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ON DIVERSITY AND CONNECTIVITY, AS HISTORICAL EXPRESSIONS OF ECOSYSTEMS[1]

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Abstract: Diversity is an historical property acquired in the growth and development, not only of ecosystems, but also of any system made of replicable subsystems. Its basic expression involves the equivalent of an averaging of quantitative ratios, between any possible pair of components, of most of their extensive and intensive properties. Diversity, like information in general, grows around itself, in analogy to the evolution of vorticity in fluids. In another approach, diversity can be contemplated as a result from interaction between dynamics of total biomass and dynamics of genetic differentiation inside the same biomass. Connectance, the ''syntaxis of ecology'', should be placed inside the boundaries of diversity, and is subjected to major constraints. Connectance is bounded between the increasing rigidity of the system and its risk of falling apart into separate systems.

General attitudes of ecologists

To put it bluntly I would like to begin saying that we need not less statistics, but more thermodynamics, and that evolution is not only driven by natural selection, but also, unavoidably, by a background of accumulated complexity in the ecosystems. In my opinion, the attempt to base most ecological work exclusively on statistics, with the only theoretical background of natural selection is incomplete, so far as it does not appreciate history enough. History is the gradual increase of complexity, or information, somewhere, as one fraction of the equivalent of the increase of entropy in the exchanges of energy going along over all the same system. It is at least intriguing, and may be profound, that the barycenter, or center of gravity of primary production, and the center of gravity of respiration are not coincident. Their distance is better measured along the vertical axis defined by light and gravity.

Most natural scientists can agree that the only rational basis for prediction is thermodynamics; but ecologists seem to trust excessively the mechanistic models of interacting populations. These models separate strictly state variables and constant coefficients of interaction. But, actually, all are variables and should be treated as such. Interaction parameters are rarely ''observed'', but they are chosen to produce ''desirable'' results, - that is, a steady state that is, as such, improbable -. The situation needs to be clarified if ecology has to progress. Evolution too often is considered in a ''void'', we do not care enough about the almost unavoidable increase of complexity along history: both genetical and ecological. Natural selection works on a scenario inherited from the past, and moreover there is a selection of the ways of selection.

In my experience there is a widespread and noticeable dislike for the concepts of diversity and succession, expressed by ecologists that are otherwise fond of statistical approaches and pretend to be the genuine reductionists. Actually, reductionism can be practiced at both ends of the spectrum: either trying to base ecology on a painstaking study of distribution and physiology of individuals and of populations, including their change or, else, coming from the other end, considering ecosystems as physical systems, and using accordingly concepts like biomass, energy flow, and so on. This approach, nevertheless, is not rarely qualified as holistic, with derogatory innuendo. In any case, theoretical ecology could derive considerable inspiration from modern physics, and the study of thermodynamics in the different kinds of systems. Specially pertinent is to examine carefully the limits and ways to prediction in open systems far from equilibrium.

Most ecological models seem to be geared to a linear world, comparable to an atmosphere and hydrosphere that were devoid of vorticity. But although we know that weather prediction is a difficult job, ecology and economy continue to use models that are conceptually too simple, like embedded in a laminary flow. They disregard excessively what can be described as an historical wrapping around of successive layers of information, that is, the differentiation that goes with growth.

Diversity

We should start thinking of ecosystems as physical systems. Diversity is a very robust measure of an intensive or quality property of them, and it is in this sense that diversity can be constructed as an analogue of temperature. Being robust means that different taxocenes and different descriptors (numbers, weights, chemical compounds) provide the basis for comparable measures. Among numbers on which to compute diversities, we should include, of course, the amounts of

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sugars (substrates), enzymes, RNA and DNA in an organism or in a system. Such chemichal diversity, and general turnover of the system, and of each of the compartments, are related. Divesity is a function of the organization of the ecosystem and is expressed and should be recognized at all the levels of observation. The concept of (ecological) diversity applies almost exactly to any system made of replicable subsystems, like language, construction toys, etc.

