An Organizational Hierarchy Postulate for the Interpretation of Species-Individual Distributions, Species Entropy, Ecosystem Evolution, and the Meaning of a Species-Variety Index

Howard T. Odum; John E. Cantlon; Louis S. Kornicker

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significantly greater on the bog mat than in the marsh (115 and 30 gr/m^2 respectively).

In the marsh there was a positive correlation of the standing crop of sedges and rushes with available moisture. There was a negative correlation with the standing crop of ferns and forbs with available moisture.

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LOWELL L. GETZ

MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

EXPERIMENTAL GERMINATION OF SEED AND ESTABLISHMENT OF SEEDLINGS OF *PHRAGMITES COMMUNIS*[1]

Examination of the vegetation which volunteered on mud flats at the Mud Lake National Wildlife Refuge in Northwestern Minnesota during the summer of 1953 revealed seedlings of a grass which the senior author tentatively identified as *Phragmites communis* Trin. Identification was made on the basis of the seed coat adhering to the roots of the youngest seedlings. During subsequent conversations, the late Dr. Norman C. Fassett indicated that definite germination of this species had not been reported. This led the authors to attempt to germinate *Phragmites* seed in the laboratory and to label a number of the seedlings on the mud flats so they could be relocated and identified after they had matured.

Seeds used in the germination experiments were contained in seed heads collected from a group of *Phragmites* plants growing on one of the refuge dikes in September, 1953. Germination tests were conducted in the laboratory in St. Paul by selecting well-filled florets from the heads and placing them in petri dishes of tap water. Laboratory tests were made on samples of seed after 3-6 months storage. The 6 month's tests included seed which had been stored dry in paper bags at room temperature, seed stored wet in glass vials at room temperature, seed stored dry in glass vials at outside temperatures (alternate freezing and thawing during the winter) and seed stored wet in glass vials at outside temperature. No germination was obtained in any of these tests.

Additional tests were conducted after 7 months storage. Seeds were placed in corked glass vials that had been half-filled with water. These were set out of doors in a wooden rack at St. Paul, Minnesota, and exposed to normal variations of outside temperature and light in late April. Four such tests, which were conducted on seeds that had been stored wet at outside temperature, gave no germination. However, in 4 tests made on seed stored at room temperature for 7 months, seeds in 19 of 40 florets germinated, or an overall percentage of nearly 50 per cent. One further test was made on seed stored dry at room temperature after 8 months and 30 per cent of the seeds in 150 germinated.

Examination of the staked seedlings on the mud flats in late summer of 1954 revealed without any possible doubt that the plants in question definitely were *Phragmites communis* Trin.

While these germination tests were not of an extensive or large scale nature, they do show that *Phragmites communis* Trin. seeds can be germinated experimentally and document the establishment of seedlings in nature.

STANLEY W. HARRIS
AND
WILLIAM H. MARSHALL

DIVISION OF NATURAL RESOURCES
HUMBOLDT STATE COLLEGE
ARCATA, CALIFORNIA
AND
DEPARTMENT OF ENTOMOLOGY AND ECONOMIC ZOOLOGY
UNIVERSITY OF MINNESOTA
ST. PAUL, MINNESOTA

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AN ORGANIZATIONAL HIERARCHY POSTULATE FOR THE INTERPRETATION OF SPECIES-INDIVIDUAL DISTRIBUTIONS, SPECIES ENTROPY, ECOSYSTEM EVOLUTION, AND THE MEANING OF A SPECIES-VARIETY INDEX

SPECIES-INDIVIDUAL DISTRIBUTIONS

One of the most fascinating and heretofore unexplained properties of ecological systems is the widespread similarity in the numerical distribution patterns of individuals and species in communities. Not only are there a few species present with many individuals and many species present with a few individuals of each, but the common and rare are related in ways suggesting logarithmic functions. Some principal graphs used are the following:

Number of species vs. number of individuals per species.—Willis (1922) plotted species versus individuals per species, obtaining curves in a wide variety of communities which resembled hyperbolas superficially, but were shown by Fisher, Corbet, and Williams (1943) to more closely resemble logarithmic series.

