INFORMATION THEORY IN ECOLOGY*

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Mathematics presently used by the biologist and its inadequacy

The naturalist, as he usually expresses it, uses mathematics as an instrument and as a language. As an instrument, statistical methods have increased the precision with which observations are developed, described, and interpreted, exercising a salutary critique on the hypotheses that are precipitated therefrom. As a language, mathematics permits the biologist to formulate his working hypotheses in the form of mathematical models capable of quantitative corroboration. Expression by means of mathematical symbols frees us from the dangers of the rhetorical inertia of our verbal reasoning and allows us to advance more surely and rapidly in the development of our science. Among other branches of biology—and perhaps more than the other branches—ecology, whose object of study is the development and distribution of life in the completely natural state, and consequently the relations among organisms and between them and the environment, places much hope upon precise quantitative expression. It is not surprising that the ecologist, particularly, appreciates the effective assistance of mathematics.

The reduction of vital facts to mathematical symbols presupposes an abstraction and a consequent loss of a series of attributes of whatever is being considered. Therefore, every mathematical representation will be incomplete, reflecting only one viewpoint of the situation with which Nature confronts us, and indeed, it will frequently be possible to construct independent mathematical models on a single set of data according to the attributes we choose to consider. Both in statistics and in analysis, each individual or each event is an equivalent element in the totality of cases and must, for purposes of mathematical expression, be considered identical and interchangeable. To this day, mathematics applied to biology has worked with quantities, and the relations among these quantities have been established as such, and not according to special interactions or orderings of the elements in any particular grouping. This statement will be made more clear by an example.

Let us consider the expressions of Volterra (1926) and of other authors, proposed with similar finality, which describe and predict the dynamics of mixed populations. We may refer, as an example, to two species represented respectively by A and B. Each of our two groups possesses certain properties relating to its rate of increase and its total action on the other group. However, this formulation is not concerned with the fine spatial and temporal structure which combines the individuals of the specific populations into a mixed population. It may break down, therefore, and does, in effect, when reality differs from a crude model such as one representing a scarcely natural, totally effective predator and a prey of equally schematic character, or any other similarly artificial system. The ideas of Slobodkin (1953) on an algebra applicable to the study of population dynamics and the works of Wangersky—partly unpublished on a similar theme, carry considerably more promise, although at the cost of complications of calculation, enough to rather frighten the biologist. He feels that new paths might be sought instead of just deepening the ruts of the old roads. He asks of Mathematics new methods more relevant to the gray areas, methods which allow a better appreciation of the qualitative and which are directed toward the broadest and deepest understanding of life phenomena. If such methods were derived from statistical considerations and based on something simply descriptive that would permit us to express flexibly and in common language facts relating to structure and to its changes, without requiring a working hypothesis of the analytical type nor the introduction of new concepts, the advantage would be double. The biologist aspires to a condensed description of his reality that will permit its incorporation into a more comprehensive intellectual structure; but he wants the data which constitute his point of departure to preserve some of life's characteristics and not end up transformed into a handful of cold ashes. His goal is to capture the sensation of a living thing in the framework of a formula, within the rhythm of intellectual constructions, with the skill that Alcover praises in the poet:

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INFORMATION THEORY IN ECOLOGY

You who imprison the dragonfly in the
frames of rhyme,
Who grasp it so delicately by the wings
That not an atom of their shimmering
fragility is lost.

Information theory.

There has recently developed with surprising speed a branch of mathematical sciences called "information theory." When a word of common usage is taken to designate a scientific concept, its specialized change of meaning may appear uncomfortable to someone unfamiliar with its new role. In this case the divergence in meaning is small. To inform means first and last to give notice of something and information theory, based on statistical considerations, is concerned with how data are transmitted, ignoring, however, any human factors involved. That is to say, the theory remains a theory of information and never becomes a theory of knowledge. If the name is not too fortunate, this is because of the speed with which the new discipline, hardly twenty years old, has conquered new fields of science. The word "information" has the virtue in any case, of suggesting the idea of a message, of communication, of description by means of a combination of symbols. The same theory allows us to estimate the information value—the value of a thing a priori improbable, whether we approach it from the starting point of total ignorance or of a certain degree of knowledge regarding the universe of which it is a part—of any combination of symbols existing in time or space.

It is well to keep in mind some fundamental ideas, including an exact definition of what is understood here as "information" and how it may be evaluated quantitatively. We are confronted with a given situation, the details of which we do not know and about which we can imagine a certain number of possibilities. The number of possible solutions is reduced as the information we have about the situation increases. When this information is sufficient, only one possibility remains, of a probability equal to unity. The information is evaluated quantitatively as a function of the ratio between the number of possible answers before and after the information is received. In other words, the information is considered as a function of a quotient of probabilities—of the probability after the "message" is received divided by the probability before its reception. The probability is the reciprocal of the possible selection.

To make the information acquired in independent operations additive, a logarithmic function is chosen. Thus, the information (I) which permits us to reduce from R_0 to R_i the number of possible states of a given system is

$$I = K \ln(R_0/R_i)$$

If the information is sufficient and definitive in the sense that only one possible state remains ($R_i = 1$),

$$I = K \ln R_0$$

in which K is a constant and R_0 is the number of choices possible and equally probable, $1/R_0$ being the probability of each one. The unit of information generally used is the bit or binit, which defines two equally probable alternatives. Thus, in the final case we have

$$I_{(bits)} = \log_2 R_0 = 1.443 \ln R_0$$

In the last decade a considerable number of works have been published on information theory, and articles in Spanish journals have not been lacking. Nevertheless, the major part of what has been written has to do with those aspects relating to mathematics, physics and communication theory. Its application to biological problems of various nature is very promising, and initial trials seem to guarantee the success of the application of the new method to many old problems. I refer to the comparison of the information series and of regulation mechanisms with the function of nervous system (Wiener) and with the fluctuations in natural populations (Doi), to the efforts to evaluate the content of information in various biological systems (Branson, Linschitz, etc.), to speculations on the way life uses the information contained in the molecules of chromosomes (Gamow), to exploration of the specificity of yeasts (Quastler), to the description of ontogeny and phylogeny in terms of information theory (Jacobson). The above list is incomplete, but undoubtedly stimulating.

In the study of communities of organisms, in expressing the distribution by species of individuals in them, there have been used for some decades concepts which plainly fully belong to information theory (the "indices of diversity"), although this had not been recognized expressly until he who speaks to you did so (Margalef, 1956b). On being placed within the general framework of information theory, they acquire new significance and confront us with a vast field of new possibilities, for the application of principles and methods elaborated in other areas of the theory readily follows.

In a meeting organized by the Scripps Institute of Oceanography and the Office of Naval Research of the United States in the spring of 1956, I applied some concepts of information theory to the structure and dynamism of mixed populations or communities or organisms, and I could see how this aspect, secondary for me then, was

what aroused the greatest interest in an audience formed of persons so qualified as to not express a reaction lightly, especially since they represented very diverse scientific specialties. In the same meeting, convened expressly to discuss "Perspectives of Marine Biology," the need for a mathematical approach, and not just the traditional statistical one, to the problems of marine biology was plainly seen, and pure mathematicians were invited to explore new methematical models, some of which might aid biologists in formulating their hypotheses, thereby bringing themselves nearer to the methodology of physical oceanography.

These comments explain the choice of topic for this paper and I shall attempt to discuss and develop in it, somewhat more, aspects which until now have been viewed as accessory. The perspectives seem vast to me, for one idea suggests another. But my rudimentary knowledge of mathematics will cause my exposition to appear crude and inelegant, justifying the slight esteem which those who cultivate more exact sciences currently show toward the reasonings of biologists. Moreover, many biologists, especially those who work on a morphological, descriptive level, scarcely attempt to dissimulate the disdain they have for the recourses they could obtain from mathematics. I am fully conscious, then, of the risk of displeasing both mathematicians and biologists. It is a consolation that the pure mathematicians are beyond taking offense, if, as I remember having read, pure and applied mathematicians have never felt nor can ever feel hostility toward one another since they have nothing in common. I hope the biologist, and especially those who cultivate ecology, will take note of the possibilities which information theory offers in their field of activity and that the investigators in applied mathematics will take sufficient interest in our problems to favor us with theoretical developments adjusted to our necessities.

Description of mixed populations in terms of information theory

How information is obtained about a community, and its measurement

The chief interest of information theory is not found now in its temporal series, in the relationships between information and "noise," etc., that are of so much importance in communication, cybernetics, and physiology of the nervous system, but rather in those aspects of it which enable us to measure the order—information or negenthropy—or disorder contained in spatial or temporal structures. To enter into the subject we use an example which will be recognized at once as a type of information series—the process followed by the ecologist in identifying and describing the most apparent type of biological structure: a community of organisms or a mixed population with many species—that can as well be a forest as a sample of plankton—in which we go about identifying successively and noting down one individual after the other, randomly or following a given profile or transect. We identify the individuals, then, as they present themselves to us, and if we identify with the same letter all those belonging to the same species, we obtain a series of the type a b c a d e b a a c . . . . . , or something similar. Each symbol has a different qualitative value and the series formed by the symbols describes a structure for us better if they result from a survey planned ahead of time to take samples as they come rather than from proceding to modify them continually according to our pleasure at the time the exploration takes place. The structure exists in the separate representation of each species and in the spatial relations among individuals of the various species. If our symbols carry subspecific information—age and degree of vitality of the individuals—so much the better proportioned is our description. It might even reach the point where each animal or each plant is recognizable, being individually characterized. In one form or another, the series is a "message" containing information descriptive of the community.

Although it is true that the works of your speaker are the first in which the relation of information theory to the description of natural communities is pointed out and older concepts—indices of diversity—are placed within, and made use of within, this new point of view, whatever credit I might claim for this is reduced to a minimum when I confess that the stimulus for it came from my reading a work of Branson (1953b) on the information contained in protein molecules considered as messages in which the various amino acids are so many symbols. The idea occurred quite naturally to me to compare the amino acids to individuals and the whole molecules to communities in equilibrium made up of many individuals of different species; this then led to considerations more or less removed from those of Branson.

Knowledge of the structure of our mixed population and the acquisition of the corresponding information can be accomplished in several successive stages. It is important to recognize this fact. Establishing the limits of a study before it is undertaken is an arbitrary act which does not shut out information, but which limits the quantity of information we are able to obtain. Thus, if a system that we have limited consists of N elements (individuals); these may be arranged in N ! different ways and once the position

of each one is established in the series, we have an amount of information

$$I = K \log_n N !$$

If we remember that information is equal to the logarithm of the number of possible arrangements and, expressing it in bits and using the approximation of Stirling, we get

$$I = 1.443N(\log_n N - 1)$$

For very long series it has become customary to write

$$I = 1.443 \log_n(N^N)$$

per individual; then information is

$$I_N = 1.443 \log_n N$$

As we shall see presently, this is a minimum estimate of the total information, because the distance that separates some individuals from others in Nature is not constant and represents an uncertainty which, for the moment, we pass over.

The process by which we obtain the quantity of information expressed by the above formulas may be broken down into: 1) counting the number of species, 2) counting the individuals belonging to each species, 3) locating the individuals in each species, and 4) completing their localization by characterizing them individually. The number of species (S) may vary from one to N; when we know what it is, we establish one of N possibilities and the total information obtained is

$$I_1 = 1.443 \log_n N$$

When the number of individuals in each species is known and is neither 1 nor N, the selection is effected among the number of combinations of N - 1 elements taken S - 1 at a time, and the total information possessed is

$$I_2 = 1.443 \log_n \frac{(N - 1) !}{(N - S) ! (S - 1) !}$$

Once localization by species is accomplished, but without distinguishing among the individuals, either because it is not possible or because it is not important to the purpose of the study, certainty is to be had within a total of $N !/N_1 ! N_2 ! \ldots N_s !$) possibilities, in which $N_1, N_2, \ldots N_s$ are the numbers of individuals in each of the different species. Total information obtained is, consequently,

$$I_3 = 1.443 \log_n \frac{N !}{N_1 ! N_2 ! \ldots . N_s !}$$

The last step possible, localization individual by individual, gives us the total information we had set for ourselves at the beginning.

It is important to realize that it is not necessary to obtain a given information in order to measure it. Thus, from the very beginning we are capable of knowing the total information the complete study of the community in question will supply us ($I_4 = 1.443 \log_n N !$) and, upon counting the number of individuals in each one of the species, we know at the same time the information which the structure contains by species in the community (I_3) which, perhaps, is the most interesting value of the four we have considered.

Each one of the above values can refer to an individual, that is to say, it can give the mean information content per individual, which is obtained through dividing by N the expressions indicated, as was done in the first. It may also be useful to employ another type of relative values, for example, the ratio between the information I_3 and the maximum information I_4, which amounts to considering each individual as belonging to a different species, or the ratio between I_3 and a hypothetical information as in the case when all species are equally frequent:

$$I_{3'} = 1,443 \log_n \frac{N !}{[(N/S) !]^S}$$

It must be remembered that information has additive properties. If we know the number of species (I_1) and pass on to the study of the relative representation of each one of them (total I_2), the information that we have gained by our inventory is $I_2 - I_1$, or,

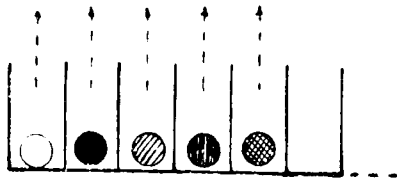
$$I_2 - I_1 = 1,443 \left(\log_n \frac{(N - 1) !}{(N - S) ! (S - 1) !} - \log_n N \right)$$

Moreover, the information obtained is independent of the manner in which the process of its acquisition is broken down.

What has been said is valid, in general, for any group of objects or of symbols (Fig. 1 on following page) and, therefore, is applicable to any form of writing. We have, for example, a line of text with N symbols; the maximum information it can contain is

$$I_4 = 1,443 \log_n N !$$

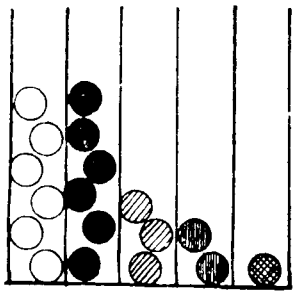
We can follow the same steps as when we study a mixed population (Fig. 1): ascertain the number of letters, determine their respective frequencies and study their sequence. If the letters are equally frequent, the expression I_3 takes us, through employing Sterling's approximation,



Up to 5 species known

I = 0.23 B/1

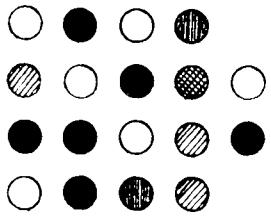
There are 5 symbols



Count the individuals in each species

I = 0.62 B/1

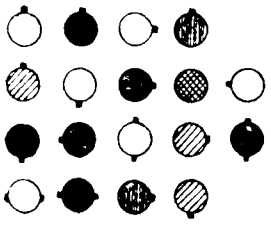
Their frequencies are unequal and must be determined



Localize by species

I = 1.66 B/1

ABADCABEABBACBABDC



Localize by individuals

I = 2.93 B/1

AβADCAβEAβBACβABDC

Fig. 1. Example of the successive stages that can provide all the information possible in a community formed of 18 individuals that belong to five species (left), not taking into account the information contained in the possible inequality of the distances which separate the individuals from one another. The "individuals" are represented by means of circles, variously shaded or striped according to the "species." When we are able to recognize the individuals, we distinguish one from another by the direction and number of the black peripheral markings. At the right the same example is reduced to a sequence of letters which, on the bottom line, are also individually recognizable. Information is given in "bits" per individual.

valid for fairly high values of N and of S, to

$$I_3' = 1{,}443 \log (S^N)$$

When the symbols (letters or individuals) are not equally frequent, the information contained is that which corresponds to I_3, less than I_3'. Then we can employ the expression

$$I_3 = 1{,}443 \log(S^{bN})$$

in which b is a positive constant less than unity, the value of which depends on how the symbols

are distributed in classes (individuals in species). This constant b has been employed in the analysis of writing from the point of view of information theory, and its value varies from one language to another. Theoretically, languages in which it has a high value can transmit a greater quantity of information with fewer printed letters. It is of interest to us because in some cases it may be useful to express the information I_3 in terms of the maximum possible information, assuming that all the species are of an equal frequency. It is easy to derive

$$I_3/I_3' = b$$

Two practical examples will help establish the ideas expounded.

Examples of the calculation of the information obtained in successive stages of the study of natural communities. Phytoplankton from the mouth of the Vigo river. Two samples taken with an interval of 10 days (Fig. 2), on following page.

