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A GENERAL THEORY OF SPECIES DIVERSITY

A thesis
submitted to the
Department of Biology
for
Graduation with Honors

Submitted by
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ABSTRACT

In this paper I have tried to develop a comprehensive theory of species diversity. By considering generally accepted aspects of the evolutionary processes, along with some interpretations of my own, particularly regarding species energy utilization, a general pattern for species diversity emerges. Much emphasis is placed on interpretation of the mean, variance and total number of species in the lognormal distribution and how they relate to patterns of species diversity, fundamental and realized niche, niche overlap, competition, genetic polymorphism, species and community energetics, predictability and harshness of environments, island biogeography, habitat extent, nutrients, and nutrient cycling. A new use for the Shannon-Weaver information statistic is proposed, and some of the consequences of this application directly parallel the results suggested by interpretation of the lognormal. Other theories relating to species diversity are shown to be included as special instances in this one.

For
Gram

VITAE

Richard E. Furnas was born in Brooklyn New York on August 10, 1952. He lived in Merrick, New York until the age of five when his family moved to Cleveland Heights, Ohio. He attended Cleveland Heights High School and was accepted to Cornell University from his Junior year at Cleveland Heights High. At Cornell he has majored in Biology while also taking advanced courses in Chemistry and Mathematics. He has been awarded a National Science Foundation Graduate Fellowship and plans to do graduate work at the University of Alaska, Fairbanks, Alaska.

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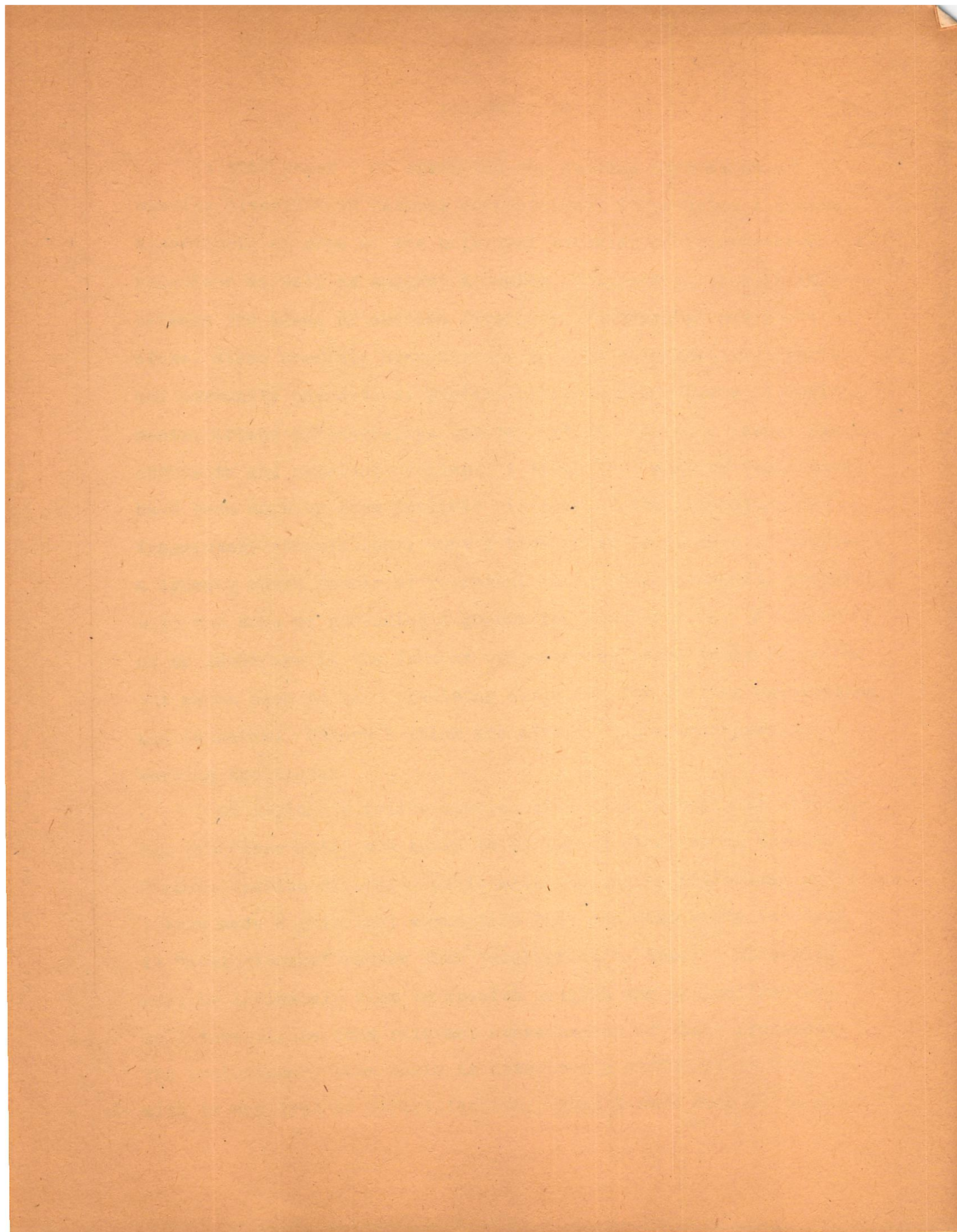
Many of the ideas in this paper have benefited greatly from discussion with other people. I would like to thank Russell F. Hansen of Western Reserve Academy, Hudson, Ohio, both for his role in giving me opportunities to develop sound intuitions about natural systems, and his thoughts on the ideas in this paper. In the early stages of developing these ideas discussions with Susan Bratton, graduate student in ecology, and Dr. Robert H. Farrell, professor of mathematics, were particularly productive. Drs. Jack Kiefer, professor of mathematics, and Robert H. Whittaker, professor of ecology and systematics, were especially helpful. Thanks are also due to Robert K. Peet and Charles L. Mohler, graduate students in ecology, and Dr. William L. Brown, professor of entomology, for their suggestions after ^{reading} copies of the manuscript. I would also like to thank the members of my family for their comments and encouragement, particularly my brother, George Furnas. Special thanks are due to Dr. Peter L. Marks, assistant professor of ecology and systematics, for sponsoring the research, and his continuing interest and moral support as well as detailed criticism of the manuscript.

APOLOGIA

This work is largely theoretical. It represents an attempt to pin down some intuitions I had shortly after being exposed to "species diversity" as a distinct problem in ecology. It also represents a perhaps somewhat reactionary approach to what I have seen as the use of mathematics in ecology. Aside from its intrinsic interest, mathematics is a powerful tool for organizing thoughts on problems. It has its potential for proposing quantitative relationships, but while these are often tactically useful for looking at specific problems, they are incomplete without at the same time mirroring qualitative relationships. There exist an infinitude of mathematical functions, and to find one which describes a certain body of data, while useful for summarizing the data, is only a beginning, not an end. I believe that much more can be asked of mathematics than summarizing data. It can point out relationships between entities. It can be used not only to describe what is taking place but provide insight into why. In this work I have tried to ask this latter type of question from mathematics; to engage in a dialectic of finding mathematical analogies to biological processes, and then biological analogs of mathematical relationships. In the course of doing this I have often felt as though ideas were spontaneously feeding back upon themselves and the scope of what was at first rudimentary relations of species diversity has grown considerably. Whenever possible I have tried to explore the biological implications of what mathematics has suggested, trying as it were to keep it "biologically honest." Things which I at first saw as problems,

or disparities, or unreasonable assumptions happily gave way to further insights, usually through what Dr. Whittaker has called "collaboration with the back of the mind" (lecture B10 668).

No attempt has been made to survey the voluminous literature on species diversity. One reason for this is its extent and the fact that there have been many other demands on my time, but the principle reason is a more active one. My early exposure to the species diversity problem gave the impression of its being a rather confused, confusing and jumbled aggregation of ideas. Somehow in my mind it was not that confusing and it seemed to me that what I first ought to do was find out what it was I really thought before pursuing the literature and thereby risk losing the intuitions I seemed to have. I have not ignored the fact that in the literature there are also data, the wellspring of good understanding, but new ideas or suggested relations have come fairly regularly and so analysis of data in the light of my ideas has not been as extensive as it might be. One claim I can make, however, which in my mind seems a reasonable justification. Any data I have looked at seem to fit into the scheme. I have made a conscious effort to envisage situations that might not fit; as well as criticisms from persons with whom I have shared my ideas. Recently I have tried to relate these ideas to some of the principal attempts at such syntheses which have been made in the past. Here I have relied principally on some major review articles to summarize ideas scattered in the literature.



