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Notes on compositional diversity

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Abstract

This paper tries to show some ways and means of simple (binary) modelling, whereby diversity can be interconnected with other attributes of a community. A new type of scaling (called characteristic scaling) is introduced for further use.

Introduction; motivation

I remember quite well of the excitement, when I first read the interesting paper of Joe Connell (1978). *Ecce, voilà*, I felt; Intermediate Disturbance Hypothesis (IDH) maybe a good guide-line for a better orientation; or, it may serve as a satisfactory '*corpus theoreticum*' around which many observations, facts, evaluations, interpretations might be arranged more properly than beforehand.

But, alas, just afterwards, the Cartesian '*omnia dubitanda*' had started to work; the clouds of a sober scientific skepticism have accumulated further during the past decade. What does the shrewd adjective 'intermediate' really mean? How can one make an operative distinction between 'intermediate disturbances' and, say, 'large-scale perturbations' (Matson & Carpenter, 1990)? Using the titleforming question of Carpenter (1989), 'do we know what we are talking about?' Is it due only to the rather idiotic fluctuations of pseudo-scientific fashions and counter-fashions that Connell (1978) is even not mentioned in any paper edited by Matson and Carpenter?

One can develop even more pessimistic views, if one starts reading the huge body of literature on 'non-linear dynamics', including recent books on systems theory (e.g. Vincent *et al.*, 1990), or on the delightful (and frightening) topic of chaos (e.g. Cvitanovič, 1979; Steward, 1979). One of the most pertinent questions is: what is the true difference between disturbance and perturbation? If both processes contain 'harmful' and 'beneficiary' components as well, how can one make a successful distinction between these types of responses?

Cutting the story of a long and tedious speculation short, the author is motivated to write this paper by the following main aspects of our actual ignorance:

(a) Theoretical weakness

IDH is still too weak for a proof or a disproof. (Using a Popperian phrase, IDH, in its present form, is not suitable either for a verification or for a falsification. Unfortunately enough, the same is true for some modification of IDH; the author has tried several versions and failed).

(b) Methodological weakness

(a) is partly due to a number of methodological defects. IDH, for instance, is a 'diversity-centered' hypothesis. But diversity, however it is measured, is usually a single property or attribute of a particular community. There is a growing need to develop such simple models, where diversity can be interconnected properly with other attributes as well.

(c) Conceptual weakness

One of the obstacles of such a modelling is that our language is still too weak in both ways. One way is mathematical where, for instance, entropy-information relations are frequently obscured with each other; the other way is biological where, even the primitive scheme, flora→vegetation, has no proper equivalent in zoology, hydrobiology.

One feels that the appropriate order is (c)→(a); that is, theoretical weakness cannot be compensated in the future otherwise than by some primary reconsideration of our methods and concepts.

Notes on composition; an iteration

Composition, even in the simplest etymological sense of the word (*con-positio* – 'collective position'), refers always to some 'mutual positional relations' of some sets of components. Even this simplistic pseudo-definition is contrary to the pragmatic use of the term is ecology, where 'composition' refers usually to some sets or weighted sets (like frequency distributions). But, we must realize, that any composition (let it be either a piece of art or a master-piece of Nature) is much more than silly '%-spectra' or similar representations. Clearly, some kind of iteration is needed.

At a start, we can think of the well-known scheme,

$$\text{flora} \xrightarrow{\qquad} \text{vegetation} \tag{1}$$

or, in a much more general context, of (2),

$$\begin{array}{c}\text{Basic sets}\\ \text{(alphabets)}\end{array} \xrightarrow{\qquad} \begin{array}{c}\text{Compositional}\\ \text{structures}\end{array} \tag{2}$$

where (2) may refer to a hydrobiological situation of some kind, and where 'large arrows' try to indicate some 'epistemiological way' of our understanding.

In order to make 'large arrows' more specific, we may decompose (1)–(2) into several and more articulate states or steps. One way of such a decomposition is shown by Fig. 1, where certain object and operations are arranged in a proper order.

