffers from the consequences of broadened environmental ranges and inconsistent recognition criteria (Stace 1989:188).

Data yield from different taxonomic schemes

The species-based scheme generates community descriptions in the form of a data matrix (k,ν), involving k species populations (rows) in ν sites (columns). Each of the ν column vectors in this matrix is a relevé. The character-based scheme with m characters (f_1, ..., f_m states respectively) generates a similar matrix (k,ν), and in addition to this, it also generates m incidence matrices (f_1,k), ..., (f_m,k). Each entry in the (k,ν) matrix is a presence/absence score (1 or 0) or some other value. The multiplication of matrices (f_i,k) and (k,ν) yields matrix (f_i,ν). Each element in the (f_i,ν) matrix is the weighted sum of a character state over the k species. Feoli and Scimone (1984) suggested analyses of matrix (f_i,ν) to reveal information about characters.

Character arrangement

Sequential (Knight and Loucks 1969) and hierarchically nested arrangements (Orlóci 1991a) are the basic types. In the sequential arrangement, a taxon is equivalent to a character state. Because of this, there are as many parallel taxonomies as there are characters in the set. In the nested arrangement the taxon is equivalent to a CST. The number of potential taxa recognizable in the hierarchical arrangement[1] may far exceed the number of taxa recognizable in the sequential arrangement. Because of this, the hierarchical nested arrangement have the potential to convey more information. The methods of analysis of data emitting from the hierarchical nested model are revisited in the following sections and extended in new directions.

The hierarchical nested model

The score matrix in Table 1 and the equivalent nested arrangement in Fig. 1 give an example. Note the CST records in the table and their mappings in the figure. The relevés which materialize as observations are vertical runs of character states with nonzero cover values. Some of the unmaterialized relevés (zero cover values) may be nonsensical, but they have to be retained to preserve the integrity of the model structure.

The following descriptions assume that the characters are numbered from top (1) to bottom (m) in the list, and the hierarchical levels from bottom (1) to top (m):

1. The defining character on hierarchical level m is character 1. The defining character set on level i includes all characters from 1 to m-i+1.

2. There are k_i nodes on hierarchic level i,

$$k_i = \prod_{j=m}^{i} s_j = s_i k_i \tag{1}$$

Take k_m+1 as 1. The character (m-1+j) corresponding to level j, to be called the characteristic attribute of level j, has s_j states.

3. A node on level i indicates the end point of a run of j character states (a j-valued CST) with point of origin on level 1. In this sense, "CST" and "node" are synonymous terms. On the lowest level, CSTs are defined by the entire character set. On the top level, a CST is a single character state and $k_m = s_m$.

4. Resemblances are computed between relevés according to the similarity or dissimilarity of their respective CST mappings in the hierarchical model. Resemblance functions derived specifically for this purpose (Orlóci and Orlóci 1985, Pillar 1992) use estimates of CST values which are the cover values at the nodes (Fig. 1).

5. Note that as CST number is reduced, moving up in the hierarchy, the CST values are summed. The value at any node b, level i, is the sum of the values at the nodes connected to node b on the next lower level i-1:

Table 1. Character score matrices of relevés from the Caatinga (NE Brazil) and the Chaco (NW Argentina). The four characters and 10 relevés are taken from a larger data set.

	Character Set Types									
Relevés	Caatinga				Chaco					
Characters	a	b	c	d	a	b	c	d	e	f
Stem tissue - succulent, woody	w	s	w	w	w	s	w	w	w	w
Stem function - regular, twin-purpose	r	t	r	r	r	t	r	r	t	t
Stem armature - thorn/spine, none	n	t	t	n	n	t	t	n	t	n
Leaf duration - deciduous, persistent, leafless	d	l	d	p	d	l	d	p	d	d
Cover (%)	6	2	1	1	2	3	3	3	2	1
	0		6			0	4	7		

$$X_{ib\gamma} = \sum_{e=1+(b-1)s_{i-1},\, i>1}^{b(s_{i-1})} X_{(i-1)\,e\,\gamma} \tag{2}$$

The incremental limits of the subscripts are: i = 2, ..., m (levels), b = 1, ..., k_i (nodes), γ = 1, ..., ν (relevés). Symbol s_{i-1} indicates the number of states of the characteristic attribute of level i-1.

Optimal character order

A consequence of the hierarchical arrangement is that the taxa on a given hierarchical level, above level 1, are determined by the characters above the level. Because of this, comparisons of communities based on the hierarchical nested model will be affected by the character order. Character order having an effect is not unknown in other types of statistical analysis as well. The computation of orthogonal functions (Rao 1952:345) is a typical example.

The effect of character order cannot be undone, only purposefully manipulated to optimize same specific property consistent with the objectives to be achieved (Pillar 1992). For example, if we wish to study the relationship of vegetation and environment, we may try to find a character order (for vegetation) that maximizes the congruence of vegetation structure and environmental structure. Similarly, if we are interested in the measurement of convergence among two plant communities, we may order the characters in such a way that they maximize the convergence of the two community structures. This is not unlike the statisticians maximization of correlation between sets of variables in canonical correlation analysis, or the minimization of a distance measure in discriminant analysis. The following describe the optimization procedure in typical cases.

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[1] To see this, consider three characters in a sequential arrangement, each with 4 states. Based on each, 4 populations can be recognized or 12 in total. The populations overlop among the characters. This is because each character covers all individuals. If the populations are arranged in a nested hierarchy, the number of nonoverlapping populations recognizable is 64, the product of the number of states.