INTRODUCTION

In this paper I am examining the general phenomenon of species diversity in natural communities. In so doing I propose a synthesis of some of the principal theories of species diversity relations as well as suggest a number of direct inter-relationships between the ideas of species diversity, fundamental and realized niche, niche overlap, competition, genetic polymorphism, species and community energetics, predictability and harshness of environments, island biogeography, habitat extent, and to a lesser extent nutrients and nutrient cycling. I think that many of these ideas have been more or less implicit in some of the literature as fragmentary observations; what I have tried to do here is propose a loosely woven fabric of relations among these community properties with the hope of providing a ground for further work. A number of my ideas are in the form of conjectures, regrettably imprecise but which seem to be promising directions for further examination and research. Others I think are already quite encompassing working hypotheses.

I am trying to relate species diversity patterns to biological processes which are known to be taking place among species. Because species diversity deals with species as biological entities, I have made a principal assumption that the time scale involved is "evolutionary" rather than "ecological." Species diversity must be intimately tied to species origins and extinctions and so I investigate some relevant consequences of these processes. The evolutionary time scale is notoriously difficult to deal with in any type of direct fashion. What I have done is to suggest

processes which may be involved in the development of species diversity--more as a tool for synthesis than as a set of readily testable hypothetical processes. Then I have looked at short-term consequences or secondary effects that such processes might generate, and it is these that I have tested against data in the literature.

In particular I have looked at the lognormal distribution of species with respect to their importance. I show that the other distributions which have been proposed may be seen as special cases of the lognormal distribution with particular ranges of values for the parameters of the distribution. I then go on to examine the properties that are held in common between communities which have been reported in the literature as giving reasonable fits to these other distributions, and then attempt to place them on a continuum generated by the interaction of biological processes which would influence the parameters of the lognormal distribution (its mean and variance).

I finally propose an application of information theory to communities which involves a sense of organisms acquiring information through evolutionary time. I feel this application of information theory describes much more about the biological interactions than the others currently in use in ecology, which seem to place more emphasis on the relations between a sampler and his community of interest than on the interactions in the community.

METHODS

The Virtues of Energy Utilization as a Master Variable

Ever since Lindeman's (1941a, 1941b, 1942) seminal works, ecologists have found increasing satisfaction in measuring energy utilization in the analysis of ecosystem function. The strength of this application has firm roots in chemistry and physics both of which put a major emphasis on describing interactions in terms of the transfer and degradation of energy. Certainly materials are also of great importance, but for purposes of discussing processes, analysis of materials relations rapidly becomes elusive and unwieldy. Throughout the living world we see examples of species performing equivalent energetic functions with different elements or compounds: there are among chordates some whose blood use iron for binding oxygen and others vanadium. Within a single organism there may be the options of aerobic and anaerobic respiration. The picture may be confused even further by the cycling of materials. If an element is in short supply, it may be cycled rapidly thereby permitting the organism or community to extract more "energetic mileage" before it is lost (viz. pelagic plankton productivity and turnover rates). With compounds there are problems of synthesis. Some organisms can synthesize the compounds they need, others must find them in the environment. All of these properties complicate the use of materials in describing community processes. To be sure, these complications are much of what makes a group of organisms or particular locality unique, but understanding grows from a recognition of both common patterns and particular details. Energy is such a shared property. It

has no substitute or equivalent and can never be recycled. Plants "eat" photons and animals eat plants and other animals. But all organisms eat energy.

In this paper I will speak of energy as though its utilization by organisms were an end in itself. Sometimes this may be so but more generally it is likely to be an indicator of ecological success. An increase in energy utilization may not be an impetus for selection in itself but if an organism can use more energy it is likely to be able to commandeer more materials from the environment, carry on more processes, and generally, be a more successful organism. Conversely, if an organism is commandeering more materials and carrying on more processes, it is also likely to be utilizing more energy. Either way, energy utilization is going to be closely linked with the success of a species.

About Lognormal Distributions

In short, a lognormal distribution is the familiar bell-shaped normal distribution on a logarithmic instead of an arithmetic base. There are two principal representations for a normal distribution. Each has its advantages and disadvantages for elucidating graphically particular properties of the distribution although each has these other properties inherent in it. Probably the most familiar representation is the bell-shaped curve called the normal density function (Fig. 1A). The horizontal (x) axis represents some measured variable, say, height of individuals of a population, while on the vertical (y) axis are numbers related to the fraction of the population having that particular height. In practice the density function is made on the basis of intervals along the x-axis and the number of individuals that have

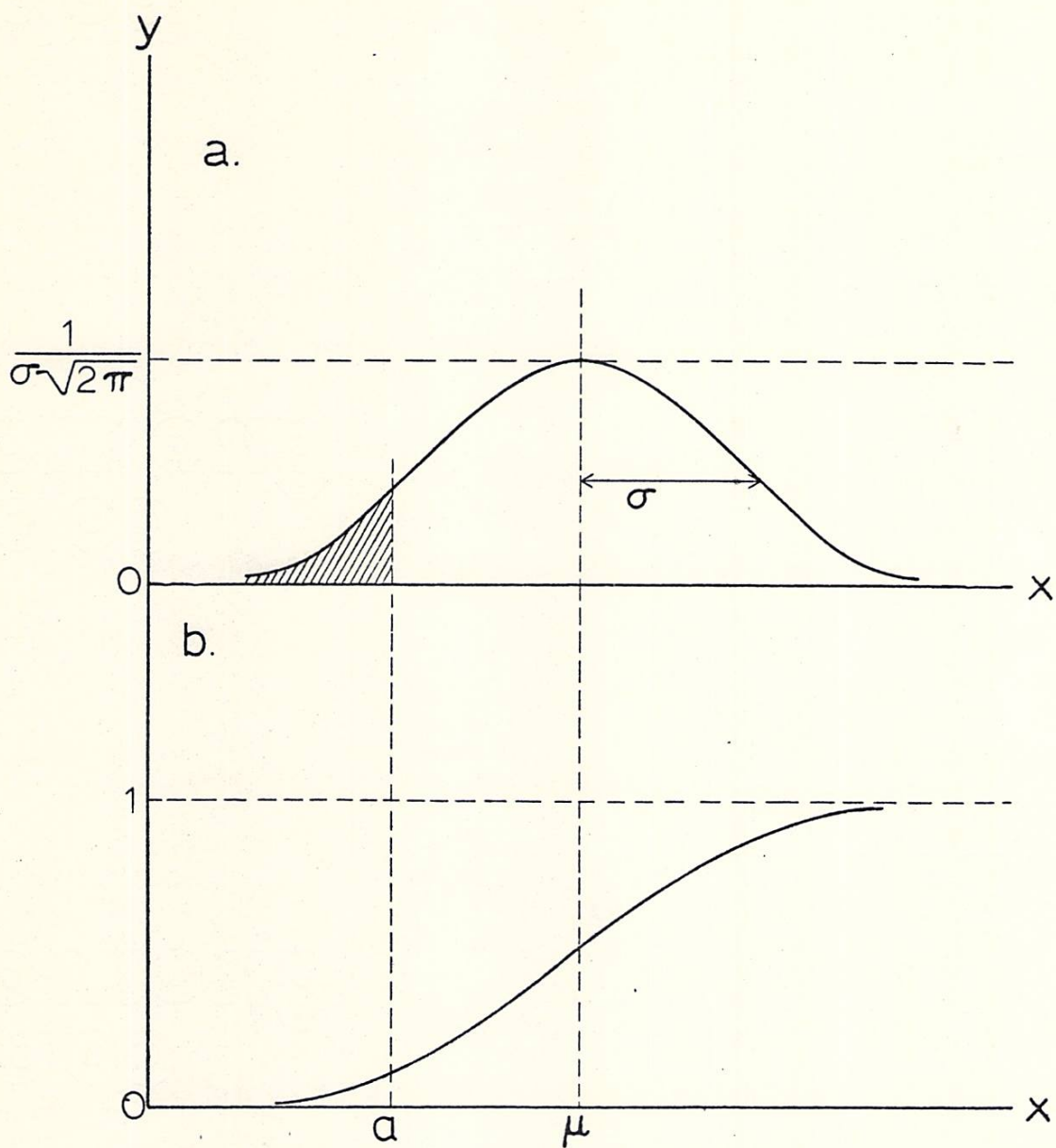


FIGURE 1
a. normal density function
b. normal cumulative distribution
function

heights falling in that interval. The alternate representation involves plotting the integral of the normal distribution with respect to the x-axis (Fig. 1B); starting at minus infinity on the x-axis, plotting the area under the bell-shaped curve (shaded area Fig. 1A) up to the point of interest, a (Figs. 1A, B).