A point set (like: flora, fauna, biota) is just a list of the components involved, without any further specification. A simplex includes abundance estimates (usually as discrete frequency distributions, called 'species-abundance' relations) but does not include representation of 'interactions' among components. The last requirement is the job of a Venn-complex (used frequently in Set Theory texts). Some properties of V-complexes are used in the construction of an S-complex where a sorted complex may be either a topological tree, a dendrite, or, it may be some ordination diagram. If an S-complex is somehow allocated into the topographical ('real') space, then an A-complex, an allocated complex is gained (where classification can be regarded as a special, 'fortunate' case).

The simplest possible primary representations of some composition are binary tables (like the primitive ones in Fig. 2.). It is to be noted at once that if we use only the marginals of such tables, then some simplex is represented, only; in order to have a better insight, the 'inner configuration' of such a table is to be taken into account. In other words, there exists a contrast between 'simplex' and 'complex' representations of diversity with many further implications.

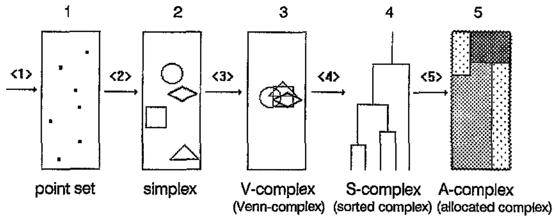

Fig. 1. Certain objects and operations in a proper order for a better specification of (1) and (2).

X_1

	sampling	units							
populations	1	2	3	4	5	6	7	8	Σ
a	0	1	0	0	1	1	0	1	4
b	0	0	1	0	1	0	1	1	4
c	0	0	0	1	0	1	1	1	4
Σ	0	1	1	1	2	2	2	3	12

X_2

	sampling	units							
populations	1	2	3	4	5	6	7	8	Σ
a	1	1	1	1	0	0	0	0	4
b	0	0	0	0	1	1	1	1	4
c	0	0	0	0	1	1	1	1	4
Σ	1	1	1	1	2	2	2	2	12

Fig. 2. Two binary tables of the $s \times m$ type, where s is number of populations and m is number of sampling units.

If one tries to follow carefully the most relevant publications in this field of study (to mention but a few: e.g. Margalef, 1958; MacArthur, 1965; Woodwell & Smith, 1969; Peet, 1974; Pielou, 1975; Grassle *et al.*, 1979; Mayr, 1984; Washington, 1984; Wilson, 1988; Magurran, 1988), then the critical reader can trace easily the funny oscillations – appearance and disappearance – of good ideals in a strange sequence. For instance, since the early guesses of Margalef and the activity of the MacArthur's group, it is quite clear (say, a scientific common-place) that without 'patterning' almost all diversity data are meaningless. But, surprisingly enough, this simple truth does not appear in the recent book edited by E. O. Wilson; as far as I can see, very few scientists are aware of it, even in the programme of IUBS, called 'Biodiversity Crisis'. One may ask: why is it so? Clearly, again, some reconsideration is needed.

Notes on diversity; another iteration

Such a reconsideration can be made concise enough by introducing a few conceptual and methodological oppositions.

§1. Scalars versus vectors

For too many people diversity means still 'number of species' (or other taxa); the 'only' tangible danger is being extinction. But, using the *ex verbis* terms of my late professor, Alfréd Rényi, 'number of components' (alias: 'richness') refers always to zero-ordered diversity, and extinction of one or more elements must considered to be a tragic end-result ('finality') of a more or less long stochastic process. If we want to study the process itself, then, to say the least, we need always vectorial representations, instead of scalars.

§2. Static versus dynamic representations

If the need for a dynamic approach is accepted, then a number of very difficult problems should be faced. As it is most commonly understood, the adjective 'dynamic' is used most frequently for temporal processes, as in the vast majority of differential or difference equations in theoretical physics and theoretical biology. In such representations, the space is still 'static' (by considering space as 'homogeneous', spatial heterogeneity as 'negligible' etc.). Contrary to this common and deceivingly convenient view, the most important biological processes (like evolution, succession etc.) are clearly spatio-temporal processes, where both space and time should be taken into account, even if the methodology involved is frequently troublesome. If we want to study diversity changes (say, during the process of a degradative succession), then we must find ways and means of comparing spatio-temporal coordinates (with special reference to the very neglected spatial processes).

