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NOTES ON DIVERSITY. PART I. INTRODUCTION

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This introductory sketch is restricted to a rough-and-ready historical outline (I.), some remarks on our present state of knowledge (II.), and some propositions for the future (III.), where a complex, plural and dynamic approach to diversity studies is advocated.

I. PRAEAMBULUM HISTORICUM

I.1 The history of diversity reasoning is practically unexplored. The very fragmentary notes presented here, of course, cannot cover such a huge field, but are intended to call attention at least to some points of interest.

I.2 As far as I can trace back, the first but fairly explicit guesses are due to Duns Scotus (1270?-1308), _doctor subtilis_, who, while attacking Thomas Aquinas, had used such dialectical arguments and eloquent phrases (e.g., _Idem et diversum_; _Posse et esse_; _Singulare et plurale_; etc.) which we might consider 'the scholastical kernel' of the matter (see e.g., Longpré 1924). This medieval debate[1] (complicated further by the counter attack by OCCAM) is somehow parallel to the amateurish sampling activity of a Samarkand khalif referred to by Williams (1963).

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[1] There is an important point, where, outside theology and philosophy, this long debate has an almost modern 'scientific touch': _the relation between individual and society_.

I.3 The old and undeservedly forgotten series of disputes at the Université de Paris and elsewhere draws the attention of the historian to the first layer of our difficulties that might be called the metaphysics of diversity. It is interesting to consider the elegant wording of A. Huxley (1937) on the 'nature of explanation' (p. 12):

'The human mind has an invincible tendency to reduce the diverse to the identical. That which is given us, immediately, by our senses, is multitudinous and diverse. Our intellect, which hungers and thirsts after explanation, attempts to reduce this diversity to identity. Any proposition stipulating the existence of an identity underlying diverse phenomena, or persisting through time and change, seems to us intrinsically plausible. We derive a deep satisfaction from any doctrine which reduces irrational multiplicity to rational and comprehensible unity...

The effort to reduce diversity to identity can be, and generally is, carried too far. This is particularly true in regard to thinkers who are working in fields not subjected to the discipline of one of the well-organized natural sciences. Natural science recognizes the fact that there is a residue of irrational diversity which cannot be reduced to the identical and the rational. For example, it admits the existence of irreversible changes in time. When an irreversible change takes place, there is not an underlying identity between the state before and the state after the change. Science is not only the effort to reduce diversity to identity; it is also, among other things, the study of the irrational brute fact of becoming...'

I.4 How to rationalize 'the brute fact of becoming'?, this is the main problem of transformists (say, Lamarck, E. Darwin), just after the canonical reduction of the diverse to the identical by Linné and others. The next and most important step is due to C. Darwin: the recognition of some degree of useful variation, 'threshold diversity' as a basic condition for any relevant evolutionary success. Darwin's turn from '*metaphysics to physics*' - as L. Boltzmann or E. Schrödinger used to put it: to a statistical mechanics of populations, *ex hypothesi* - is rightly considered to be the overture of a long-term development (cf. Mayr 1982).

I.5 Needless to say, it took again more than one century and the tedious, labyrinthic work of many biologists to go *from hypothesis to operational modelling*. A few notes might suggest some aspects of difficulties; for important details the reader is referred to some reviews and textbooks (e.g., Williams 1963, Peet 1974, Pielou 1975, 1977, May 1975, Krebs 1978, Grassle et al. 1979, etc.).

(1) Post-Darwinian and post-Mendelian scientists have been engaged for a long time in seeking *identity* (of paleostrata, genes, etc.) rather than *variation*. This is why some fields of study, like that of '*genetic diversity*' have still the air of novelty.