As a probability distribution the normal density function must have a total area of one, corresponding to the probability, say, that an individual will have some height, while the area from minus infinity up to a (Fig. 1A) corresponds to the probability that an individual has height less than a . In the case of the normal distribution, the mean, mode, and median all have the same value, μ . This value is the height (x-value) at the highest point of the curve. The variance (σ^2) is a measure of the dispersion of the distribution. Its square root (σ) is the standard deviation which directly measures the distance from the mean to the points of inflection of the curve on either side of the mean. The cumulative distribution function rises continuously from 0 to 1. In this representation the median (and hence, the mean and mode) is at the x-value corresponding to the y-value at 0.5. The variance is a bit more elusive but essentially is expressed by how rapidly the curve rises. If the variance is large, the curve rises slowly, if small then more quickly.

A convenient way of looking at normal distributions involves the use of probability paper. This is a graph paper which takes advantage of the fact that the cumulative distribution function rises monotonically. By adjusting the scale on the y-axis, it makes the sigmoid shape of the cumulative normal distribution function into a straight line. The mean and variance of the

distribution are easily read from such a graph since the mean corresponds to the x-value at 50 per cent of the total probability, while the standard deviation corresponds to the difference between the x-value at the mean and the x-value at a point a little more than 34 per cent of the probability to one side of the mean. Often this probability paper is calibrated both in terms of cumulative per cent and in terms of positive or negative standard deviations from the mean. If two normal distributions have the same mean on probability paper, they will pass through the same point intersecting the 50 per cent line, while if they have the same variance (and hence standard deviation), they will be parallel (Fig. 2).

As mentioned above, a lognormal distribution is a normal distribution on a logarithmic base. What this means is that instead of having a linear scale along the x-axis, the scale is logarithmic. When using probability paper, the same relationship holds, and instead of a linear scale, a logarithmic one is used. In using a logarithmic scale the base of the logarithm is of no consequence as long as one is consistent throughout. Since changing the base of the logarithm merely involves a multiplication by a constant, for purposes of graphing, a choice between different logarithmic bases is merely a choice between the units one is to use to calibrate the scale and is of absolutely no consequence whatsoever--the representations will be equivalent in every respect.

In the situations described so far, the use of probability paper has assumed that the full range of theoretically possible values for a particular character could in fact be measured. In some situations such as the distribution of soil particle sizes

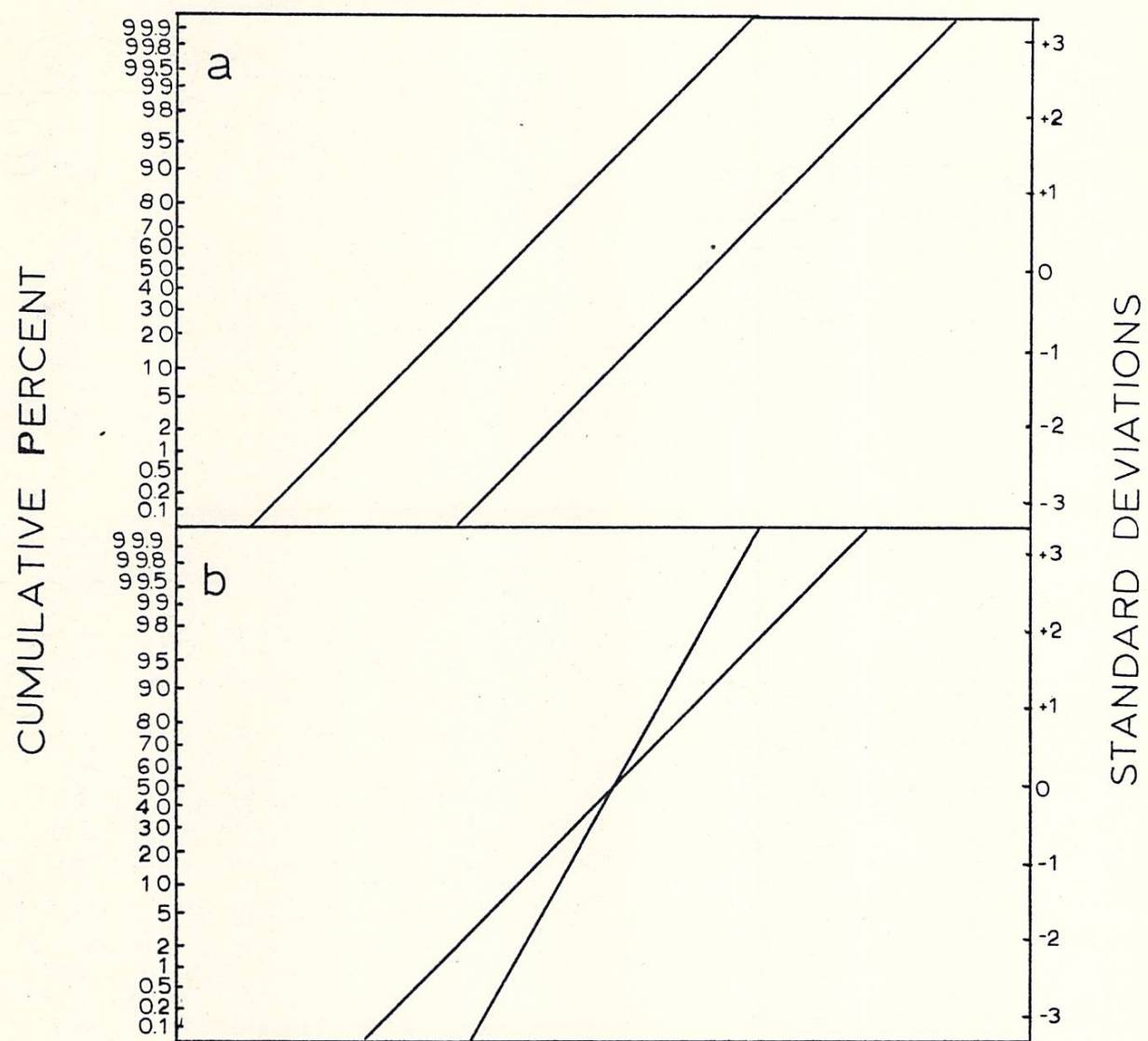


FIGURE 2

Normal distributions plotted on probability paper:

a. same variance, different means

b. same mean, different variances

after going through a sieve, this is not the case and either very small or very large values may be excluded from measurement, thus truncating the range of values. The density function obtained would correspond to the unshaded region of Fig. 1A if, for example, low values were excluded. When using probability paper to analyse such data, the straight line of the complete distribution is no longer straight and instead it goes almost straight and then drops precipitously near the zone of truncation. Fig. 3 is a plot of a full normal distribution and normal distributions with various degrees of truncation (after Hald 1952).

Since straight lines are readily discriminated by eye, and since the data analysed here give reasonably straight lines on probability paper, I have done nothing further in curve fitting.

See also Fig. 4 for the shape of confidence isopleths for probability paper (after Hald 1952) .

When plotting species in such a treatment some problem arises. The entire assemblage of species represents 100 per cent and each species is taken as contributing the fraction $1/N$ (where N is the total number of species) to the total assemblage. The difficulty is that when the last species comes to be plotted it goes at positive infinity. I have dealt with this problem by simply assuming that the first species is observed when there was a probability of $.5/N$ of its observation and the last one was observed when there was probability $(N - 0.5)/N$ of its observation. This small manipulation makes very little difference except to move all points onto the range of the graph.

