

DIVERSITY AND STABILITY: A PRACTICAL PROPOSAL AND A MODEL OF INTERDEPENDENCE

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Introduction

Diversity and stability can be considered as functions intended to express "organization" of the ecosystem. Diversity is related to the distribution of present biomass, to the instantaneous complexity. Diversity, as such, may be an useful concept, but as a measure of organization is incomplete, and has to be complemented by some expression of the persistence along time, or order. ^{1, 2} It is a matter of choice, and may be confusing, to apply the name of stability to this quality of persistence. It seems necessary to agree up to a certain point about what is meant by diversity and by stability, taking into account that any empirical ~~experimental~~ approach, to be useful, requires that both functions be computed on independent parameters.

Diversity

Diversity in ecology has its roots in the consideration of the richness and variety of species in a community, but can be applied to any distribution of the elements of a set in subsets, as when summarizing the distribution of the individuals of an unispecific population in year classes, or of a mixture of molecules in chemical species. Diversity is dependent from our decision or from our capacity to discriminate: in the classification of individuals we can go down to species, or to genotypes or to kinds of DNA. Any monotonous function can be used to express diversity, with a minimum when all the present elements belong to the same class and a maximum when every one of the elements belongs to a different class. Selection of the adopted function is a matter of expediency and it seems that what we need is a function almost invariant to the usual accidents in the sampling and treatment of data. For instance, the function should be relatively insensitive

to the size of the sample, to any random selection inside of the sample and, if possible, to operations that strictly are not random, such as those depending on the method of sampling and on the taxonomic groups selected for study. Taxonomic groups that cover a broad ecological spectrum -as chydoridae do in freshwater lakes- are in a better position to give an estimate of the distribution of overall diversities, with all their implications, than groups ecologically more specialized, as are the diatoms of the marine plankton.

The usual function of ^{Shannon}~~Shannon~~-Weaver is acceptable on the mentioned points. The factorial expression, basically equivalent, has the advantage to be more intuitive to the biologist, as it visualizes² diversity as proportional to the number of relations that can be established among the elements of a set, and this may have some bearing to the number of actual feedback circuits effective in the system. The set of all possible binary products between the actual numbers of individuals (meaning the probabilities of interaction at the individual level) gives the same value of equitability³ or evenness⁴ than the set of numbers of individuals, and this is also a desirable property of the chosen expression of diversity.

The regularity in the distribution of individuals into species fascinated the firsts students of diversity. It is a consequence of the fact that classes in which the individuals are distributed, are linked by definite relations. The most simple example is offered by the age classes in an unispecific population: if mortality is constant, stable distribution follows the law of geometric progression; but if there is an acceleration in the addition of juveniles, diversity drops. Equally, the interactions inside the ecosystem generate and alter the quantitative relations between the numbers of individuals of the different species. Although diversity appears as an instantaneous property, it is a result of the function of the ecosystem.

The preferred expression for diversity, a statistical function in which computation enter the numbers of individuals of all the species, is not exempted of the sort of criticism that has been levelled against other expressions based

on statistical or deterministic hypothesis about the regular distribution of individuals into species. Perhaps the most critical aspect is the dependency on size of sample. The relations between diversity and space make necessary the consideration of a spectrum of diversity, implying perhaps a hierarchy of structures that leads to recognize and separate the simple diversity at a low level and a pattern diversity.⁵ As the example presented in fig. 1 shows, it is possible to have the same value of diversity for a given sample size inside of completely different structures. As we can see later, the form of the spectrum appears related to the stability.

Diversity, measured in bits per individuals as usual, reaches its superior limit around 5, perhaps as a consequence of limitations of a topological nature set to the possibility of interaction between elements. Thus, the scale offered by diversity as a measure of the complexity of an ecosystem is rather limited. If there is need or desire to enlarge it further, one has to use spectra of diversity or introduce the complementary point of view of stability.