(2) Although several pioneers of plant sociology (e.g., Jaccard, Raunkiaer, Kylin) have been able to conceive at least the contours of '*coenological diversity*' in the first decades of this century,[2] their results and methods were monopolized, and mostly *misinterpreted*[3] by a few aggressive schools (Zürich, Montpellier, Uppsala). According to their 'classificatory mania', the main effort of these schools was to reduce diversity to identity. It is to be noted that - history repeats itself - practically the same thing happened to *numerical syntaxonomy*, whose 'classical phase' was quite insensitive to any diversity reasoning, in particular, to the important problem of *how resemblance is related to diversity* and *vice versa* (for a 'blank' see, e.g., Whittaker 1973).

[2] The reinterpretation of Jaccard's data by Williams (1963) is fairly convincing.

[3] DuRietz (1921) gives a bunch of terrifying examples for the fatal misunderstanding of his own Scandinavian ancestors.

(3) When the forties and fifties witnessed the first explicit diversity functions and speculations (by R. A. Fisher, et al., Simpson, and Margalef, etc.), the vast majority of biologists remained practically intact and uninterested. Since the ice was broken by E. G. Hutchinson, R. H. MacArthur and E. C. Pielou and others, there exists a boom of 'diversity fashion' with strange pro and dubious contra reactions.

II. STATUS PRAESENS

II.1 *In medias res,* it may be instructive to consider the cons and pros

II.1.1 by quoting Pielou's (1980) drastic criticism on Grassle et al. (1979). Pielou, *inter alia,* says that '... I was distressed to find that so many people treat 'diversity' and 'diversity index' as synonyms. It will be evidently news to many statisticians that an ecologist studying diversity is not merely engaged in devising, and estimating, an index that is the qualitative analogue to variance. Ecological diversity is a biological phenomenon...' She requires, further, that our investigation should concentrate on some relevant 'biological laws', rather than on certain properties of some functions and indices. One feels that Pielou is partly right.

II.1.2 On the other hand, one feels also that the problems posed by Grassle et al. (1979) are in majority important and inevitable. What are the axioms and postulates that govern our diversity reasoning? Which family of functions is able to represent diversity and related phenomena? How to choose properly a function and methods of estimates in a particular situation? It is only fair to say that these and a number of similar problems cannot be avoided. I think that the volume in question has made some important contributions to a better understanding of the future.

II.2 One of the obstacles to progress in better understanding is the simultaneity of phenomena which is present in all diversity analyses. Moreover, this simultaneity has a biological aspect, [BA], a mathematical aspect, [MA], and a coupled version of [BA] and [MA]. Suppose we have some concrete entity (observational unit) or a set of definite entities and consider briefly some features of our difficulties.

II.2.1 [BA] means that several (e.g., genic, genetic, biochemical, epidemiological, etc.) kinds of diversity exist, even for the same entity, simultaneously. One of the best examples is Homo sapiens and human society.[4] The scholar, who is engaged in studying, say, morphological diversity of different families during phylogeny and finds that, for example, D(Orchidaceae) > D(Alismataceae), would perhaps be interested in more than one type of biological diversity. In addition, he should be interested in studying relations between 'useful' and 'residual' variation during evolutionary processes. [BA] shows clearly that the present-day hegemony of 'species/individual diversity' is in many cases unjustifiable or even sometimes quite ridiculous.

II.2.2 [MA] means that several kinds of functions (e.g., Fisher's LSD, entropy estimates of Fisher, Shannon, Rényi and Gini type and indices of variation) can be used in order to represent some degree of biological diversity. The coupled version of [BA] and [MA] is concerned with some proper modelling in an operational situation. The adequacy of a model is the 'garantia exclusiva' by which we arrive at the very true statement that 'ecological diversity is a biological phenomenon'. (Our model might be either fairly simple or rather sophisticated, depending on the [BA] of the particular problem).

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[4] Several points of a diversity reasoning are indicated by Izsák and Juhász-Nagy (1982, 1983).