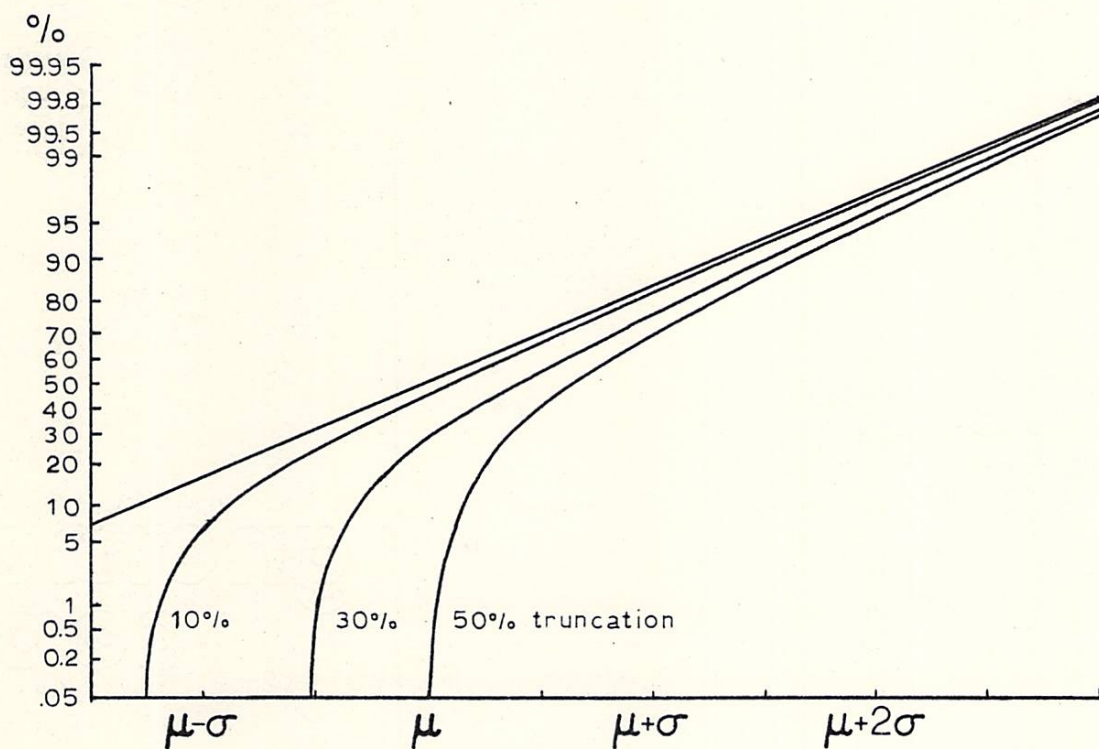


FIGURE 3
EFFECT OF TRUNCATION ON
the shape of cumulative distribution
functions plotted on probability paper

(AFTER HALD, 1952 p.146)

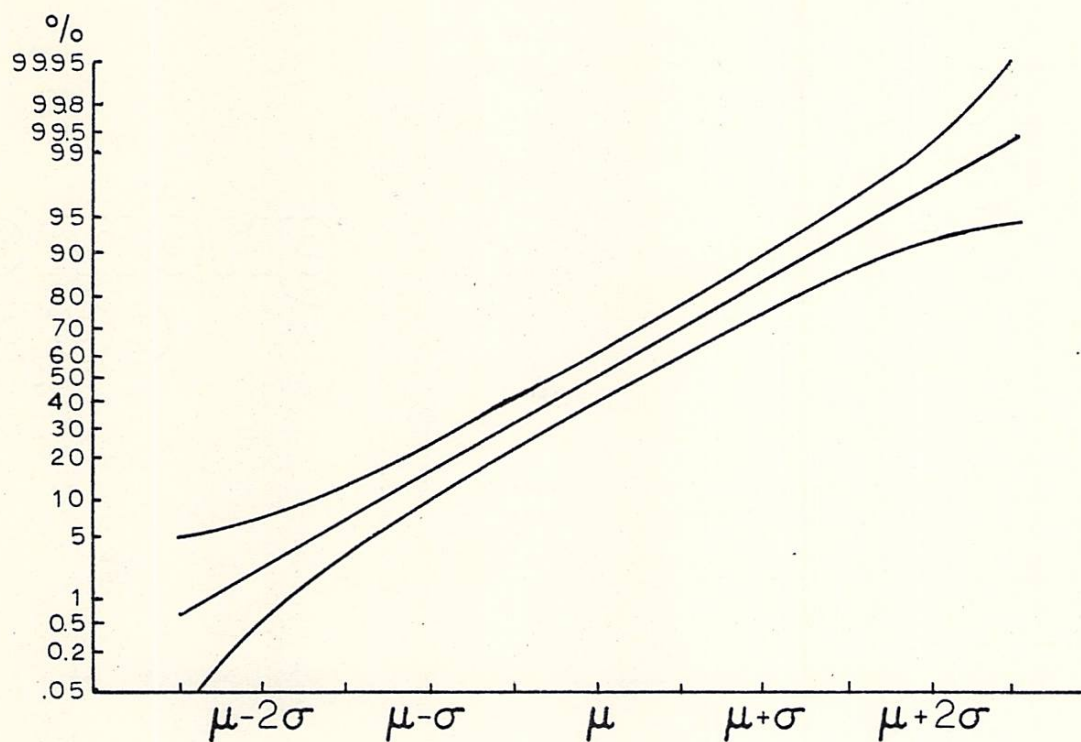


FIGURE 4
 GENERAL SHAPE OF 95%
 confidence region for normal
 distribution on probability paper
 (case of sample size of 100)

(AFTER HALD, 1952 p139)

Lognormal Distributions and Species

In discussing the lognormal distribution of species I will start with an empirical observation on how species segregate with respect to their importance (energy utilization or other measures which are probably nearly proportional to energy utilization are taken as referred measures of importance). The generality of this distribution in describing much of species-importance data is well documented (Preston 1948, 1962, Whittaker 1970, p. 35 ff., 1965, Patrick 1954, 1967, 1968a, b, 1971, Patrick et al. 1968), and later I will show that the other principal distributions which have been proposed are in practice indistinguishable from lognormal distributions.

The lognormal distribution has two parameters, its mean and variance (or standard deviation) and in practice when considering species it assumes another, the total number of species encompassed in the measurements. Each of these parameters can be thought to change independently of the others. I have examined a variety of biological processes involved in species interactions and then tried to evaluate their expected influence on the parameters of the lognormal distribution. Each of these processes will be discussed separately, as though each could take place in the absence of the others. This will describe a much wider range of possible situations than actually ever exists, but if carefully applied this type of reasoning can be very useful.

"Perhaps I can best make clear . . . by quoting a remark dropped casually by Eddington in a recent book--

'We need scarcely add that the contemplation in natural science of a wider domain than the actual leads to a

far better understanding of the actual.' (P. 267, The Nature of the Physical World).

For a mathematician the statement is almost a truism. From a biologist it would suggest an extraordinarily wide outlook. . . . The ordinary mathematical procedure in dealing with any actual problem is, after abstracting what are believed to be the essential elements of the problem to consider it as one of a system of possibilities infinitely wider than the actual, the essential relations of which may be apprehended by generalized reasoning and subsumed in general formulae, which may be applied at will to any particular case considered" R. A. Fisher (1958), preface to The Genetical Theory of Natural Selection (p. viii - ix).

I have tried to develop such a larger system and then test to see if the observed phenomena are consistent with the results suggested by this larger system.

The Question of Why a Lognormal is Observed at All

In the literature there are several mechanisms of species interaction which may be construed to yield a lognormal distribution (MacArthur 1960, Whittaker 1970, p. 27). These generally describe events that occur on an ecological time scale and, therefore, I am somewhat suspicious of their validity. I have contemplated analagous processes operating on evolutionary time scales, but my knowledge of some of the more exacting aspects of probability theory is inadequate to pursue these ideas at present. I have discussed these ideas with people in the math department but we have not yet been able to adequately formalize my ideas. The problem of the cause of the lognormal distribution is related to,

but not a prerequisite for, the observations^{and} discussion which follow. Causes of the lognormal and implications of its existence must each be founded upon the empirical observations of the lognormal distribution and as such would rest first on those observations and then rely on each other for possible new directions of inquiry.

THEORETICAL OBSERVATIONS AND DISCUSSION

A View on Previous Models

A number of models have been proposed which deal with species dominance-diversity relations. What I show here is that they all may be viewed as special cases of the lognormal distribution. I then suggest an interpretation of these distributions and the communities they have been used to describe in terms of the lognormal distribution and its parameters.