The concept of diversity, as stated inside the domain of ecology, has no necessary implications concerning information or thermodynamics. Nevertheless, the consideration of conceptual connections with information theory may be useful: in a very diverse community, every element is bearer of a higher amount of information and also more work (a larger sample) is necessary to get an equivalent knowledge of the system. A more diverse system is usually a more predictable system, in the sense that diversity is proportional to the amount of accumulated and assimilated information that allows to anticipate environmental change. In this sense, diversity is related with stability, implying some relation between changes accounted for and changes not accounted for. But although in nature a more diverse system is often also a more stable system, the independence of both properties is apparent in the context of informations: Diversity (D) refers to the width of the communication channel¹, stability (S) is related to the deterioration of

information during its transmission, to the noise, and, thus, the actual effectivity of the channel can come close to the difference $D - \frac{1}{2}$.

Stability

In usual speech, a system is stable if, when disturbed from a condition of steady state, it develops forces which tend to restore the system to its original condition. The imprecision of the concepts of stability, regulation, and the like, is stressed by many authors ^{6,7,8}. Ashby ⁷ states that in the notion of stability there is something linked to the fact that, although a system is passing through a series of changes, there is some aspect that is unchanging: a statement about general conditions that the interactions fulfill may be a statement concerning the stability. A set of states that are interconvertible, but generate no new states, is another element to be included in the notion of stability, as well as the existence, around this set of states, of another set on which the system does not go spontaneously, but if led to it can return to the interior first set. If led outside the exterior set, no prediction is possible. This can be represented by the diagram of fig. 2, left. A matrix can be an appropriate practical representation, and in cybernetic terms we can speak of a system of feedback circuits in which the negative (or stabilizing) ones predominate.

The usual form to write down the interactions between the elements of an ecosystem is an appropriate starting point to discuss the concept of stability. In the degree that an ecosystem is described by such a matrix, it can reach a stationary state. The outputs are the changes in numbers of the different species (the set of dN_i/dt), and these act as inputs for a new cycle, until we have a situation stationary or with regular rhythms. This model is equivalent to the core of fig. 2, left. Changes not accounted for (changes in the environment, immigration or emigration) can lead the system to the peripheric field of the same fig. 2, but the changes can be eventually assimilated or buffered by the play of the same input-output matrix. Perhaps some changes will drive to a structure so different from the initial one that the convenience of referring to the same ecosystem may be questioned: nevertheless

the mechanism of building up complexity works as al/ways.

If stability has to be an useful concept, it needs quantification. But the enterprise to find a way to quantify it looks forbidding. To begin with, a matrix like the ideal one, but~~h~~ with reference to a concrete ecosystem, has never been specified. But suppose this could be done. We might choose as an expression for stability the ratio~~d~~ between the dimension of the whole map of the states from which the system can return -including the effects of moderate environmental disturbance, massive migration, etc.- and the area covering the set of spontaneously interconvertible states -including adjustment to or anticipation of predictable environmental change as well as cycles generated by interaction between species-. This would be the ratio between the areas B and A in fig. 2. It seems that both areas under consideration are always more or less related, that is, systems that spontaneously fluctuate more, can return also from a wider range of induced deviations. Moreover, the boundary between both areas cannot be precised practically, as it is difficult to decide what environmental changes are regular and how far they have affected the evolution of the associated species.

All the aspects of the problem of the stability of ecosystems are pervaded by history^{OR}. To subject a system to hypothetical change has almost no meaning; anything that has passed through a temporal set or succession of selective filters can be named stable, be complex or simple, variable or almost constant. If the capacity to return from a far away state is never needed or realized, the system could not prove itself stable. Reasoning along this way, the whole notion of stability becomes hopelessly confuse.

We should decide if it is preferable to consider stable a system if it survives many changes, but preserves a certain recognizably similar structure (up to at which point?), exchanging species, shifting the proportions of their representation, using alternative paths in food nets, and so on, or else a system that remains similar to itself and whose presumed stability is never tested. The same

dilemma can be expressed in terms of information: a system may be considered stable because it can pick up continuously information from environment and change accordingly, or because it has already the available information and nothing new happens for which its organization is not prepared. The second alternative means that the system has attained a degree of homeostasis that makes inconsequential further changes, so far they fall inside the usual range. Perhaps we could speak of extrovert and introvert ecosystems.