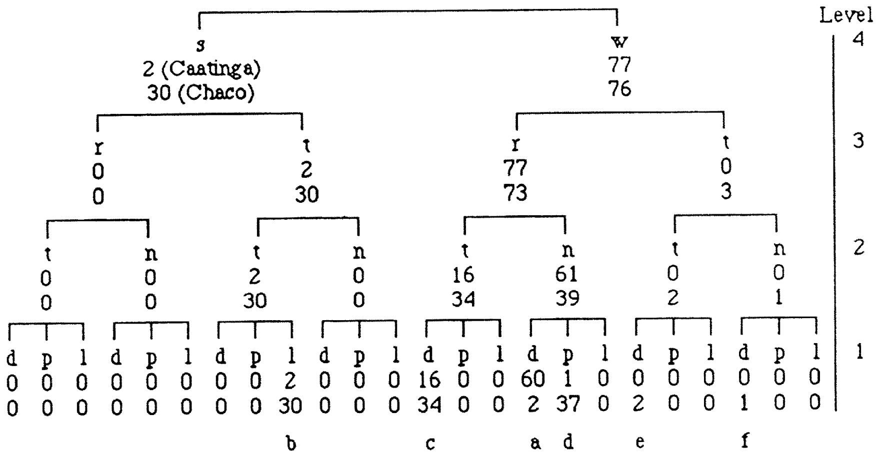

Figure 1. Hierarchical nested structure of the character set in Table 1, showing character state symbols and CST cover values in the Caatinga or Chaco relevés. Vertical runs of letter sets, such as w, r, t, d identify CSTs. Letters b, c, a, d, e, f at the base identify the CSTs materialized in the sample. The upper and lower rows of numbers indicate cumulative CST cover values in the two relevés. Height scale and horizontal spacing of nodes are arbitrary.

1. Structural congruence

The following describes derivation of an optimal character order for measurement of structural congruence in vegetation and environment:

a. Define vegetation structure $\mathbf{D}_i$, hierarchical level i, as a v x v matrix of relevé dissimilarities (with a characteristic element, relevés j and k, d_{ijk}) based on CST performance mappings at the nodes or some transformations of these.

b. Define environmental structure Δ as another v x v matrix of relevé dissimilarities (with a characteristic element, relevés j and k, δ_{jk}) based on environmental variables or their transformations.

c. Measure congruence by an appropriate function. We used for this purpose the matrix correlation

$$\rho(\mathbf{D}_i;\Delta) = \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}\, \delta_{jk} \tag{3}$$

This involves the $v(v+1)/2$ distinct off-diagonal values in $\mathbf{D}_i$ and Δ. The values of $\rho(\mathbf{D}_i;\Delta)$ range from -1 to +1. Positive values indicate congruence (cf. Sokal and Rohlf 1962, Sneath and Sokal 1973:97;280).

d. Rearrange the character set and repeat steps in an orderly iterative process (see further details below) until $\rho(\mathbf{D}_i;\Delta)$ is maximized on each hierarchical level (above level 1).

2. Structural convergence

The hypothesis of convergent evolution is a perennial topic for much discussion in the ecological literature (Cody and Diamond 1975, Orians and Solbrig 1977, and Orians and Paine 1983) . "How convergent" or "how significantly convergent" are typical questions[2]. The following algorithm optimizes the character order to maximize convergence:

a. Assign the v relevés to n groups (say, floristic regions) and map the groups into the same character hierarchy (Fig. 1).

b. Construct m level-specific dissimilarity matrices

$\mathbf{D}_i$, i = 1, ..., m

An element d_{ijk} in the ith such matrix is the dissimilarity value of relevé j and k on hierarchical level i. The elements are arranged by groups whose convergence is to be determined. The groups may be equal or unequal in size.

c. Compute dissimilarities among the groups. This may be done on a group-to-group basis, or over all the groups as an average dissimilarity ,

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[2] The correlation coefficient has been interpreted as a measure of both convergence (positive side) and divergence (negative side), or the lack of both (zero, Orlóci *et al.* 1986). In the case of similarity functions with domain from 0 to 1, values that are extremely high indicate convergence, and extreme low values indicate divergence, but there is no natural point indicating the lack of both. We believe that a division point can still be found by way of some randomization algorithm as a midpoint between probability limits on the extremes.

$$\sigma_i = \frac{1}{\sum_{e=1}^{n+1} \sum_{f=e+1}^{n} \nu_e \nu_f} \sum_{j=1}^{\nu-1} \sum_{k=j+1, g_j \neq g_k}^{\nu} d_{ijk} \quad (4)$$

In this, ν signifies the total number of relevés in the n groups; ν_e and ν_f are the sizes of group e and group f; g_j or gk is a label of the group to which relevé j or k belongs. When Euclidean distances are involved, and if these are squared, σ_i is an average square centroid distance.

An alternative to average dissimilarity when the groups are excessively dispersed, is the average of the dissimilarities of all relevés of one group to their closest neighbour relevés in the other groups:

$$\sigma_i = \frac{1}{\nu} \sum_{j=1}^{\nu} \mathrm{INF}\,[d_{ijk}, k=1,...,\nu \text{ and } g_j \neq g_k] \quad (5)$$

In this INF is the lowest value function. Other symbols are defined similarly as in (4).

d. Change the character order and recompute σ_i. Continue in like manner until on all levels σ_i is minimized. A correction factor may be applied to discount increases in the nominal value of convergence due to overlapping floras (Orlóci *et al.* 1986).

