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HOW TO INTRODUCE CONNECTANCE IN THE FRAME OF AN EXPRESSION FOR DIVERSITY

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Two frequently used indices of diversity are: the index borrowed from information theory, $H = -\sum p_i \log_2 p_i$, and Simpson's index, $S = \sum p_i^2$. We take the individuals as elements, and the species or reproductive units as subsets. The probability of each particular individual belonging to species i is p_i and $\sum p_i = 1$.

The numerical value of Simpson's index is inversely related to the naturalistic or intuitive quantification of diversity, and, for common use, diversities are expressed as $1 - S$, or as $1/S$. We propose to combine both ways, in a new expression $D = (1 - S)/S$. This expression is the ratio between the probability that two individuals, taken at random, are of different species, and the probability that they belong to the same species. It is an expression of the maximum possible number of interspecific interactions measured against the maximum number of intraspecific interactions. To emphasize this meaning it is convenient to write the index as follows

$$D = \frac{\sum_{i \neq j} p_i p_j}{\sum p_i^2} \quad (1)$$

It is difficult to obtain homogeneous quantitative information about interspecific interactions in nature. Perhaps data on flowering plants and their insect visitors would be suitable to help develop this model (Margalef 1980). For the moment, in order to give some substance to an exercise in speculation that we hope will be applicable to ecosystems, we have considered "second-order organisms" subjected to Darwinian evolution, viz., electronic circuits and mechanical models made with construction toys in which connections between elements are evident. We have studied 78 electronic circuits and 104 Meccano models taken at random from manuals or from information accompanying different instruments. The range of compositional richness of the electronic systems spans from 2 to 222 kinds of different parts or different sorts of components; the range is from 4 to 109 in the Meccano systems. Diversity has been computed on the distribution of all parts into the different sorts of components.

Both H and D have also been computed for a number of samples of phytoplankton (fig. 1). Correlation is good (see fig. 1) and it is appropriate to compare H with