In fact there is a continuous range of possibilities, extending from the required plastic stability --extended even to the annihilation of the system? -- to the permitted rigid stability. We could characterize this by a monotonous function. The eventual desire to apply a qualification (stability) that has a certain tradition remains the only pseudoproblem. We are at a loss to decide if it should be applied to the head or to the tail of our nice serpents. Perhaps it would be wiser to refer to both ends with separate names, for instance, adjustment or lability to the first one, and conservatism, endurance or persistence to the second.

A measure of stability (Peristence)

We cannot presuppose eventual and unknown changes in the environment and responses of the ecosystem to them, and moreover we must assume that the set of relations linking the elements of the system has passed the proof of time and reflects the past interactions between environment and community. Two useful approaches have been proposed along these lines. Both are basically similar, since both repose on the general expression of interdependence between species and between species and environments:

$$dN_i/dt = e_i N_i + \sum a_{ij} N_i N_j$$

where the a's are positive or negative constants, and e_i stands for the environment and eventually can be decomposed in a sum of terms relating to different factors.

Leigh⁹ relates (conservative) stability to the inverse of the frequency of

fluctuations. These can be recognized when the density of the species crosses its average value. The model of Leigh is particularly interesting, because stability thus defined appears related to other synthetic or "macroscopic" properties of the ecosystem, showing a positive correlation with biomass and number of species, and a negative correlation with production.

Kerner^{10,11} represents the possible states of an ecosystem as a cloud of probability in a multidimensional space, in which the dimensions stand for the species -or for environmental factors either-. The cloud is denser where the easily interconvertible states are mapped. Kerner characterizes the cloud by a parameter that he names "temperature". High temperature means a larger cloud with the possible states more evenly distributed; low temperature is, in consequence, a synonym for conservatism or persistence. We can appreciate the correspondence with the sketch of fig. 2 left, and the pertinence of the concept, if not, perhaps, of the name, with all implications in a further application of statistical mechanics to ecology. Kerner's concept is particularly relevant in the sense that it can lead to identify maximum stability with the lowest free energy in the system.

Other considerations might enter also in a measure of stability, as the anticipatory power of the system (prevalence of endogenous rhythms over direct responses), the relative importance of negative and positive feedback circuits, the ratio between actual and possible change (a ratio of one would mean no capacity for change when needed), and perhaps the ratio between individual growth and reproduction, related to average individual size. Important as these considerations may be, they remain forcibly too theoretical.

What is needed is a practical way to compute an appropriate function that we may name stability, that could be compared with diversity and with other parameters of the ecosystem. In my opinion we should follow a criterium analogous to the one that led to the acceptance of Shannon's function in diversity, that is, select a function that gives a fair idea of what is meant, practical to compute and resistant to the common hazards of the ecological circumstance.

There is a risk of disposing of the whole concept of stability by a sleight of hand, but this I do not believe.

I would propose to partition the total biomass in species and to associate an extinction function with any one of them. If b_i is the proportion of the species i in the total biomass ($\sum b_i = 1$), m is the instantaneous mortality rate, or alternatively t is the time necessary for the biomass (population) to be halved by mortality, any one of the two following expressions may serve our purpose:

$$(1) \quad S = \sum b_i / m_i \qquad (2) \quad S = \sum b_i t_i$$

Their acceptance should be based on merits of these functions; some interesting qualities are:

- (a) They are a measure of the capacity of storage (of energy, information, etc.) expressed as an average residence time. The dimension is appropriately T .
- (b) Contribution of every one of the species to the stability of the ecosystem is made proportional directly to its biomass and inversely to its mortality. Biomass is a good expression of influence on other species and mortality reflects the impact of other species or of environmental factors. Increase of size increases storage capacity and lengthening of life span means a major independence from time. The species of higher trophic levels make a relatively more important contribution to stability, in the sense that their extinction value is lower. The average sum of the ratios over the system is a measure of the degree of realization of a trend towards homeostasis.
- (c) Biomass and mortality are easy to measure or, at least, less difficult than other parameters. It seems advisable to consider distributions of biomasses and not of numbers of individuals, but mortality rates can be applied conveniently to the selected form of expression. Plants are apt to have very different extinctions in different parts of the body: the trunk of trees contributes more to stability than the green parts; in such cases, perhaps the b 's should be subdivided further, below the species level.