Sample A. May 6, 1953. 1,032 individuals distributed in 21 species, N = 1,032, S = 21. The frequencies of the different species (N_1, N_2 . . . N_s) are: 500 : 152 : 109 : 87 : 61 : 51 : 12 : 12 : 9 : 8 : 8 : 4 : 4 : 4 : 2 : 2 : 2 : 2 : 1 : 1 : 1.

Operation	Calculation	Information in bits: Total	Information in bits: Per individual
Count the number of species . . .	$I = 1{,}443 \log n\ 1032$	11,5	0,01
Distribute the individuals according to species	$I_2 = 1{,}443 \log n \frac{1031!}{1011! \times 20!}$	144,6	0,14
Localize the species	$I_3 = 1{,}443 \log n \frac{1032!}{500! \times 152! \times .}$	2550	2,47
Localize species of equal frequency (hypothetical situation)	$I_3 = 1{,}443 \log n \frac{1932!}{(49!)^{21}}$ (b 2550/4470 = 0.57)	4470	4,32
Localize the individuals (maximum information)	$I_4 = 1{,}443 \log n\ 1032!$	8840	8,67

Sample B. May 16, 1953. 631 individuals distributed in 17 species. N = 631, S = 17. Represents a volume similar to that of sample A. The frequencies of the different species (N_1, N_2, . . N_s) are: 504 : 52 : 15 : 14 : 10 : 7 : 7 : 4 : 4 : 3 : 3 : 2 : 2 : 1 : 1 : 1 : 1.

Operation	Calculation	Information in bits: Total	Information in bits: Per individual
Count the number of species . . .	$I_1 = 1{,}443 \log n\ 631$	9,3	0,01
Distribute the individual according to species	$I_2 = 1{,}443 \log n \frac{630!}{614! \times 16!}$	93,5	0,15
Localize the species	$I_3 = 1{,}443 \log n \frac{631!}{504! \times 52! \times .}$	827	1,39
Localize species of equal frequency (hypothetical situation)	$I_3 = 1{,}443 \log n \frac{631!}{(37!)^{17}}$ (b = 827/2550 = 0,32)	2550	4,03
Localize the individuals (maximum information)	$I_4 = 1{,}443 \log n\ 631!$	4990	7,92

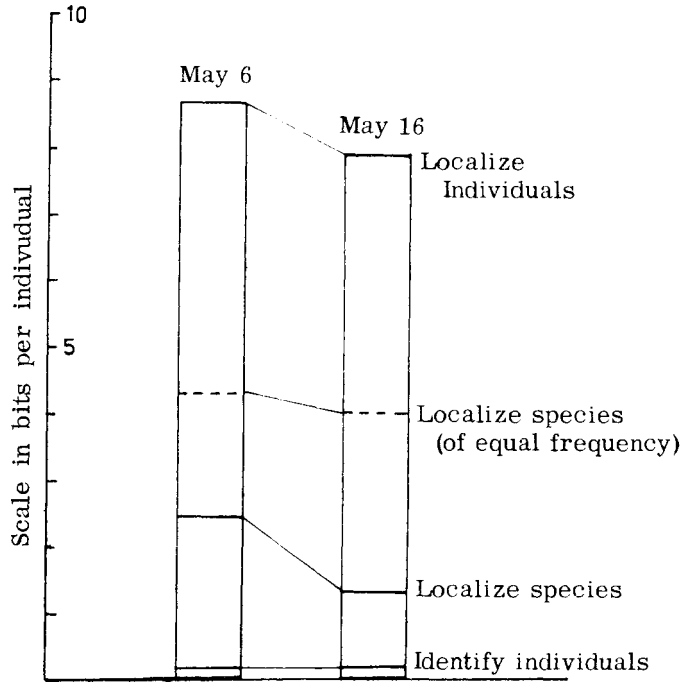


Fig. 2. Graphic representation of the information accumulated in successive operations (detailed at the right) of the study of mixed populations of phytoplankton. The levels of the lines represent purely hypothetical situations. See Text.

Information having to do with the distances between symbols

We have witnessed the transformation of a community of organisms into a temporal series by means of our nervous system, which can only function in this way, effecting one identification after another. This temporal series can represent an instantaneous structure, as when we analyze a sample of fixed plankton or take the inventory of a forest whose plants are not visibly growing.

From a practical point of view, the structure of natural communities can oscilate between two extreme types. The most simple ones are those constituted by moving organisms or organisms without active movement suspended in a liquid, in which their respective positions continually changing can be viewed with a certain indifference, except when colonies or epibiosis are formed with more or less rigid mechanical relations in a part of the total mixed population. The other extreme is represented by rooted vegetation where the different individuals occupy positions definitely relative to one another that are fixed, the spatial structure arising from intimate relations in the putting forth and development of roots, branches, etc. Animals, in the main, occupy a position intermediate between these two extremes.

If we note carefully, the problem is always the same; what varies is the value of time in relation to the possibility we have of studying the system. Plankton moves about continually in the water, but the successive positions of the individuals constitute ecological facts fundamentally no different than the germination and growth of an oak or the aimless wanderings of a squirrel; on the other hand, if a mass of water is not frozen "in place," we cannot study in detail the spatial structure of the plankton population in it. Let's imagine for a moment that trees begin to sprout, grow and die with the speed we are accustomed to see in diatoms, or that, armed with note book and pencil, we move through the forest with a speed a thousand times less than that of a snail.

It seems to us that the "fixed" spatial structure—the forest—holds greater possibilities of information—of order—than a suspension of plankton, with "uncertain" and variable position of the individuals. This is what has been called the "degree of organization" of vegetable communities, which permits ordering them according to their degree of "sociological progression" from plankton to forests (Braun-Blanquet).

Nevertheless, in all cases, the information content is the same, ℓ n N !; all that varies is the possibility we have of obtaining all this information. Some information always escapes us, of greater order, obviously, in the case of plankton, for on taking a sample of these organisms suspended in water, we destroy an instantaneous spatial structure no less real than that of the forest. Therefore, we are perfectly justified in calculating the information represented in localizing the species and even the individuals in a volume of ocean water, even though we are unable to obtain it. However, the information we can really obtain plus that which escapes us, which we could consider subjectively as an enthropy, always equals K ℓ n N !, where N is the number of elements of the system, be they pines or diatoms.

In the foregoing considerations we have concerned ourselves only with equidistant symbols, hypothetically situated along a lineal series. Reality is more complex and this complication effects all the different types of communities, from plankton to forests, although it might seem of less importance in relation to the simpler communities or those from which we can extract relatively less information (plankton).

The distance between individuals noted successively in a list of identifications represents another system of symbols associated with those referring to the individuals themselves. Possibly the most useful analogy within the field of information theory is to consider individuals as signs of different kinds which may be of different duration (distance separating them). The problem becomes extraordinarily complicated, for the distances may vary continually, increasing the total information of the system to infinity. Moreover, it is obvious that in reality the individuals do not constitute a lineal series, but rather a tridimensional system (practically speaking, bidimensional among dwellers of the emerged land masses) and this complicates even more the problem of spatial relations as information bearers. This problem offers exceptional interest in oceanography, for it links the study of heterogeneity in the distribution of organisms with that of the hydrodynamic structure of water masses.

The analysis of crystalline structures, which has also been considered from the point of view of information theory (Brillouin, 1956) does not seem to offer any useful ideas, for it has to do with structures of an essentially periodic nature.

To sum up, although spatial relations among individuals really contain information, there do not seem to exist, at the moment, methods to measure and utilize it, so in what follows we shall ignore the problem of distances and take as the principal information contained in a system that given by the expression K ℓ n N ! which, of course, recognizes the fact that individuals of the same species are not identical.

Redundancy and prior information.

If we wish to proceed with the greatest possible rigor, we must reject any human evaluation of the information and give it the purely objective restrictive sense of a probability. But the determination of this probability may proceed from an arbitrary limitation, as when we undertake to study a group of N individuals or select a language with N symbols, resulting from the elaboration of prior information or from information we obtain as we go along. If we study a sample of plankton and see that the cells of Chaetoceros densus are nearly always accompanied by cells of a Vorticella, on noting down one of these organisms on our list we know that the probability is great that its companion will appear too; if it does, the information gained is slight, since it was already anticipated. Similarly, we know that after the letters cio in Spanish it is much more likely that the n appear than the e. This is what is known as redundancy, repetition, which occurs in language just as in the study of a mixed population. Redundancy results in a diminution of the total information.

In a series descriptive of a community of organisms, redundancy gradually increases and when we have identified up to 500 individuals, any subsequent identifications probably contribute little to our final description of the community; therefore we usually stop noting down species when we have identified a good collection of individuals. However, it would be foolish to interrupt a study after identifying no more than half a dozen individuals, for if we were to continue we might encounter a species not yet observed, or at least arrive at a different numerical proportion among the different species. We all know that after studying a community for a long time the chance of adding new species to our inventory diminishes and that increasing the sample improves our accuracy regarding the relative numbers of individuals of different species, although only very slightly toward the end. Nor will an excessive prolongation of the study supply new data as to the intraspecific and interspecific groupings of the individuals, to the internal correlation which has caused the information value of each identification to diminish.

It is important to realize that to have an equivalent amount of information, with respect to that contained in the total structure of a community, the length of the information series, measured by the number of its elements—that is, by the number of individuals identified—does not always have to be the same. There are communities where species are few and of such characteristics—low index of diversity—that the identification of a short series of individuals is

sufficient to gain an idea of the whole—as is the case in the population of a dune or of a Scandanavian forest. Other communities, more diversified, or of a richer structure—higher index of diversity (tropical forests, for example)—require the preparation of a longer series before an equally significant description can be presented. In the first case the relative mean information value per individual is higher than in the second. Information is measured by the degree in which the data received diminishes our ignorance (total at the beginning) regarding the system in question. Our initial state of ignorance is equivalent for both types of systems, but since a shorter series of identifications is necessary for a knowledge of the first, it is obvious that each element of the series has a relatively larger information value.

We may return again to the example of the two samples of plankton which served to illustrate the information content of natural communities. In the preceding discussion of redundancy we did not distinguish among individuals but took all members of the same species and their effect on the structure of the community or mixed population to be equal. Therefore, maximum information is equal to I_3, or 2.47 bits per individual in sample A and 1.39 bits per individual in sample B. The smaller information of the latter represents a greater redundancy, which results from the peculiar distribution of the individuals by species. The value of $\underline{b}$ is a measure of the redundancy. If $\underline{b} = 1$, there is none, but b is 0.57 in sample A and 0.32 in sample B. Once we know how the individuals are distributed by species, the information actually obtained as compared to that contained in the structure of the community—as given above—equals $0.14/2.4 = 5.67\%$ for A and $0.148/1.39 = 10.65\%$ for B. All this means that the nature of community B is more easily known than that of A because of its greater redundancy, or in other words, because of the relatively greater information value of each of the elements of which it is composed.

Another way of representing the information in a group of different symbols (species) with different <u>a priori</u> probabilities (different frequencies) is that adopted by Shannon:

$$I = - KN \sum_{j=1}^{j=S} p_j \log p_j$$

in which p_j are the probabilities corresponding to each of the "species" S, and $\sum_{i=1}^{S} p_j = 1$.

Information is maximum when all the p_i are equal. This expression is equivalent to Brillouin's expression, $I = k \log \frac{N!}{N_1! N_2! \ldots N_s!}$ (Baer, 1953a).

We should remember now that whatever expression we use, the redundancy—that is, the diminution of information owing to an internal correlation—is related to the value of a sum of terms, each of which has the form $p_i \log p_i$ in Shannon's expression or $N_s \log N_s$ in Brillouin's. Redundancy depends also on how the individuals are distributed by species, reaching a minimum when all are equally frequent and a maximum when one species is represented by $N - S + 1$ individuals and the remaining ones by one.

The redundancy of a series may be determined by studying the series itself, analyzing its internal correlations; but it may also arise from previous knowledge, from prior information which reduces that provided by the series. An example given by Brillouin (1956) illustrates this well. Let us consider two numerical tables, one consisting of random numbers and the other of values corresponding to a given function. In general, a number of $\underline{n}$ digits contains approximately 3.3 $\underline{n}$ bits of information, and if there are N numbers in the table, the total information is $I = 3.3 Nn$ or 3.3 times the total number of digits. If the table is made up of random numbers, laying aside any fortuitous internal correlation which might be discovered, the total information cannot be affected by any prior knowledge. Very different is the case of the table containing values of a function. If we do not know the nature of the function, any regularity or internal correlation discovered among the values given in the table will constitute a measure of redundancy and reduce its information value. If we know the function in an imprecise way, the table will be useful to us for certain values, but its information content will be lowered considerably. Finally, if we know exactly what the function is, we know beforehand what the tabulated values will be, so that each figure we see has been anticipated, and simply verifying its presence has nothing to do with the probability of its occurrence. In the latter case, the table contains no information at all. It seems paradoxical that a table of values calculated for a given function may be very useful to us and yet contain much less information than a table of numbers selected at random. Let it be remembered, however, that we did not define information according to its degree of usefulness but for what it has of unpredictability. So, it may be said that the speech of a madman or the paintings of some modern schools contain a greater quantity of information than more conventional forms of expression. This, of course, in no way reflects on the value of the theory of information.

Information and organization.

The organization characteristic of life, be it in an organism, or a system of organisms or a mixed population, involves the existence of a rather large number of (organic) correlations among the elements of the system. In terms of information theory, organization signifies redundancy, therefore the quantity of information contained in a system cannot be considered an indication of the degree of order or organization of its elements. Nevertheless, when the information contained in a system is not taken by itself, but rather in relation to prior information pertaining to a wider system, then the quantity of information may be indicative of the degree of organization. In applying information theory to the study of mixed populations, these ideas must be made very clear. Perhaps this may best be accomplished by means of a very simple example taken from everyday life which the ecologist can immediately relate to the practical cases presented by the study of natural communities.

We enter a house and examine the contents of any drawer. In it we find a certain number of objects of various kinds. Let us suppose it is a very disorderly drawer containing a large variety of objects, duplicates of each item, naturally, being few in number. Examination gives an information series of many different symbols, each having about the same number of elements. Redundancy is small and the information content large. The series gives, in fact, many indications as to what is in the house—among other things, that a great disorder reigns in it. This inference, however, does not come from the series itself, but rather from our knowledge of what to expect in a house. Going on to the case in which we find a very orderly drawer containing objects of only one or of just a few kinds, with some items—if there are various—represented a large number of times, the information series is made up of few symbols and its redundancy is great. Its information content, as a message in itself, is small and actually gives little indication as to what might be expected in other parts of the house in which the drawer represents a sample. However, assuming that in every house there is a similar piece of furniture, the careful segregation of objects of the same kind in a single drawer speaks very much in favor of the order reigning in that house. It should be noted well, however, that we deduce this from knowledge having nothing to do with the series studied.

If we take into account not only the number of different objects but also their position, the information they provide may be measured by means of the now familiar expression

$$I_3 = 1{,}443\ bN\ \ell n\ S$$

A disorderly drawer gives us a series in which the value of b approximates unity and S is very high, so that the total information or the information per element (which is proportional to $b\ \ell n\ S$) is quite high. In the house in which all is arranged in an orderly manner, few kinds of objects and a large number of each kind are found in every drawer, which means that b and S are small and information—total, or per element—is low.

Let us not forget that information has been defined as a function of a quotient of probabilities. If the initial possible selection, determined by examination, is established a posteriori, it is obvious that a more organized or "simple" system will lead us to restrict the number of initial possibilities thus devaluating the information obtained. But the difficulty disappears if we permit the utilization of prior information about the universe of which the group we are going to study forms a part. Or, what amounts to the same thing, as seen in our example, from what we know what is usually to be found in a house, we may judge the degree of disorder present in a drawer examined at random. From this new point of view, if the drawer is so disorderly that it contains all the elements we might expect to find in a house, the quotient of the probabilities following and preceding our investigation will approximate unity and its logarithm zero—that is, the information obtained through our prying is practically nil. We have reference here, of course, to the information contained in the distribution of the objects by classes; their arrangement in space still admits of many possibilities, the one in our example being but one among a great number possible, so that if we determine their position exactly, the information obtained is still considerable.

Not much more can be gained by juggling our example further, so let us move on to a consideration of communities of organisms.