3. Redundancy

Redundancy is the repetition of the some information by different characters. The topic is well worked in the vegetation literature (see Orlóci 1978:17) and also elsewhere (Sokal 1965, Jardine and Sibson 1971:171, Sneath and Sokal 1973:103). Redundancy helps to give weight to individual characters proportional to their capacity to minimize the loss of information should they be removed selectively step-by-step from the character set. The following algorithm orders the characters by level of redundancy:

a. Compute a ν x ν symmetric matrix $\mathbf{D}_i$ of vegetation relevé resemblances on hierarchical level i.

b. Measure a character's redundancy on this level with regard to a previous level according to

$$\rho(\mathbf{D}_i;\mathbf{D}_{i-1}) = \sum_{j=1}^{\nu-1} \sum_{k=j+1}^{\nu} d_{ijk}\, d_{i-1jk} \quad (6)$$

This is similar to (3) except that here structures of adjacent levels ($\mathbf{D}_i$, $\mathbf{D}_{i-1}$) are compared. For data sets with only two relevés, (6) has a simpler form,

$$\rho(\mathbf{D}_i;\mathbf{D}_{i-1}) = 1 - \frac{|\, d_{ijk} - d_{(i-1)jk} \,|}{\mathrm{SUP}\,(d_{ijk}, d_{(i-1)jk})} \quad (7)$$

Symbols, d_{ijk} and $d_{(i-1)jk}$ signify dissimilarity values between relevés j and k. SUP selects the largest dissimilarity.

c. Select the character order above level i-1 which maximizes (6) or (7).

d. Repeat the steps on all levels above level 1.

Common to the algorithms is a recursive procedure, similar in spirit to successive approximation (Poore 1956, 1962, Orlóci and Pillar 1989, Orlóci 1990, 1991b) by which they find the character order that maximizes the structure evaluation functions (3), (4,5), or (6,7). The problem in this is one in determining the influence of the individual characters on the total data structure. The algorithms identify the less relevant characters and places them to lower levels in the hierarchy. Agglomerative or divisive versions exist. In the agglomerative version, character evaluations start at the top of the hierarchy (level m) and moves down to the second highest, third highest, etc. levels. Considering level i, the character added to the set, chosen from among the remaining pool of i unassigned characters, is such that its inclusion maximizes the relevant structure evaluation function. The divisive algorithm starts with finding an optimal character arrangement for hierarchical level 2, and continues the same for level 3, 4, etc. On hierarchical level 1 (bottom of the hierarchy), the data structure is unaffected by character order. On any higher level i above level 1 (i > 1), m-i! character arrangements are to be evaluated in the case of congruence and convergence. In the case of redundancy, there are

$$\frac{(m-i+2)!}{(m-i+1)!1!)} = m-i+2 \quad (8)$$

different character subsets with m-i+1 characters in each to be evaluated. These subsets differ by one character removed from the m-i+2 characters of level i-1. As a character is removed, one of the residual subsets will maximize redundancy. At that point the missing character is given rank m-i+2 (placed on level i-1 of the hierarchy). The problem on the next higher level is to find the character among the remaining m-i+1 characters that should be given rank m-i+1 (placed on level i of the hierarchy). This requires the evaluation of m-i+1 character subsets. The computations continue in like manner until each character is assigned to a hierarchical level. The agglomerative and divisive versions are not expected to produce identical orderings of characters. Furthermore, if the optimal character order is established according to increasing redundancy, the invariant characters will be judged completely redundant.

Optimal taxonomy

An optimal character order defines an optimal taxonomy, specific to structural properties in the sample. The practice of linking the optimality of a model or a decision to the relationship of structures has many precedents. Closely related cases involve dendrograms (Sokal and Rohlf 1962, Sneath and Sokal 1973:277, Orlóci 1978:264, Podani and Dickinson 1984), species number and data types (Orlóci and Mukkattu 1973, Orlóci 1978:34), sampling unit size and shape (Podani 1982), and sample size (Orlóci and Pillar 1989).

Table 2. Character set in vegetation description on the Elk Lake survey site. Only states materialized in the data are listed for character 1. 'Stem' and 'leaf' refer to stem and stem-like or leaf and leaf-like plant structures.

Growth-form (Barkman 1988)

1. Form (gf). 6:polythrichid, 8:pleuroziid, 20:caespitose graminid, 23:decumbent herb, 24:arching herb, 26:scapos-rosulate herb, 27:erect scapose herb, 30:arctostaphyllid shrub, 31:andromedid (vacciniid), 34: sambucid, 38:piceid, 39:betulid

Stem

2. Consistence (co). 1:succulent, 2:herbaceous, 3:semi-ligneous, 4:ligneous, 5:no stem
3. Direction (di). 1:erect, 2:erect diffuse, 3:creeping, 4:climbing, 5: no stem

Leaf

4. Shape (sh). 1:needle, 2:graminoid, 3:broad, simple, 4:compound, 5:thalloid, 5:no leaf
5. Epidermal surface (ep). 1:glabrous, 2:glaucous, 3:trichomous dense, 4:trichomous sparse, 5:no leaf
6. Width (wi). 1:< 2.5 mm, 2:2.5-5, 3:5-10, 4:10-50, 5:50-100, 6:100<, 0:no leaf
7. Length (le). 1:<5mm, 2:5-25, 3:25-75, 4:75-125, 5:125<, 0:no leaf