Ideally, a numerical index of diversity should be independent of the size of the sample. With reference to the distribution of individuals into species, it has been assumed that the multiplications by a conventional factor of the size of the sample, will result in the addition of a number of species that is always the same, or otherwise regular. Then, a good index of university might be the average number of new species that enter the check list when the total number of identified individuals is doubled. Indices borrowed from information theory, like Shannon-Weaver's, are acceptable and have many advantages. But, in fact, the size of the sample, and the extraction of replicate samples, cannot be made independent from organization and growth. This is at the origin of many statistical difficulties. The systems expand and cover the space, and growth breeds internal differentiation. Samples cannot be considered as equivalent and extracted from an ideal uniform universe. The limits of usual statistical approaches to diversity should be evident. It is possible, of course, to apply simple statistics to the study of a large number of temperature measurements; but this is quite different from the more interesting study of temperature in terms of statistical mechanics. What the ecologist asks from the statistician is an analogue of this second approach, not forgetting completely some advice in relation with the more pedestrian first question. It can be suspected that number of individuals and number of species might be related among them also in the frame of approaches that assume organization, like allometrics and fractal theory.

Naturalists have a feeling for diversity, and are fond of the graphs made of a sequence of vertical bars that stand for the respective representations of the different species, ranked in order of decreasing abundances. The search for a magic interpolatory expression is probably futile and surely irrelevant. In any case, a statistical approach has a hard task in finding suitable null hypotheses. More than the total number of species, what is important is the overall style of the distribution, either steep or flat, which means that the ratios between the abundances of any pair of species tend to be, respectively, high or low.

After folding repeatedly a sheet of paper, the respective surfaces of the resulting areolae, each one limited by a polygone of creases, follow a distribution quite similar to the representation of the different species in a community. This "diversity" is higher if the process of folding has gone for one step more. Otherwise, the pattern of distribution seems not to be different when the successive folds are produced at random, from when there is a "purpose" in their ordering, as it may be in a particular job or exercise in origami. This should show that eventual telelogical interpretations are irrelevant in the study of diversity. The fractal approach to the geometry of nature opens new possibilities in the pursuit of numerical approximative descriptions. They are relevant in providing an image of the propagation, over all the extension of the ecosystem, of a similar pattern of dependence and organization, as well as in the consideration and quantitative analysis of boundaries. But the progress in the consideration of diversity which all of us wish for the future should not exclude more simple approaches. For example, to correlate with the environmental temperature, through seasonal or geographical series, the number of species of butterflies in 1000 specimens collected at random in each one of a number of places: this may introduce a statistical exercise that could lead to deeper questions.

There is a large literature on diversity. From time to time, I feel guilty of having contributed to its dismal growth in many ways. Here I will not deal specifically with the question of the spectra of diversity in space: remember that usually dD/dx is correlated with D, being D any appropriate measure of diversity; this reminds of the Liapunov measures of stability, where the decrease in the rate of change is positively correlated with the rate at which such rate decreases. Another current topic is about criteria for choosing the "best" index. A paper by Hurlbert (1971), about the "non-concept" of diversity, ends adding another index of diversity to the already available, and I follow the example here, after these critical remarks, proposing another index (k). But this is done in an oblique way and only as a way to explore further aspects, and to keep the discussion alive.

In fact, I would feel sorry if k were generally adopted. In my experience it is dangerous to provide simple recipes for any numerical treatment. I cannot assess the damage done by the books on statistical methods, but the provision of apparently easily computable indices of diversity has assisted the proliferation of many irrelevant tables, with diversities, expressed usually in the Shannon-Weaver index, and not uncommonly (specially in papers on water pollution) computed on unlikely lists that can include, as equivalent "items", *Plesiopapus noctivagus, Chironomidae*, assorted worms, and miscellaneous things.

A dynamic approach to diversity

Diversity pretends to express in an abridged form how a set is distributed into subsets. This definition sounds formal and is only helpful as it restricts the meaning of any particular "diversity", to the application of the principle that has been used in the division of the set. If, as usual, the whole set of individuals is distributed according to species, any measure of diversity on such basis may be directly relevant only to the interaction among species. It has to do with dynamics of populations, that generate some semblance of order in the subsumed numerical richnesses of each one of the species. There is a need to understand how diversity is maintained or changed along time. In my book of 1974 (p. 368), I used the Brillouin presentation of the most used index, to work out the changes in its numerical value, through manipulation and shifts in the representation of the different species. It is both simple, and instructive for students interested in conservation, to see how any substitution of one individual of a rare species by an eventually "equivalent" individual of another species that was already more common, decreases systematically the index of diversity. This approach can be elaborated as convenient.