In preceding paragraphs we have seen how it is possible to calculate the information contained at different levels of the structure of organic communities. In most cases, the most appropriate level seems to be that of the relative location of individuals, but taking those belonging to the same species to be equivalent and interchangeable. This is the value represented by I_3. The simple, direct calculation of this information does not give a quantity proportional to the degree of organization of the community, but, rather, an inverse correlation frequently exists. This is because the information content decreases as redundancy increases, and redundancy depends on the intensity of the internal correlations—an index of organization. This reasoning may be presented in another way. Since in nature the number of species is very great, practically without limit, of many groups

composed of the same number of individuals, the one including the smallest number of species, and the most unequal representation of the same, is the one representing the most intense selection or segregation (as a consequence of the action of certain organizing forces—ecological and historical factors, competitive and complementary relations among different species) and is, in brief, the least probable. The presence of a single species, to the exclusion of all others, is the least probable type of natural community and, therefore, represents a maximum information. But if we calculate its information content by means of current procedures, on observing that there is no more than one species we say, a posteriori, that our study has not provided any information at all, since all states and combinations are reduced to a single possible one.

One of the most serious problems encountered in information theory, found at the root of the paradox that troubles us, is that of utilizing prior information to evaluate information received. The difficulty lies in the fact that very different systems may be involved and in the transfer or translation of information from one to another there is always a human element which must be eliminated in order to maintain the necessary scientific rigor.

Ordinarily information calculated according to usual procedures will be in inverse ratio to the organization of a community—that is to say it will constitute an "entropy" rather than information, (Margalef, 1956b). To avoid misunderstandings it will be better to speak hereafter of "diversity," but calculating it just as "information." Therefore, a community of low diversity represents a structure having more order and less probability within the whole biological sphere. To express our knowledge of it, a short information series suffices. A more diverse community requires for its description a longer information series and in consequence each of its elements possesses a relatively smaller information value; it represents a more probable state, a smaller degree of segregation within the biological complex.

Inasmuch as the invention and use of the indices of diversity—which will be spoken of in greater detail later—reflects a need felt by ecologists before they ever heard of information theory, Ecology's interest in this theory does not spring from curiosity in something new but responds rather to the necessity of finding a broader mathematical base for concepts which the naturalist comprehends perfectly through having used them.

Information theory should provide a flexible language for the description of many structures and processes found in organic nature. For one thing, the ecologist would like to have a method for judging the degree of organization or disorder in a system made up of elements discontinuous in space and time, whether absolutely or in relation to a broader system, taking into account statistical inaccuracies in the original data which, in the form observations usually take, also affect the boundaries of space and time. A system of this type should be analyzable by parts and in its evolution in time, so that its heterogeneity, and the way this undergoes modification in terms of order and disorder, may be seen. It is to be hoped that ideas derived from information theory will help accelerate the crystallization of some principals of ecological science and also, perhaps, to purify and simplify its vocabulary a little.

In what follows I shall attempt to illustrate some applications of information theory to concrete problems planted by the structure and dynamics of natural populations. In every case the point of departure will be that "diversity"—a very familiar concept to ecologists—may advantageously be measured quantitatively by means of the recourses offered by information theory.

THE DIVERSITY OR ABUNDANCE OF SPECIES IN MIXED POPULATIONS

Generalities.

We know that the number of species varies from one organic community to another. Some are made up of a great number of species; in others the individuals are distributed among fewer species and therefore, assuming an equal mass in the samples compared, the number of individuals in each species is greater. In general it may be said that the conditions of life under which a great diversity of species is possible are extremely varied; very special or extreme conditions foster the formation of groups composed of a small number of species where each is represented by many individuals (Thieneman, 1920).

When we speak of diversity of species in a natural community, we refer to the characteristic noted, not also to something else—to the fact that the diverse species are represented by a different number of individuals. This disparity makes the quotient $\frac{\text{number of species}}{\text{number of individuals}}$ valueless as an index of diversity; the index $\frac{\text{number of species in common}}{\text{total number of species}}$, sometimes used with the object of discovering and evaluating the possible affinity between two different communities, also is incorrect.

The number of individuals in the different species preserves a certain regularity. If we form a series in which the species are ordered according to decreasing abundancy, it will be seen that those represented by many individuals are few and that the proportion of those more and more scantily represented increases gradually. This type of distribution is repeated in other natural groupings. It is found in every mixed population, but also in sections of the same population made up of animals or plants belonging to the same taxonomic group. The individual plants and animals that live in a cubic kilometer of marine water are distributed by species with a regularity not fundamentally different from that observed in the tintinides (ciliated) in the same mass of water. The same rule may be seen in the distribution of species per genus within a systematic group (genera with one, two, three species, etc., are progressively scarcer), not only world-wide, but also within a limited area. The distribution by species within a mixed population will still have this form if, instead of taking the number of individuals, we compare the total weight of those belonging to each species, although in this case the order of each species within the complete series may be different, as shown in studies on fish populations (Yoshihara, 1951).

Causes of unequal abundance of species.

The causes for the regularity which has been indicated are complex. The diversity of groups in which it is found—including surnames in a telephone book, the number of publications written by scientists (Williams, 1944b) and even, to a certain point, the distribution of taxpayers into income tax brackets—seems to indicate a very generalized basic combination of self-multiplication and selection. Although the resulting distribution may appear simple in form, the unequal number of individuals in the different species and the regularity they have comes from the integration of a large number of properties and phenomena having to do with mixed populations. Some of these have been discussed in a previously published article (Margalef, 1956a) and the account that follows cannot be exhaustive but simply enumerative, leaving room for other possibilities. We begin with a provisional grouping in three sections:

1. Structure of the community. The chains of alimentation permit us to distinguish distinct levels in the community—vegetables, phytophagues, zoophagues of first and second degree, etc.,—and together they may be represented by a pyramid (Elton's pyramid), since the number of individuals in the larger species on the higher trophic levels is smaller than that of species at a lower level; nevertheless, the small-sized species at the lower levels of the pyramid are able to subsist together better, competing more intensely among themselves than the species at higher levels. In every biotope of some complexity the relative size of niches or habitats follows a distribution similar to that mentioned: to the larger or principal one are added portions of others, which, naturally, shelter less numerous species. A lake serves us as an example: it presents a mass of surface waters of great extension, a deep-water region that is rather homogeneous and of smaller dimensions, although still of considerable size, and a large variety of shore environments of progressively smaller dimensions. The distribution of the species, which are adapted to precise conditions, adjusts itself to the biotopic structure and the number of the respective individuals reflects the relative size of the habitats. This also holds true on a smaller scale; any sample takes in what represents a principal habitat plus fragments of others or organisms roving beyond them. The role of cycles is similar, and at any instant within an annual sequence of populations there exists a nucleus of favored species plus another of scantier ones, the residue of preceding populations or the seed of future ones.

2. Differential reproduction. The fecundity of the species depends on an unlimited number of factors, as does also their death rate. In a mixed population in equilibrium, the rate of reproduction and the death rate of each species are balanced and no correlation exists between the reproductive rate and the abundance of a species. Nevertheless, in moments of instability, it is safe to suppose that the net rates of multiplication (subtracting the death rate) for the various species are distributed according to a normal curve. Since the number of individuals increases in geometric ratio, a normal distribution of the net reproductive rates would give a distribution of the individuals per species similar to the "lognormal" postulated by Preston (1948), although the latter was prudent enough not to include with his purely empirical expression an "explanation" such as given here, which appears to be only partly valid, if at all. Competition means a decrease in the relative net rate of multiplication for some species; these stand at the bottom, distribution-wise, and are eventually eliminated, if no ecological segregation occurs.

3. The effects of evolution. The biotic community represents on a small scale the pattern followed in the natural survival of species. This must be interpreted in the sense that in nature few species are represented by many individuals—widely distributed, eurychoric and euryoichic—and there is an increasing number of more localized and restricted species represented by few individuals—to the despair of collectors. Reality fits this picture, a consequence

of the normal progress of evolution. The species with fewer individuals form smaller populations or are reduced to a small number of individuals at certain times, affording greater opportunities for isolation and genetic change. Evolution is a self-accelerating process. The number of species increases geometrically once in the groove of progressive specialization and differentiation; but there always remains "primitive" or non-primitive forms which become euryoichic. The result is a characteristic distribution preserved through the probability of extinction, which increases when the species become very rare.

For the reasons given and, without doubt, other supplementary ones, we may expect a type of distribution like the one observed; but the foregoing reasonings are only qualitative. They are not sufficient to undertake in a logical way the construction of an approximate mathematical model and the adjustment to it of what has been observed. Although statisticians of prestige have presented some of the expressions that follow, among them Fisher (Fisher et al., 1943; Quenouille, 1949), their development stops in accepting simply that a certain natural distribution fits a γ function, or some other type—that is, no causal analysis arrived at.

Information theory provides another example in which frequency distributions similar to those of the species in a mixed population are found. Reference is made to the normal forms of language and writing which, it may be assumed, in the appearance of new symbols (phonemes or letters), the double employment of some symbols, with one form used more than another, the act of selecting from among existing symbols, the reduction of some to the condition of vestiges and their final disappearance, follow laws not altogether unrelated to those governing the multiplication and evolution of species of organisms.

According to information theory, maximum efficiency in the transmission of a message composed of symbols of different duration—that is, the maximum value of the mean information represented by each symbol—is obtained when the symbols are of unequal frequency and their frequencies (N) have the following relation to their respective durations (t):

$$p_s = e^{-ct_s}, \qquad \ln(N_s / N) = - ct_s$$

in which p_s is the probability of the occurrence of the symbol s, $p_s = (N_s / N)$, t_s the duration of the same and c a constant.

Mandelbrot (1953; quoted by Brillouin, 1956, and Cherry, 1957) has applied these principles to the analysis of language, in which the frequency of the different words follows a rule similar to the distribution by frequency of species in a community: a few words of very frequent use and an increasing number of words of a more limited use. A generally accepted postulate is that the nervous system tends to operate with the greatest possible efficiency; for a communication based on symbols (letters, words, etc.) of unequal frequency to have a maximum efficiency, the symbols must be unequal as to time consumption—that is, they must be of different duration, with their duration inversely proportional to their frequency (probability). As a matter of fact, it is undeniable that shorter words have a greater frequency in language than longer ones. But the substitution "cost" may be made for "duration," assuming that in the central nervous system words are codified in some way, quantitatively characterizable by something that may be called "cost." All this is no great help to us, but it does have the merit of showing how similar problems are presented in the study of natural communities and in the study of languages, with the hope that the similarity will facilitate the finding of solutions applicable in one case and the other. Just as the equal frequency among species which would give the maximum information content in a system is lacking in natural communities, so in the various languages the frequency of letters, phonemes and words is other than what would be considered optimum for the communicatory mission these symbols have. This fact runs counter to the more or less well-founded prejudice that there is a tendency to order and maximum economy in the world of living things. As we saw in the discussion on organization and information, such a contradiction, as far as mixed populations are concerned, is more apparent than real. Quite probably language does not represent a sequence of symbols trying to achieve a maximum information per symbol, but rather what should be viewed as a pattern or model involving structural blocks of a type determined by factors comparable to those operating in a community of organisms. This line of investigation, in any case, is indebted to information theory and is a topic equally exciting to biologists and linguists.

Before leaving the theme, we should see if the study of language structure can provide any provocative ideas. The concept of "cost" could be applied to the species; the rarer ones would "cost" more—collectors will subscribe to this assertion—and, in fact, one example of a rare species would have the information value of several examples of a more common one. Mandelbrot, in his hypothesis that the "cost" of a word is determined by its frequency in a language—as informatimn theory requires for maximum efficiency of the language—calculates the function relating the order of a word in a series in which all are arranged according to their relative frequencies, greater to lesser, to the

actual frequency of each one. Passing over the mathematical operations we have the expression

$$p_z = P(Z + B)^{-\gamma}$$

in which p is the probability (frequency) of the species (or word) in position Z and P, B and γ are constants. This expression describes quite well a natural distribution we used as an example (tintinides of Mediterranean plankton, Fig. 3).

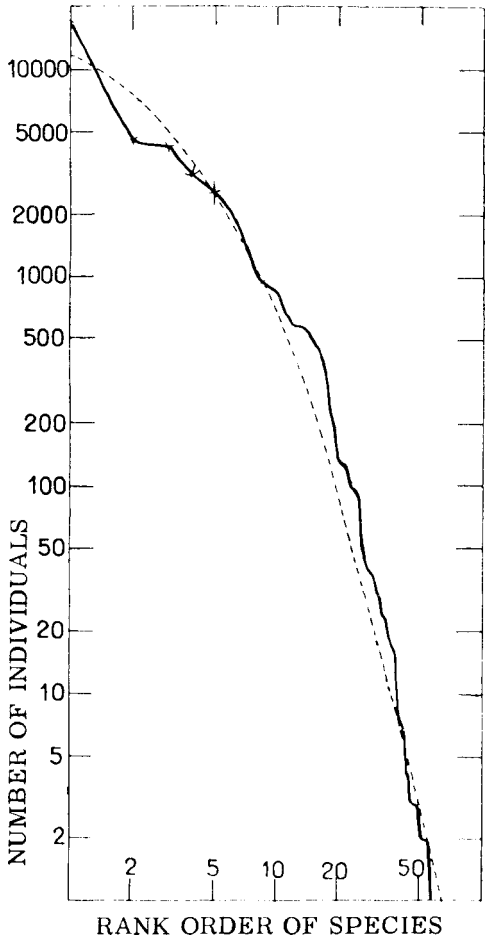


Fig. 3. Distribution of individuals (by number, on the ordinate axis) into species (arranged according to rank, from most to least frequent, on the abscissa) in a mixed colony made up of several varieties of Mediterranean tintinides (infusory planktonic). The dotted line is a theoretical curve plotted according to Mandelbrot's function, p_z (etc.), making B = 8.4 and γ = 4.5. The value p_z is the probability of the species (on the ordinate axis, proportional to its frequency), Z its rank according to frequency abscissa).

Indices of diversity. The regularity of the distribution of individuals by species is such that several empirical mathematical expressions have been proposed to describe it, although it should be remembered that these were presented either before information theory came to be spoken of or else in ignorance of its development. The best known expressions are the "geometric progression rule" of the Japanese (Motomura, 1932 and 1947; Usida, 1943; cited by Yoshihara, 1951; Ito, 1949), the "logarithmic series" of Fisher, Corbet and Williams (1943), applied by the same authors (1943 and after) to a host of cases, and the "lognormal distribution" of Preston (1948). In botany the relationship between the number of species and the logarithm of the area studied (proportional to the number of individuals) has been considered linear for some time (Gleason, 1922) and this relationship implies a definite distribution of the individuals by species, similar to the "geometric progression rule" (Margalef, 1956a). In any of the hypotheses, the distribution of individuals by species is related to a definite correspondence between the total number of individuals and the total number of species; and the way the relationship between the number of species and the number of individuals varies, as we increase the size of our sample, depends on the type of the distribution.

Accepting one expression or another and finding a proper agreement between the natural community and a theoretical distribution, we can calculate a characteristic parameter for each community which expresses an intimate characteristic of its structure, manifested by the way the individuals are distributed in species. This parameter is called an "index of diversity" and the first condition it must satisfy is that it be independent of the size of the sample, assuming that this is taken from a "homogeneous" mixed population or community. The index of diversity represents the wealth of species. It is high in communities that include a great number of species and in which the number of individuals of each species decreases relatively slowly on passing from the more abundant to the less abundant ones. The index of diversity is low in communities of few species with a rapid decrease in the number of individuals per species on passing from the dominant ones to those successively less important numerically. Among the various indices of diversity proposed and discussed in the basic publications that have been referred to, the simplest, and by no means the worst is

$$d = (S - 1)/\ln N$$

based on the presumed linear relation between the number of species and the logarithm of the area or the number of individuals. As always, S represents the number of species and N the number of individuals.

Indices of diversity calculated in this manner are definitely useful. They permit us to establish the characteristic "wealth of species"

and to use it in comparing communities of very diverse types. They enable us to solve satisfactorily problems that are difficult to work with, such as minimum area and floristic affinity in the study of vegetation (Margalef, 1951). They lend themselves to interesting biogeographic considerations, comparing the indices of diversity of local fauna and flora and relating them to the effects of glaciation, drouth cycles, etc., as factors tending to lower their value, or to the continuance of the biota and the consequent accumulation of species in lands of more conservative characteristics at the periphery of regions subjected to intense climatic cycles, where the indices of diversity are high. The geographic distribution of the indices of diversity facilitates localizing centers of accumulation of the species. Careful study of the problems indicated leads to a natural solution of the discrepancies existing among the various schools of plant ecology, particularly of those having to do with the concept of fundamental biocoenotic unity, which each school sees against the background of the vegetation with which it is familiar. Since the indices of diversity constitute a way of evaluating quantitatively the degree of complexity of each type of community (low indices on the tundra; very high ones in the tropical forest), they help establish common patterns that unify the types of units used and even the methods of the various schools.