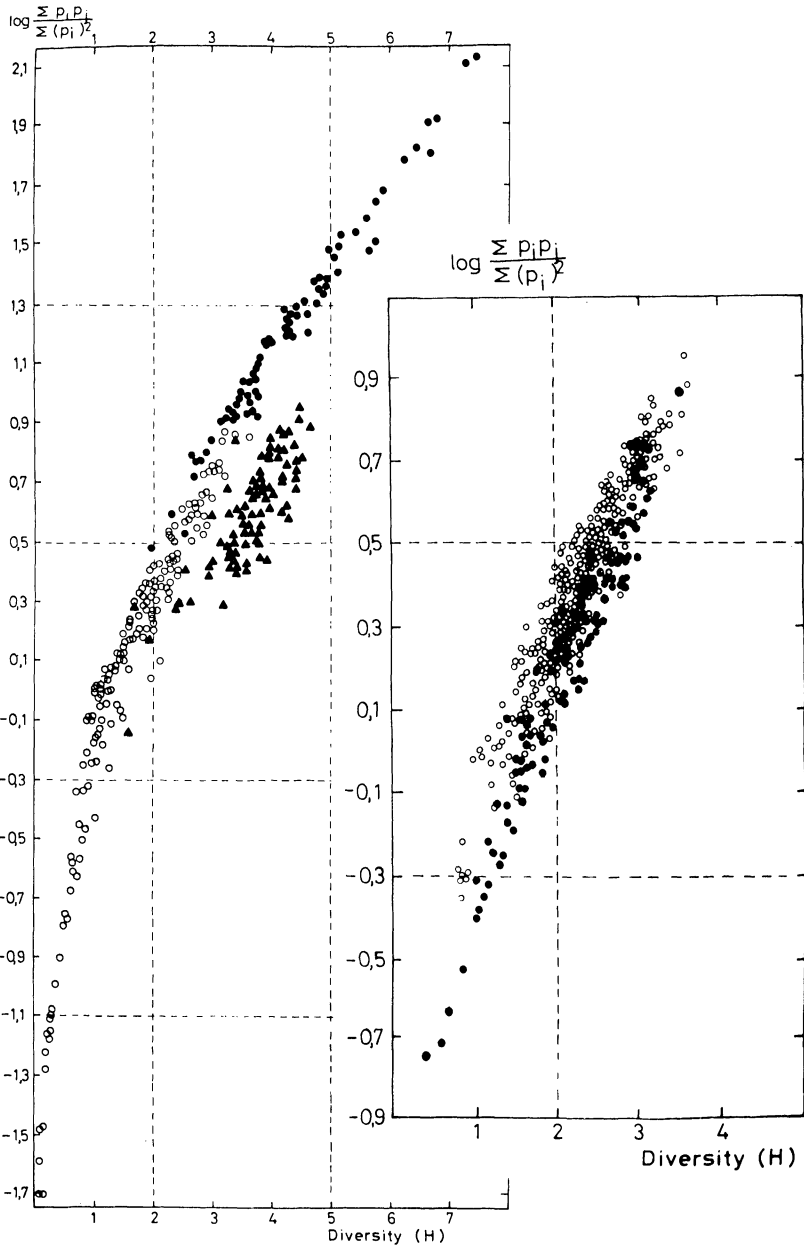


FIG. 1.—Values of Shannon's diversity (H) and of the log of the new index of diversity D , in a number of communities and artifacts. *Right*: open circles = marine phytoplankton populations of NW Spain; solid circles = phytoplankton populations in marine microcosms. *Left*: open circles = Mediterranean phytoplankton; solid circles = electronic circuits; triangles = functional models made of Meccano parts. Note the different scales.

$\log D$, as could be expected from the construction of the respective indices. Besides, we have computed diversities for the two sets of artifacts: working models assembled with parts of the construction toy, Meccano, and standard electronic circuits. The concepts of diversity and of connectance can be applied to any system made of discrete elements, with specific connections among the parts, that has been subjected to a process of selection, effective both at the level of the components and at the level of the system. The systems represented by electronic circuits tend to have rather high values of diversity and it is easy to provide an explanation. Small electronic components, such as resistors, are not assembled combining standard values—they may be so if the models are constructed with materials contained in multipurpose boxes—but are made to required specifications, because they are cheap to produce. The result is a large number of “species” represented by single individuals, that would not have much chance to breed and survive if they were biological species. The construction and evolution of integrated circuits suggests new lines of thought important in theoretical systems theory, and probably also in biology. Spare and interchangeable parts in a construction box are much more like biological species; they should be versatile enough to be used in the construction of a number of models, a condition that the parts have to fulfill in order to be maintained in the production line.

The mass action law makes probability of reaction proportional to the concentrations of reactants. Expressions like $N_i N_j$, or $p_i p_j$, introduce such an assumption in ecology. But, as a matter of fact, intensity of interaction is not necessarily related to the probability of encounter, and probability of encounter may differ from the product of the respective densities. A factor of activity, a_{ij} , needs to be adopted; if $a_{ij} = 0$, species i and j are unrelated, if $a_{ij} = 1$, the species are connected and interaction is proportional to the product of their respective densities. The distribution of the values of the a_{ij} 's is an expression of the connectance of the system under consideration.

If the values of a_{ij} for each interspecific combination are introduced in expression (1), we have

$$D_c = \sum_{i \neq j} a_{ij} p_i p_j / \sum p_i^2, \quad (2)$$

a new index that compares the actual interspecific interactions against the intraspecific ones. These, if necessary, could be adjusted also with specific coefficients a_{ii} . The expression (2) divided by expression (1) provides an index of connectance

$$C = \sum_{i \neq j} a_{ij} p_i p_j / \sum_{i \neq j} p_i p_j = D_c / D. \quad (3)$$

The index of diversity (1) represents the upper limit of a measure of the capacity of the system to construct a net of relevant interactions, and in our opinion this is an advantage, since it relates two concepts that in the past have led to disagreement. See Gardner and Ashby (1970), May (1972) among others.

It has been argued that high diversity systems might be unstable, and should simplify themselves and decay. This reasoning is based on the erroneous assumption that all possible interactions are realized. Actually, interactions in the ecosystems are restricted and more or less hierarchical; there is a definitely structured net of interspecific interactions that covers only one fraction of the grand total of possible connections. McNaughton (1978), among others, gives attention to this subject and finds that in any natural communities only about 60% of the possible links materialize.

We briefly have considered connectance in relation to the synthetic study of electronic circuits. Any large electronic circuit, if its assemblage is justified—that is, if it has passed “natural selection”—must have a limited number of connections. Otherwise it is short circuited and useless.