Before I proceed, a word about the relations to be expressed is in order. There have been two principal approaches to describing the relations which exist in dominance-diversity data. The first and most common representations have involved plotting the importance value of the species along the ordinate and the rank of the species along the abscissa. The geometric series (Motomura 1932, Fig. 5b) and random niche boundary hypothesis (MacArthur 1960, Fig. 5c) have explicitly addressed themselves to this type of description. The lognormal distribution (Preston 1948, 1962, Fig. 5d) and the logarithmic series (Fisher, Corbett, Williams 1943, Fig. 5a) have been used to describe the number of species (or species density) at a particular importance value or range of values. Needless to say the two representations can be interconverted although the actual relationship which exists between the two representations has been absent from what literature I have seen. Simply stated, by appropriate rotation and reflection of axes, the former representation may be seen as the integral of the latter one. If the distribution is incomplete (as is usually the case since very rare species are not represented) the

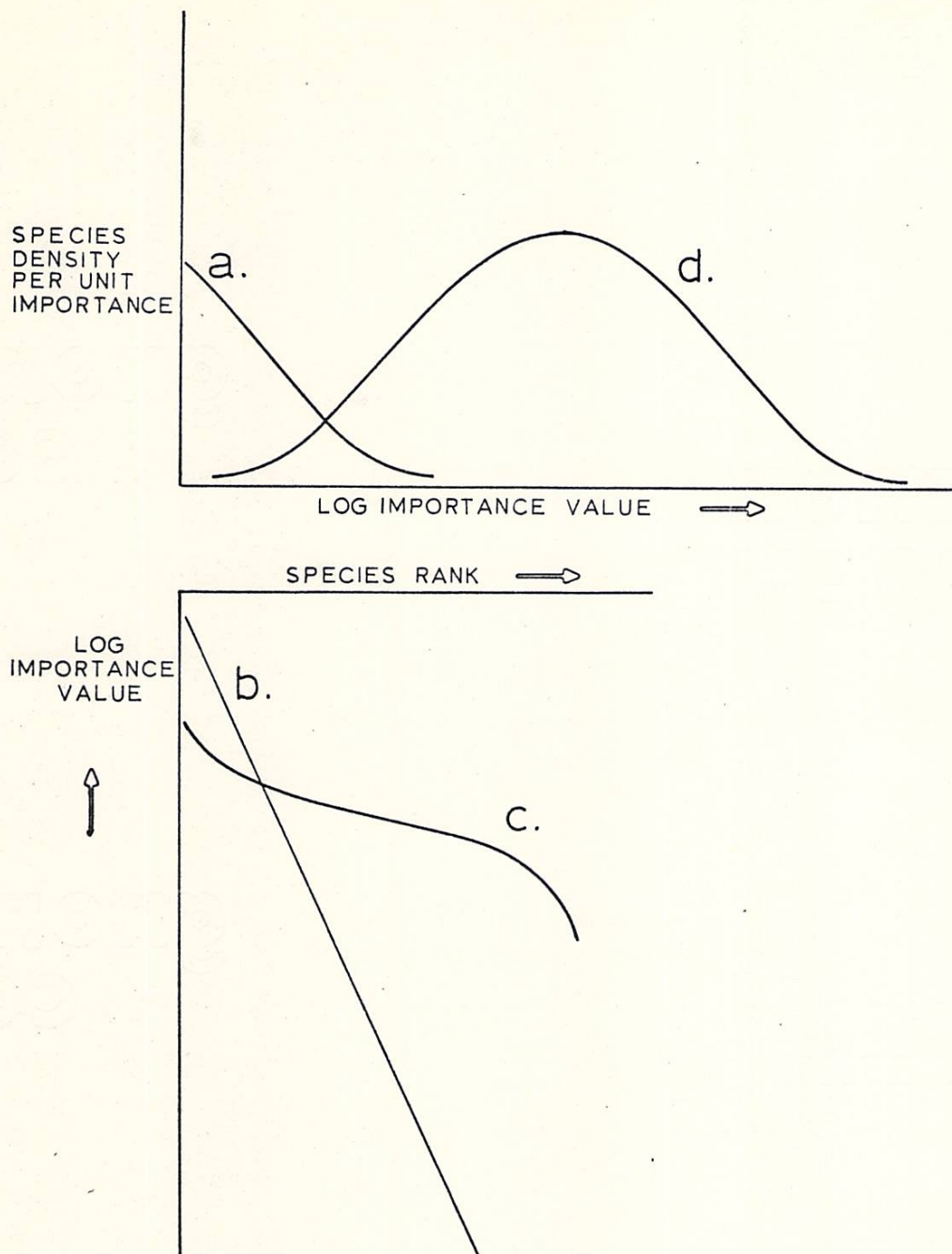


FIGURE 5

DOMINANCE-DIVERSITY CURVES:

a. logarithmic series

b. geometric series

c. random niche boundary hypothesis

d. lognormal distribution

relation is most conveniently seen if one integrates from the right (see Fig. 6).

I have already mentioned that there are four particular distributions which have been proposed to describe dominance-diversity data: the logarithmic series (Fisher, Corbett, Williams 1943), the geometric series (Motomura 1932), the random niche boundary hypothesis (MacArthur 1960), and the lognormal distribution (Preston 1948, 1962, see Fig. 5a, b, c, d). In his 1948 paper, Preston remarks upon the logarithmic series and suggests that it may be considered equivalent to a lognormal distribution which has been truncated on the left by insufficient sampling. Since measuring the importance of species in a community involves sampling from the community, there is a tendency to miss rare species in the process of sampling. The agreement of the logarithmic series with empirical data may then be interpreted as an artifact of insufficient sample size. In fact, more intensive sampling invariably does show this to be the case (Preston 1948).

The geometric series suggests that species divide up resources sequentially with each species taking a fixed fraction of what remains after its predecessors in the sequence have taken their share. If species importance is plotted logarithmically against species rank, a straight line results with its slope determined by the value of the fixed fraction (Fig. 5b). Given the relationship between the importance vs. rank representation and that of number of species at a given importance value (species density), the geometric distribution may be converted to the species density vs. importance value form of representation by simply taking its derivative, which on the logarithmic plot becomes a constant (Fig. 7a).

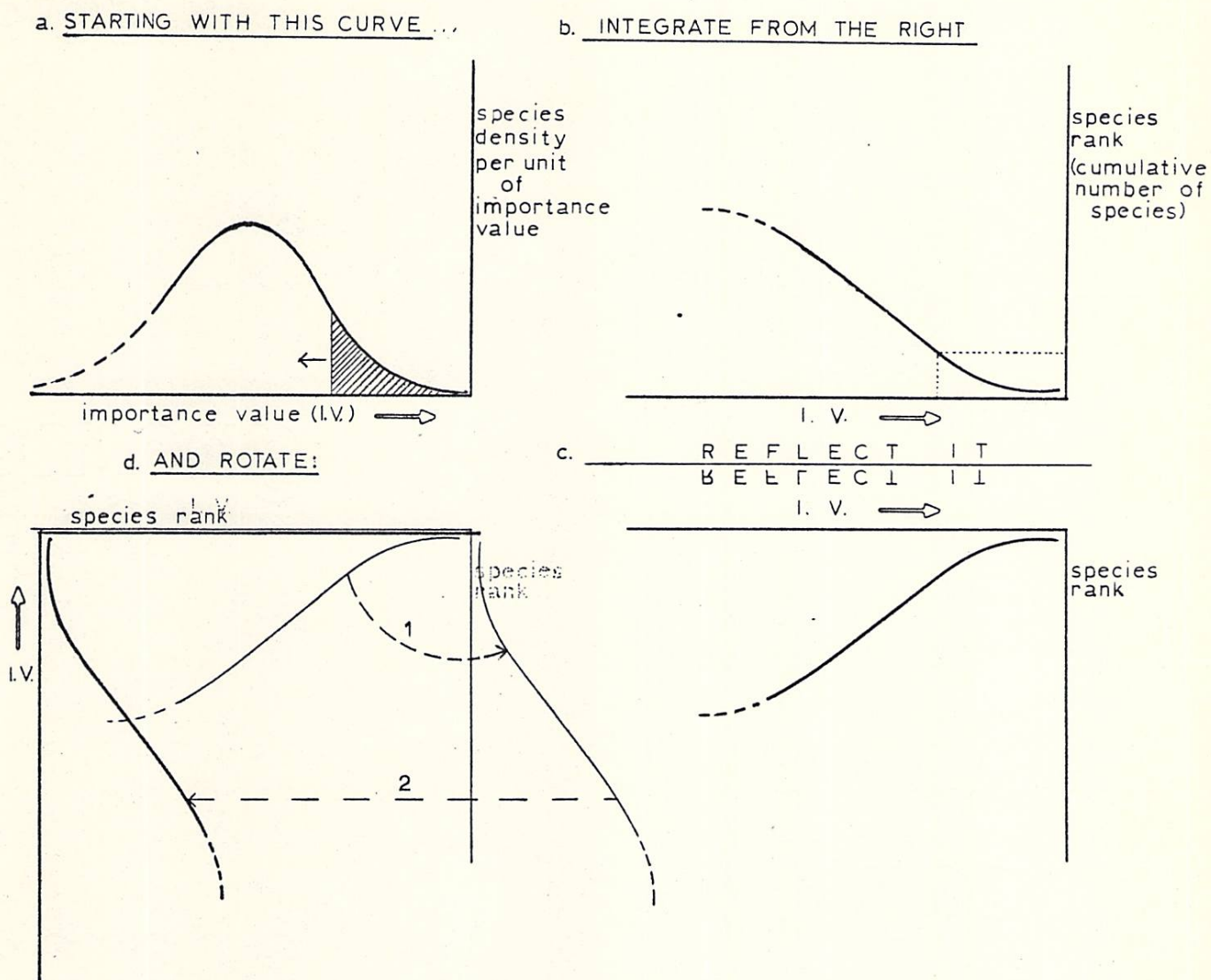


FIGURE 6
INTERCONVERSION OF THE TWO
principal representations for
species-importance data

(arrow → indicates increasing I.V.)