- (d) The expression includes an obvious and desirable reference to flow of energy. The ρ a's in the expressions of Leigh and Kerner are rates of flow accompanying every possible combination of individuals of different species. Here I propose to use only total loss (mortality plus emigration, litter production in trees) rather than include rates of increase. m represents the difference between the maximum possible change (r) and the realized change ($r-m$). Resting stages and unicellular organisms in the moments of rapid multiplication without mortality, contribute very much to stability in the expressed sense.
- (e) The same difficulties present in the computation of diversity are encountered here, as the estimates of stability or persistence should be based on incomplete samples, that is, on a selection, more or less arbitrary, among the species present in the ecosystem. Perhaps some stratified sampling could be advised, considering the prospective contributions of the different groups of organisms: bacteria, for instance, contribute negligibly to stability, and perhaps contribute more in a resting state than in activity.

As in diversity, there is a need to consider spectra of stability (persistence), both in space and in time. A good example of what is meant by a spectrum of stability in space is offered by the consideration of plankton communities. In a small cell of observation, there is a rather high probability that after a short time many individual cells will be found outside: extinction in the context of our cell of observation is very high. As the dimension of the cell of observation is enlarged, extinction in the adopted sense decreases as some power of the dimension and in dependence also from the turbulence of water and the motility of cells.

A spectrum of diversity with reference to time would mean to average biomasses and mortalities over increasingly longer periods, and, in doing so,

iron out small fluctuations. The contribution of resting stages to stability during the cold season is high; although their mass may be not important, their mortality or probability of extinction is also quite small. Regular migration is encompassed appropriately in the frame of both spectra, over space and over time.

Diversity, stability and productivity

Diversity and stability, computed as proposed on different sets of measurements are complementary and together they describe the actual capacity of the ecosystem as a channel of information at the species level, in the proposed form $D = (1/S)$. If stability is very high, diversity is more "valuable".

It has been assumed often that diversity and stability (in the sense of persistence) run more or less parallel. This may repose on empirical evidence afforded by the study of succession, but examples supporting such opinion can be found also in communities actually not linked by relation of succession, for instance, benthic communities are frequently more diverse than planktonic ones and obviously more stable. But I do not see a way to link logically both parameters in a simple way, and it seems that the frequent positive correlation between both -in the sense adopted in the present paper- comes from the correlation between $(r-m)$ and m . r and m design, as usual, instantaneous rates of multiplication and of mortality, but in a rather loose sense, also applied to sets of species and even to whole ecosystems.

Together, diversity and stability are expressions of the degree of organization of an ecosystem. All the known data, albeit in a very general form, point to the existence of definite relations between organization and relative energy flow ~~in~~ in the ecosystems. As a convenient measure we can take the primary production divided by the total biomass of the ecosystem (P/B). For short, and according to the spirit of latin-derived languages, this ratio can be named productivity.