The connectance has been computed as the fraction of the realized connections against the total number of theoretically feasible connections between parts [$n(n-1)/2$]. The expression (3) represents a weighted average of the connectivity in the system, and can be compared advantageously with the expression of connectivity that results from dividing the number of actual links by the number of possible links. It is convenient to keep both converse interactions, a_{ij} and a_{ji} , because the coefficients may be different (De Angelis 1975). To a dog, a tree is a different thing than a dog is to a tree. For our particular set of electronic circuits, the following empirical relations have been found:

$$\log D = 0.2907 H - 0.3503 \quad (r = 0.987) \quad (4)$$

$$\log C = -0.29 H + 0.554 \quad (r = 0.925) \quad (5)$$

$$\log D + \log C = 0.2037 \quad D_c = D \times C = 10^{0.2037} = 1.5984, \quad (6)$$

and from expression (5) the following relations can be illustrated

diversity, H	connectance, C
1.91	1.0
4.59	0.6
5.35	0.1
→ infinite	→ zero.

The relations observed in electronic circuits may provide hints of what, perhaps, can be expected also in other systems, particularly, in ecosystems. The inverse relation between (total) diversity and connectance probably holds also for biotic communities, although the constants might be different. At least such sort of relations (fig. 2) are consistent with the fact that functional segregation in the ecosystems breeds diversity. Completely unrelated individuals could belong to an indefinite number of species. Of course, such assemblages do not exist, exist only in museums, or in any case, would not qualify as systems. Connectance is positively correlated with a weighted expression of turnover (primary production/total biomass) and here we have another way of access to the self-arrangement of parts in a system that remains functional.

The product of the connectance (C) by the number of species, or of kinds of parts in the artifacts, tends to fall inside a rather close range of values. For our electronic circuits, it is between 2 and 6, in most cases around 4, and it reaches up

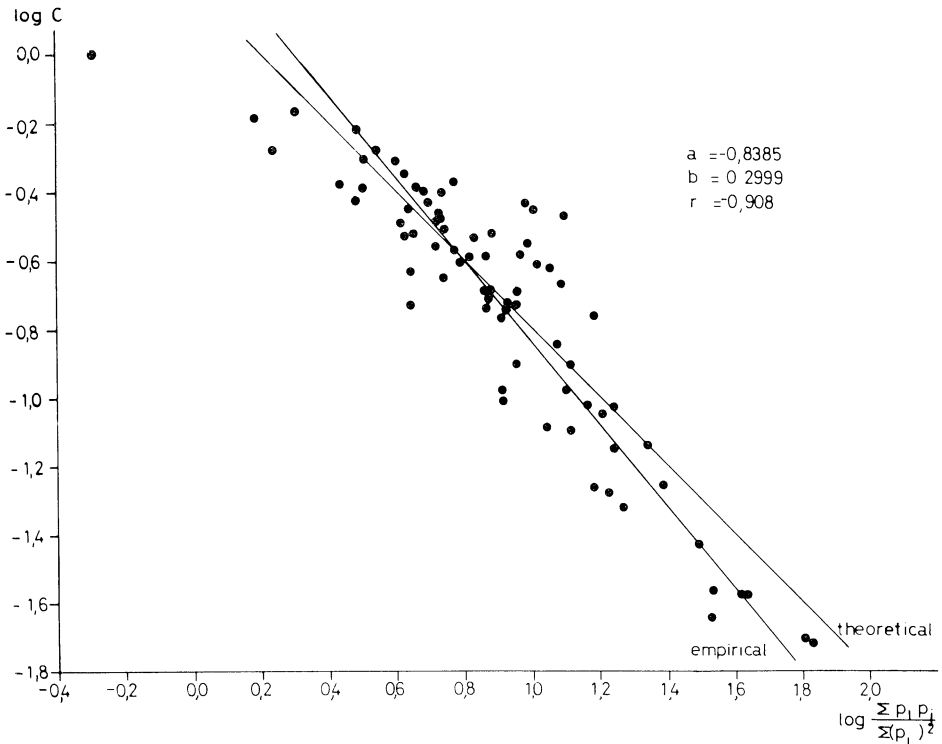


FIG. 2.—Relation between diversity (as $\log D$) and connectance (C) in a series of 78 electronic circuits of different complication.

to 12 only if diversity is high (H higher than 5). This can be related to some findings in natural communities. McNaughton (1978) has related connectance and number of species; for 31 communities composed of plants and phytophagus animals, Rejmánek and Starý (1979) found that the product connectivity \times number of species always remains in the range from 2 to 6. In the same way the a_{ij} 's values (specific connectance) that affect every couple of the different interacting components notably reduce the variance of the diversity indices. In this case we have worked with expression (1), because with this expression we can insert these values independently for all connected couples of components that we have computed for the 78 electronic circuits systems (fig. 3).