II.3 Unfortunately enough, the true value and position of modelling in ecology is a highly controversial subject, even in the works of the same author. For instance, the curious overstatement of Pielou (1969 p. 1) suggests that modelling is almost omnipotent. ('The fact that ecology is essentially a mathematical subject is becoming even more widely accepted'). The other type of exaggeration is shown again by Pielou (1981), a rather dim view and a very sceptical 'stock-taking'. This kind of mental oscillation is a permanent spource of amazement on behalf of those philosophers, mathematicians and theoretical physicists who have at least some intention to look at the strange zigzag development of theoretical ecology. Their wise comment and advice would perhaps the 'aurea mediocritas'; some sober simultaneous perception of prospects and limitations.

II.4 The importance of modelling is shown clearly by considering diversity patterns of several kinds (see, e.g., Fischer 1960, MacArthur 1965, Pianka 1966, Pielou 1975, 1977, Cody and Diamond 1975, Krebs 1978, etc.).

II.4.1 A primary difficulty is that, besides the simultaneity of II.2, there exist a multiplicity of diversity patterns, according to their dimensions, scaling properties, etc., and a huge number of possible mechanisms behind phenomenological patterns. Suffice it to say that such problems as taxon/abundance relations, niche relations, resource partitioning, etc., cannot be treated successfully without a multiple pattern approach (see, e.g., May 1975, 1981, Engen 1978, DeVita 1979, and Tilman 1982).

II.4.2 Secondly, because diversity in itself may be sometimes quite meaningless, the perception that diversity should be coupled with other types of basic phenomena (like resemblance, preference and heterogeneity) is becoming a very urgent task of ecology. In other words, the traditional trinity of theoretical ecology (diversity - complexity - stability) in many cases cannot be tackled without a proper interconnection between diversity and other structural properties of some supraindividual objects (see. e.g., Patil and Rosenzweig 1979, May 1981, Tilman 1982, Juhász-Nagy and Podani 1983, Juhász-Nagy 1984).

II.4.3 Thirdly, II.4.2 implies at once the need of a pattern and process approach, i.e., a dynamic (preferably spatio-temporal) generalization of a static diversity reasoning. The dynamic generalization seems to be fairly difficult, because our knowledge is very limited even in case of spatial processes and related problems, e.g., diversity processes in the topographical space according to some characteristic ordering (see, e.g., Juhász-Nagy 1967, Dévai et al. 1971, Cormack and Ord 1979, Kobayashi 1981, Juhász-Nagy and Podani 1983, Podani 1984).

II.4.4 Finally, as for a better understanding of II.4.3, we can choose the key-word diversity state, [DS], and some of its implications. Speaking in simple terms, [DS] is some diversity vector of a certain kind. The primary relevance of [DS] is shown by the fact that a number of further concepts (e.g., diversity transitions, transformations of [DS]) and methods (e.g., analysis of diversity gradients, coenoclines, ecoclines, etc.) might be based on that concept. Hopefully, the notion of [DS] can be further developed to a state-space (or state-variable) approach, where some difficult problems of theoretical ecology (e.g., limits of diversity, diversity and stability, etc.) are going to be tractable (see, e.g., Loucks 1970, Noy-Meir 1974, Casti 1979, May 1981, Tilman 1982).

III. PROPOSITIONES FUTURAE

III.1 As a main conclusion of the previous discussion, suppose that the most important future task is to find the operational means of representing generalizations of II.4. It is to be noted at once that our present-day terminology and methodology are quite inadequate to the work that must be performed. A few notes may suggest some points of interest.