§3. Single vectors versus classes of vectors

By reiterating argument § 1, it is fairly important to consider at least the contours of a 'singularistic' versus 'pluralistic' dilemma. Figure 2 shows how deceiving it can be to say that X_1 and X_2, two binary tables (where '1' and '0' mean presence and absence, resp.) are practically the same, because their raw marginals as vectors are identical and column marginals have only a small degree of difference. (De facto, using weighted Shannon's estimates, single raw marginals have 19.02

bits in both cases; single column marginals of X_1 and X_2 can be characterized by 32.27 and 35.02 bits, resp.) In order to have a better insight, it is relevant to see the difference between 'inner configurations' (composed of raw and column vectors, resp.); in some way, X_1 can be regarded as a 'random' composition, whereas X_2 as a 'regular' composition. In a more explicit way, let us consider first set Q, $Q = \{a,b,c\}$; secondly, Q', the power set of Q (set of all possible subsets), $Q' = \{0,a,b,c,ab,ac,bc,abc\}$; thirdly, the fact that X_1 uses all elements of Q' once, but X_2 uses only two elements of Q' (a,bc) four times. In consequence, $m\hat{H}_1 = 24$ and $m\hat{H}_2 = 8$ bits, where both quantities are weighted Shannon's entropy estimates for X_1 and X_2, resp.; and where $m = 8$ (number of sampling units). In a more detailed way,

$$m\hat{H}_1 = 8 \log_2 8 - 8\,(1 \log_2 1) = 24,$$

$$m\hat{H}_2 = 8 \log_2 8 - 2\,(4 \log_2 4) = 8.$$

§4. Diversity versus dependence

Even this over-simplistic case and the main properties of this type, say, 'combinatorial type' of diversity – which may be called biotic diversity – shows properly that diversity in most cases should not be used *per se* but it is to be interconnected (coupled) with other types of phenomena *viz.* processes. Let us consider now the simple (pairwise) comparison of raw vectors in Fig. 2 (say, as an interlocal comparison), using the well-known 2 × 2 contingency tables as they are shown by Fig. 3. It is easy to see that all contingency tables for all pairs of X_1 represent the clear-cut case of stochastic independence, whereas all tables for X_2 represent maximum degree of dependence (i.e. 'non-independence'). In a more explicit way, and concentrating on the (A,B)-pair, the values of joint entropy functions are:

$$m\hat{H}_1([A,B]) = 16 \text{ bits}; \; m\hat{H}_2([A,B]) = \\ = 8 \text{ bits};$$

the values of simple (marginal) entropy functions are clearly identical:

X_1

	1	0	Σ
1	2	2	4
0	2	2	4
Σ	4	4	8

X_2

	1	0	Σ
1	0	4	4
0	4	1	4
Σ	4	4	8

or

	1	0	Σ
1	4	0	4
0	0	4	4
Σ	4	4	8

Fig. 3. 2 × 2 contingency tables for X_1; and X_2 of Fig. 2.

$$\begin{aligned} m\hat{H}_1(A) &= m\hat{H}_1(B) \\ &= m\hat{H}_2(A) \\ &= m\hat{H}_2(B) \\ &= 8 \text{ bits}; \end{aligned}$$

in consequence, the values of contingency information (say, association) functions are:

$$\begin{aligned} m\hat{I}_1(A,B) &= m\hat{H}_1(A) + m\hat{H}_1(B) - \\ &\quad - m\hat{H}_1([A,B]) \\ &= 8 + 8 - 16 \\ &= 0; \end{aligned}$$

$$\begin{aligned} m\hat{I}_2(A,B) &= m\hat{H}_2(A) + m\hat{H}_2(B) - \\ &\quad - m\hat{H}_2([A,B]) \\ &= 8 + 8 - 8 \\ &= 8 \text{ bits}. \end{aligned}$$

This relevant difference can be described by the usual notation of set theory as well [i.e. $m\hat{H}_1(A) \cap m\hat{H}_1(B) = \emptyset$; $m\hat{H}_2 \cap (A) \cap m\hat{H}_2(B) = m\hat{I}_2(A,B)$]; or, it can be depicted my means of the usual Venn-diagrams (see Fig. 4). In addition, Fig. 4 shows a third case, X_3, where the intersection of $m\hat{H}_3(A)$ and $m\hat{H}_3(B)$ is neither empty, nor 'full' than beforehand. Note that in all Venn-diagrams of this type diversity appears always as some 'envelope' and dependence does as some non-empty intersection.