Centering the discussion not on any suitable measure of diversity, D, but on its change, dD/dt, it is evident that numerical expression of diversity decreases when it is easier to add a species than to add an individual, that is, when there is a limit to biomass, but not to genetic differentiation. In this dynamic approach, diversity may be seen as an expression of the transitory relations between the tendency to change the biomass or the total number of individuals (N), and the tendency to change the number of species (S). We might consider either dN/dt and dS/dt separately, or combine both in an expression dS/dN. An approach that ecologists understand easily is to write $N^k = S$, or $k = \log S/\log N$, in which k is another suitable index of diversity, providing numbers acceptably correlated with the values of more usual indices computed on the same sets.

In a monoculture, or in a chemostat, k = 0, and in a system like a museum display case (close comes Noah's ark), in which each individual belongs to a different species, k = 1. An obvious lesson of these examples is that diversity is modulated by the flow of energy pushed through the system (Fig. 1). Ecosystems, according to their ratio P/B (primary production/total biomass) fall somewhere between the chemostat and the display case, centered inside the first half of the range, around values of k between 0.2 and 0.3. This means that, on a global basis, number of individuals should stand perhaps between the cube and the fourth power of the number of species. It can be doubted if it has always been so, along the history of our planet. In any case, what can be said is that human exploitation decreases systematically the ratio P/B in the rest of the biosphere and, in consequence, a loss of diversity around us is unavoidable. Standard ecological theory predicts that, in undisturbed dynamics, K-strategists have to take the lead (Margalef, 1974, p. 658) and under such conditions one should expect a gradual subdivision of "niches". In consequence, what is expected to happen in the exploited and disturbed world around us goes against the "natural" trend. But, of course, increase of diversity should have a limit, among other reasons, because even non-humanized nature is subjected to a quite rigorous spectrum of disturbance.

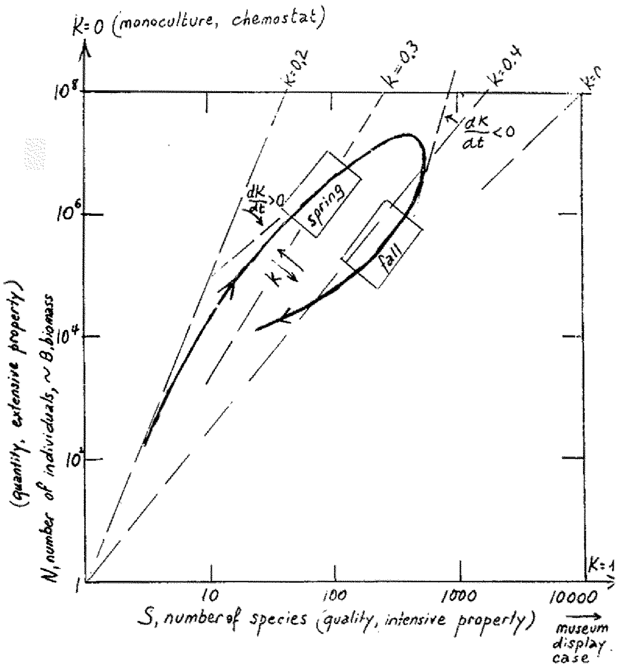

Fig. 1. Idealized representation of a field of possible relations between total biomass and number of species, in ecosystems. Time is associated either with continuous trajectories, as is clear from the comparison between spring and fall aspects in any temperate ecosystem, or in the consideration of "normal" succession, or with discontinuous trajectories in the response to disturbance.