III.2 *Simplex versus complex diversity.* Let Q be the *biota* of a T *topographicum*, $Q:=\{a,b,\ldots,s\}$. Let Q' be a *joint space of the binary type*, $Q' := 2\times 2\times 2\ldots\overset{s}{\smile}\times 2$, realized, further, as a contingency table with 2^s cells. (It is permitted, of course, that Q' may be a joint space of the n-nary type, *mutatis mutandis*.) Let, further, Q'' be an empirical *finite scheme* (sensu Yaglom), i.e., a relative frequency distribution in a one-to-one correspondence with Q' (see Rényi 1962). In other words, Q'' is an ordered pair, $\langle Q', F_j\rangle$, where the frequency distribution F_j is gained by a j-specified *sampling procedure* related to T. (The j-specification should contain all the relevant relations between T and T_j, where T_j is a set of sampling units.) Let $\hat{H}_j^{(\beta)}$ be an entropy estimate of the Shannon-type of F_j, called the *biotal diversity*[5]. At the same time, we can define $\hat{H}_j\{L\}$, $\hat{H}_j\{L\} := \{\hat{H}_j(A), \hat{H}_j(B), \ldots\}$, the set of *local entropy estimates* for all elements of Q, where $A:=[a,\bar{a}]$, $B:=[b,\bar{b}]$,... An important property of $\hat{H}_j^{(\beta)}$ is that it represents an *overall diversity bound* for $\hat{H}_j\{L\}$ as shown in Fig. 1. The relation between $\hat{H}_j^{(\beta)}$ and $\hat{H}_j\{L\}$ becomes particularly interesting if we consider some initial 'mental steps' that should be taken when one wants to move, say, *from flora to vegetation* (see Fig. 2). First, by (1),

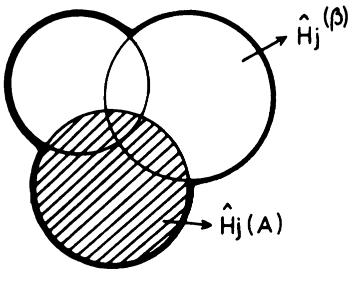

Fig. 1.

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[5] Note that biotal diversity corresponds to *faunal diversity* (Dévai et al. 1971), *florula diversity* (Juhász-Nagy and Podani 1983) or to *floral diversity* (Juhász-Nagy 1984).

the basic flora[6] (as a 'point set') is to be built up. Secondly, the elements (points) of such a flora are to be characterized by such simplex quantities as the elements of $\hat{H}_j\{L\}$, etc. (where no Descartes operation, ×, is involved). Thirdly, if operation × is meaningful, then some complex quantity, like $\hat{H}_j^{(\beta)}$ becomes interpretable. (Needless to say that any further steps, e.g., construction of dendrograms, allocation, etc., are based on [3] of Fig. 2).

III.3 Singular versus plural interpretations. A complex measure, like $\hat{H}_j^{(\beta)}$, has the immense advantage that it permits a huge number of decompositions of a complex set (see Juhász-Nagy 1984), gaining conditional, multiple or partial diversity estimates. We can define, for instance, complete dissociation of element 'a', $\hat{H}_j(\{A\}) := \hat{H}_j(A|[B,C,\ldots,S])$, as a multiple conditional entropy estimate (see Fig. 3). Likewise, we can define total dissociatum of a complex set as a sum of

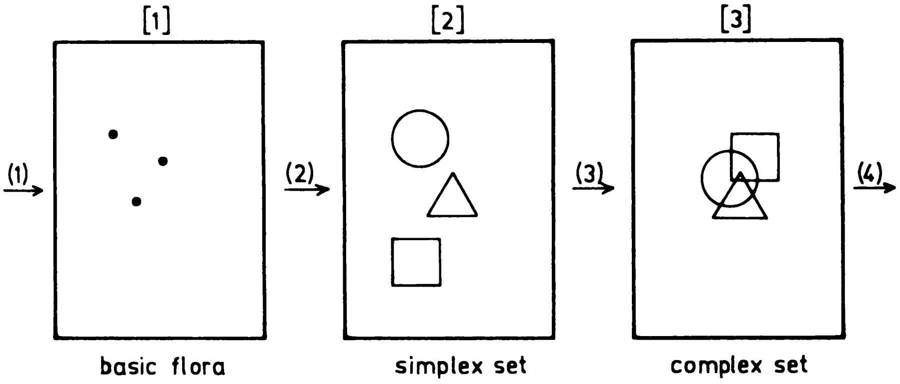

Fig. 2

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[6] If Q is the basic flora ('floral universe') of T, then Q' is the set of all subsets of Q.