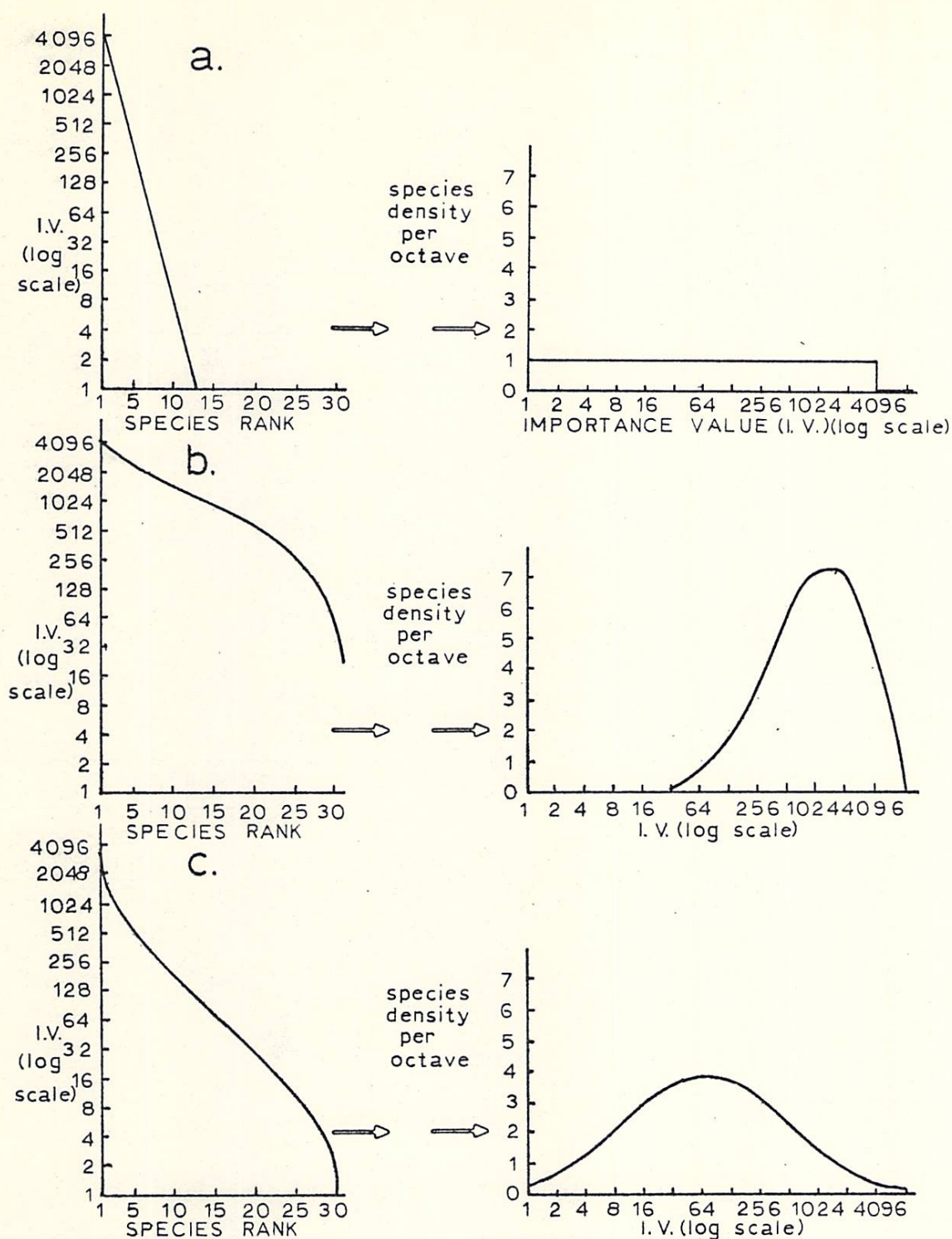


FIGURE 7

THEORETICAL DOMINANCE-DIVERSITY
curves in each representation
a. geometric distribution
b. random niche boundary hypothesis
c. lognormal distribution

The geometric series appears to fit data from communities with only a small number of species and strong dominance. These typically although not invariably are found in severe environments. If the distribution as strictly defined is plotted on probability paper, a horizontal line coinciding with the 50 per cent probability line results (Fig. 8). Data from particular communities produce no such line due to the finite number of species; rather a sloping line results (Fig. 8 -- data from Whittaker 1966).

The random niche boundary hypothesis (MacArthur 1960) is based upon an assumption that species randomly partition a resource hypervolume (an n-dimensional volume with each dimension representing a particular resource). This relationship then rests on a knowledge of the total number of species in the community, to permit the calculation of the various species importance. This distribution has met with much enthusiasm because of its structural analogy to community process. However, there are serious mathematical difficulties with it which Pielou (1968) outlines. If it is viewed in terms of species density (with respect to importance) vs. importance it yields a steeply peaked distribution which is somewhat skewed (Preston 1962, Fig. 7b).

The MacArthur distribution has been successfully used only in the description of "small samples of taxonomically related animals from narrowly defined, homogeneous communities. . . primarily for higher animals with stable populations and relatively long life cycles" (Whittaker 1970). MacArthur (1960) has also noted a systematic tendency for the common species to be too common and the rare ones too rare compared to the model. Significantly, this deviation is in the direction of greater normality

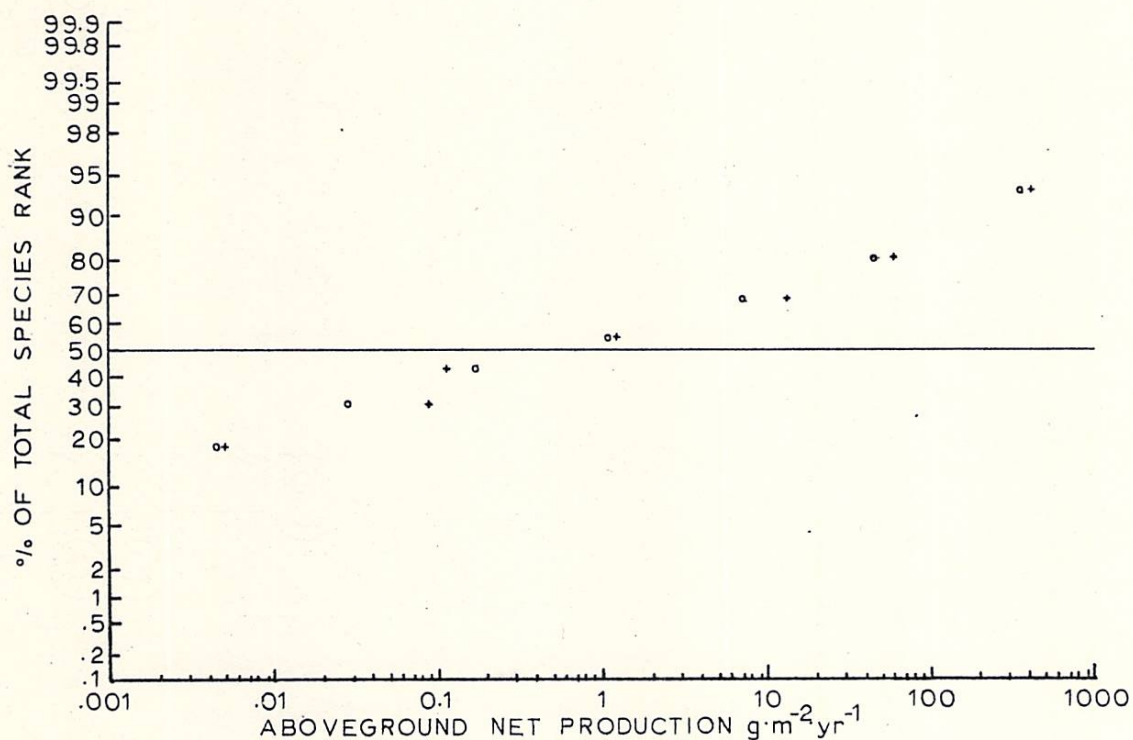


FIGURE 8

THE GEOMETRIC DISTRIBUTION ON probability paper:

The horizontal line is one interpretation of how it should be plotted (a continuous geometric series)

The small circles are the predicted values for a geometrically distributed community of stature similar to that shown by...

The crosses---data from south slope Fraser fir forest, Great Smoky Mountains, Tenn.