Although an appropriate development of this approach is not yet ready, as it stands now, it might help to visualize how changes in diversity are generated. They are the outcome of the interference between mechanisms that regulate the numbers of species and those that are operative in relation with the total biomass or abundance. The application to seasonality is forthright: during spring, numbers of individuals increase faster than number of species, and diversity drops (dk/dt < 0); in fall, number of individuals decreases, but number of species less so, since many of them remain as eggs, hibernating stages, and the like, and then dk/dt > 0. (Suppose that you go repeatedly through your text, in a word processor, and change a few words each time, with a wish to be less repetitious: so works nature in the dynamics of diversity).

Different species have different life spans. As a consequence, trains of waves are introduced in the values of diversity. We can understand easily the origin of the complex and diversified patterns expressed through the graphic representation of diversity as a sequence of vertical bars, in the form commonly used by the plant ecologists, and marine biologists (Frontier, 1985).

Consider the widely adopted expression of growth with negative feedback, as $dN/dt = aN^{h} - bN^{h'}$, that in the usual tradition dating from Verhulst, has been impoverished to the almost exclusive form $dN/dt = rN - (r/K)N^{2}$. The number of species may depend, following the theory of insular biogeography (Mac Arthur and Wilson, 1967), on the balance between introductions and extinctions, being the extinctions more dependent on the extant species, in the general form $dS/dt = cS^{m} - dS^{m'}$. Make $dN/dt = 0$. $dS/dt = 0$, and $B = \log (bc/ad)$, with the result of $K = B\,(h'-h)/(m'-m)$. Remember that the condition for regulation is to have $h' > h$, and $m' > m$. This gives to k the quality of a measure of the interaction and the relative strengths of two feedback mechanisms. Naturally if limitation in total numbers of individuals or of biomass is more rigorous, diversity can go up. If, reciprocally, number of species is more strongly limited, diversity will decrease. It is easy to draw analogies comparing the length of a discourse - in letters -, or its number of words, and the classes of words in it. Moreover, longer words, as big animals in nature, tend to be rare in the first draft.

Some insight can be gained through a very simple and general way of representation on a graph defined by two coordinates, one of them extensive or quantitative, the other intensive or more related to quality (figs.). Such sort of graphs, defining a space on which events play, are very useful in physics and in ecology. In our case it recommends itself to have the logarithm of the number of species as ordinate, and the logarithm of total biomass along the abscissae (Fig. 1). The devolpment of a population simple or complex, or an ecological succession can be plotted on such a graph. It should be clear on it the difference between enlarging a "sample" and assessing the development of a system, in space or in time. Biomass increases at first very fast, and then growth slows down; in the meantime number of species increases steadily and one can never be sure of the point of saturation. Disturbance often will be more detrimental to biomass than to the already genetic diversification. The important point is that the way back never retraces in reverse the previously followed path. For this reason this diagram ressembles many others used in science, like those that represent, for instance, accumulated heat/temperature in a lake, and volume/temperature of the universe.

Thus, in its infinitesimal expression, diversity reduces to state what should be easier, if to add a new individual, or to add a new species (or genotype) to an ecosystem. The tentative answer may be profound, although it cannot be discussed here with all its implications.

Webs, connectivity, and hierarchy

The usual way to compute and express diversity concerns the probability of occurrence of each species (or class, or subset), taken independently, in a large collection of individuals (or in a given biomass). The probabilities of contact, interaction or spatial proximity between any pair of components, either of the same or of different species, in a first step seem to be besides the point, but can be usefully considered in some of the possible approaches to diversity.

Consider such couple of elements (individuals) as a new unit entity, and compute the diversity of the possible combinations. In the usual Shannon-Weaver index, the diversity of the binary combinations is expected to be equal to twice the simple diversity. If it is not so, there is attraction or repulsion among the components of each ideal couple. If diversity of flowers is D_F and diversity of bees is D_B, the mutual adjustment between flowers and bees makes that the index of diversity computed over all the possible binary combinations is below the sum of precedent indices. One of the best indices of diversity, (Gini - Simpson, is conceptually binary from the start, in the sense that it is based on the probability that two individuals extracted at random, from the spece under study, belong or do not belong to the same species. The probabilities that they belong to the same species is Σp_i^2, and the corresponding probabililty that they belong to different species is $\Sigma p_i p_j$, in which expressions the p–s stand for the separate probabilities ($\Sigma p = 1$) of occurrence of species i, j...