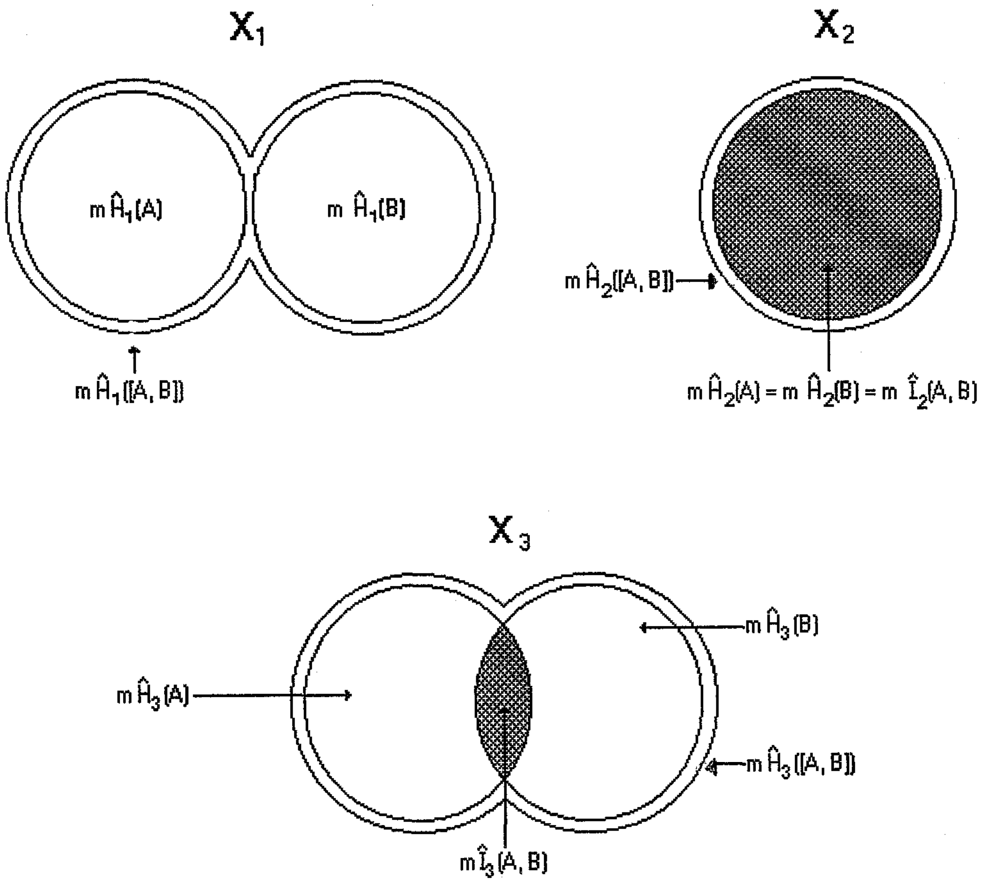

Fig. 4. Venn-diagrams for a pair of populations (a, b).

§5. Entropy versus information

The last statement remains true even if we do not consider elementary (pairwise) comparison. In the case of our primitive example, it is straightforward to introduce triple comparisons, for all elements of Q (by means of 2 × 2 × 2 tables). Such a comparison is depicted in Fig. 5, quite analogous to Fig. 4. It is easy now to identify the quantities at the end of §3; namely, $m\hat{H}_1 = m\hat{H}_1$ ([A,B,C]) = 24, $m\hat{H}_2 = m\hat{H}_1$ ([A,B,C]) = 8 bits, where the actual valuation is due to the fact that for X_1 all the possible intersections are empty (and, therefore, the value of joint-triple entropy is of *maximum*), while for X_2, since all intersections are being 'full' (with maximum values), therefore, the value of joint entropy is of a *minimum*. Even this primitive contrast shows why it can be very dangerous to interpret entropy-information relations in a vulgar way ('the less the uncertainly, the greater our information'). Instead, it is much better to think always in terms of *posse-esse* relations, as even Duns Scotus guessed it rightly, in the dawning period of our age (see e.g. de Muralt, 1991). In a more explicit way, we may introduce here the function mI_j (A,B,C), or, in brief, $m\hat{I}_j(\lambda)$,