Indices based on information theory.

With all their usefulness and significance for biology, obvious in that they were proposed independently in various areas of investigation and reflecting, therefore, a need in the study of Nature, the usual indices of diversity have the drawback of attempting to adjust a natural distribution to a simple mathematical expression of more or less arbitrary form, and this does not always work.

Information theory provides a way to escape this difficulty, adopting as an index of diversity a more exact expression of the information contained in the structure of a community. In the section devoted to a discussion of the relationship between information and organization it was concluded that "diversity" and "information"—the latter calculated directly from the sample—may be considered equal for practical purposes—that is, for the purpose of obtaining a parameter representative of certain characteristics of a mixed population.

The information contained in a community can be calculated for various levels. Choosing the level (and the form of expression) most suitable for indicating the diversity is not difficult. It must include precisely that information requiring for its calculation a knowledge of the distribution of the individuals by species. Information calculated from these data measures that contained in the localization of the individuals with reference to each other, considering all those of the same species to be indistinguishable. Certainly, we could ask for no better description of the structure of a community. The expression is, as we already know,

$$I_3 = K \log_n \frac{N!}{N_1!\, N_2! \ldots N_s!}$$

Unlike the most commonly used expressions for calculating indices of diversity this one (Brillouin's) gives the actual number of individuals by which each species is represented in the sample. This advantage is achieved at the expense of unavoidably complicating the calculations necessary, to the point that if adequate factorial tables are not available (Stirling's approximation is frequently utilizable, since high numbers are involved), as well as mechanical means of calculation, using formulas derived from information theory becomes excessively laborious in practical work and requires numerous appraisements of diversity.

The above expression gives ever higher values as the number of individuals increases. For the comparison of groups of different total size to be meaningful, relative values relating the results to some unit must be used. The value given by the formula should be divided by the size of the space from which the sample comes, by the number of individuals N, or by the maximum value the expression gives. This maximum may be conceived in two ways: the maximum total information contained in the system, as if each individual belonged to a different species, or the maximum obtained by assuming a correct total number of species but averaging them out, that is, hypothesizing that all are equally frequent. The mean diversity per individual will coincide with the mean diversity per unit of volume when dealing with populations of equal total density. In the table on the following page are given different expressions of the indices of diversity, D, based on information theory. Only absolute values will be expressed in bits.

The value $\underline{b}$ represents the redundancy arising from the unequal frequency of elements of different kinds. It is a good index of diversity since it depends on the way individuals are distributed into species, having a maximum value of one, representing the independence and equal probability of the different species—that is, the maximum diversity in a mixed population. The index of diversity D_n depends on both $\underline{b}$ and the number of species. Possibly it is still too early to give preference to either of the two expressions D_n or D_m; perhaps either one may be the better in a given case.

INFORMATION THEORY IN ECOLOGY

Diversity	Expression	Alternate forms**
(Total information)	$*I_3 = \ell n \frac{N!}{N_1 ! N_2 ! \ldots N_s !}$	$*I_3 = Nb \ell n S$
Per unit of volume (V) or of surface	$*D_v = \frac{1}{V} \ell n \frac{N!}{N_1 ! N_2 ! \ldots N_s !}$	
Per individual (N)	$*D_N = \frac{1}{N} \ell n \frac{N!}{N_1 ! N_2 ! \ldots N_s !}$	$*D_N = b \ell n S$
Relative to the maximum, assuming an equal number of species, S	$D_m = \frac{1}{N \ell n S} \ell n \frac{N!}{N_1 ! N_2 ! \ldots N_s !}$	$D_m = b$
Relative to the maximum, differentiating among individuals or assuming S = N.	$D_x = \frac{1}{\ell n N!} \ell n \frac{N!}{N_1 ! N_2 ! \ldots N_s !}$	$D_x = b \frac{\ell n S}{\ell n N}$

*To obtain value in bits multiply by 1,443.
**When all species are equally frequent, b = 1.

All of the hypotheses on which are based the indices of diversity proposed before information theory rest on the assumption, in a general way, that the successive factors of the product $N_1 ! N_2 ! \ldots N_s !$ preserve such a regularity that it is not necessary to employ their real values but rather that the value of the product may be obtained by means of a much simpler expression employing the total number of individuals and the total species. Transforming any of the expressions in the table above and employing Sterling's approximation, we have

$$\ell n \left(\frac{N^N}{S^{bN}} \right) = \sum_{j=1}^{j=S} N_j \ell n N_j$$

which reminds us of the information expression adopted by Shannon. If we let $\ell n N_j = n_j$, the sum of the second member of the above equation becomes

$$\sum n_j e^{n_j}$$

This way of representing it could facilitate the finding of relationships between the hypotheses on which the old indices of diversity are based and information theory. Thus, for example, according to the rule of "geometric progression," the successive values of n in the last quantity would form an arithmetic progression. Some of my efforts to study the old indices of diversity from the point of view of information theory have not resulted in anything positive, perhaps because of an inadequate recourse to mathematics; but the impression gathered is that those expressions are rather crude approximations without any special significance.

Nevertheless, the agreement between the old indices of diversity—including even the simplest of them—and the "modern" indices derived from information theory is sufficient for them to continue to be used as a first approximation, thereby saving considerable time over that required in using expressions derived from information theory. The example given in Figure 4 (on following page) is instructive in this regard, and it should be added that Williams' indices of diversity, based on "logarithmic series" also give perfectly comparable results. Precisely for this reason it is unfortunate that, mathematically, no special significance in terms of information has been found for the old indices.

The relationships between organisms and their environment.

In all the foregoing considerations we intentionally avoided characterizing the biotope from which our population sample was taken, except in arbitrarily limiting the space it occupied. All we have is a group of individuals divided into a given number of species and having a certain distribution in space.

Though we may not do much with it, it is well to remember that information theory provides recourses for evaluating the degree of attachment between a given species and a certain type of environment. Species can be handled in the same way that Augenstine and his collaborators (1953) study the distribution of normalized

frequencies $\frac{N_1}{N/S}$ in the amino acids of proteins or the letters of a language. For a group of biotopes, or of more or less diverse communities, the more euryoichic species show a distribution higher than expected. The ecological valence of the species can also be determined by employing the method followed by Quastler (1953) to measure the specificity of elementary biological reactions (for example in yeast/substratum systems), substituting species for yeasts and biotopes for substrata. Either of these methods or still others, but likewise growing out of the principles of information theory, can be of considerable help in formulating in a more exact and uniform way certain ecological facts.

THE STUDY OF SPATIAL STRUCTURE IN COMMUNITIES

The spatial heterogeneity of mixed populations.

For the time being we will neglect any relation with time. That is, no distinction can be made between a relatively fixed structure such as that of a forest and another more subject to change in time such as that of plankton. The problem of how the relative positions of the individuals vary with time is relegated to another plane.

In terms of ordinary observation we can say that the spatial structure of a community is not homogeneous. It is as different as can be imagined from the regularity of a crystal lattice. It certainly doesn't resemble the model we could prepare by putting together a series of species in which each is represented by the number of individuals corresponding to its actual frequency (abundance) and mixing and arranging the individuals together until a maximum homogeneity is attained. Studies with theoretical models of such "homogenized" populations have been made, of course, and they are useful in clarifying some biocoenotic concepts (Cottam & al., 1953; Curtis & al., 1950), but the structure of natural communities differs, more or less, from that of these artificial models. In fact, their greatest utility lies in furnishing a base for studying the degree to which the structure of natural populations departs from the accidental.

Hutchinson (1953) systematizes the causes of heterogeneity in a number of "fields": 1) vectorial, depending on the unequal local intensity of certain ecological factors; 2) reproductive, based on the densification of descendants around their progenitors—the origin of contagious distribution in many plants; 3) social, dependent on aggregation, territorial instinct and other social factors; 4) coercive, the result of competition among the species; 5) random causes. There

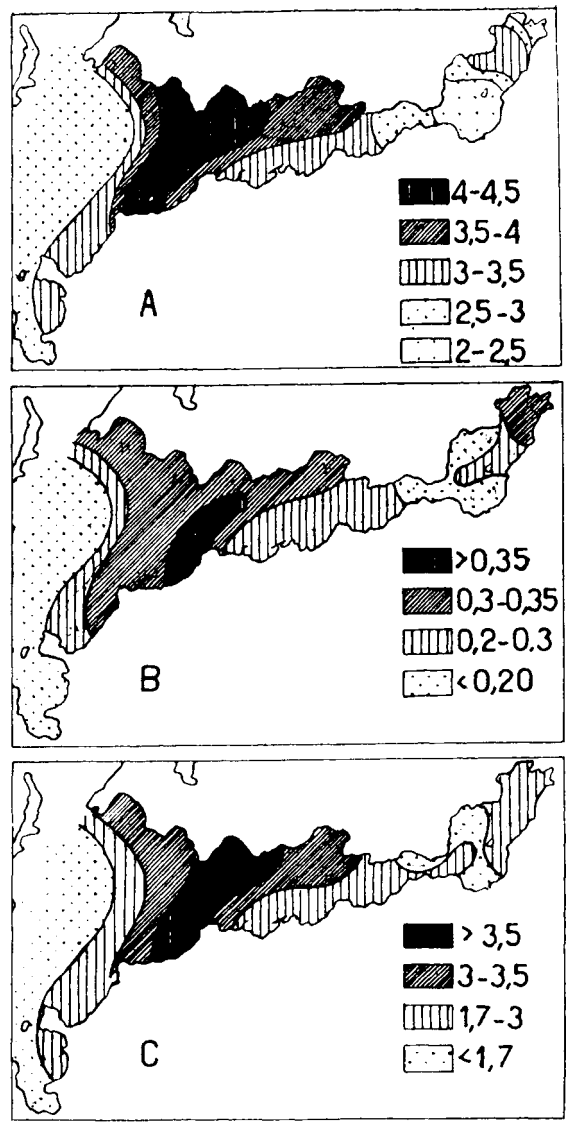


Fig. 4. Distribution of diversity in surface phytoplankton from the mouth of the Vigo, Aug. 25, 1955, based on a study including 27 stations.

A. Index of diversity $d = (S-I)/\log n\ N$.

B. Index of diversity $Dx = \frac{1}{n\,N\,!} \log n \frac{N\,!}{N_1\,!\ N_2\,!\ \ldots\ N_s\,!}$

C. Index of diversity $D_N = \frac{1{,}443}{N} \log n \frac{N}{N_1\,!\ N_2\,!\ \ldots\ N_s\,!}$

exists a considerable literature on the problems of aggregation, inter-dispersion, contagious distribution, etc., for which we give a few basic references (Archibald, 1948, 1949; Cole, 1946; Dice, 1952; Elton, 1949; Hopkins, 1954; Holmes & Widrig, 1956; Mako, 1955; Moore, 1954; Neyman, 1939; Nielsen, 1954; Numata, 1950; Romell,

1926; Shinozaki & Urata, 1953; Skellam, 1951, 1952; Thomson, 1952). The reading of these works is very stimulating to the ecologist, but they do not interest us directly because they do not deal with aspects of the fundamental problem as seen from the point of view of information theory.

The structure of a community can take various forms. There are "fine grain" ones, that is, with small heterogeneous nuclei which give rise to many similar structures which are repeated indefinitely. There are also relatively large surfaces or volumes occupied by individuals distributed in a relatively uniform manner but differently than in other contiguous spaces. Finally, the heterogeneity may pass from one plane to another in a gradual way so that "grains" or structures are not distinguishable. It is very difficult to systematize ideas in this domain and the above phrases pretend only to call to mind what every naturalist knows very well and can represent satisfactorily with symbols on a diagram. Hopkins (1957) has recently attacked this problem as it affects vegetation, establishing a series (3 to 7, for example) of basic structural units that combine in various ways and at times are joined together as one, as a result of the attraction or repulsion among the species as deduced from their fortuitous association in small areas.

The causes of heterogeneity in the structure of the living tapestry covering our planet are the same as those inter-relating the elements of the biosphere (see Hutchinson's listing above) and therefore the study of heterogeneity can scarcely be separated from the determination of biocoenotic units. Defining heterogeneity according to biocoenotic criteria or determining biocoenotic criteria or determining biocoenotic structure from the starting point of simple heterogeneity is an approach of little practical use. I believe that heterogeneity must be evaluated independently, without reference to the relationships among organisms which form the basis of biocoenotic systems, and in this no small service is rendered to biocoenology.

Usual methods of studying heterogeneity.

Heterogeneity is usually evaluated by measuring, in terms of probability, the extent to which an observed distribution corresponds to or departs from a theoretical homogeneous distribution. The many studies made of the distribution of plankton are typical. A series of samples are taken at different points the length of a section and their composition is evaluated statistically in relation to the mean obtained by taking all the samples of the series together (Barnes, 1953; etc.). This procedure may be refined by applying it to two samples at a time and noting the different species, though this complicates it considerably.

The literature referred to in the preceding section treats statistical problems of interest according to the approach indicated.

The method derived from information theory.

The principle is very simple. We have two groups, A and B. Each one of them provides a given information: I_a and I_b. Obviously, if both groups are homogeneous, that is, if one of them represents a simple prolongation or repetition of structure of the other, the information obtained from the study of both together cannot be much greater than I_a or I_b. For all practical purposes any extra work would be wasted on redundancy. But if the two groups are different, then the information provided by their combined study may be as much as the sum of the information of the two parts, I_a and I_b.

It seems to me that in practice the investigation of diversity must be based on the study of a function which describes the way information ("diversity") varies as the space from which a sample is taken changes (increases).

Our point of departure is a small sample with a given information or diversity value. We increase it, adding to it contiguous fragments from the biosphere and the diversity remains the same, if the degree of "order" in the amplified sample has not varied—that is, if the homogeneity is perfect. The diversity increases when the richness (information) of the structure grows with the addition of a heterogeneous blob. Then the whole is more varied; as a message, it contains more information. But, considered as a part of the biosphere, it represents a less intense selection or segregation, an "inferior" degree of organization.

The first characteristic demanded of the simple indices of diversity proposed before, or independently of, information theory, was that their value be independent of the size of the sample. At first glance it is obvious that the ratio $\frac{\text{number of species}}{\text{number of individuals}}$ does not fit this specification and therefore it cannot be utilized as an index of diversity. But the problem has more meat to it. The usual indices of diversity are based on properties observed in a considerable number of natural mixed populations and they are expected to remain invariable when a sample from a "common type of community" is increased, though the community may manifest a certain intrinsic heterogeneity taken as normal. Experience shows us that the value of the indices of diversity of a community increases when we include in our sample fragments of a community manifestly different from the first.

We see, therefore, that this whole line of reasoning rests on a vicious circle; an index of diversity is sought whose value does not vary as long as it has to do with a community reasonably homogeneous, but the only way to recognize this homogeneity is by means of the invariability of the index of diversity. This false type of reasoning is frequent in biocoenology: associations are defined by their characteristic species and the characteristic species by their occurrence in given inventory groups which serve to define the associations. Although they do not appear in a presentable logical dress, such vicious circles are born of an intuition that passes over steps not yet broken down through formal reasoning.

Information theory may be of help in finding a more satisfactory base that will clothe the indices of diversity more decently and continue their utilization. We only have to see how the indices of diversity whether the old ones or those based on information theory vary, as a sample, started with just one individual, is slowly increased. A natural community, developed in two or three dimensions and with the complication of a variable distance between successive elements, does not lend itself readily to this procedure; but writing gives us an absolutely equivalent model, although simpler, since it develops in only one dimension and eliminates the factor of variable distances. We can imagine that each letter represents an individual of a given species and that the sequence of letters is a series of identifications of contiguous individuals, a comparison we have already used. We calculate the indices according to the groups formed by the first symbol, by the first two, the first three, etc., indefinitely.

As an example, we may take the beginning words of the preceding paragraph as they would be in Spanish; the same set of words in English and a random assortment of digits. In the word samples, spaces and punctuation marks count as symbols. We have, then, the following three samples:

1. La teoria de la informacion nos puede ayudar a . . .

2. The* information theory may be of help in the . . .

3. 03473473869774246762167662276612568592 6 . . .