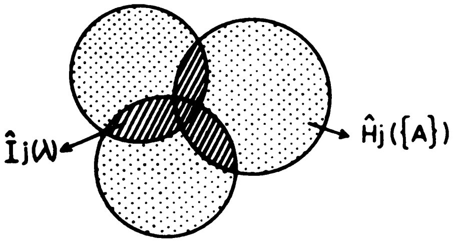

Fig. 3

complete dissociation estimates of all elements. Similarly, by introducing the quantity

$$\hat{H}_j([L]) := \hat{H}_j(A) + \hat{H}_j(B) + \ldots$$

called the local distinctiveness, we obtain

$$\hat{I}_j(\lambda) = \hat{H}_j([L]) - \hat{H}_j^{(\beta)},$$

called the associatum, as a joint contingency information for all elements of Q (see Kullback 1959). Although associatum and dissociatum are more or less complementary to each other (showing some degree of 'common' and 'uncommon' local behavior' of populations, respectively), these quantities are not necessarily additive, because of the existence of interassociatum ($[\hat{H}_j(A) \cap \hat{H}_j(B) \cap \cap \hat{H}_j(C)]$ in Fig. 3), i.e., the frequent existence of 'negative information'. Despite some computational difficulties, a plural interpretation of diversity may be very useful, because it permits to make distinction between autophenetic and synphenetic patterns, and to explore several compositional properties of vegetation (or, other objects).

III.4 Static versus dynamic diversity. All forms of the representations in III.2-3 are static, if survey sampling T_j is characterized by the ordered pair $\langle t_j, \tau_j \rangle$ where t_j is a topographical, whereas τ_j is a temporal scalar. On the other hand, if we have a $\underline{T}_u$ vector field of some kind, $\underline{T}_u := [T_1, T_2, \ldots, T_j, \ldots]$, then we can achieve a number of dynamic representations. Even in the relatively simple case, where only the size of sampling units (of the same shape, etc.) is changed (see, e.g., Dévai et al. 1971, Podani 1984), some unordered versus ordered diversity estimates are to be confronted. If, for instance, the change of biotal diversity along a topographical vector can always be characterized by at least one local maximum ('maximum area' or maximum volume'), and similar relations are true for all those mentioned above, then any meaningful complex diversity estimate is to be related to such a characteristic size of the topographicum. Moreover, using local and global extreme values as a reference basis for an *elementary scaling*, several useful concepts (e.g., *characteristic points*, *characteristic intervals*, *characteristic ordering*) can be introduced in order to study some *compositional rules* of communities.

III.5 *As a summary* of this fragmentary outline, it is to be noted at once that the vast majority of practical diversity calculations are based on some *simplex*, *singular* and *static kind of reasoning* (particularly in the case of species/individual diversity). On the other hand, the difficulties mentioned in II.4 clearly require some *complex*, *plural* and *dynamic approach*, where such a problem as 'limits to diversity' can be taken into account hopefully. The further parts of this series of notes will have this aim in view.

REFERENCES

Casti, J. 1979. Connectivity, Complexity and Catastrophe in Large-scale Systems. Wiley, New York

Cody, M. L. and J. M. Diamond (eds). 1975. Ecology and Evolution of Communities. Harvard Univ. Press, Cambridge, Mass.

Cormack, R. M. and J. K. Ord (eds). 1979. Spatial and Temporal Analysis in Ecology. Internat. Co-operative Publishing House, Fairland, Maryland, USA

Dévai, I., K. Horváth and P. Juhász-Nagy. 1971. Some problems of model building in synbiology. Part 1. Spatial diversity process of the binary type in a simple situation. Annal. Univ. Sci. Budapest, Sectio Biol. 13:19-32

DeVita, J. 1979. Niche separation and the broken-stick model. Amer. Nat. 114:171-178

Du Rietz, G. E. Zur Methodologische Grundlage der Modernen Pflanzensoziologie. Holzhausen, Wien