$$m\hat{I}_j(\lambda) = sm\hat{H}_j(\mathrm{L}) - m\hat{H}_j \qquad (3)$$

where $sm\hat{H}_j(\mathrm{L})$, local diversity, is entropy estimate for all raw marginal values, where $m\hat{H}_j$ is again biotic diversity, and $m\hat{I}_j(\lambda)$, called associatum, is contingency information for all elements of a set Q. Since in the tables of Fig. 2. raw marginals are identical, $sm\hat{H}_1(\mathrm{L}) = sm\hat{H}_2(\mathrm{L}) = 24$ bits, therefore, $m\hat{I}_1(\mathrm{A,B,C}) = 0$, and $m\hat{I}_2(\mathrm{A,B,C}) = 16$ bits (as a special kind of *maximum* value). Again,

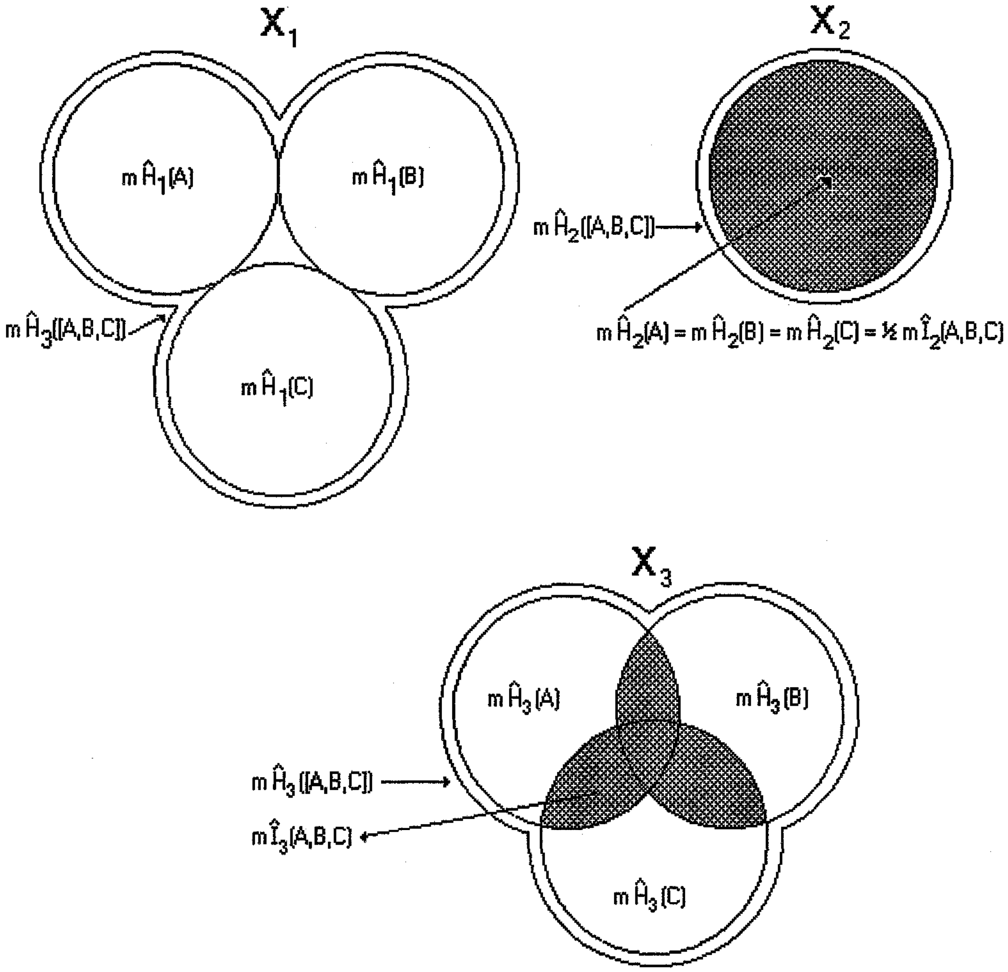

Fig. 5. Venn-diagrams for a triplet of populations (a, b, c).

if some intermediate third case, X_3, is introduced, then it is expected to have 'intermediate values' between the *extrema* indicated above. This shows clearly why it is so important to know always the proper *extrema*; how to manipulate with relevant relations (e.g. $\leq$, $\geq$); how to use the so-called 'sigma-conditions', proposed by the best authors in the field of information theory (e.g. Khinchin, 1957; Kullback, 1959; Rényi, 1962 etc.). Note that 'Σ-conditions' means roughly 'perfect' additivity and subadditivity relations within an envelope. Note also that these conditions and the introduction of proper inequalities make superfluous in most cases the majority of 'diversity versus evenness' arguments in ecology.