Cumulative species vs. logarithm of number of individuals.—Gleason (1922) and Cain (1932) plotted species accumulated versus the area sampled to obtain the now familiar species-area curve. With the species on a linear scale and the area on a logarithmic scale, many graphs are relatively straight (Vestal 1949, Goodall 1952). The counting of species per area was done to estimate the effectiveness of sampling for counting species.

Gleason (1922) and Williams (1944) also plotted species cumulated vs. the *individuals* found. Such graphs are independent of the size of the organisms, permitting the comparison of curves for the large and the small. For example, algae in Silver Springs (Yount 1956) may be compared with the trees of a rain forest. Fisher, Corbet, and Williams (1943), in an effort to obtain an accurate descriptive formula, compared such curves with the straight line that one obtains from a logarithmic series plotted on these same coordinates. However, Preston (1948) and Williams in a later paper in 1953 indicated criticisms of the logarithmic series as a mathematical description. For purposes of this paper this type of graph, of which Figures 1-3 show examples, is of greatest significance.

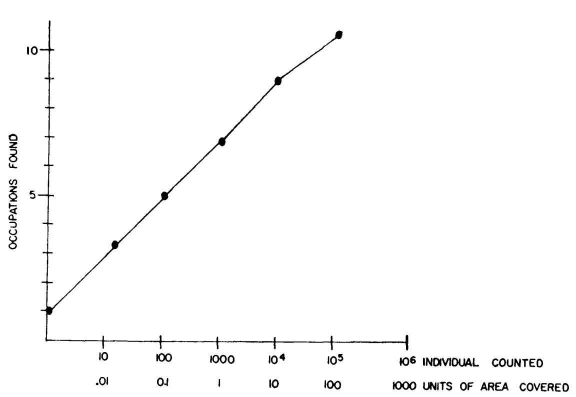

FIG. 1. Graph of occupations found versus logarithm of cumulative individuals counted based on the synthetic data which were formulated in Table I according to the hierarchy postulate of per capita relationship of occupations.

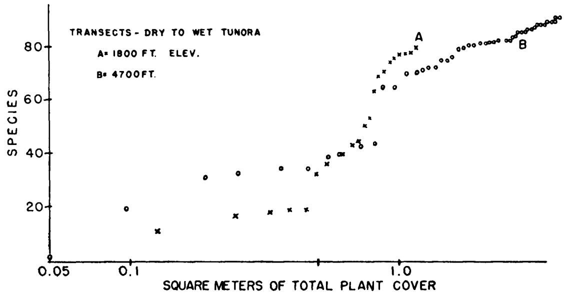

FIG. 2. Graph of species versus logarithm of cumulative cover of plants taken across conspicuous environmental gradients in Arctic tundra. Cover rather than number of individuals is used where plant individuals are difficult to determine. Curve A shows two conspicuous rises as cover is accumulated from a dry hill top, down a moderate to poorly drained slope into a marsh. In curve B the middle type is poorly represented. These data are from a study aided by a contract between ONR, Department of the Navy, and the Arctic Institute of North America. Their reproduction in whole or in part is permitted for any purpose of the United States Government.

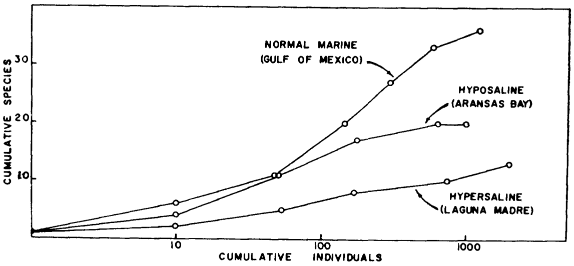

FIG. 3. Graph of species versus logarithm of cumulative individuals for molluscan shells in three marine environments of different environmental severity. Aransas Bay has low salinities; Laguna Madre has high salinities and the Gulf of Mexico has relatively normal and stable salinities.