Plant height

8. Height class (he). 1: < 0.1m, 2: 0.1 - 0.5 , 3: 0.5 - 2, 4: 2 - 8 , 5: 8 - 10, 6: 10 - 25, 7: >25m

Table 3. Character order in the Elk lake data set. Plant characters are described in Table 2 and the environmental variables include exposure, slope, soil depth, and soil texture. Decreasing congruence of vegetation structure (D_i, hierarchical level i) and environmental structure (Δ) is the ordering criterion. The congruence measure is $\rho(D_i;\Delta)$, defined as (3) in the text, and the algorithm is divisive. The D_i matrix has characteristic element $2(1 + r_{ijk})$ in which r_{ijk} represents a nominal product between standardized relevés j and k, hirarchical level i (Orlóci and Orlóci 1985). The Δ matrix is similarly defined. Asterisks indicate the characters that account for maximum congruence in the subsets.

$\rho(D_i;\Delta)$	Order in character subset
0.524235	gf
0.445153	co
0.534043	*di
0.227612	sh
0.120588	ep
0.047395	wi
0.37611	le
0.257664	he
0.459472	di gf
0.70103	di *co
0.108908	di sh
0.128919	di ep
0.12804	di wi
0.604726	di le
0.431131	di he
0.480543	di co gf
0.441492	di co sh
0.326616	di co ep
0.211398	di co wi
0.580569	di co *le
0.486461	di co he
0.554961	di co le gf
0.544541	di co le sh
0.521539	di co le ep
0.33591	di co le wi
0.577934	di co le *he
0.537012	di co le he *gf
0.536784	di co le he sh
0.517702	di co le he ep
0.308429	di co le he wi
0.537138	di co le he gf *sh
0.518702	di co le he gf ep
0.31246	di co le he gf wi
0.518772	di co le he gf sh *ep
0.312416	di co le he gf sh wi
0.336037	di co le he gf sh ep wi

Example 1

Our objective is to find the optimal taxonomy which maximizes congruence between vegetation structure and environmental structure in secondary sub- boreal vegetation near Elk Lake, Ontario (Orlóci and Pillar 1989). The plant characters are listed in Table 2. The environmental variables include elevation, exposure, slope, soil depth, and soil texture measured on 43 plots laid contiguously in a belt transect. Table 3 contains the step-by-step results and Fig. 2 displays the congruence profiles for optimal and suboptimal character orders. The highest ranking character is "stem direction" (di). This is the single most effective character in the set of 8 characters in accounting for structural congruence (0.534 on a scale from 0 to 1). "Stem consistency" (co) is the second (0.701), and leaf width is the last (0.336). The character order in the optimal taxonomy is {di co le he gf sh ep wi}.

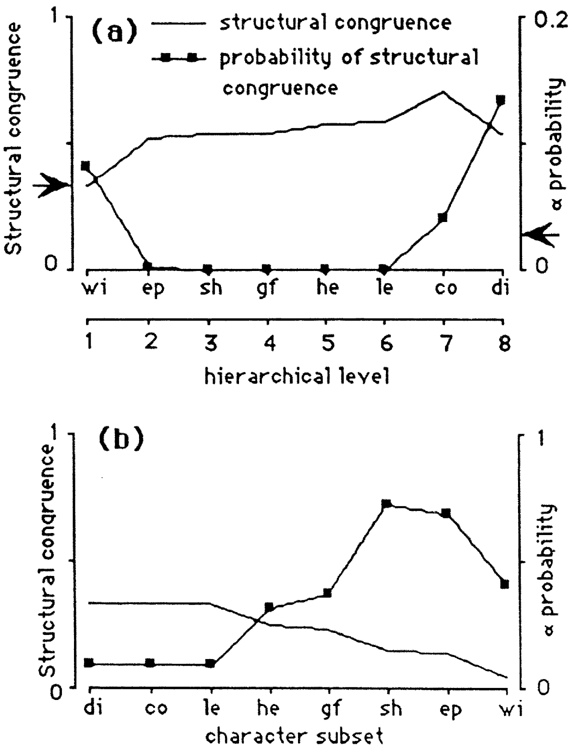

Figure 2. Profiles of structural congruence per character subset and corresponding α probabilities in the Elk Lake sample. The α value is the probability of obtaining a congruence level at least as large as the observed under the null hypothesis that CST presence in a community is a chance event. In graph (a) the characters are arranged in optimal order for congruence (Table 3). In graph (b), the character arrangement is suboptimal. Character labels are explained in the caption of Table 2. Arrows point to congruence level and probability level attained in a species-based analysis. Note that the optimal character order reveals higher congruence with generally much lower α values than do the suboptimal character order or the species-based analysis on any level.

Results corresponding to an optimal and a suboptimal character order are displayed in Fig. 2. It is noted that the degree of congruence achieved under a suboptimal character order is lower than under an optimal character order. Congruence in the species-based analysis (indicated by the arrows in Fig. 2) is also lower than under optimal character order. Each congruence under optimal character order. Each congruence value is associated with a probability value (α). The probability values, generated by Pillar's (1992) randomization algorithm under the null hypothesis that random dispersion and establishment defines the CST composition of the community in the site, are direct measures of the weakness of structural congruence in the community. Only values associated with low probabilities indicate significant congruence.