(DATA FROM WHITTAKER, 1966)

on a logarithmic base. Fig. 9 shows a plot of the MacArthur distribution for 100 species on probability paper as well as a plot of the bird data (from Saunders 1936) which MacArthur used to exemplify his distribution. The lognormal relationship appears to yield a better description of the data.

The lognormal distribution (Preston 1948, 1962) has been proposed primarily as an empirical observation. It describes most of the data quite well particularly in communities with large numbers of species (Whittaker 1970). Its integral is sigmoid in shape (Fig. 7c), this is the form seen in a dominance-diversity curve from a lognormal distribution.

Each of the other distributions may be seen as special cases of the lognormal distribution. The geometric distribution can be interpreted as a lognormal distribution of large variance. In fact, the variance (which would need to be interpreted as infinite if the distribution were strictly accepted) need not be very large at all since the number of species involved is finite and there is a most important member. The random niche boundary hypothesis likewise yields to such scrutiny. It may be readily seen as a lognormal of usually rather small variance. In point of fact, however, each of these distributions must be considered as descriptions for data. I have shown that at least in some cases the data can fit the lognormal better even than these other distributions.

As a means of showing dominance-diversity data Whittaker (e.g. 1963, 1972) has made extensive use of the log importance vs. species rank type of plot without attributing any particular distribution to the resulting curves. The curves nearly always

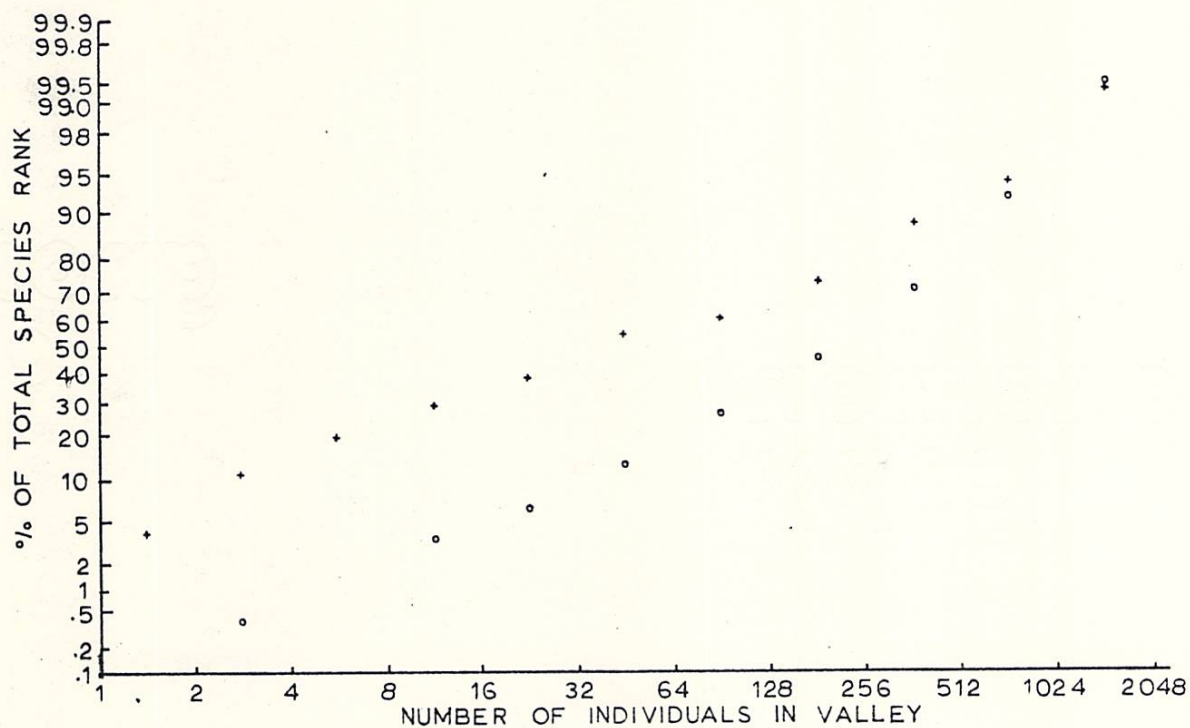


FIGURE 9

THE RANDOM NICHE BOUNDARY hypothesis (circles) and data said to be described by it plotted on probability paper. The data (birds of Quaker Run Valley... shown by crosses) is described well by a lognormal distribution.

(DATA ORIGINALLY DUE TO SAUNDERS, 1936 taken from PRESTON, 1948)

tend to be sigmoid, with the possible exception of assemblages with very few species which give the appearance of the geometric distribution (Whittaker, pers. comm.). As pointed out above, a fit involving only a few species may readily be interpreted as a lognormal distribution of moderate variance since the number of species is small.

In looking at this set of distributions in terms of the lognormal distribution there seems to be a progression from a large variance to a small variance in going from the geometric series to the random niche boundary hypothesis (the logarithmic series being a function of sample size). The types of communities to which these distributions have been applied show a similar, parallel progression: from low diversity, immature (in the sense of Margalef 1968: not well-developed) communities such as stressed and early successional communities toward communities of higher diversity or greater maturity such as those of later succession, mesic environments or within an advanced taxon.

A Supposition....

The progression outlined in the last section suggest an analogy. Suppose that species are making "random observations" on how to survive in the environment. The processes of mutation and recombination are the "experiments" being performed and the outcome after selection might be thought of as the final observation after the experiment. Each species represents a different set of these observations, genetically isolated from the other species in the community. The analogy goes further; the lognormal distribution empirically fits the data from a great many communities. The other distributions suggest a contraction of the variance

of the distribution with increasing "maturity" of the community. Suppose that this were an instance of the law of large numbers operating to contract the variance through evolutionary time. The law of large numbers, from probability theory, essentially says that the more observations one makes, the better one's estimate of the mean. A familiar form of this result is the relation often used in statistics: the standard error of the mean is reduced by increasing sample size. This would suggest that the variance of the lognormal distribution may be related to the degree of refinement of the organisms' adaptation to the environment of the community.

There are a couple of implicit assumptions in the last statement. The argument suggested really only applies if the environment is in some sense stable and predictable and if the species composition is held constant. These constraints obviously seldom apply for any length of time in nature but they nonetheless suggest some further relationships I will discuss before examining the effects of removing these constraints. A contraction of the variance of the lognormal distribution would suggest that species are making major changes in their energy (importance) utilization relative to one another. In particular, the initial suggestion is that species of low energy utilization will tend to increase their energy utilization while those of high energy utilization will tend to decrease theirs. An average reduction in the energy utilization by important species seems unlikely except due to especially intense interspecific competition. More likely is the possibility that species on an average increase their energy utilization and so it seems that there might be a second order

correction to the initial observation: that the contraction of the variance is primarily a consequence of species of low importance making proportional increases in their energy utilization faster than those of high importance. This seems more reasonable since proportional increases by species of low importance do not seem likely to effect corresponding proportional decreases in more important species due to the large differences in absolute magnitudes of energy utilization. These differences in energy use are likely to be associated with similar differences in the material resources for which there is apt to be more direct competition.

Another interpretation which is in many ways analagous relates to Hutchinson's (1958) ideas of the fundamental vs. realized niche. This analysis suggests that species of high importance are apt to be closer to the borders of their fundamental niche than species of low importance. This is quite consistent with the definitions which he has suggested for fundamental and realized niche since one of the principal sources of restriction into a particular realized niche is competition with other species. It seems reasonable to suppose that species of high importance feel less impact of the presence of other species than ones of low importance.

The second order correction of low importance value species rising in importance faster than ones of high importance value suggests a systematic distortion of the basic normal curve: a slight excess of species among low importance values and a slightly diminished assemblage among high importance value species. This has been reported by McNaughton and Wolf (1970) for a number of communities.

The Effect of Polymorphism as a Strategy

I suggested above that energy utilization may be interpreted as an expression of the size of the realized niche of a species. Dobzhansky (1970, p. 127) has stated that in addition to heterotic polymorphism balance, possibly even more important in nature is that maintained by diversifying selection. "Diversifying selection favors different genotypes in different subenvironments. . . ." This description suggests that polymorphism plays an important role in expanding the realized niche of a species at a given place in space and time.

Mayr (1963, p. 389 ff.) has commented that frequently polymorphism within a species shows a central-peripheral geographic distribution. The central parts of a species range tend to have high polymorphism while the peripheral regions show reduced levels of polymorphism. This is consistent with the trend I have suggested above since the center of a species range tends to be a situation of high input of genetic variability (Brown 1957) and hence the rate at which "observations" are being made is apt to be higher--this would also result from higher population levels. The peripheral regions on the other hand are smaller in population and furthermore are subject to swamping of advantageous genomes by occasional influxes from the central populations.