Three expressions have been calculated: the simple index of diversity d, the mean information per symbol in bits (D_N), and the information which a structure made up of the same number of individuals and the same number of species would give when the latter are assumed to be equally frequent. Since Stirling's formula was used in obtaining them, the values are not correct for a small number of individuals. Actually, it should begin with 1 instead of zero, but it is left as is to show a better correlation with the values of the other indices of diversity. The results are given in Figure 5 on the following page. In general the indices of diversity increase rapidly at first until they reach a nearly stable value at about 40 symbols or individuals. The irregularities at the beginning of the curves are of a statistical type and represent the largest probable error that can be expected when working with a small number of elements. The segment of the curves extending between 50 and 90 symbols represents a stable zone for the functions. In dealing with organisms, we would say that the minimum sample ("minimum area" for phytosociologists) is found at about 50 individuals. When the sample is increased by adding to it a group made up of the same symbols, but arranged somewhat differently and with some symbols having a different frequency (which is what happens when we pass from the English text to the Spanish) the diversity of the whole increases. But it soon becomes stable and even decreases, through "assimilation" of the two groups. Another disturbance in the development of the curves comes about in passing from letters to numbers. In the series of numbers taken at random, the frequencies are more equal than in the case of letters and moreover there are fewer whole numbers than letters, but the expressions derived from information theory are not affected by opposing tendencies and do not give a true picture of the change, as does the simple index of diversity d. At all events, the marked parallelism shown by the curves in Figure 5 guarantees the propriety of the index of diversity d.

Figure 5 was prepared to show how the indices of diversity vary as a sample beginning with one element is increased and also to show that in a "reasonably homogeneous" system their values tend to become stable. It may be asked if there occur in natural communities levels of stabilization like those shown in the Spanish text, the Spanish text plus the English text, and these two plus the numbers of the example, or if in nature the heterogeneity is more continuous, giving a more level curve without ups and downs. My impression, arrived at through the partial analysis of some data, is that natural communities exhibit discontinuities similar to those in Figure 5 and even greater.

*This violation of English usage appearing in the original had to be preserved, because the subsequent calcuations have been based on the sample as given [Ed.].

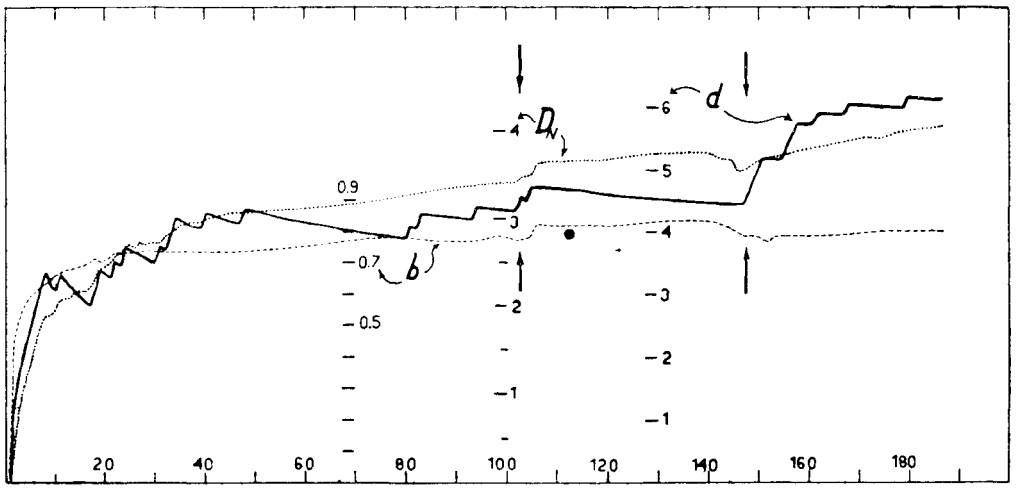


Fig. 5. Diversity values for groups growing progressively larger made up of the series of symbols: "La teoria de la informacion nos puede ayudar a buscar una base mas satisfactoria, que nosi servira para: The information theory may be of help in the 0347347386977424467621676622766125 6859926." Each successive group includes an additional symbol, from one to 187. See text. Three indices of diversity are employed:

$$d = (S - 1)/ \ln N. \qquad D_N = \frac{1{,}448}{N} \ln \frac{N!}{N_1 ! \, N_2 ! \, . \, . \, N_s !}$$

$$b = D_m = \frac{1}{N \, nS} \ln \frac{N!}{N_1 ! \, N_2 ! \, . \, . \, N_s !}$$

The transition from Spanish to English is made at 102/103 and from English to the numerals at 147/148 (indicated by arrows).

In the procedure followed, on increasing the size of a sample indefinitely, considerable heterogeneities may present themselves when the series is already so long that they may be "diluted" in the series of information already accumulated. In studies of heterogeneity it would be advisable once the information series has reached a sufficient length to begin suppressing initial symbols as others are added at the end, so that it is mobile, moving along the text or cross section studied. In this way heterogeneities are detected more easily.

In theory, the value of D_m is independent of the number of species and only reflects the way the individuals are distributed in species; D_N equals the value of D_m multiplied by $\ln S$. When the number of "species" varies—as is the case in the example given in Figure 5 and in the majority of the examples taken from mixed populations—it seems preferable to use the index D_N, that is the mean information per symbol or individual.

The way the original sample should be increased to measure any possible heterogeneity presents new problems. It could be done by concentric areas or volumes so that every point in space would correspond to a series descriptive of the way the diversity of the system increases as areas more and more removed from the point are annexed. If the successive terms of the series show a great regularity, a more simple expression may be substituted. In a more refined analysis we would study increments of diversity separately along each of the directions radiating out from the starting point, using either information series increasing indefinitely in length and including always the initial point or else mobile series of limited length. In either case we obtain vectorial quantities. The heterogeneity around a point would be defined by means of a system of vectors set up at that point, each describing the way diversity varies in a certain direction as the initial sample is increased by the addition of individuals encountered as we move along in that direction. Putting the ideas contained in this paragraph into practice requires an amount of work usually out of all proportion with the results expected. Nevertheless they may give rise to other ideas useful in practical work.

The analysis of heterogeneity in plankton.

In applying the methods presented and carefully analyzing heterogeneity in the light of information theory, it is very convenient in the study of vegetation to use diagrams or plans showing the location of the individuals belonging to different species. In my investigations I have not done this, but, rather, inventoried the individuals found in samples of plankton taken in a uniform way over a large area. Examples of this will serve to illustrate the possibilities in some of the methods proposed. It should be mentioned in passing that these samples were not obtained synchronically (this very rarely is possible), thus introducing an element of error, and the spatial structure from which a sample came—possibly not the same for all samples—was destroyed when the samples were mixed together and specimens were selected fortuitously for identification and inventory.

In groups where the distribution of the individuals by species agrees quite well with one of the theoretical models postulated for the application of the simple indices of diversity, it is convenient to use these, at least as a first approximation, especially if they are seen to correlate well with the more laboriously calculated indices derived from information theory. This justifies the continued use of the simple expression $d = (S - 1)/\ell n N$.

We may begin by locating the value of the index of diversity of each sample in its proper place on the map and tracing isograms. Graphs of this type (Fig. 4) are of considerable interest, especially in discovering states of tension relating to succession or the progress of succession, which we shall see, is one of the fundamental causes of spatial heterogeneity. The ecotones or boundaries between different natural communities show overlapping where both populations are in contact, and the points at the border show the highest diversity. Therefore, mixed zones may easily be discovered. In the example in Figure 4 is shown the contact between a community belonging to the interior of the river's mouth and another coming in from the ocean. The peculiar form of the mixed zone results from the fact that waters from the Atlantic penetrate principally along the northern shores of the mouth of the river.

The analysis of the distribution of diversity takes in one of the aspects of heterogeneity, but it does not satisfy completely. It is possible to imagine two adjoining areas with the same index of diversity, but it may be that this results in each case from absolutely different complexes of species. To establish the existence of such heterogeneity, recourse should be made to the principle discussed above—studying the way the indices change as the size of the sample increases. When we commingle, by pairs, samples from adjoining localities, the increase of diversity generally shown is a measure of the heterogeneity existing between the two points the specimens come from.

In studying heterogeneity in the distribution of surface plankton on different dates in the mouth of the Vigo, a great number of samples were taken on each cruise. The diversity of each one was calculated and then the diversity of amplified samples formed by combining two original samples from adjacent stations. Showing the combining of the samples on the diagram from the detailed inventory of each of the original samples presents its problems. Should an equal number of individuals be taken from each sample or should the number of individuals, equal or not, in equal volumes be used? In the examples given the second method was used.

The following expression was used as a measure of the heterogeneity between two points, A and B, separated by the distance L.

$$H = \frac{d_{AB} - [(d_A + d_B)/2]}{L}$$

in which d_A, d_B and d_{AB} are the indices of diversity of samples A and B and of A and B together, in equal volumes. For reasons that will be understood later, we could debate whether it might not be better to use the logarithm of the distance rather than its arithmetic value.

Once all the data had been obtained, a map could be traced for each situation, in which the heterogeneity is represented graphically by means of a network traced in such a way that in going from one collection point to another on the map the same number of lines would be cut as there were "degrees of heterogeneity" between the two. As a suitable degree the value of the preceding expression multiplied by 10 was selected. In practice, short lines were drawn for each pair of stations (some 30), perpendicular to the straight line joining the collection points; the remainder of the network was completed freely, imagining a certain regularity in the degrees of heterogeneity. The maps this gives provide an excellent total idea of the conditions of heterogeneity, and if they are prepared for different time intervals they show very clearly the changes in the distribution of heterogeneity that accompany succession. In the advanced stages of succession and during stable water conditions there is always a greater heterogeneity. Zones of greater water movement contain more homogeneous populations. Figure 6 (on the following page) reproduces two of a series of maps presented in another publication (Margalef, 1957) which show, respectively, a moment of little heterogeneity and another of high heterogeneity.

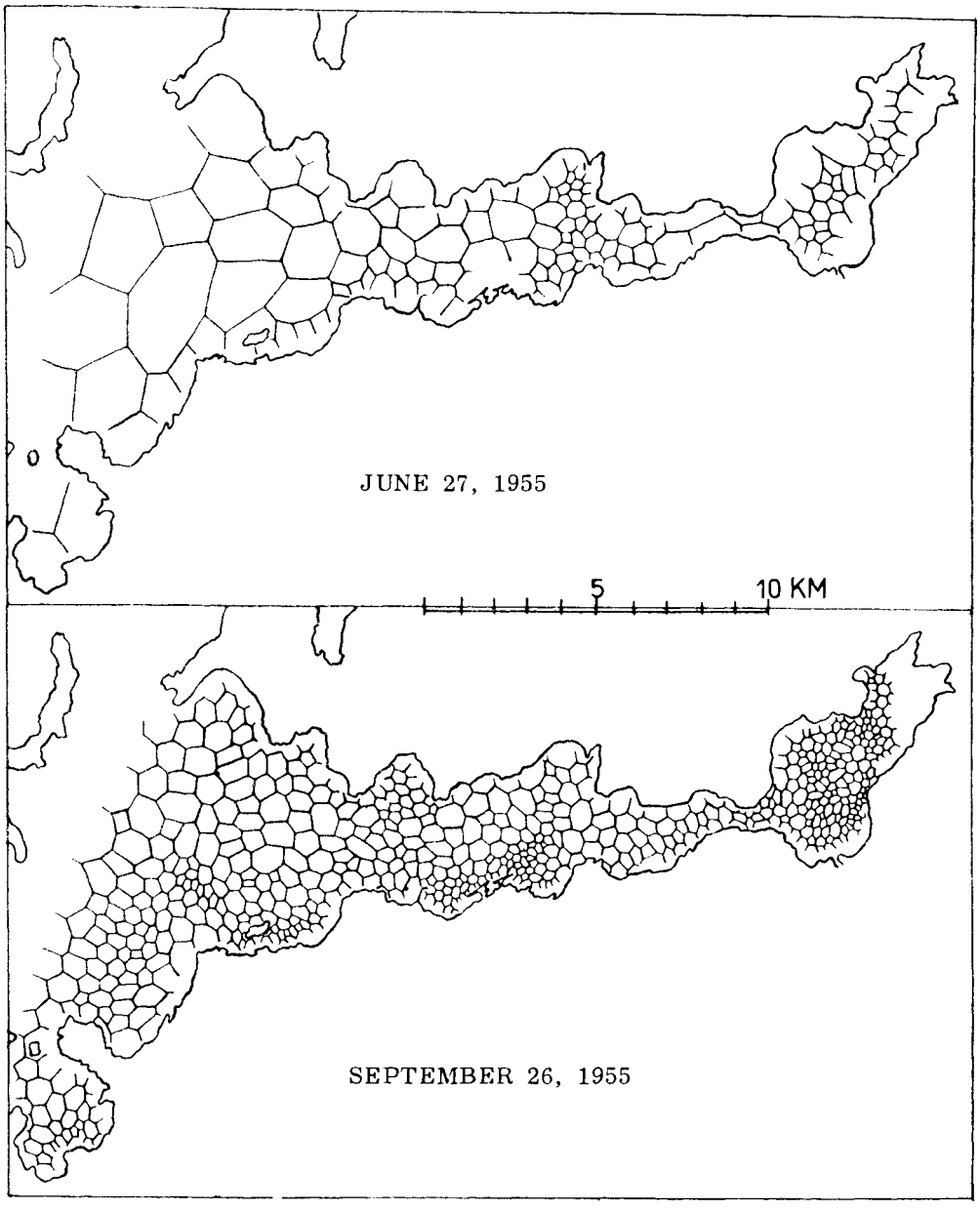


Fig. 6. Heterogeneity in populations of surface plankton in the mouth of the Vigo at two different intervals. The network is traced according to principles explained in the text. The number of lines that must be crossed in going from one point to another is porportional to the heterogeneity existing between the two points. Each area enclosed by lines might be viewed as a "unit" of heterogeneity, a "kernel" in the structure of the whole population. The greatest heterogeneity is found where the mesh is finest. Notice how the degree of heterogeneity varies from one location to another. In June the heterogeneity is much less than in September.

Certainly many improvements could be made in the rather crude procedure described. Replacing L with $\ell n\, L$ affects the results only slightly because the distances separating pairs of stations are of the same order. The substitution of the index of diversity $\underline{d}$ for the mean information per individual would give results of a greater general value. It should be remembered moreover, that the heterogeneity starting from a point in a given direction is a vectorial quantity. Normally, the diversity at A and B is different, so that

$$\frac{d_{AB} - d_A}{L} > \frac{d_{AB} - d_B}{L}$$

In the elementary procedure followed above, heterogeneity has been calculated "coming and

going," subtracting from the diversity of the two samples combined the mean diversity of one of the two samples. In a graphic representation such as that attempted this simplification can hardly be avoided.

The same data may be elaborated in another way that does not give us the fine structure of the community in space, but does give a synthesis of its characteristics as a whole. If we compare the mean diversity of all the groups formed by taking pairs of contiguously located specimens with the mean diversity of each single specimen, we obtain a measure of the mean increase in the diversity of the community on passing from the smallest unit to the next—that is, from tens or hundreds of meters to two or three kilometers. Likewise the mean diversity may be calculated for groups of samples taking in increasing areas until the whole mouth of the river is included. The comparison of these values provides a reference to the distribution and organization of heterogeneity in successive volumes of varying size within the total structure.

Such an analysis was made over a period of time, with the results shown in Fig. 7. The relationship between the amplification of the area

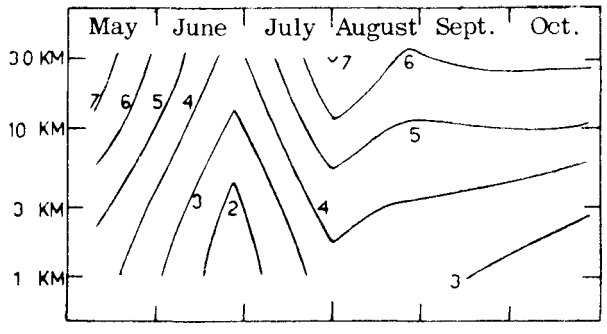


Fig. 7. Values of diversity in areas of increasing maximum dimensions (ordinates), at different times, (abscissa), for surface phytoplankton in the mouth of the Vigo, 1955. Values determined monthly for each area of the dimensions indicated. The curves have been interpolated freely from the data. See text.

and the increase of diversity remained about the same for the whole series, from simple samples to the whole content of the river mouth, suggesting a progressively complex structure for the whole system. The value of diversity in the cases indicated increased linearly with the logarithm of the maximum dimensions of the area from which the samples were taken. This empirical finding suggests the convenience of comparing heterogeneity with the logarithm of the distance between the two points compared. At the same time, the possibility of calculating a new index suggests itself, equal to

$$d_L / \ell n\, L$$

in which d_L is the index of diversity of the whole complex of populations, more or less heterogeneous, in an area with the maximum dimensions L. It should not be forgotten that our comments have to do with just one example, relating to marine plankton, and that another type of community might present different relationships and problems. New attempts should be made using better data taken from other types of natural communities.