Ecological (usually "trophic") nets have two complementary aspects, either as a set of knots, or as a set of links or arcs. The second aspect has been much studied in a synoptic way, but the first one has been relatively neglected (see, for example, in Ulanowicz, 1986). What is in a link? And how many are of them? Links to be counted can be defined in different ways (Gardner & Ashby, 1970; MacArthur, 1972). I would propose that only links including a negative feedback loop should be counted. To their class belongs the most studied of all links: the one existing between predator and prey. These are direct relations. MacArthur speaks of strong and weak interactions, and suppose that most of them are in the border line. I would prefer to ignore indirect links and for good reason: Each knot is a terminal station and a center for decision, yes or no: Stop. Patten and his coworkers are of a different opinion (see Patten, 1985).

My point of view emphasizes the role of each knot as a center of accretion of information: it behaves like a semiconductor in an electric network. The non identity of the knots or centers at both ends of each link, allows to speak of the asymmetry of each link, that is not necessarily implied in the link as such. The possibility of this asymmetry is accepted in a discussion by

Carpenter & al. (1987) in what concerns ways of learning, and should be the general case in ecosystem webs. Think of the link between the population of an insect that is selected for a character of immediate effectiveness, and the population of a bird that is selected for its capacity of learning. Such kind of asymmetry should be general.

Until an analogous view - the individuality of the neuron, and the asymmetrical function of its extensions - entered the study of the nervous system, no great progress could be made in the corresponding area of science. This may contain a forewarning. The problem of organization of ecosystem webs faces also the ambiguity of having to work both with the consideration of relations among individuals and the highly idealized reconstruction of relations among species. Much more typification and uncertainty are introduced when larger units are preferred, like "niches", compartments of convenience, or trophic levels. And do not forget that qualities of the ecological webs are closely related to diversity, and to the changes in diversity.

When speaking of quantitative approaches to the complexity of ecosystems - the syntaxis of systems, as it were -, reference is made to diversity and to connectivity. Connectance, properly, is the ratio of the number of realized links to the number of possible links, and is related to diversity in many ways. It is obviously related to any diversity, when computed on the number and kinds of realized binary connections, and measured against the number of possible binary connections (usually the double of the simple diversity). The crude quotient of the number of interspecific detected kinds of relations, divided by the number of the possible ones, is usually stated as a percent. In a set of S species the minimum number is S–1, below that the system breaks in two. The maximum number is S (S–1)/2. The real number of connections is well below the maximum number of possible connections. The necessary internal flexibility of any system could not be maintained otherwise. Any electronic device totally connected is shortcircuited and useless. In this sense, connectivity is the contrary of a "progressive" character. Decrease of connectivity means cutting potential relations, which leads to the development of a hierarchy, or of a "chain of command". We could choose to quantify hierarchy, this one certainly seen as a "progressive" property, by (1–C) or by any other suitable expression. Here, it remains only to remind that language has also a hierarchy of the same nature, from which study some useful suggestion could be derived.

In a quest for a more precise terminology, it has been proposed to call connectivity the (average) number of connections per component, and connectance (C) the percentage of the total possible arcs or loops in the web that are realized. But probably further new concepts and definitions will be needed. A weighted expression of absolute connectance is $C' = \Sigma a_{ij} p_i p_j / \Sigma p_i^2$. A study of electronic nets suggests that the values for this expression (dimensionless) can peak around 1.6. If the same trend prevails in all sort of nets, which we do not know, perhaps this constant could be more important than the 5.3 that seems to be an upper limit to diversity, when expressed by the Shannon-Weaver index. A parallel exrpession for relative connectance, might be $C = \Sigma a_{ij} p_i p_j / \Sigma p_i p_j$. Everywhere the as are between 0 and 1, but not necessarily 0 or 1, and may be made equivalent to the coefficients of interaction generally used in ecological theory.