Everything that has been published before about the serious limitations of point diversities and in favor of the appropriate expression of its spectral quality must be extended to the connectance. This becomes more necessary when, as in our proposal, we choose a common or related quantitative frame to express both measures.

The elements of the electronic circuits are either connected $a_{ij} = 1$, or disjoint $a_{ij} = 0$, or not directly connected. Ecosystems include a further complication. Not many organisms of different species are permanently connected as are certain parasites, mycorrhizae, etc. The rule is that the interactions between individuals of

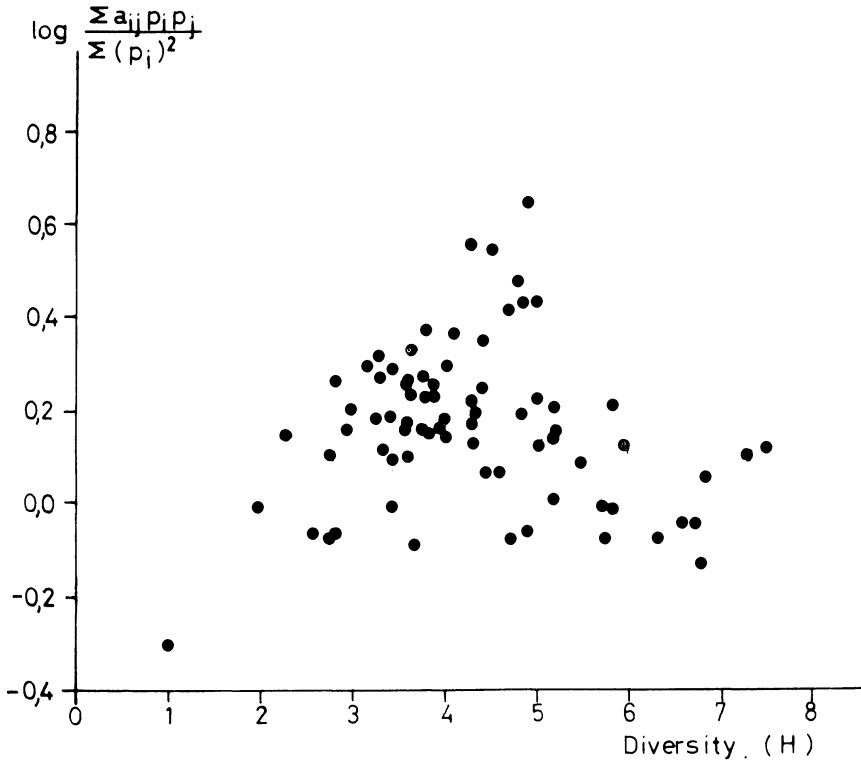


FIG. 3.—Product of diversity (D) \times connectivity (C) as compared with the diversity computed according to Shannon's expression (H). Set of 78 electronic circuits. The variance of the product $D \times C$ is rather limited.

different species, and also of the same species, are discontinuous or intermittent. The length of the periods of separation depend on life histories, motility, accumulation of reserves, total length of life, and so on. Such intermittent contacts make smaller the numerical expression of the connectance of the system. It is assumed that a system of high diversity, to persist for awhile, must have a low connectance. If it is so, it may be concluded that the temporary character of most contacts among species, a natural consequence of the discontinuity of life and the discreteness of individuals, becomes a powerful agent of stabilization. The game is slowed down and lasts longer.

SUMMARY

Systems made of parts that are totally connected do not work, neither ecosystems nor artifacts. Relative connectance is inversely related to diversity, and both magnitudes can find a common frame of expression, in which some constant expressing the constraints of any organization might be embodied. If S is Simpson's index, the expression $(1 - S)/S$ as a measure of diversity offers some advantages or, at least, helps further reasoning. Such expression is the ratio

between total interspecific possible interactions and possible intraspecific interactions.

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