In any comparison between productivity and organization, if we start the

comparison with one of the components of organization, either diversity or stability, the other provides a welcome expansion of the scale. Some trivial examples can illustrate this point. In a chemostat, if flow is accelerated, we can arrive at an unispecific population; its diversity cannot decrease anymore but its stability can still be reduced a bit further, before the population is swept away. A plankton community may attain a diversity of 4.5 bits per individual, and about the same value for the diversity can be computed in a forest. Yet the forest has a much higher stability, as measured by the proposed standard, and the expression $D - (1/S)$ is much more realistic as an expression of the degree of organization than just D , and, more matter of factly, gives a more reasonable number to be compared with P/B . I have pointed out (fig. 1) that spectra of diversity concerning plankton may exhibit an excessive diversity at small ranges, a result from mixing and turbulence; their stability at the same range is extremely low, and the expression $D - (1/S)$ is a much more faithful indicator of organization than simple diversity; in short, it normalizes the spectrum. Deep sea and cave populations are among those of lowest energy flow and lowest turnover, yet, its diversity is not extremely high, at least among cave dwellers. But stability is actually very high, and again the expression $D - (1/S)$ appears much more meaningful than just D in what concerns general organization and relations with energy flow.

In general, diversity is negatively correlated with productivity, but it is not possible to understand the relation without considering change, that is, without a dynamic model. Placing the events in a temporal perspective, an increase in productivity means a decrease in diversity, independently of the present numerical relationship between both ~~parameters~~ quantities. Adequate evidence is found in situations of rapid change, as in plankton cultures or in chemostats. Any sudden increase of the total biomass is unevenly partitioned among the different species and diversity drops.

It is easy to develop conceptual models: Net rates of increase may be rank correlated with the number of individuals of the set of species, and if they are not, soon they become correlated. Any increase in total biomass makes that the relative abundances of the different species come apart; another contribution to the decline of diversity comes from the species dependent on others, and with time lags in their responses. In the expression of diversity using factorials, it is simple arithmetic to follow the changes step by step, each step consisting in the addition or separation of one individual, or in the substitution of one individual of one species by one of another species; the substitution of an individual of a rarer species by one of a commoner species decreases diversity, and viceversa.

The comparison between diversity and productivity in assorted ecosystems (fig. 3) has also some interest in what concerns definition and nomenclature of stability. In one end we may have great changes in productivity associated to quite small changes in diversity, that is always rather low and this is the domain of adjustable stability, or low stability in the nomenclature adopted here. In the other end, small changes in productivity are associated with considerable changes in diversity, and this is the area of conservatism, persistence or "true" stability. The general pattern of relations suggest rather a semilogarithmic function, but is clear that different kinds of ecosystems fall on different functions (fig. 3).

We arrive at the same semilogarithmic relation through another way. Returning to the model of a changing ecosystem, assume that, after increasing suddenly, the rate of change of the biomass is kept constant (we can put $r-m = k$), then diversity, after the initial drop, remains constant, representation of the different species is stabilized and the system has caught on in a regime of change. Acceleration of the biomass (we could write $d(r-m)/dt = k$) leads to a sustained drop in diversity. Elsewhere ¹² I have tentatively related derivatives with respect to time of biomass and diversity, but without being satisfied. The suggested expressions and the precedent comments can be summarized writing simply

$$D = K - (r - m) , \quad \text{or} \quad D = K - \ln \left(\frac{P}{B} + 1 \right) + m$$

This expression is written using the different symbols in a not very definite sense, and representing averages over whole systems or part of systems. K is a constant; r and m ~~xxxxxxx~~ are instantaneous rates of multiplication and of mortality, with the convention that $P/B = e^r - 1$.

The changes of diversity so far discussed do not imply changes in stability. Stability can be introduced in this expression if we remember that $1/S$ is a measure of the rate of mortality m , and this is most clear in the hypothesis of one single species. We are led in consequence to write

$$D - \frac{1}{S} + \ln \left(\frac{P}{B} + 1 \right) = K$$

where, in the maximal degree of maturity, $S \rightarrow \infty$, $P/B \rightarrow 0$, and $D \rightarrow K$; so that K can be considered as the superior limit of diversity (five ?).

We can put also $P/B = (P/R) \cdot (R/B)$, leading to write

$$D - \frac{1}{S} + \ln \frac{P}{R} + \ln \left(\frac{R}{B} + \frac{R}{P} \right) = K$$

where often $\ln(P/R) = 0$.