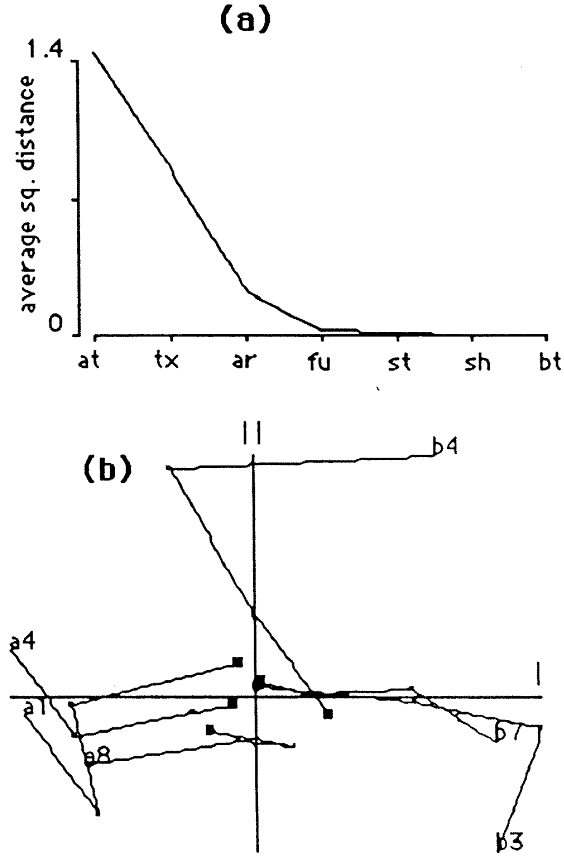

Figure 3. Comparison of the Caatinga and the Chaco based on the relevé groups in Table 4. Graph (a) displays the changing values of equation (4) over hierarchical levels identified by character labels. The distance measure of relevés is a nominal squared chord distance. Character order (horizontal axis) is optimal for structural convergence (Table 5). Graph (b) displays relevé trajectories in procrustes mappings. Relevés al, a4, a8 are from the Chaco, and b3, b4, b7 from the Caatinga. The points in (b) with a relevé label represent level 1 in the hierarchy where the trajectories begin.. The large squares indicate the end points of the trajectories (top level in the hierarchy). Note the appearance of increasing convergence (declining interpoint distances) between the Chaco and Caatinga relevés through hierarchical level.

Table 4. Caatinga (Brazil) and Chaco (Argentina) data sets. Three relevés are described in each set based on a total of 25 CSTs. Characters and character states: (bt) biological type - 6 cactoid, 7 other; (st) stem type - 1 succulent, 2 herbaceous, 3 woody, 4 no stem; (fu) stem function - 1 regular, 2 twin-purpose, 3 no stem; (at) armature type - 1 thorn/spine, 2 none, 3 no stem; (tx) leaf texture in a scale - 1 (herbaceous) to 5(leathery), 6 plant leafless; (sh) leaf shape - 2 linear, 3 other, 4 plant leafless; (ar) leaf arrangement - 1 simple, 2 compound, 3 plant leafless. Entries are character states under CSTs and cover-abundance values under Relevés.

CSTs							Relevés					
							Caatinga			Chaco		
bt	st	fu	at	tx	sh	ar	b3	b4	b7	a1	a4	a8
7	3	1	1	1	3	2	1	16	6	6	22	21
6	1	2	1	6	4	3	2	2	2	11	4	2
7	3	1	2	3	3	2	1	16	0	0	0	0
7	3	1	2	2	3	2	32	0	15	5	5	15
7	3	1	2	4	3	1	3	5	5	15	5	0
7	3	1	2	3	3	1	16	32	16	0	0	0
7	3	1	2	4	3	2	2	0	0	0	0	0
7	3	1	2	2	3	1	1	1	1	0	0	0
7	3	2	2	1	3	1	1	0	0	0	0	6
7	3	1	2	1	3	1	1	1	0	0	0	5
7	3	1	2	5	3	1	1	5	0	5	15	1
7	2	1	2	1	3	1	0	15	0	0	0	0
7	3	1	2	5	2	2	0	1	0	0	0	5
7	3	1	1	3	3	1	0	0	0	15	15	15
7	3	1	1	4	3	1	0	0	0	15	15	15
7	3	2	1	5	3	1	0	0	0	1	0	6
7	4	3	3	5	3	1	0	0	0	1	0	0
7	3	2	1	4	3	1	0	0	0	1	5	0
7	3	2	1	1	3	2	0	0	0	1	1	0
7	3	1	1	1	2	1	0	0	0	1	1	0
7	2	2	2	1	3	1	0	0	0	0	5	0
7	3	2	1	1	3	1	0	0	0	0	0	1
7	2	2	2	1	3	2	0	0	0	0	0	5
7	3	1	1	2	3	1	0	0	0	0	0	5
7	2	2	1	1	3	1	0	0	0	0	0	1

Table 5. Characters order for maximum structural convergence. The data set describes the Caatinga and Chaco vegetation (Table 4). Asterisks indicate character sets which minimize equation (4) on the hierarchical levels. Relevé dissimilarity, d_{ijk} in (4), is measured as a nominal squared chord distance. Optimal character order: bt sh st fu ar tx at.