Number of species of particular abundance vs. logarithm of abundance.—Preston (1948) followed by Williams (1953) and Patrick, Hohn, and Wallace (1954) found a fit of species-individual data in a graph of the number of species having a particular abundance versus the logarithm of that abundance. Hump shaped curves were obtained which were compared with theoretical log-normal curves on the same graph.

Abundance vs. logarithm of the rank.—MacArthur (1957) and Hutchinson and MacArthur (1959) provided still another type of plot relating a measure of the abundance of a species to the rank order of abundance indicated on a logarithmic scale. The observed graphs were compared with some theotrical curves based on the hypothesis of a normal distribution of niche size. Difficulties with this and other plots are discussed by Hairston (1959). In all four of the types of graphs listed, logarithmic functions are involved.

SPECIES-DIVERSITY INDEX

The logarithmic species-diversity index probably originated with Gleason (1922) and has been used by a number of authors (Fisher, Corbet, and Williams 1943, Williams 1950, Yount 1956, Odum and Hoskin 1957, Margalef 1957). It is the slope of the graph of cumulative species versus logarithm of individuals.

$$\frac{\text{Increment in cumulative species}}{\text{Increment in logarithm of individuals counted}} = \frac{\Delta S}{\Delta \log I} \qquad (1)$$

Fisher, Corbet, and Williams (1943) also considered the slope of the species-log individual graph as a proper measure of community species diversity particularly where the graph was straight. Since these authors postulated that the graphs were manifestations of the logarithmic series they used a constant derived from the logarithmic series for an index instead of the slope. One number may be derived from the other with the nomogram of Figure 8 of their paper. A table of standard error is also provided.

Even without theoretical implications, the slope of the species vs. log individuals graph is useful as an empirical measure of the diversity of communities. One may compare diversity of communities of all sizes, communities with different amounts of data, and communities sampled with different methods and sample sizes.

Recently Margalef (1957) has indicated that the logarithmic species diversity index (equation 1) has the mathematical form of negentropy (information). He used the index to determine the amount of informational content in the plankton species of an estuary.

In the descriptive, graphical, and mathematical formulations so far presented to relate species and individuals there have been few efforts to indicate how the particular distributions come about and how such distributions are related to community function and survival (Goodall 1952). As Hutchinson (1953) stated, "It is likely that something very important is involved here, but for the present what it may be is a mystery." In later papers Hutchinson and MacArthur postulate that development of many species aids in establishing community stability. They attempt to show that the species divide the available spaces and niches in a random manner.

In this communication a different explanation is offered to account for the logarithmic properties of species-individual distributions cited above. The patterns are derived from postulates of a high degree of organization in nature, the very antithesis of random functions. However, Brian (1953) cautions ". . . lest the j-shape of the population form suggest to the ecologist intense interspecific competition, . . . it is well to recall that Kendal (1948) has shown that theoretically negative binomial distributions can develop where no competition or interference either between or within species occurs . . . [and] where immigration was . . . negligible the form tended toward that of a logarithmic series." Thus, it is perhaps prudent to assume that several kinds of phenomena may contribute to this logarithmic relationship including patterns which serve to regulate interaction.