Since in these examples dealing with the mouth of the Vigo the function relating the increase in diversity to the amplification of the area studied is always about the same, the index $d_L / \ell n\, L$, in whatever form it might be given, will be proportional to the difference between the diversity for the whole river mouth and the mean diversity of each of the stations. These values are given in the table on the following page.

The above data have been given only to show that no relationship exists between the "heterogeneity structure" indicated by the values in the column at the right and the diversity of the primary populations or of all of them taken together. They should be interpreted as follows: when the total diversity is large and the value in the last column relatively small, as in May, populations of high diversity but little heterogeneity are involved. Contrasting with this—the situation in September or October—are populations of low diversity that are very different one from another, giving to the whole a "fine grain" structure.

Quantitative study of the causes of heterogeneity.

When we have at our disposal methods for measuring heterogeneity, it is legitimate to speculate about possible models or expressions relating heterogeneity to its causes. In doing so, of course, we leave the realm of information theory, though not without profit.

In the course of the study referred to, the distribution of nearly all the species was mapped separately; for some of these, data was available on their net increment under the prevailing conditions. Excepting the case where it is possible to recognize several communities apparently distributed according to environmental differences and bound together by wide ecotones, generally, when the characteristics of the medium are more uniformly distributed, there is a considerable lack of correspondence between the types of distribution of one species and another. The total distribution, reflected in the indices of diversity and of heterogeneity, results from

INDICES OF DIVERSITY d FOR PHYTOPLANKTON IN THE MOUTH OF THE VIGO

Date	Index of diversity for the whole river mouth	Index of mean diversity for each sampling	Difference
May 9, 1955	7,44	4,47	2,97
June 27, 1955	3,54	1,53	2,21
July 30, 1955	7,01	3,59	3,42
August 25, 1955	5,90	3,22	2,68
September 26, 1955	6,26	2,90	3,36
October 24, 1955	6,28	2,43	3,85

the integration of a series of apparently unrelated distributions. The study of distribution in unispecific populations should be approached, then, species by species.

At this level there are, undeniably, certain irregularities. Ordinarily, the heterogeneity in the distribution of a single species, conveniently represented in this case by the quotient σ^2/m (the variance divided by the mean number of individuals per unit of volume in the series of 27 stations) is related to dynamic characteristics of the species. The heterogeneity is larger in species that increase very rapidly and less in those that multiply slowly and are also able to move about actively. (Table at bottom of page)

The findings of Baldi and his collaborators at the Italian Institute of Hydrobiology are in agreement with what has been said, as shown in their studies on genetic differentiation at a low level, wherein they reveal a heterogeneous distribution of the crustaceans of lake plankton in a horizontal plane, with a low heterogeneity in robust species with exceptional swimming ability, a long life span and a lower reproductive rate (Cyclops strenuus, for example) and a very high heterogeneity in species of shorter longevity, less swimming ability and a more rapid rate of reproduction (Daphnia longispina is a typical example) (Baldi, 1950).

Provisionally it can be assumed that heterogeneity in the distribution of a species is related to an expression of the form RL^2/D, in which R is the net rate of increase, D a difusion value which in phytoplankton will depend on the turbulent diffusibility of the water, and L the distance between the two points concerned. In stabilized water the diffusibility in a vertical direction is very small, resulting in a strong stratification of communities. This heterogeneity is reinforced by ecological segregation—differences in lighting, etc.—which cannot be included in the above expression.

Kierstead and Slobodkin (1953) assign a minimum horizontal dimension to a water mass surrounded by masses which have other properties or are unsuited to the growth and conservation of the species under consideration. The rate of multiplication of the species must exceed the number of those lost and the order of its magnitude is the ratio of the diffusibility to the square root of the dimensions of the region in the zone of maximum diffusion. It is expressed as

$$L = K\sqrt{D/R}$$

in which K is a constant which varies according to the geometric form being considered—a channel open at both ends, a horizontal section of a water mass, a cylindrical section, etc. This expression is the same one we had arrived at before, and in reality, the possibilities of preserving a population are the same as the possibilities of its remaining separate from neighboring ones—that is, the possibilities of preserving a heterogeneity. As one more

Some Examples of Heterogeneity in the Distribution of Species of Phytoplankton in the Mouth of the Vigo River (1955)

Species	Date of observation	σ^2/m
Nitzschia delicatissima	July 30	168,5
Nitzschia delicatissima	August 25	146,0
Sceletonema costatum	July 30	109,9
Eucampia zoodiacus	July 30	4,55
Ceratium furca	July 30	1,26

example of the relationship between concepts of physics and biology, it is well to remember that the expression used in giving the minimum volume of a mass of fissionable materials capable of initiating a chain reaction may be used to define the characteristics necessary for a population to grow or to preserve its independence within the body of a liquid (Kierstead and Slobodkin).

The serious problem that faces us, still unsolved, but perhaps not insoluable, is to integrate in a simple manner the properties of unispecific populations, in order to arrive, by analytic means, at an expression of heterogeneity that will fit in with the way it is presented in terms of information theory. Since diffusibility and distance mean the same for the passive species such as phytoplankton, the problem reduces itself to a consideration of the different ratios of increase and the possible active locomotion of a particular species, assuming to begin with, a uniformity of ecological conditions.

In these terms we move on now to a consideration of the dynamics of populations, their succession as a cause of heterogeneity, leaving thus the theme expressed in the heading to this section.

THE DYNAMICS OF MIXED POPULATIONS

The Concept of Succession.

Every mixed population is characterized by a structure and this structure may change with time. Therefore, the indices of diversity or any other expression of instantaneous properties of that structure having to do with organization or information content are modified with the development of the population, and the values they attain at successive intervals give some idea of certain over-all properties of succession—so called—the different stages of which are characterized by values determined by those indices.

The concept of succession has been expounded repeatedly in ecology texts. It is understood as the process by which biotic communities replace one another in the same place as time passes. In this the action of the environment (stabilization of water masses, erosion of rocks, etc.), the reaction of the organisms themselves (exhaustion of nutritive elements, accumulation of metabolites, etc.), and interactions among the various species (alimentation, non-exploiatory relations (ectocrinic), competition) all play a part. The modification of communities in time becomes slower and slower, attaining finally a state of near equilibrium with the environment characterized by the dominance of the species that have won out in the competition, whether because of their greater or more efficient productivity, because of the way they have conditioned the medium in their favor, or because of an antibiotic effect exercised on other organisms.

In a more general way, succession may be defined as a gradual, irreversible change in the structure of a mixed population in the direction of a replacement of systems slightly structured and having a rapid dynamics, made up of relatively small organisms, having a high productivity/biomass relationship, adapted to the rapid utilization of the resources of the medium, by other, more stable, communities made up of larger organisms with a greater thermodynamic output, adapted to an efficient utilization of the resources and having a lower productivity/biomass relationship. Thus, for example, the initial phases of a phytoplankton are characterized by an inefficient utilization of light, and the organisms duplicate their mass in a short time and become quickly and entirely consumable by animals; while in more advanced stages it will be so structured as to make better use of the light, nutritive substances, etc. afforded by the biotype, accumulating a great mass of organic material, respiring and non-respiring which fixes and immobilizes a considerable quantity of materials, slowing down the speed of its cycle (its regeneration).

The ratio between the actual productivity and the exploitative capacity of the medium tends to approach a maximum value of one. The ratio between a consumption proportional to the biomass (represented by respiration and all sorts of destructive agents) and the productivity also tends toward a maximum value of one, for the biomass increases gradually when the productivity surpasses the degree of consumption. By virtue of these two relations the biomass tends to exist as a function of the capacity of the medium; but this does not occur without a certain tension, for the immobilization of organic material by a growing biomass involves a reduction of the possibilities the medium affords for production. All supplementary exploitation of a natural community, such as that practiced by man, when added to respiration and the "natural" agents of destruction proportional to the biomass cause the latter to diminish until an adequate productivity/biomass relationship is established. Of necessity, every community exploited by man should be in a preclimactic state, that is, before the climax or final stage of equilibrium has been reached, whether it is a populatin of fish in which the climax is characterized by an excess of old individuals that eat much and grow but little (low productivity/biomass relationship) or a forest where at the climatic stage the production of wood slows down to the point where its destruction is compensated for by the very elements of a community in equilibrium.

Changes in the structure of a community that accompany succession

The changes described in the general economy of a community are accompanied by internal readjustments governed by competition and other types of relationships among the organisms which lead to important modifications in the specific composition. The species capable of maintaining the productivity/biomass relation at a low value, that is, those which because of their greater size or other properties have a smaller intrinsic respiration as well as those which are consumed less by other creatures, survive longer and continue to increase as succession advances. The accumulation of metabolites may diversify the conditions of life and facilitate the existence of other beings; in the case of plankton, for example, this accumulation fosters the establishment of populations of dinoflagellates of great specific diversity. As succession proceeds, there begin to appear organisms of large size which prey on the smaller ones necessary to their existence, not however, to the point of extinction, so that in time the trophic chains extend upward and the structure of the community becomes more complicated. Competition leads to the exclusion of some species, but also to a local segregation, temporary or ethological, of species that were able to compete at first, thus enriching the structure of the community. In the case of forests, coral reefs, etc., certain dominant species provide a spatial structure for the community and increase the number of ecological niches or habitats in it. All this shows that succession is normally accompanied by an amplification of the structure of the community, or of what is sometimes called its "sociological complexity."

The stability of mixed populations.

The greater the number of avenues by which energy may flow through a complex system, the stabler it is. MacArthur (1955) has shown this very clearly, as the principle applies to communities of organisms. The greater the indifference of the species in choosing their food, or the greater the number of species existing at the same trophic level (on the same "story" of Elton's pyramid), the greater the stability of the system, because the energy circulating through it has more alternative avenues to choose without the edifice's breaking down. I do not know if I should venture to link this concept of stability with that of resonance. In reality, a community exhibiting great stability—in the sense of MacArthur—is comparable to a system easily interconvertible within a series of equivalent systems.

In this sense, stability means, basically, complexity. A natural forest, with its complete complement of species, is much more stable as a biological system than a forest regulated by man, forceably preclimactic, with a few dominant species that are subject to violent oscillations through the effects of disease (Tischler, 1955, p. 345). The intrageneric complexes I shall refer to, characterized by high indices of diversity, are also highly stable, because of the near ecological equivalence of their elements.

In the MacArthur sense, stability acts to guarantee the survival of a biological structure in the face of environmental changes or chance variations in the number of some of its components. If the environmental conditions vary little, there is no necessity for a stable structure and such a one will be replaced by another apparently less stable but more efficient: stenographic species replace euryphagic ones, each ecological niche tends to be occupied by only one species, and the intrageneric complexes are reduced to the status of curiosities—in comparison with the much more frequent establishment of an intense competition among closely similar species. Stability, as interpretated by MacArthur, does not always increase as succession progresses.

MacArthur gives an expression quite theoretical in nature and formulated much like entropy for quantitatively evaluating the degree of stability in a community of organisms.

Succession and diversity.

The specific composition of a community depends, on the one hand, on the conditions of the biotope, which exclude many species of an ecology unsuited to it, and, on the other, on the circumstances permitting the access of species momentarily capable of being introduced and later either assimilated or rejected from the system of a community in the process of succession. Both groups of factors constitute the materials that succession has to work with, but they have nothing to do with succession itself, which is of much more general nature. Those of greatest interest from the point of view of information theory are 1) structural complexity, 2) internal correlations, 3) stability, 4) competition.

Structural complexity. When the complexity of a community increases, as in passing from meadow to thicket to forest, the system accepts, generally speaking, an increasingly large number of species. There is an accompanying increase in the indices of diversity. The community takes on an increased information content—in terms of a message—but it resembles more and more the total biosphere.

Internal correlations. As succession progresses, increasingly better defined and more intense relations are established among the different organisms making up a mixed population. As all ecologists know, the initial stages of any

succession are rather unpredictable, in great measure because of the accidental nature of the first colonization. Communities which may be considered equivalent, since in time they give rise to the same type of terminal community, may be completely different in the beginning. Communities in the climactic state are much more highly organized and therefore more uniform. In terms of information, the existence of internal correlations in any series means redundancy and a loss of information. Information, in the sense of message, and, therefore, the equivalent of diversity, must diminish as organic correlations among the components of a community increase in importance.

Stability. In the meaning attached to it by MacArthur, stability depends on the number of interconvertible states. It may be assumed that this number is greater when there is also a greater number of possible states. Information is measured by the logarithm of the number of choices. A high stability will represent, then, a high information content or an index of diversity of high numerical value.

Competition. This may be understood in a very broad sense. Succession is the result of the varied rates of multiplication of the different species plus the possible introduction or extinction of others. When the total number of species remains constant, the progress of some species at the expense of others may be considered a manifestation of competition.

Any differential multiplication of the species, basic to the concept of succession, will result eventually in a lowering of the index of diversity. In studying the indices of diversity based on information theory we arrived at the summation $\sum n_j e^{n_j}$, where e^{n_j} represents the number of individuals in each one of the species (N_j). The value of the summation is inversely related to the index of diversity (or information) and its minimum value, which represents maximum diversity, is reached when all the quantities involved are equal ($e^{n1} = e^{n2} = e^{ni} \ldots$). If we recall that the general expression for the increase of a unispecific populations is $N_t = N_o e^{rt}$, in which N_t is the number of individuals at the end of an interval t, and r is the characteristic rate of increase, it will be seen that if the rates of increase are not equal, that is, if a differential multiplication exists, the terms of the summation will tend to be unequal, increasing the value of the total and bringing about, consequently, a decrease in information or diversity.

From a group of species having the same or slightly unequal number of individuals, the transition is gradually made to another group usually made up of a smaller number of species in which a few abundant (dominant) ones are followed by others in which there is a rapidly and regularly diminishing number of individuals. The case has never been observed in which, starting from an initial inequality, the rarer species have increased more rapidly than the abundant ones, tending toward a numerical equality; but even if this hypothetical case should become reality, the final development of the community would lead again to a state of low diversity. Rearrangement of the distribution of individuals by species leads normally to the extinction of some, assuming an invariable sociological complexity. Summing up, as a result of competition, the community will contain a smaller quantity of information—considered as a message; but within the general system of the biosphere it will represent a less probable situation, a greater tendency to order.

The consideration of the relations between the indices of diversity and competition leads to the examination of some very curious phenomena which up till now have been given very little attention. Usually it is assumed that species belonging to the same genus compete more intensely among themselves than do those in less closely related groups, so that the existence together of congeneric species in a community at any one time should occur less frequently than what might be expected by chance (Cabrera, 1932; Elton, 1946). But, surprisingly, there is no lack of proofs exactly to the contrary (Williams, 1947a). Populations of algae, planktonic as well as benthonic, provide copious arguments in favor of the belief in a frequent association of species of the same or similar genera. Think, for example of the summer populations of Mediterranean plankton in which may be found together up to two dozen species of the genus Ceratium, or of the winter flowering of diatoms with no few species of Chaetoceros associated together. Perhaps even more noteworthy are the intrageneric complexes of species of desmids in turbulent waters, of euglena, of heteroconta and egodoniales in fresh waters of other types. In such cases the indices of diversity are high and do not decrease as succession progresses; it seems as though the different species have arrived at a status quo, with a very low competitive pressure among them. Incidentally, this slight degree of competition may explain the extraordinary specific differentiation in most of the groups indicated. The exact causes of this state of affairs are not known; but it seems probable to me that the action of ectocrinic substances provides an explanation, even though only partial. Dinoflagellates with a strong toxic action (Goniaulax, for example) can inhibit the development of species belonging to other groups, but they do not affect congeneric species that are biochemically

similar and also produce in higher or lower degree the same antibiotics. Another indication in favor of the action of organic substances dissolved in the medium is had in the fresh water algae previously mentioned. They develop especially in waters that favor the conservation of dissolved organic substances, whereas in waters where the organic substance coming from the organisms is destroyed, an intense intrageneric competition and "brutal" domination arises (example: Cladophora). Regardless of what may be made of this, the phenomenon undeniably exists and must be taken into consideration in evaluating variations in the indices of diversity in the succession of certain types of communities.