σ_i	Character subset	σ_i	Character subset
0.005931	*bt	0.03513	bt sh st *fu
0.015619	st	0.880767	bt sh st at
0.033512	fu	0.83422	bt sh st tx
0.816232	at	0.206312	bt sh st ar
0.813563	tx		
0.007005	sh	0.882241	bt sh st fu at
0.174443	ar	0.821455	bt sh st fu tx
		0.225749	bt sh st fu *ar
0.015619	bt st		
0.029937	bt fu	1.08819	bt sh st fu ar at
0.805232	bt at	0.857027	bt sh st fu ar *tx
0.813563	bt tx		
0.007005	bt *sh	1.4439	bt sh st fu ar tx at
0.174443	bt ar		
0.017036	bt sh *st		
0.033767	bt sh fu		
0.828185	bt sh at		
0.8139	bt sh tx		
0.176464	bt sh ar		

Example 2

We seek the character order that maximizes convergence for two sample vegetation structures, one from the Caatinga (Brazil) and the other from the Chaco (Argentina). We use the data sets in Table 4, and present the results in Tables 5, 6, and Fig. 3. The latter

Table 6. Eigenvalues of the Caatinga and Chaco data set (Table 4, Fig. 3b) for ordination on different hierarchical levels. Ordinations use optimal character order for maximum convergence (Table 5, Fig. 3b).

	1	2	3	4	5
1	55.37	25.20	12.65	4.87	1.91
2	48.23	28.62	14.19	6.56	2.40
3	73.27	14.83	8.88	2.45	0.57
4	52.34	31.13	15.23	1.25	0.05
5	71.66	24.07	4.22	0.04	
6	89.49	10.50	0.01		
7	99.98	0.02			

displays a convergence profile which allows level-by-level (character-by-character) examination of the relationship of the two structures. Fig. 3 also displays the trajectories of the Caatinga and Chaco relevés (as moving spatial points) across the hierarchical levels as mapped in eigenordination. The eigenvalues are given in Table 6. The profiles and trajectories clearly show the strong effect of character order.

Example 3

We seek the character order in which characters placed lower in the list are more redundant than the characters placed higher. Redundancy is defined based on the contribution of the character to structural distance on two adjacent levels. Suppose that with the ith character included, the distance of two relevés (j,k) is d_{ijk} and with character i excluded $d_{(i-1)jk}$. Distances are defined according to equations (6) or (7). The character considered most redundant on level i is the one whose removal from the set minimizes the difference $|d_{ijk} - d_{(i-1)jk}|$. To test the algorithm the original data set (Table 1), we made the last two characters identical which makes one of them totally redundant (Table 7). The results are presented in Table 8.

CST types: crisp or fuzzy

Our earlier work on character set analysis (Pillar and Orlóci 1991) suggests that fuzzy CSTs can reduce the analytical indeterminacy in the sample owing to absences, and can sharpen the appearance of structural connections between vegetation and environment. Our new results (Figs. 4, 5, 6 and in Table 9) suggest further that fuzzy CST analysis is also less affected by varying the character order than a crisp CST analysis:

1. Under optimal character arrangement in fuzzy CST analysis, depicted in Fig. 4a, high structural convergence (low average nearest neigbour distance) detected on the higher levels is also detectable on the lower levels. This is not so in a crisp CST analysis in which the effect of high structural convergence on the higher levels, as seen in Fig. 4a, dissipates on the lower levels.

Table 7. Character score matrix of two relevés taken from the Caatinga and Chaco sample (Table 1). Character "stem tissue" (#1) is repeated as #5.

CSTs #	Characters 1 2 3 4 5	Caatinga	Chaco
a	w r n d w	60	2
b	w r t d w	16	34
c	w r n p w	1	37
d	s t t l s	2	30
e	w t t d w	0	2
f	w t n d w	0	1

2. The trends observed in relevé trajectories is influenced by the optimality criterion adopted in character ordering. This given, divergence is revealed with clarity in the fuzzy CST analysis (Fig. 5, see eigenvalues in Table 9).

4. Similar considerations apply when the analysis is aimed at maximum congruence with an environmental structure (Fig. 6). A crisp CST analysis with optimal character order for maximum congruence reveals stronger structural congruence (the vertical 0 to 1 scale in Fig. 6a) on the higher hierarchical levels than on the lower ones. A fuzzy CST analysis reveals relatively higher structural congruence also on the lower levels. When the character order is suboptimal (Fig. 6b), the congruence revealed by crisp CST analysis is generally low, while in fuzzy CST analysis congruence is generally at the same level as that under optimal character order.

Synopsis

Any character set can define a taxonomy, but the character arrangement, whether sequentially or hierarchically nested, matters. Logic dictates that the states of each character should cover the entire plant multitude. If they do, the sequential arrangement of m characters creates m parallel taxonomies with overlaps. Under the nested hierarchical character arrangement the number of taxonomies is also m, one on each hierarchical level, but the taxonomy of a lower hierarchical level is always an expansion of the taxonomy on the next higher level. Therefore, in the hierarchical arrangement, the order in which the characters are presented matters.