Functional Hierarchy of Occupations and Species

The proposed hypothesis can be presented as it was conceived using an analogy previously used by Elton (1926) in formulating a niche concept. The species in an association of organisms are compared to the occupations of humans in an army or in an urban community where something of the same distribution of commonness and rarity may occur. In such a community there is often a basic occupation that is the major reason for the existence of the community, such as agriculture or the making of some product in some central large industry. These workers and their occupations in the primary industry are most numerous. The occupations that serve and are dependent directly upon the basic occupation are less numerous such as wholesalers, truckers, salesmen, advertisers, and managers. Even further away functionally from the dominant occupation are those occupations that serve primarily the second stage occupations and are twice removed, such as special suppliers of specialized items needed in the secondary occupations. There may be even rarer occupations that serve only the third stage occupations and so forth. As one counts progressively more individuals one includes rarer occupations. The number of individuals who can make a living at the occupations far removed from the most common occupation becomes successively smaller. It takes an increasingly larger number of persons and an increasingly larger town to provide support for the more specialized jobs. This is natural since the cost of the most specialized services must be divided among those being served if the whole system is to have economic competitive value and not cause a collapse of functional chains due to inefficiency failure at some occupational link. Whether these comments about human occupations are exact or not, it is not the purpose of this communication to establish. The human analogy is used only in order to make the principle clear as advocated for ecological systems. Certainly the hypothesis applies to the table of organizations of military systems.

Many occupations such as grocers, druggists, and residential fuel suppliers service all of the others. The number of individuals in each occupation is not only due to the proximity of function to the basic occupations, but to the volume of occupational activity relative to the volume of basic function. Some occupations may be much more important to the community survival than their numbers indicate. Doctors, lawyers, teachers, and other specialists may be examples. In these cases as well as with the other occupations, the density of the occupation depends on the number of persons it serves.

Both in human communities and by analogy in biological communities, the occupational structure might be described as one in which the basic occupations which first bring energy into the system are determined by the energy and materials source whereas the remainder of the occupations are related on a per capita basis. Each dependent occupation has a definite and characteristic range in per capita requirement. There are ratios between each specialized occupation and the number of people being served.

Hierarchy Postulate

As long as the rarer occupations are related to the commoner occupations in constant per cent ratios, the relationships of occupations to individuals is by definition logarithmic. The reason a plot of cumulative species and logarithm of cumulated individuals is a straight line in such a case is no mystery. If the per cent change in individuals with adding of species is constant, the following may be expressed.

$$\frac{dI}{IdS} = k \qquad (2)$$

Where S is number of species and I is the number of individuals. Integrating, the hierarchy postulate yields the following

$$\log I = kS + C \qquad (3)$$

and

$$S = K \log I \qquad (4)$$

which is a straight line on the plot of cumulative species and logarithm of individuals counted. The equation of the graph (4) is also the expression that Margalef recognized mathematically as of the same form as the expression for information where H is the information

$$H = K \text{ log (number of states)} \qquad (5)$$

(macroscopic negentrophy). Margalef (1957) comparing equations (4) and (5) reasoned that the number of species must be a measure of information. The reason that the number of species is a measure of the informational content now becomes apparent from the hierarchy postulate. Rothstein (1952) and others have shown that a hierarchy such as in a military organization could be described in units of information. An ecological heirarchy may be similarly described. Negentropy of information and organization of species are all measured by the same quantity. Constants in the equations are all different.

When a per capita hierarchy exists, organization exists, and equations 2-5 pertain. The degree to which these apply is the degree to which simple logarithmic, per capita structure exists. Since there is often some tendency for a straight line on graphs of species and log individuals, it must be concluded that to a considerable extent, communities tend to be organized into hierarchies in their relationships of species.

For an example consider the hypothetical table of occupations in Table I constructed on the one single basic principle that each occupation requires a certain number of individuals to support it although the per capita requirement may vary greatly from one occupation to the next. Suppose that letters are used to represent occupations that are necessary to community survival. Three types of dependence are illustrated: occupational niches dependent on one other niche, occupational niches dependent on one other niche but requiring a large per capita support, and occupational niches dependent on the total number of all individuals present.

TABLE I. Some fictitious occupations and per-capita requirements for their support.