In summary, the development of internal correlations in the community and competition among the species lead to a diminution in the indices of diversity. An increase in the structural richness of the community, which may parallel an increase in stability, leads, on the other hand, to higher indices of diversity. So the resulting tendency arises from the conflict or interaction of "forces" operating in opposite directions. Usually succession is accompanied by an initial increase in sociological complexity and stability (in the sense employed by MacArthur) which soon comes to a stop. But the effects of the differential multiplication of the species are in evidence throughout the succession; the relations among the species, the internal correlations of the community, continue to perfect themselves even after the structure has reached saturation. We expect, then, that the indices of diversity will increase in value at first, when the richness of the structure is increasing more rapidly than its internal adjustment through correlation and competition; later the value of the indices will diminish when the final tendencies are predominant.

If we keep in mind the fact that two elements are involved in diversity—the number of species and the distribution of the individuals by species—we can carry the analysis one step further, using the specialized (in one sense or the other) indices of diversity based on information theory. The mean information per individual (D_n) depends as much on the number of species as on the distribution of the individuals by species. But the theoretical information, assuming the species to be equally frequent (D_m) only gives an idea as to the effects of the particular distribution of the individuals into species. An increase in diversity through the enrichment of the structure of a community should affect the indices of diversity more, through an increase in the number of species, than altering the redundancy, while competition as well as the strengthening of internal correlations should have a greater effect, at least theoretically, on the redundancy due to the unequal probability of the species. This would appear to leave a door open to a more careful analysis. Some observations on the variation of the simple indices of diversity during succession agree with the preceding theoretical prediction of an initial increase followed by a slow decline. Nevertheless, it should be noted that only a few examples of marine plankton have been studied (phytoplankton and tintinids) (Margalef, 1956a and 1957; Margalef et al., 1955).

The value of time during succession.

When we measure the information contained in a system of symbols or particles, we assume that we are dealing with a synchronic, fixed system or that we shouldn't worry about the time that elapses as we note down one element and then another, since they are all there waiting for us. But organic systems confront us with something not foreseen in physics: the reproduction of elements of unequal velocity and dependent on a store of historical circumstances not at all easy to express. Imagine the perplexity of a mathematician if the elements of the combinations he is dealing with were to reproduce themselves, and at different velocities, moreover, right while he is manipulating them. I suppose that new developments in physics have reached a point where problems of this sort have been encountered. The application of the concepts of information theory to successive states separated by such events is of a conventional usefulness. We determined the information contained in successive states—assumed to be instantaneous—of a succession, but can we, using the same theory, bridge the distance in between?

There is a relationship between the complexity of phenomena (measurable in terms of their information content) and the scale of dimensions—including time—which gives the point on one side of which they are "exact" and on the other "statistical and historical." The significance of time and the degree of its irreversibility is proportional to the complexity of the systems in which it is manifested. We could establish a relation between the value of time and the information content in the same system. (It is of little use to remember the distinction between information calculated with the mixed population taken as a message—which we have more properly called diversity—and the degree of organization or of small probability of occurrence of the same population.) We can assert that in a natural community with a high index of diversity, a single unit of time can represent changes equal to those taking place in several units of time in a community with a lower index of diversity. The value of time varies, then, through the course of succession. In its final

stages (lower index of diversity for equivalent sociological comlexity) time, measured by the passage of events, flows with the same rapidity as in the life of the aged, while time in the initial stages is more comparable to that in the child. After all, the phenomenon of succession is not essentially different from that of the growth, development and cicatrization of a wound. Cells are involved in one case, individuals in the other, and in each, differential multiplication leads to a stable phase. The stimulating speculations of Lecompte Du Nouy (1936) on time and life, illustrated especially by the phenomenon of cicatrization, are well known. Branson (1953a, p. 37) conceived the idea of introducing a biological time, within the field of information theory, showing himself in agreement with Du Nouy's data. The latter deduces differences in the value of time in different subjects according to the progress of the cicatrization of their wounds. Perhaps the unequal speed at which different successions take place permits us to distinguish territories or types of communities that are "younger" than other "older" ones. Certainly communities in which restitution is more rapid ("younger ones") win out over types of communities that recover more slowly.

Relations between succession and heterogeneity.

Vegetation around a lake is usually arranged in more or less concentric zones, each of which represents a progressive stage in the process (succession) of terrestial adaptation. These zones continue to move outward until the water mass is left behind. This provides an example of the spatial structure of a succession; heterogeneity lies in the presence at various points of different phases of one type of succession. Complications may arise when, because of the nature of the land, the velocity of the succession is not the same at all points equidistant from the water, resulting in a quicker appearance of some stages or even their total disappearance at certain points, a phenomenon given the name of wedging (coincement) by Dansereau (1956). In systems made up of planktonic communities comparable situations are to be found, usually somewhat more complicated.

A study of phytoplankton in the mouth of the Vigo River, published only in part elsewhere (Margalef, 1957), has demonstrated that the spatial structure—or the heterogeneity in the distribution of the plankton—can be interpreted as the result of a heterochronic succession at different points of a water mass, complicated by movements within the mass. This way of interpreting heterogeneity permits of an exposition that is simpler, and possibly more elegant, than an evaluation based on expressions involving speeds of multiplication, diffusibilities and distances all at the same time—which is not to say that this second way is any less valid.

In a dynamic conception of heterogeneity, for all the natural uncertainties involved—multiplied here because they affect time and space and the relations between the two—some general rules can be formulated: The succession begins with the emptying or renewing of the waters of the river mouth, which may take one of two main forms, depending on whether surface or subsurface water comes in from the Atlantic. The characteristics of the river mouth are such that surface water gains its greatest entrance along the northern bank. The succession proceeds most rapidly where the water is stillest, that is, in the shallow areas of the inner river mouth and also in those least affected by tidal currents. The persistence of vertical circulation or of a high degree of turbulence in the upper layers of the water favors the prolongation of the initial stages. This irregularity in the speed of succession is what gives rise, at first, to the heterogeneity in the distribution of the phytoplankton. As the water grows more and more stable the succession slows down all over the river mouth and it tends toward an over-all similarity in its make-up—plankton of dinoflagellates. But this very stability leads to local differences, many of stochastic origin, fortified by the play among certain movements of the water (internal waves) and the mobility, in the later states, of the predominant organisms, capable of phototaxtic movements. The most mature stage of the succession, under undisturbed conditions consists of an antoplankton of dinoflagellates, the greatest mass of which is located very close to the surface and subdivided in dense nuclei, to the point where the heterogeneity in the distribution of the phytoplankton can be clearly seen in the form of blotches of red water in the residue of the sea. The driving force is constituted by the factors bringing about the succession: stabilization of the water and the increasing loss of non-swimming organisms, the consumption of nutritive elements, the accumulation of metabolites and the selective action of planktophagic animals. The interaction of these general forces with local conditions and special distributions of an accidental nature gives rise to local advances or retardations in the progress of the succession manifested in a synchronic heterogeneity in the distribution of the plankton.

Differences, at successive intervals, in the indices of diversity and the distribution of the heterogeneity in the river mouth agree perfectly with the picture of the succession as sketched. Examining one after another the maps showing the heterogeneity at different times, one can imagine a relation between succession and heterogeneity analogous to that in vegetation at the

shores of a lake. It seems to me that the simplest way to describe these phenomena, in a very general way, is by use of indices which express concepts relating to information theory.

Heterogeneity cannot be conceived of separate from succession, nor can succession be expressed without taking into account heterogeneity. The idea that succession and its climax are something spatially heterogeneous and can attain a very complex structural complexity is an idea not at all new. Likewise, heterogeneity must be considered dynamically as a structure that is the seat of a "force" actuating succession. Since the indices of diversity and other concepts derived from information theory can be used to establish comparisons in space and time, they lead us also to relate heterogeneity with succession.

Other applications of the indices of diversity to the study of succession.

The value of heterogeneity can be studied for increasing areas, as has been seen in another section. Adding time as another dimension, it is possible to obtain an idea as to how the "grain" or texture of the heterogeneity of a system evolves as the succesion progresses (Fig. 7). Thus, for example, between August and October, 1955, the index of diversity of the phytoplankton in the mouth of the Vigo increased very little—from 5.90 to 6.28—while the mean index of diversity, corresponding to a space of several hundred meters, decreased from 3.22 to 2.43. This should be interpreted as an indication of the acquisition of a "finer grained" structure, with segregation of the plankton into small blobs, each one more uniform, but at the same time differeing more from its neighbors.

We have already seen that in studying heterogeneity the comparison of local indices of diversity is insufficient, because the case may arise where systems are made up of totally different species, and yet, by chance, have indices of exactly the same numerical value. For this reason the procedure of increasing the size of the group was suggested so that the corresponding variation in the indices of diversity would enable us to recognize the true structure of the system.

The same reasoning can be applied to the study of succession, comparing the larger group formed by uniting two successive ones at times t and $t + a$ with the group corresponding to t, namely,

$$\frac{d_{t,\,t+a} - d_t}{a}$$

In this case time imposes a single signification and the new index—of discontinuity, as it may be called—has the form of the difference between two indices of diversity divided by the time elapsed between the two moments that are compared. The first index of diversity relates to a totally arbitrary aritificial group and consequently is undoubtedly crude and justiable only for the lack of something better.

The index of discontinuity so defined has been applied to the study of sequence in algae (Margalef, Duran & Saiz, 1955) and planktonic animals (Margalef, 1956a) and its greatest advantage lies in permitting a distinction between what is succession and what is translation, not always easy when dealing with planktonic populations. Very high values of this index of discontinuity indicate such great changes in the nature of such communities, that in most cases it must be recognized that they are the result of a change of water masses, replacing one population with another of diverse origin—that is, a translation and not a succession as such.

As has been seen, moments of maximum discontinuity correspond to high values of the indices of diversity, the result of a mixing of populations. Then, in the segment of succession leading up to the next discontinuity, the index of diversity usually follows the tendency normal for any succession—that is, it decreases slowly, often after an initial increase. In the examples studied in relation to the mouth of the Vigo, the maximum values of the index of discontinuity characterize the moments separating one planktonic succession from another, coinciding therefore with a vigorous renewal of the waters of the river mouth.

It might be well to emphasize that the proposed index of discontinuity, and any other of the same type in which successively examined groups are added together—with the possibility of taking the same individuals twice in an unknown number of cases—cannot be justified at all within information theory and should be considered solely as empirical indices having a certain practical utility, but not as a basis for further development.

APPLICATIONS TO OTHER ORGANIC STRUCTURES

Comparison of the community with an organism.

The simpler indices of diversity and, to a greater degree, those based on information theory may be applied to a great number of systems. These need only be made up of discrete elements capable of being classified in a certain number of classes. The universe offers models of this type from the subatomic to the sidereal, but here we are interested only in systems endowed with life.

A topic that may be considered now is the comparison of a community, of a biocoenosis,

with an organism. Just as the first is a structure made up of individuals, so the individual organism, it seems to us, is similarly made up of cells. The species, as well as the natural community, are systems that remain constant or vary with time according to the inheritance, uniform or differential, respectively, of a given system of genic frequencies. There exist, however, between a biocoenosis and an organism fundamental differences: the first is a closed, uncentralized entity; the second, a centralized organization, open with regard to the flow of matter and energy. Therefore, our comparison is not undertaken in a formal way, but only as a possible source of ideas in the application of certain methods.

The same methods used to obtain a synthetic view of the structure of a community can be employed to describe the molecular composition of the cell, the composition of the tissues of an individual, the distribution by different allelomorphs of a chromosomic locus in a community. The similarity goes beyond the purely methodical. Growth consists in an increase in the number of elements—cells in this case—and differentiation appears in that this increase is not uniform in the different tissues—inasmuch as the cells of one proliferate more rapidly than those of another—and varies from one part of the organism to another, giving rise to allometric growth.

One aspect of this comparison which opens up wide horizons is that ontogenic differentiation, as well as phylogenetic evolution and biocoenic succession, all result from a differential multiplication of various classes of elements: in the first, of the different tissues and regions; in the second, of the different allelomorphs, through natural selection; and in the third, of the different species, through competition. Another similarity appears in relations with time. The varied rates of the changes that may be described in terms of information as a basis for the definition of a "biological time" make it possible to distinguish a "juvenile" phase, a "mature" one, and finally one of "senility"—in the life of an organism as well as in the life of a race or the development of a succession. If we determine the information contents at successive moments, we have a common pattern for comparing different growths, distinct phyletic lines and different successions. The comparison may be carried even further. In the same way that biotic succession advances at varied speeds in a large area, accelerating in some spots and falling behind in others, giving rise to a spatial heterogeneity of the communities, an analogous local diversification of "biological time" is exhibited in organisms in the form of allometric growth.

We would not be justified in seeing in this more than a purely external similarity, useful at best as a rhetorical recourse or as a mnemonic device, if it were not for a very significant circumstance. The differentiation of an organism in growth, the evolution of a race and the succession of a community are brought about through structural changes which take us from one state to another, each of which may be described in a simplified way in the same phraseology, in terms of information and entropy, that is, in terms of something closely related to the basic differences between the organic and inanimate worlds. In all three cases, through a differential multiplication of elements, a similar life process is manifested which can be described as a tendency toward the diminution of the indices of diversity. According to the considerations expressed previously when comparing information and organization, this diminution of diversity represents an increase in the degree of organization.

The information contained in organisms.

Organisms begin life with a store of information that they use in the form of negentropy (negative entropy). Acquiring information, and even copying it, represents an increase of entropy. According to Brillouin (1956), herein lies the fallacy of Maxwell's Demon. The Demon's supposed success would arise from the information it possesses, overlooking the fact that the acquisition of this information signified an at least equivalent rise of the entropy of the system. As is well known, information can also be measured in thermodynamic units. If we have information in bits, we can pass to units of entropy multiplying by 0.96×10^{16} . In physical systems, the information represents an element that can be neglected, but not in organisms. According to Linschitz (1953), a bacterial cell contains an information of the order of 10^{13} bits. The body of a mammal is made up of cells numbering in the order of 10^{12}, so the arrangement of the cells represents at least 4.10^{13} bits; if we add to this the infracellular structure, the total information reaches values that are not inconsiderable from the point of view of thermodynamics.

Reading printed matter recovers information without destroying it, with a cost, in terms of entropy, that is relatively low. Brillouin (1956) discusses the problem of the reactivation of latent information, applicable in good part to the problems presented by organisms. The organism uses information in developing its soma without destroying the key to this information, and produces, moreover, a new "edition" of the same in its germinal cells. Obviously, the use of latent information contained in the hereditary storehouse signifies a consumption of energy which is degraded in the course of the

organism's growth, so that the total entropy increases in the physical system of which the organism forms a part. But it is doubtful if the simple process of making copies of the information accumulated throughout the history of the race represents a consumption of energy sufficient to establish here also the equivalency between entropy and information—latent information, at least. The problem here becomes part of the much discussed theme of the thermodynamics of living things.

If information theory helps to better explain the reproduction and transmission of latent information by living things, the results will be directly applicable to the study of mixed populations. They should enable us to bridge time, escaping the limitation of having to compare instantaneous successive states in order to arrive at conclusions regarding possible intermediate events.

Evolution.

In unispecific natural populations, each chromosome locus may be occupied by a certain number of different alleles. The proportions of the different alleles may remind us of the distribution of the individuals of different species in a community. This coincidence arises from the operation of similar "forces." Genetic mutation does, in fact, resemble the introduction of a new species into a community, and natural selection is found among alleles as well as in the species of a community, and may lead to the eventual elimination of some of them. In both cases situations of equilibrium may occur, in the form of heterozygotes with favorable characteristics and of intrageneric complexes, respectively. Note that the alleles of the same locus are exactly comparable to species occupying the same ecological niche. The extension of a single allelomorph through a whole unispecific population (increase of homozygosis) and the dominance of a few species in a mature community are comparable phenomena in that they may be described by a diminution of the respective indices of diversity. All this, starting with an indefinite initial combination, tends toward the segregation of types of elements, reducing the number of them found in a limited space or time and assisting Creation as an agent capable of giving form, structure, or organization to what in the beginning lacked these, altogether or in part. In this sense, natural selection is creative, although, actually, the true creative forces lie in the capacity of information elements to reproduce themselves and in the possible appearance of new types of these, whether as mutations in unispecific populations or as an introduction of a new species in mixed ones.

We have compared a locus with a biocoenosis; we must compare the whole genome with a biocoenosis. The evolution of genetic systems by duplication, which apparently has had an important function in the evolution of the vegetable kingdom (Schussnig, 1927) is worthy of comment in relation to the comparison we have made. When genomes duplicate themselves, genes which were identical, or at least homologous, have new possibilities to become different and thereby increase the number of classes in a whole. The entire structure becomes enriched, as when a community acquires greater sociological complexity (as in going from thicket to forest, for instance). Moreover, this duplication establishes a greater number of possible interchangeable states, which means greater stability—in the sense of MacArthur. In reality, evolution by polyploidization leads to a stabilization of morphological types, so manifest in phanerogams. In this case diversity increases as in the first stages of a succession.