We do not believe that criteria of universal applicability exists to order characters, but we consider it appropriate to define a character order according to optimality criteria established by specific objectives. These may have to do with congruence, convergence, or redundancy of vegetation structure vis-a-vis environmental structure, or one vegetation structure vis-a-vis another vegetation structure. We propound a pragmatic solution to finding an optimal character order in

Table 8. Character ordering in the Chaco and Caatinga relevé groups (Table 7) based on redundancy. The algorithm is divisive. Asterisks indicate the character subset, carried to the next higher level, after the most redundant character is removed. Since there are only two relevés, the distance measure is (7). Using subsets of 4 characters, lowest rank is assigned to character 5. Using subsets of 3 characters, the next lowest rank is assigned to character 1. Character 2 and 3 are the third and second highest ranking characters. Character 4 is assigned the highest rank. Note that in ambiguous cases, such as on level 1 with characters 5 and 1 completely redundant, the algorithm arbitrarily removes character 5, the first of two equally most redundant characters encountered in the list.

Level	Squared chord distances	$\rho(D_i;D_{i-1})$		Charact. subset	Charact. out	Character rank
1	1.5820		*	1 2 3 4 5		
2	1.5820	1.0000	*	1 2 3 4	5	5
2	0.4201	0.2656		1 2 3 5	4	
2	0.7535	0.4763		1 2 4 5	3	
2	1.5407	0.9739		1 3 4 5	2	
2	1.5820	1.0000		2 3 4 5	1	
3	0.4201	0.2656		1 2 3	4	
3	0.7535	0.4763		1 2 4	3	
3	1.5407	0.9739		1 3 4	2	
3	1.5820	1.0000	*	2 3 4	1	1 5
4	0.4439	0.2806		2 3	4	
4	0.7535	0.4763		2 4	3	
4	1.5407	0.9739	*	3 4	2	2 1 5
5	0.5217	0.3386		3	4	
5	0.6921	0.4492	*	4	3	4 3 2 1 5

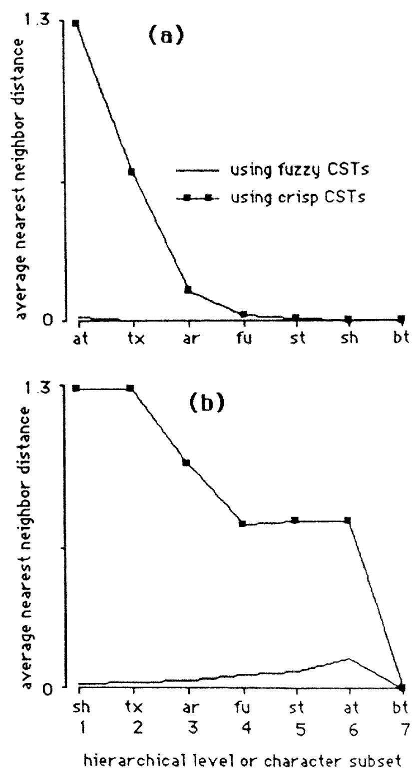

Figure 4. Profiles of average nearest neighbor distance between the Chaco and Caatinga relevés groups (Table 4). The character order is optimal for maximum convergence (Table 5) in (a) and suboptimal in (b). The order in (a) and (b) differ by the position of characters sh and at. Note that fuzzy CST analysis reveals higher convergence (smaller distances) on the lower levels than the crisp CST analysis does.

that we entreat character orders and select the one that best satisfies the relevant criterion. Beyond this, we seek improvements by way of fuzzy taxa. In these, each plant unit has degrees of belonging to all the taxa.

The type of structure sought is an *a priori* decision and character selection to describe these structures is a necessity. But characters are selected on the basis of suitability to describe a structure and the analysis may

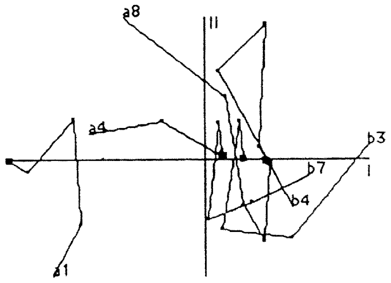

Figure 5. Ordination trajectories of the Caatinga and Chaco relevés (Table 4) in fuzzy CST analysis. The analysis is an extension of the comparisons displayed in Fig. 4. Trajectories are given for relevés a1, a4, a8 (Chaco) and b3, b4, b7, (Caatinga). Each trajectory begins with a relevé label and spans 7 hierarchical levels starting with the 1st. The character order maximizes convergence (Table 5, Fig. 4a). The dissimilarity function of relevés is a nominal squared chord distance and the ordination method is eigenanalysis. Ordination axes I and II are described in Table 9. Note the trend of increasing convergence with increasing hierarchical level, and compare this to the relatively small distances of fuzzy CST analysis in Fig. 4. Also compare the trends to those in Fig. 3b of the crisp CST analysis.

appear "loaded". Addressing this point, Sneath and Sokal (1973:95) observe:

> "when we use only a set of characters known to show resemblance between certain groups, the similarity coefficients that will result from this study will reflect that choice".

Further, paraphrasing Dale (1968), there is circularity in an analysis where character analysis supports the character choice which then are analyzed to reveal information about the characters. These may be true, yet the desire for parsimony, and also other common sense considerations will tolerate no random selection of characters for analysis.

Table 9. Eigenvalues in ordinations corresponding to hierarchical levels in the Caatinga and Chaco data (Table 4). The scattergram for the 1st and 2nd components is shown in Fig. 5. The analysis uses optimal character order for maximum convergence.