§6. Diversity versus complexity

We may call the configurations of Fig. 4 elementary Venn-complexes (where the adjective 'elementary' refers here to a pairwise comparison of some kind). If we have s kinds of populations (the cardinality of a set Q), and if $s>2$, then we may get some non-elementary Venn-complex (see Fig. 6). Although it is much beyond the scope of this short paper to show the proper methodology (e.g. how to manipulate with $2\times 2\times \ldots.^{s}\times 2$ tables), we may guess at least some simple properties of such a complex. First, it has like beforehand, an overall diversity envelop, represented by some joint entropy functions. (*Nota bene*: since such a complex has or may have several 'inner subenvelopes' of different orders as well, there-

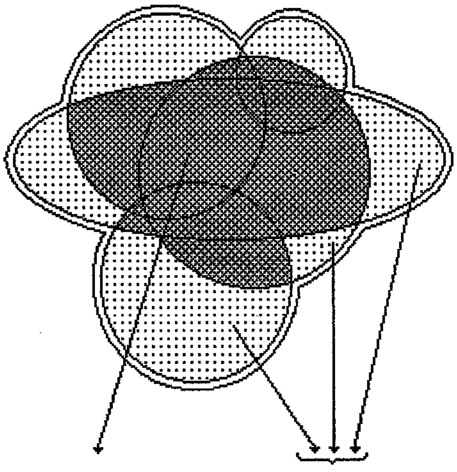

Fig. 6. A general Venn-diagram, where biotic diversity (as an envelope) can be subdivided into associatum and dissociatum.

fore, a relevant but still missing concept, subdiversity, should be taken into account.) Secondly, such a complex can be subdivided roughly into an 'overall intersectional region' and an 'overall outer region'; the former can be represented as a multivariate association (called associatum), the latter as a multivariate dissociation (called dissociatum), referring to the 'common' and 'uncommon' (particular) behavior of the populations, respectively. (*Nota bene*: due to the subdiversity relations of such a complex, a number of subassociata or subdissociata relations can be distinguished, representing coalitional relations of groups of populations.) Thirdly, the ordering relations mentioned above make possible to study at least some main features of complexity of our objects (including such seemingly innocent questions: how to relate 2 × 2 or 2 × 2 × 2 etc. structures to $2 \times 2 \times ...^{s} \times 2$ structures.) Fourthly, it is very relevant to study a nonelementary Venn-complex 'in motion', when a number of its properties (like the sized of intersections) may change in a spatio-temporal referential system.

Without listing further possible oppositions, some tentative conclusions derived from § 1 § 6 can suggest

- that there are many types of diversity (i.e. diversity includes a highly 'diverse body' of phenomena);
- that a particularly relevant and fairly inclusive type of diversity may be termed compositional diversity (and biotic diversity is one example of such a category);
- that compositional diversity makes good sense only if it is related to other attributes (like dependence) of our object.

Surprisingly enough, the simplest binary representations can generate more consistent and much richer families of models than the nonbinary (miscalled 'numerical') representations (of e.g. Juhász-Nagy,1976, 1984; Juhász Nagy & Podani, 1983).

Fragments of a case-study; some illustration

Some reasoning of the previous section can be illustrated, at least *pro parte*, by some results of an old case-study (cf. Dévai *et al.*, 1971; Juhász-Nagy *et al.*, 1973).

The basic data have been obtained from a survey of Cladocera fauna during ten days (summer, 1968), by counting 66 565 individuals collected from a shallow fish-pond at Bánhalma (in the Great Hungarian Plain, near the village Kenderes). The number of taxa has been ten ($s = 10$); e.g. *Bosmina longirostris* (O. F. Müller) (with four well-distinguished varieties), *Daphnia longispina* (O. F. Müller), *Chydorus sphaericus* (O. F. Müller), *Ceriodaphnia pulchella* G. O. Sars, etc.