As a system incrases complexity, new species that are introduced do not connect with all the species existing previously, but interact or establish a relation of dependence only with a few species, as preys or symbionts. Connectivity decreases as total number of species grows and several works (MacNaughton, 1978; Rejmanek & Stary, 1979) have noticed that in ecosystems the product S.C is kept between 2 and 12. The different richness of individuals with which the species are represented, influence that kind of relationship. An improvement is to write $C.2^H$ equal to a number Q that varies inside a smaller range, precisely between 2 and 4 (Margalef & Gutiérrez, 1983). These are tentative results, obtained more through the study of technological electronic circuitry than in the consideration of ecosystems, where the published data, besides being scarce, are not always reliable, and often are uncertain in relation with the quality and quantification of the assumed link. Ecologists use the concept of equitability E, related to S and to H (Shannon-Weaver index of diversity) through $S^E = 2^H$. Then, $C.S^E$ is equal to Q.

Again, from the data concerning electronic circuits, and on the basis of general experience about ecological nets, one can be sure that the range between 2 and 4 may be narrow in appearance for reasons of scale, but in reality covers all possibilities and degrees of organization. Perhaps the values tend to peak around 3.5. Q could represent a scale of the quality flexibility-rigidity of organization.

It has been found convenient to construct a representation on a plane of the connectance (C) or, better, of its complement (1–C), against diversity (Fig. 2). The difference (1–C) is a measure of "hierarchy", since it represents the proportion of links that have been cut, with the corresponding development of a "chain of command". The graph reminds the representation of number of species against biomass in Fig. 1. It suggests that the way "hierarchy" (that is, 1–C) increases, expressed against diversity, might be another important property of the organization of systems. At this stage this should remain as a simple suggestion about a possible meaning of Q.

The examined synoptic properties of ecosystems cannot be conceived outside a context of historical development. It should be apparent how efficient is life

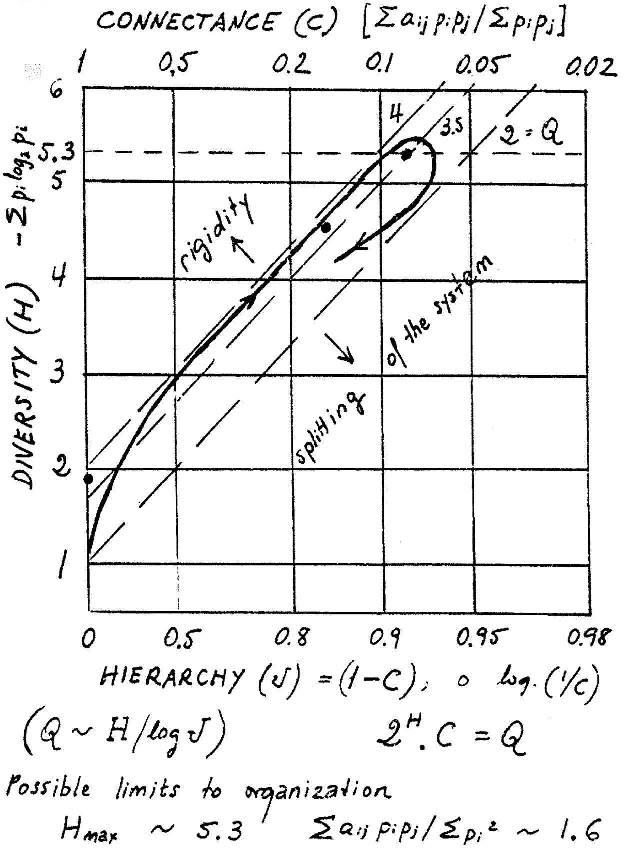

Fig. 2. Idealized representation of a field of possible relations between diversity and connectance, or with "hierarchy". The available conceptual space is limited between the risk of rigidity and the risk of breaking down the system into independent systems. Q is a tentative new measure of the relative distance from both limits.

in the preservation, as usable information, and in several levels of organization, of the invisible byproduct of the incessant metabolism that scientists associate with an "increase of entropy". This goes with time, and changes continuously the dynamic properties of the ecosystems. The ecosystems behave at least as machines, and with more reason than usual machines that never can turn twice remaining absolutely identical, show in their organization and in their operation the consequences of the accumulation of history. Think that in language, the meaning of words, and sentences, shifts slowly, in function of the speaker, of the hearer, or of the context, as they are used again and again. No wonder that the available simple ecological models fail in their purpose, but there is hope of improving them.

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