Level	Ordination axis				
	1	2	3	4	5
1	88.93	7.46	3.35	0.19	0.05
2	77.19	13.67	8.52	0.41	0.20
3	74.51	15.93	8.87	0.64	0.05
4	69.83	17.97	12.02	0.18	
5	78.24	20.31	1.44	0.01	
6	95.26	4.73	0.01		
7	99.98	0.02			

We prefer to pose the problem of choice differently. We specify functions and constraints under which we seek structures. We do not specify the structures themselves. This is a practice in no ways different from choosing the covariance as the measuring function in a MANOVA, or the generalized distance in discriminant analysis. Selection of a measuring function is the same as selecting scale and the reference framework through which we try to detect structures and relationships in the sample. As for selecting characters, what we do is no different from deciding what we have to measure within a range of natural possibilities. This is not different in essence from selecting variables for statistical analysis.

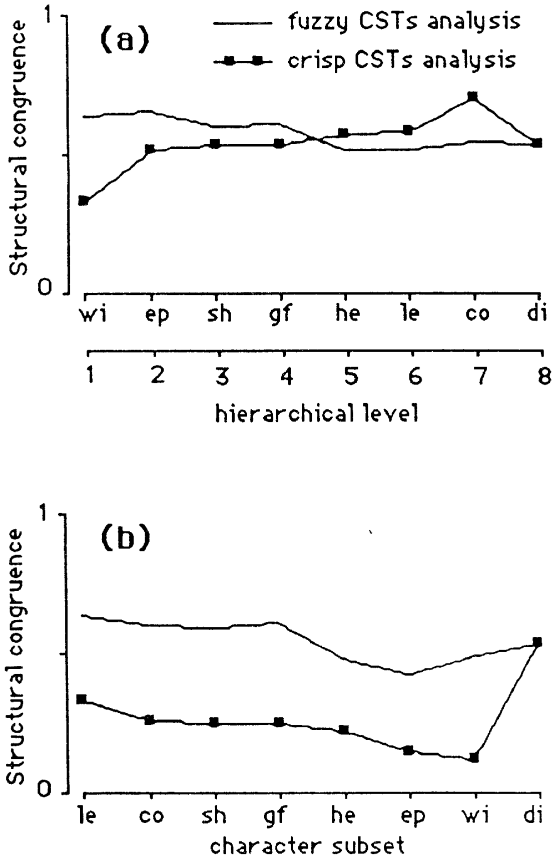

Figure 6. Congruence levels of vegetation and environmental structures in a sub-boreal environment as revealed by fuzzy and crisp CST analysis. Character order in (a) is optimal (Table 3). It is suboptimal in (b). Note in (b) the relatively strong congruence revealed by the fuzzy CST analysis, despite the fact that characters with low rank (ep and wi) are placed on high levels (6 and 7).

We know of examples which use random subsets of characters, but to our knowledge no one has yet suggested to chose a character set, the measuring function, or method of analysis at random. Nothing else left to fall back on, we have to come to terms with the inevitable: reasoned choices cannot be replaced by random ones and that the choices affect the outcome.

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ERRATA

COENOSES 8(1):53-66, 1993
V. De Patta Pillar & L. Orlóci

p. 55 1st col. Line 45; 'Codgers' should read 'Congress'.

p. 56 1st col. Line 12; ...'The relevés which materialize' should read 'The CSTs which materialize'.
Line 14; 'unmaterialized relevés' should read 'unmaterialized CSTs'.
Equation (1); '$s_i\ k_i$' should read '$s_i\ k_{i+1}$'.
Line 27; 'Take k_m+1' should read 'Take k_{m+1}'.

p. 56 2nd col. Legend Table 1; 'four characters and 10 relevés' should read 'four characters and 10 CSTs'.
Equation (2); '$X_{(i-1)}e\gamma$' should read '$X_{(i-1)e\gamma}$'.
Line 17; 'optimize same' should read 'optimize some'.

p. 57 1st col. Equation (3); '$\rho(\mathbf{D}_i;\Delta) = \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}\delta_{jk}$' should read

$$'\rho(\mathbf{D}_i;\Delta) = \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}\delta_{jk} \left(\sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}^2 \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} \delta_{jk}^2 \right)^{-\frac{1}{2}}\ ',$$

p. 58 1st col. Equation (6); '$\rho(\mathbf{D}_i;\mathbf{D}_{i-1}) = \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}d_{i-1jk}$' should read

$$'\rho(\mathbf{D}_i;\mathbf{D}_{i-1}) = \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}d_{i-1jk} \left(\sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{ijk}^2 \sum_{j=1}^{v-1} \sum_{k=j+1}^{v} d_{i-1jk}^2 \right)^{-\frac{1}{2}}\ ',$$

p. 59 1st col. Legend Table 3; '$2(1 + r_{ijk})$' should read '$2(1 - r_{ijk})$'.

p. 59 2nd col. Caption Figure 2; 'explained in the caption of Table 2' should read 'explained in Table 2'.

p. 60 1st col. Line 7-8; delete 'Each congruence under optimal character order.'

p. 61 1st col. Line 21; 'we made the last two characters identical' should read 'we made the first and the last characters identical'.

COENOSES 8(3):140, 1993

Errata to Coenoses 8(1):53-66, 1993.

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The Editors regret the inadvertent misplacement of the authors marked galley proofs and request for corrections.