The 3-dimensional shape of a sampling unit was approximately a cube. The sizes of sampling units (V_1, V_2, ...V_j...) were selected according to the increasing power of 2, from 1 to 8, that is, we took *ca.* 2, 4, 8, 16, 32, 64, 128, and 256 ml. water for the different sampling volumes. The number of sampling units was 64 ($m = 64$) for all sizes. The lay-out of sampling points was of the random type. The instructions were constructed by obtaining a table of pairs of random numbers, where the first column represented random numbers for a compass (0–360), the second one the number of oar-strokes to be made in a given direction. In such a way the sampling procedure was somewhat similar to a 'Brownian motion' in the surface of the lake; i.e. all points of the surface have been selected more or less equiprobably.

Omitting many details, it may be of some interest to see the values of the three functions (Table 1), labelled by § 3 in the previous chapter,

- where $\hat{H}$(L), local diversity, entropy estimates of raw marginals of 10 × 64 ($s \times m$) tables;
- where $m\hat{H}_j$ is biotic diversity;
- where $m\hat{I}_j(\lambda)$, associatum, overall association for 10 populations as a gain of information (divergence) measure, gained by the difference of the entropy estimates.

Note that all quantities are given here in *nits* ('*n*atural un*its*'); i.e. *log. nat.* was used.

The 'trends' of the three sequences of data are clear enough. First, it is to be noted that in V_8, where all components are present (and the table is completely full of '1'-*s*), all functions have zero value. This size (or, better to say, some size between V_7 and V_8) may be called min-volume (closely related to the concept 'minimal area', used from the beginning of this century in terrestrial plant coenology). Secondly, note that such a minimum cannot be expected at the 'starting points' of a V-scale; instead, even small sizes have considerable values. Thirdly, it is to noted that all sequences have some relative maxima ('peaks') in V_3 and V_5; these sizes may be termed max-volumes (realizing that min-max-volumes should have a mutual reference to each other; guessing that these maxima may be the optimal sizes for a number of analysis, like cluster analysis of some kind). The author, having an experience in land communities, has never get such a coincidence of maxima; usually, the maximum of associatum is due to a smaller point – or interval – of scale than the maximum of biotic diversity.

Table 1. Associatum values gained as differences between values of local and biotic diversity.

	$m\hat{I}_j(\lambda)$	=	$sm\hat{H}_j$ (L)	–	$m\hat{H}_j$
j = 1	20.30		158.26		137.96
2	25.52		198.54		173.02
3	50.35		252.58		202.23
4	30.23		207.63		177.40
5	47.62		241.69		194.07
6	22.53		179.02		156.49
7	16.50		162.44		145.94
8	0.00		0.00		0.00

In order to have a still better insight of such sets of data, it is interesting to consider the '*posse-esse*' relations as they are shown by Table 2. Note that the vast majority of the $\binom{10}{k}$ possibilities (1,10,45,120,210,252,...) are never 'realized'; in other words, Nature never uses all the possible combinations of elements in any given situation. (This trivial statement corresponds well with the experience of field biologists.)

Some outlook; vistas and perspectives

In order to have some outlook of our urgent agenda, a possible way is to see first some simple generalizations of the previous results, and then to speculate a bit on the perspectives of our research area.

First of all, leaving alone now some more advanced ways of inference (see Cliff & Ord, 1981; Ripley, 1981, 1988; Podani, 1984), some simple means of a spatial processing is to be considered. Such a processing is realized many times by *T*, a topographical vector whose points represent the geometrical sizes of sampling units in an ascending order. For the sake of a reliable evaluation, it is always supposed that $s < \mathrm{m}$, $m \rightarrow \infty$, and the lay-out is random. If we put *T* versus *F* (where *F* is a function, or a family of function of chapter 3), then we get some graphicons (vulgo: 'curves'), like in Fig. 7. Although, for the sake of simplicity, Fig. 7. shows two graphicons only, we may have here quite a number of graphic representations) e.g. according to the reasoning of § 6 in chapter 3).