Occupation	Number of other kinds of individuals required for support of one in this niche	Number of persons this occupational niche supported per area
A (primary occupation)	—	1000
B	10 A	100
C	10 B	10
D	10 C	1
E	10 D	0.1
F	10 E	0.01
G	10 F	0.001
H	100 A	10
I	100 B	0.1
J	100 C	0.001
K	100 D	0.00001
L	10 A—n	100
M	100 A—n	10
N	1,000 A—n	1
O	10,000 A—n	0.1
P	100,000 A—n	0.01

When the data in Table I are plotted as in Figure 1, a linear type curve results like those in many natural associations. The distribution of rarity in species tends to be logarithmic because directly or indirectly each rare species requires or is required by a definite number of the more common species for its survival and support. We might define a community as organized when the numbers of occupational niches are related on a per capita support basis.

Some of the successive hierarchy of relationship to the basic energy users may correspond to the trophic passage of energy. However, there are many routes of community coaction other than those involving major energy transfer, e.g., those concerned with transfers of materials or information. Such logarithmic hierarchy, thus, is not restricted to food chain relationships. It is likely, however, that any coaction involves an effect on energy budget.

The almost universal report of cases suggesting at least partial hierarchy of species indicates the universal similar organization of systems. Odum and Hoskin (1957) found organized cases in an artificial stream microcosm similar to those in nature.

DEVIATIONS FROM SIMPLE HIERARCHIAL ORGANIZATION

In many instances the graph of species cumulated versus individuals counted turns upward, turns downward, or has inflexions. There are several hypotheses which may be stated concerning the significance of such curves. A curve that turns upward has more organization and diversity than the straight (logarithmic) comparison line. A curve with downward curvature has less organization and diversity.

Diversity with homogeneous sub-areas.—An upward curve may be expected where one is counting in homogeneous small areas which are taxonomically different from adjacent homogeneous areas. As one counts, one is within the area of maximum functional interaction of species. With larger number of individuals counted one passes over wider areas and includes more than one homogeneous area thus including species at a faster rate than one would within a smaller area.

Communities which are sub-organized.—When the graph turns down (flattens) as the number of individuals counted increases, one may infer that there is less hierarchy than is possible. The system is under-organized. If organization has survival value for the system, such systems will have poor competitive value and be displaced by systems with higher organization. Under-organized systems may be expected where the environment is so new either in the invasion, successional, or evolutionary sense that adequate higher order species have not become established. The curvature and the slope of the curve in the upper zones is thus a measure of the degree of fulfillment and saturation of the evolution or growth of the organization.

Inflexion and Edge.—The graph of species and log of individuals or cover may be used to indicate discontinuity in organization of communities. Sharp upward turns of a graph indicate an edge (Figure 2).

The diversity of species may be related to the biomass counted or to the cover of the biomass as well as to the separate individuals. This makes it possible to count where the existence of separate individuals is uncertain as in Arctic ground cover (Figure 2). Such comparisons make possible comparison of the organization and the biomass.

SPECIES DIVERSITY INDEX IN PALEOECOLOGY

The considerations of diversity, organization, and the species diversity index may be used with fossil assemblages as well as with living systems. Since the species diversity index is independent of taxonomic content and little affected by dilution or concentration, it may be used to characterize the faunas of ancient seas. For example in Figure 3 shelled populations, living and dead from hyposaline and hypersaline environments with restricted diversity are compared with shells from a normal marine environment of the Gulf of Mexico. Such indices in ancient strata may help indicate the generality of logarithmic structure in past ages, the evolution of ecosystems with trends in organization, and the difference between normal environments and extreme ones.

SUMMARY

A postulate of per capita hierarchy of function in communities leads to logarithmic properties like those observed in many species-individual graphs. The hierarchy postulate explains why species-diversity index is a measure of organization in units of information and negative entropy as Margalef has postulated. The value of the organizational measure for paleoecology is illustrated with data on shells.

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HOWARD T. ODUM[1]
JOHN E. CANTLON[2]
AND LOUIS S. KORNICKER[1]

[1] INSTITUTE OF MARINE SCIENCE, PORT ARANSAS, TEXAS
[2] DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
MICHIGAN STATE UNIVERSITY, EAST LANSING