This is not the first time that evolution has been considered in relation to information theory. But the point of view of other authors (Young, 1954, p. 281; Jacobson, 1955) is very different. That of Jacobson is expressed in a very concise and thought-provoking way: "Informational language describes this process very elegantly, and without contributing any new concepts, as follows. The information in specifying the organization of the organism, as such, defines a message. The message is transmitted around a feedback loop (the life cycle). Occasionally, noise (mutations) arises in the message. The noise affects the gain of the message around the feedback loop (fertility of species). Those messages which pass through the filter (environment) with a gain equal to, or greater than, unity cause positive feedback (self-sustaining continuation of the species). Those noisy messages which cannot pass through the filter (unfavorable mutations) are rejected (bred out of the species) after a sufficient number of transmissions about the loop. Eventually the message takes on a character which is primarily due to the filter, in which the gain is maximized (natural adaptation). And these maximal gain messages may be vastly more complex than the original message (evolution)."

In an area less subject to speculation, and perhaps of more immediate practical interest, certain relations between evolution and the properties of communities are obvious which can be expressed by means of the indices of diversity, especially when these are taken as indicators of "dynamic niches" (Watheman, 1957), which may increase or decrease in number in the course of the changes undergone by mixed populations, establishing variable competitive pressures on given categories of species and thereby affecting their possible microevolution. The two extreme types of communities—1) having a few dominant

species and strong intrageneric competition (low index of diversity); 2) complexes of species of the same genus, in equilibrium through intense ectocrinic activity (high index of diversity)—represent mediums having very different properties as far as the origin of new systematic forms is concerned. Black, Dobzhansky and Pavan (1950) point out the genetic importance of the differences in diversity among temporate and tropical forests. A high index of diversity limits the genetically effective population, which cannot but influence the type of evolution.

The study of indices of diversity gives us knowledge as to the rapidity with which communities change—planktonic more rapidly than benthonic, and among the latter, vagile ones faster than sessile ones—or the rapidity with which they have changed in the past—lower indices of diversity in the biotas of regions which have been subjected to intense climatic cycles. Having a quantitative pattern for comparison facilitates the study of relations between the renewal of communities and evolution.

Final Considerations.

The different aspects of biology which we have examined permit the use of a common language proceeding from widely separated scientific fields. In ecology it is immediately adaptable and supplies a real need. In this last section there have been examined, too rapidly and not too clearly, other fields of the biological sciences in which information theory is also applicable. Understandably, I have limited myself to problems similar to those presented by ecology, without even mentioning other biological problems on which information theory may cast some light (Wiener, 1948; Quastler, ed., 1953). The possibility exists of making commensurable phenomena which, by tradition, have seemed to have little in common. Especially applicable to the study of life are those concepts which delimit order and disorder, in all their forms. In thermodynamics, succession can be described as the acquisition of greater efficiency in exploiting the medium and reducing to the minimum the dissipation of energy. Information theory describes the evolution of structured systems, divisible into elements qualitatively different, into states representing a greater degree of organization, in the individual as well as in the race and in the biosphere. A broader biophysics is possible which does not consist in the application of physical-chemical principles to the study of life, but in the generalization of certain concepts on a higher plane which takes in, without any preference, both the living and the inanimate.

Information theory provides an appropriate form of expression when we deal with these properties of the Universe, when we wish to express concisely the manifestations of the sublime force which has lifted life out of chaos. It is noteworthy that a part of its operation can be described in terms of information theory, that is, in a scientific language which has grown out of the rigorous study of the way rational beings have of communicating with each other. This concidence causes us to mediatate on the creative value of the word and on the message value has.

BIBLIOGRAPHY

ANGELIER, E.--1953. L'indice de diversite de C. B. Williams et son interet en biogeographic. C. R. Som. Soc. Biogeogr., 258: 25.

AUGENSTINE, L., H. R. BRANSON & E. B. CARVER.—1953. A search for intersymbol influences in protein structure. Information theory in Biology, ed. Quastler, 105-118.

ARCHIBALD, E. E. A.—1948. Plant populations I. A new application of Neyman's contagious distribution. Ann. Bot., N. S. 12: 221-235.

———1949. The specific character of plant communities. I. Berbaceous communities. II. A quantiative approach. J. Ecol., 37: 260-274-288.

BAER, R. M.—1953a. Some general remarks on Information theory and Entropy. Information theory in Biology, ed. Quastler, 21-24.

———1953b. Biological systems and information dynamics. Information theory in Biology, ed. Quastler, 208-214.

BALDI, E.—1950. Phenomenes de microevolution dans les populations planktiques d'eau douce. Viertelsjarhsch. Nat. Ges. Zurich, 95: 89-114.

BARNES, H.—1953. Considerazioni statistiche sulla distribuzione spaziale di alcuni organismi planctonici raccolti su un lungo percorso nel golfo della Clyde. Mem. Ist. Ital. Idrobiol., 7: 109-127.

BLACK, G. A., T. DOBZHANSKY & C. PAVAN.—1950. Some attempts to estimate species diversity and population density of trees in Amazonian forests. Bot. Gazette, 111: 413-425.

BLUM, H. F.—1951. Time's arrow and Evolution. Princeton Univ. Press., Princeton. ix 222 pp.

BOND, T. E. T.—1952. Applicability of the logarithmic series to the distribution of the British Hieracia and other plants. Proc. Linnean Soc. London, 163:29-38.

BRANSON, H. R.—1953a. A definition of Information from the thermodynamics of irreversible processes. Information theory in Biology, edit. Quastler, 25-40.

_____ 1953b. Information theory and the structure of proteins. Information theory in Biology, edit. Quastler, 84-104.

BRAUN-BLANQUET, J.—1951. Pflanzensoziologie. Springer Verlag, Wien. 631 pp.

BRIAN, M. V.—1953. Species frequencies in random samples from animal populations. J. Anim. Ecol., 22: 57-64.

BRILLOUIN, L.—1956. Science and Information theory. Academic Press, New York, 320 pp.

CABRERA, A.—1932. La incompatibilidad ecologica, una ley biológica interesante. An. Soc. Cienc. Argentina, 114:243.

CALILLEUX, A.—1953. Biogéographie mondiale. Presses Univ. France, Paris, 128 pp.

CAIN, S. A.—1938. The species-area curve. Amer. Midl. Nat., 19: 573-581.

CHERRY, C.—1957. On Human Communication. A Review, a Survey, and a Criticism. The Technology Press of the Massachusetts Inst. of Technology, 333 pags.

COCHRAN, W. G.—1949. The present status of Biometry. Congreso de Ginebra (1949), núm. 28. 19 pp.

COLE, L. C.—1946. A theory for analyzing contagiously distributed populations. Ecology, 27: 329-341.

COTTAM, G. J. T. CURTIS & B. W. HALE.—1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology, 34: 741-757.

CURTIS, J. T. & R. P. Mac INTOSH.—1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology, 31: 434-455.

DANSEREAU, P.—1956. Le coincement, un processus écologique. Acta biotheoretica, 11: 157-178.

DAWSON, G. W. P.—1951. A method for investigating the relationship between the distribution of individuals of different species in a plant community. Ecology, 32: 332-334.

DICE, L. R.—1952. Measure of the spacing between individuals within a population. Contribut. Labor. Vertebrate Biol., Univ. Michigan, 55: 1-23.

DOI, T.—1956. Dynamical treatment of exploitation of aquatic resource. II. Effect on the aspect of appearance of recruit by feedback of information of the size of catch. Bull. Tokai R. Fish. Res. Lab., 13: 73-84.

ELTON, C.—1946. Competition and the structure of ecological communities. J. Anim. Ecol., 15: 54-68.

ELTON, C.—1949. Population interspersion: An essay on animal community patterns. J. Ecol., 37: 1-23.

EVANS, F. C., P. J. CLARK & R. H. BRAND.—1955. Estimation of the number of species present in a given area. Ecology, 36: 342-343.

FISHER, R. A., A. S. CORBET & C. B. WILLIAMS.—1943. The relation between the number of individuals and the number of species in a random sample of animal population. J. Anim. Ecol., 12: 42-58.

GAMOW, G.—1956. (Conferencia peonunciada en La Jolla, Universidad de California, en abril de 1956).

GLEASON, H. A.—1922. On the relation between species and area. Ecology, 3: 156-162.

GOODALL, D. W.—1952. Quantitative aspects of plant distribution. Biol. Rev., 27: 194-245.

GRUNDY, P. M.—1951. The expected frequencies in a sample of an animal population in which the abundancies of species are log-normally distributed, I. Biometrika, 38: 427-434.

HOLMER, R. W. &. T. M. WIDRIG.—1956. The enumeration and collection of marina phytoplankton. J. Conseil, 22: 21-32.

HOPKINS, B.—1954. A new method for determining the type of distribution of plant individuals. Ann. Bot., 18: 213-227.

_____ 1955a. Species-area relationships of plant communities (Abstract). J. Anim. Ecol., 24: 504.

_____ 1955b. The species-area relations of plant communities. J. Ecol., 43: 409-426.

_____ 1957. Pattern in the plant community. J. Ecol., 45: 451-464.

HUTCHINSON, G. E.—1953. The concept of pattern in ecology. Proc. Acad. Nat. Sc. Philadelphia, 105: 1-12.

ITO, T.—1949. On the law of geometrical progression in limnoplankton. (Nombre de la revista en japonés) 14: 127-132.

JACOBSON, H.—1955. Information, reproduction and the origin of life. American scientist, 43: 119-127.

KENDALL, D. G.—1948. On some modes of population growth leading to R. A. Fisher's logarithmic series distribution. Biometrika, 35: 6-15.

KIERSTEAD, H. & L. B. SLOBODKIN.—1953. The size of water masses containing plankton blooms. J. Mar. Res., 12: 141-147.

LECOMPTE DU NOUY.—1936. Le temps et la vie. Gallimard, Paris, 268 pp.

LINSCHITZ, H.—1953. The information content of a bacterial cell. Information theory in Biology, edit. Quastler, 251-262.

MacARTHUR, R.—1955. Fluctuations of animal populations, and a measure of community stability. Ecology, 36: 533-536.

MAKO, H.—1955. A consideration on the density

index of fish populations. Bull. Jap. Soc. Sci. Fish., 21: 67-72.

*MANDELBROT, B.—1953. Contribution a la théorie mathematique des jeux de communication. Publ. Inst. Statist. Univ. Paris, 2: 80-102.

MARGALEF, R.—1949. Una aplicación de las series logaritmicas a la fitosociología. P. Inst. Biol. Apl., 6: 59-72.

_____ 1951. Diversidad de especies en las comunidades naturales. P. Inst. Biol. Apl., 9: 5-27.

_____ 1956a. La diversidad de especies en las poblaciones mixtas naturales y en el estudio del dinamismo de las mismas. Univ. Barcelona. Tomo homenaje póstumo al Dr. F. Pardillo, 229-243.

_____ 1956b. Información y diversidad específica en las comunidades de organismos. Inv. Pesq., 3: 99-106.

_____ 1957. Temporal succession and spatial heterogeneity in natural phytoplankton. Perspectives in marine Biology, Univ. California (en prensa).

MARGALEF, R. M. DURÁN & F. SAIZ.—1955. El fitoplancton de la ría de Vigo de enero de 1953 a marzo de 1954. Inv. Pesq., 2: 85-128.

MOORE, P. G.—1954. Spacing in plant populations. Ecology, 35: 222-227.

NEYMAN, J.—1939. On a new class of "contagious" distribution applicable in entomology and bacteriology. Ann. Math. Stat., 10: 35-57.

NIELSEN, C. O.—1954. Studies on Enchytraeidae, 3. The micro-distribution of Enchytraeidae. Oikos, 5: 167-178.

*NUMATA, M.—1949. On the variation-rate of a species curve and the density of species. Seibutu, 4: 31-32.

_____ 1950. The homogeneity of plant communities. Bot. Mag. Tokyo, 63: 203-209.

ODUM, H. T.—1956. Efficiencies, size of organisms, and community structure Ecology, 37:592-597.

*ODUM, H. T. & R. C. PINKERTON.—1955. Times speed regulator, the optimum efficiency for maximum output in physical and biological systems. Amer. Scientist, 43: 331-343.

PRESTON, F. W.—1948. The commonness, and rarity, of species. Ecology, 29: 254-283.

QUASTLER, R.—1953. The measure of specifity. Information theory in Biology, edit. Quastler, 41-71.

_____ (Editor) 1953. Information theory in Biology. University of Illinois Press, Urbana, 273 pp.

QUENOUILLE, M. H.—1949. A relation between the logarithmic, Poisson and negative binominal series. Biometrics, 5: 162-164.

ROMELL, L. G.—1926. Bemerkungen zum Homogenitätsproblem. Svensk. Bot. Tidskr., 20: 441-455.

SCHUSSNIG, B.—1927. Die pflanzliche Zelle im Lichte der Phylogenie. Heim, Wien.

*SHANNON, C. & W. WEAVER.—1949. The mathematical theory of communication. University of Illinois Press, Urbana.

SHINOZAKI, K. & N. URATA.—1953. Apparent abundance of different species. Res. Population Ecol., 2: 8-21.

SIMPSON, E. H.—1949. Measurement of diversity. Nature, 163:688.

SKELLAM, J. G.—1951. Random dispersal in theoretical populations. Biometrika, 38: 196-218.

_____ 1952. Studies in statistical Ecology. I. Spatial patterns, Biometrika, 39: 346-362.

SLOBODKIN, L. B.—1953. An algebra of population growth. Ecology, 34: 513-519.

THIENEMANN, A.—1920. Die Grundlagen der Biözonotik und Monards faunistische Principien. Festschrift fur Zschokke, 4: 1-14. Basel.

THOMAS, M.—1949. A generalization of Poisson's binomial limit for use in Ecology. Biometrika, 36: 18-25.

THOMSON, G. W.—1952. Measures of plant aggreagation based en contagious distribution. Contr. Labor. Vertebrate Biol., Univ. Michigan, 53. 1-17.

TISCHLER, W.—1955. Synökologie der Landtiere. Gustav Fischer, Stuttgart, 414 pp.

VOLTERRA, V.—1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. accad. Lincei, s. 6, 2:31-113.

*WADLEY, F.—1950. Notes on the form of distribution of insect and plant populations. Ann. Ent. Soc. America, 43: 581-586.

WANGERSKY, P. S.—1956. (Exposición privada).

WATERMAN, T. H.—1957. (Discusion de la communicacion de Margalef). Perspectives in marine Biology. Univ. of California (en prensa).

WIENER, N.—1948. Cybernetics. John Wiley & Sons, New York, 194 pp.

WILLIAMS, C. B.—1943. Area and number of species. Nature, 152:264.

_____ 1944a. Some applications of the logarithmic series and the index of diversity to ecological problems. J. Ecol., 32: 1-44.

_____ 1944b. The number of publications written by biologists. Annals Eugenics, 12 (2): 143-146.

_____ 1947a. The generic relations of species in small ecological communities. J. Anim. Ecol., 16: 11-18.

_____ 1947b. The logarithmic series and its applications to biological problems. J. Ecol., 34: 253-272.

WILLIAMS, C. B.—1947c. A diagrammatic method of analysing the interrelationship of the faunna or flora of several different localities. Proc. Linnean Soc. London, 158:09-103.

_____ 1947d. The logarithmic series and the comparison of island floras. Proc. Linnean Soc. London, 158:104-110.

_____ 1950. The application of the logarithmic series to the frequency of occurrence of plant species in quadrats. J. Ecol., 38: 107-138.

_____ 1951. A note on the relative sizes of genera in the classification of animals and plants. Proc. Linnean Soc. London, 162: 171-175.

_____ 1952. Diversity as a measurable character of an animal or plant population. Colloque intern. Centre nat. rech. Sc. sur l'Ecologie, Paris, 1950, p. 129-141.

_____ 1953. The relative abundance of different species in a wild animal population. J. Anim. Ecol., 22: 14-31.

YAMAMOTO, G.—1951. Benthic communities in Mutsu Bay. Bull. Japan. Soc. Sci. Fish., 16: 433-439.

YOSHIRATA, T.—1951. Some example of the law of Geometrical progression of an animal population. Bull. Japan. Soc. Sci. Fisheries, 16: 185-187.

YOUNG, J. Z.—1954. Memory, Heredity and Information. Evolution as a process, edit. J. Huxley, A. C. Hardy & E. B. Ford, pp. 281-299. George Allen & Unwin, London, 367 pp.

*Original reference not consulted directly.