Engen, S. 1979. Stochastic Abundance Models. Chapman and Hall, London

Fischer, A. G. 1960. Latitudinal variation in organic diversity. Evolution 24:61-81

Grassle, J. F., G. P. Patil, W. K. Smith and C. Taillie (eds). 1979. Ecological Diversity in Theory and Practice. Internat. Co-operative Publ. House, Fairland, Maryland, USA

Huxley, A; 1937. Ends and Means (An Inquiry into the Nature of Ideals and into the Methods Employed for their Realization). Chatto and Windus, London

Izsák, J. and P. Juhász-Nagy. 1982. Studies on lognormality of mortaility statistics. Biometrical J. 24:731-741

Izsák, J. and P. Juhász-Nagy. 1983. One the explanation of the changes in the age of the concentration of death causes. Z. Alternforschung 39:31-36

Juhász-Nagy, P. 1967. On some 'characteristic areas' of plant community stands. Proc. Colloqu. on Information Theory edited by A. Rényi, Akadémiai Kiadó, Budapest. pp. 269-282

Juhász-Nagy, P. 1984. Spatial dependence of plant populations. Part 2. A family of new models. Acta Bot. Hung. 31 - in press

Juhász-Nagy, P. and J. Podani. 1983. Information theory methods for the study of spatial processes and succession. Vegetatio 51:129-140

Kobayashi, S. 1981. Diversity indices: relations to sample size and spatial distribution. Jap. J. Ecol. 31:231-236

Krebs, C. J. 1978. Ecology. 2nd ed. Harper and Row, New York

Kullback, S. 1959. Information Theory and Statistics. Wiley. New York

Longpré, P. 1924. La philosophie de Duns Scot. Seuill, Paris

Loucks, C. L. 1970. Evolution of diversity, efficiency, and community stability. Amer. Nat. 10:17-25

MacArthur, R. H. 1965. Patterns of species diversity. Biol. Rev. 40:510-533

May, R. M. 1975. Patterns of species abundance and diversity. In: Cody and Diamond (1975), pp. 81-120

May, R. M. (ed.). 1981. Theoretical Ecology: Principles and Applications. 2nd ed. Sinauer, Sunderland, Mass.

Mayr, E. 1982. The Growth of Biological Thought. Harvard Univ. Press., Cambridge, Mass.

Noy-Meir, I. 1974. Catenation: quantitative methods for the definition of coenoclines. Vegetatio 29:89-99

Patil, G. P. and M. Rosenzweig (eds). 1979. Contemporary Qunatitative Ecology and Related Ecometrics. Internat. Co-operative Publ. House, Fairland, Maryland, USA

Peet, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5:285-307

Pianka, E. R. 1966. Latitudinal gradients of species diversity: a review of concepts. Amer. Nat. 100:33-46

Pielou, E. C. 1969. An Introduction to Mathematical Ecology. Wiley, New York

Pielou, E. C. 1975. Ecological Diversity. Wiley, New York

Pielou, E. C. 1977. Mathematical Ecology. Wiley, New York

Pielou, E. C. 1980. Review on Grassle et al. (1979). Biometrics 36:742-743

Pielou, E. C. 1981. The usefulness of ecological models: a stock-taking. Quart. Rev. Biol. 56:17-31

Podani, J. 1984. Spatial processes in the analysis of vegetation. Theory and review. Acta Bot. Hung. 30:75-118

Rényi, A. 1962. Wahrscheinligkeitsrechnung, mit einem Angang über Informationstheorie. VEB Deutscher Verlag der Wissenschaften, Berlin

Tilman, D. 1982. Resource Competition and Community Structure. Princeton Univ. Press, Princeton, N. J.

Whittaker, R. H. (ed.). 1973. Ordination and Classification of Communities. Junk, The Hague

Williams, C. B. 1963. Patterns in the Balance of Nature and Related Problems in Quantitative Ecology. Academic Press, London

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