This expression is consistent with many empirical relations, but has also some difficulties. Essentially it embodies nothing new, but as it relates four parameters (D , S , P , B) of paramount signification in ecology, all ~~xxxxxxx~~ of them measurable independently, ~~xxxxxxx~~, it can be tested and perhaps prove useful for prediction and for the indirect estimation of some of the parameters. Here the expression is proposed only to serve as a starting point for discussion. At this stage, the form of the expression is only tentative. Empirical evidence will introduce modifications or reject it altogether.

In what concerns the relations between diversity and stability, the expression embodies my opinion that they repose on the fact that species with a higher turnover react quickly to environmental change, that is, in the usual correlation between $(r-m)$ and m .

The study of organization in space.

Any expression of the sort of the one proposed would remain inoperative so far it is not able to take into account that ecosystems are spatial structures as well as temporal ones. Perhaps one dimension of space (one to begin with) can be introduced in expressions using derivatives, like the following one

$$- \frac{dD}{dx} = \frac{dB}{dt} \cdot \frac{dB}{dx}$$

As other expressions suggested along this paper this one has no pretence; it is just shorthand for ecological reasoning and sets the possibility forth of enlarging the validity of the expression proposed in the last section. As the last expression stands, it is obvious to see that according to the value of dB/dt , superior or inferior to zero, we may have parallel or crossed gradients in diversity and biomass. If production decreases, gradient of diversity may be parallel to the gradient of biomass, but if the biomass is increasing, the gradient of diversity will be probably opposed to the gradient of biomass. Comparing transects in the margin of fertilized and unfertilized fields, one gets the impression that this is precisely what happens.

A very general approach that has the advantage to be ~~uncomplicated~~ unsophisticated consist in adding over large spaces of expressions valuable in smaller spots, following of the form, with K constant (non summable):

$$D_1 = \frac{1}{S_1} + \ln \frac{P_1}{B_1} + \ln \left(\frac{R_1}{B_1} + \frac{R_2}{P_1} \right) = K$$

$$D_2 = \frac{1}{S_2} + \ln \frac{P_2}{B_2} + \ln \left(\frac{R_2}{B_2} + \frac{P_1}{R_2} \right) = K$$

It is easy to see that this process of summation implies that if productivity is uniform over a large space, and diversity does not increase further as the area is enlarged, this should be linked to an increase of stability if the expression must hold. On the contrary, if diversity keeps increasing, as in the case of communities of different composition mixing along a boundary, stability should decrease. In general, in an area of uniform productivity (P/B), local differences in diversity (stability) should be associated with opposite gradients in

stability (diversity).

Two subsystems may be in such relation together that they exchange production, and the values of P/R are complementary in them. To remain in equilibrium it is postulated that the one having the larger value P/R (the more autotrophic) should have a lower value of diversity or a ~~greater~~ ^{lower} stability, and possibly both. In the coupled, heterotrophic, system, diversity may be high (dystrophic lakes) or low (polluted water), but diversity and stability may be strongly dependent on the quotient R/B, usually very high in such situations.

In general the expressions seem to fit quite well to the behaviour of ecosystems.

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Figure 1

Figure 1. Averaged diversity for ~~various~~ phytoplankton populations pooled over spaces of increasing dimension, in two neighboring segments of a square intensely sampled. Western Mediterranean, July 1968. The populations in the inferior NW section were rich in diatoms, with an exaggerated diversity at the lowest range of ~~size~~ sample size. The populations of the upper SE section were rich in dinoflagellates, giving a "normal" spectrum of diversity.

Figure 2. Left, a mapping of stability. States inside the area A are spontaneously interconvertible; if the system is led inside the area B from here it can regain the area A. Right, in the small square a system of equations of the form $dN_i/dt = e_i N_i + \sum a_{ij} N_i N_j$ should be imagined. The changes in N_i act as inputs for further change. Change of the magnitudes not accounted for may be considered as a test for stability.

Figure 3. Approximate relations between productivity (primary production per total biomass) and diversity in a number of typical ecosystems. The scale of productivity has been cut diagonally. The concept of stability is necessary to give more consistency to the expressed regularities.