Secondly, let us introduce now the simple convention of elementary scaling, where only max-min-values of such graphicons are used. As it is shown by Fig. 7, this convention generates in the axis *T* (or, in a more advanced case, in both axes) some sets of characteristic points, intervals, orderings of topographic nature which sets can

Table 2. Relations between possible and realized events. Possible events are given here by the 10th row of the Pascal-triangle.

Number of possible events	$\binom{10}{0}$	$\binom{10}{1}$	$\binom{10}{2}$	$\binom{10}{3}$	$\binom{10}{4}$	$\binom{10}{5}$	$\binom{10}{6}$	$\binom{10}{7}$	$\binom{10}{8}$	$\binom{10}{9}$	$\binom{10}{10}$
Sampling volume	Number of realized events										
V_1	1	6	8	0	0	0	0	0	0	0	0
V_2	1	6	10	7	4	0	0	0	0	0	0
V_3	0	2	7	9	8	3	1	0	0	0	0
V_4	0	0	1	4	7	5	4	2	0	0	0
V_5	0	1	1	2	5	7	7	6	1	0	0
V_6	0	0	0	0	1	4	4	4	3	3	1
V_7	0	0	0	0	0	0	1	3	5	4	1
V_8	0	0	0	0	0	0	0	0	0	0	1

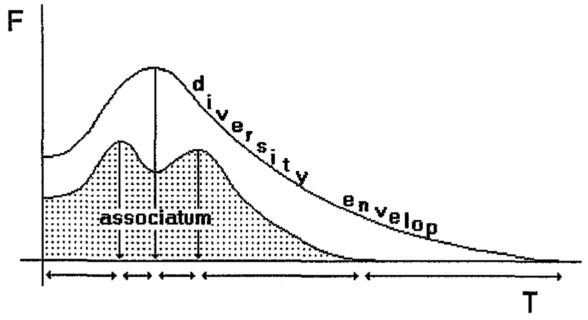

Fig. 7. Characteristic scaling in a plane of T *versus* F, where T is a topographical vector, F is a characteristic function. Only min-max values are used for scaling.

be regarded as relevant scaling attributes of a particular objective. (Needless to say, the more functions we have, the property of 'being characteristic' is more reliable.) In a somewhat metaphorical sense of the word, we can say that this type of characteristic scaling shows the ways how a community of some sort can 'sense for itself' different degrees of spatial heterogeneity. Note that in such a way, by means of some T-screening, can one detect scaling relations between maximal and minimal volumes, mentioned before.

Note also that some proper use of dynamical Venn-complexes makes possible to introduce diacretic modelling, where the dynamical behavior of particular populations or coalitions can be studied with relation to other (preferably: all) partner populations of a study.

Thirdly, a very relevant question is how characteristic scaling changes in time; how can one interconnect spatial attributes with results of temporal periodicity (see Reynolds, 1984). Such an interconnection would be imperative for a better understanding of 'mechanisms of succession' (see Reynolds, 1988); including such difficult problems as the activities of strategies and forced cycles (see Tilman, 1988; Sommer, 1991), or, the results of 'role analysis' of some kind (see Padisák, 1991). Clearly, some ways and means of a 'pattern and process' approach is indicated (see e.g. Juhász-Nagy, 1992), where spatial and temporal moments can be related to each other in an operative way.

Finally, a few remarks are needed in order to show why it is so important that these methodological efforts can reach a satisfactory theoretical framework as soon as possible. One of the most relevant problems of ecology, without doubt, is the acceptable explanation of stable coexistence of populations. But, because there are several types of coexistence and there are many types of stability (e.g. Lyapunov-types, assymptotic, interconnective, robust stability), we may guess that such a plurality needs a number of explanations (preferably: a minimal number). At the same time, one feels that the 'twelve explanations' of Wilson's (1990) fine paper represent somehow an 'over-plurality' but it is rather difficult to say how a proper reduction can be made; partly, because the verbal statements of Wilson's are far from being 'sharp enough'. It is somewhat depressing to see that since the period that Scudo and Ziegler (1978) have called the 'golden age', our theoretical tools (like Gause's hypothesis, IDH etc.)

were not able to reach the acceptable levels of testability. 'Towards more testable hypotheses'; I think that this way is indicated for theoretical ecology.

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