A reversed situation exists in the Hawaiian Islands (Michael Soulé, pers. comm.) where *Drosophila* polymorphism increases toward the more remote islands. This may be interpreted as a condition where invasion and swamping are likely to be far less common. Exchange with the other islands is going to be severely reduced by both the ocean barrier and the winds which tend to blow transverse to the axis of the island chain. This allows the

species on the more remote islands to refine their adaptation to the island environment. The proximate islands are also larger and tend to have more species. Presumably a different species represents a more substantial and better structured difference in ecological exploitation pattern. At the same time it is going to leave less room for less efficient forms of other species which might have been able to use similar resources. This amounts to character displacement (Brown and Wilson 1956) among species reducing the polymorphism of the species involved on the near islands with character release taking place on the more distant ones.

A general pattern seems to emerge from these observations. Diversification of species is a method whereby more energy may be harvested. In the absence of speciation, polymorphism will be increased as a result of such diversification but isolation is required to permit diversification in useful directions (without swamping). New species in the community represents a better structured method of exploiting the environment because it is not subject to normalization toward other strategies (see Mayr 1963, p. 422 ff.). This results in displacement of other species, however, with a concomitant reduction in polymorphism.

Relations Involving Island Biogeography

I have suggested a pattern involving a contraction of the variable of the lognormal distribution under conditions of constant or predictable environment and constant species composition. The closest approximation to this situation would be a community on a large, remote tropical island. The island must be large to

permit large populations, thereby reducing the probability of extinction. It must be remote to prevent a significant influx of alien species, and it should be tropical to provide for the criterion of a predictable environment. Relations involving the variance of the lognormal have seldom been investigated but from data reported by MacArthur (1969) it appears that my suggestion of a small variance for the lognormal distribution is observed in just that sort of situation --- the tropical continental land masses. His data also suggest the impact of changes in these initial constraints may have on the lognormal distribution. He says that mean values of σ^2 for the birds of tropical mainland are: $0.972 \pm .157$, temperate mainland: $1.861 \pm .233$, and island: 3.871 ± 1.437 . The tropical mainland has the smallest variance of the three localities.

These observations suggest a number of general relationships. It seems unnecessary to make a fundamental distinction between islands and continents. They represent a continuum of sizes of land masses and the inherent species dynamics may well yield to similar analyses in "both" instances. MacArthur and Wilson (1967) have suggested a number of relationships which exist among species on islands. One of these relations involves the number of species present on an island at a particular time. They suggest that this number of species is going to be directly related to the rate of colonization and inversely related to the rate of species extinction or extirpation. They also suggest that these rates vary as a function of the total number of species already present and that often they equilibrate one another at a fixed species number. I would suggest that this may be so but primarily

for time scales which are sub-evolutionary. The species present at a place are either colonists from somewhere else, or species which have evolved in situ from other species (which ultimately were colonists from elsewhere). Since the process of speciation is taking place, the picture gets slightly complicated to view just in terms of equilibria. It is certainly true that the total number of species present on an island is equal to the number of new species which have arrived on the island, minus the number which has gone extinct. New species arrivals are defined non-dimensionally (species defined in terms of genetic isolation on a local scale, Mayr 1963, p. 17) at the time of arrival. Over an evolutionarily short period of time the number of species present will then be largely a function of rates of colonization from elsewhere, and local extinction rates. The evolution of new types, either on the land mass being considered or on the land masses which provide colonists, will result in increments in species present over and above the basic colonist-extinction consideration. This permits a straightforward extension of the MacArthur and Wilson theory to continental land masses where species evolution is apt to be a more important source of new species than successful colonization by forms derived elsewhere.

On the basis of the processes I have described thus far, extinction of species may have a complex effect on the form of the lognormal curve. The extinction of a species represents a loss of a set of "observations" on how to survive in the environment. In another sense, however, that set of observations was not good -- it let the species go extinct. In a situation where the extinction rate is high such as might be due to a low degree of predictability

of the environment of enforced small population size due to small area, the effect of extinction will be to remove species more or less at random. The species that remain are in an environment where the competitors are constantly changing drastically and so the effectiveness or relevance of their "observations" through time will be seriously compromised. We might expect then that the variance of the lognormal distribution in such a situation would increase much as the extinction rate was increased.

Invasion by other species (colonization) will also influence the variance of the lognormal distribution. A low invasion rate will tend initially to permit species to adjust to one another and their environment (barring a high extinction rate, hence decreasing σ^2). Slightly higher invasion rates would tend to cause a perpetual sequence of species displacements with respect to one another and σ^2 would tend to increase. If invasion rates are quite high compared to evolutionary time (often the case on near islands) they may result in a decrease in σ^2 by permitting a natural selection among colonizing species rather than among individuals of the species present at a particular time. That is: if the rate of colonization is very high (and extinction also) there would tend to be a selection for favorably balanced assemblages of species resulting in steady-state assemblages of species which were well-adapted to one another. An increase in the size of the "species pool" (the species which are "available" as colonists) would also have a similar effect.

In 1954, Patrick adopted the use of the lognormal distribution as a tool for describing the diatom flora of streams. Since then she has done a number of studies (Patrick 1967, 1968, 1971,

Patrick et al. 1968) documenting various patterns in diatom floras as they relate to environmental parameters. Of particular interest is her 1968 paper which examines diatom communities in similar ecological conditions. She observed that the communities tended to have lognormal distributions of similar variance and total species number when they were in similar ecological conditions. Her paper of 1967 dealt directly with the influence of invasion rates, species pool and size of area on the structure of the diatom communities. Unfortunately, her observations on the effect of species pool were not in a form I could use. She experimentally modulated invasion rate into her introduced substrates for growth and obtained results fully consistent with the patterns I suggested above. Invasion rates were all high (relative to evolutionary time) and in this range an increase in invasion rate caused a decrease in the variance of the distribution as I suggested above would be the case. In her analysis of the effects of area, she examined the diatoms in streams of similar chemistry in Maryland and on the island of Dominica. The Maryland community had a lower variance than the ones on Dominica, again consistent with both the scheme I have proposed and the suggestion by MacArthur and Wilson (1967) that land mass is going to be inversely related to the extinction rate.

Unfortunately the data in the literature are too scanty and not in a form suitable for quantifying these relationships between extinction, invasion, speciation and species pool and the shape of the lognormal curve. A further mathematical treatment is probably possible but seems likely to involve premature assumptions about the details of the interactions and does not

seem justified in view of the absence of any data to suggest reasonable directions. Besides, I lack the necessary mathematical tools to carry the analysis much further, in that direction.

A Relativistic Perspective on Environmental Stability,
Favorability, and Predictability

The problems of environmental stability, favorability, and predictability inevitably come up in discussing patterns of species diversity. They are particularly elusive concepts to define precisely and seem to me to have little or no meaning in any absolute sense. I find something predictable if and only if I both know how to predict it and can somehow obtain the necessary information required to use that knowledge. A flip of a coin is usually considered unpredictable, but if I have an "educated thumb" this is no longer so and I may be able to predict the outcome of a toss quite reliably. Favorability is a similarly relative concept. No a priori judgement of favorability can be made. If an appropriate strategy can be found, the problems encountered under particular circumstances may be completely overcome. In a sense, organisms find an environment favorable if they have a strategy for surviving in it while if they do not, it is unfavorable. The amount of success organisms have in exploiting an environment is then likely to be related to how much experience organisms have with similar situations as well as the degree of "pre-adaptation" they have to that environment.

Certainly before there were any terrestrial organisms, the land environment represented a harsh, unfavorable environment. The properties which made it so have not changed appreciably but

organisms have found strategies for exploiting the terrestrial environment and have become enormously successful on land. Several things may be seen to contribute to this success. While organisms have been gaining much "experience" surviving in the ocean, once the land was invaded a number of problems present in the ocean environment ceased to exist. The autotrophs suddenly found themselves in a much more favorable light environment--they were no longer competing with water molecules for light. Plants and animals alike found gas exchange much more rapid and the less soluble nutrients generally became more available once the move to the terrestrial situation was accomplished. Hutchinson (1970) has pointed out that in the marsh there is perhaps the best of all possible worlds with abundant water, soil with its associated nutrient exchange capacity, and good gas exchange with the atmosphere. Not surprisingly this habitat is also one of the most productive in the world although at one time, by all rights it must have been among the less favorable of environments.

Over most of the earth's surface there are wild fluctuations in the availability of light in any 24-hour period. We call these day and night and they trouble us little because we have reliable means for predicting the cycle. Without a means of predicting the light and dark cycle we would consider the light environment tremendously unstable. This cycle is so familiar that we scarcely consider it but it is probably a capability which is carefully cultivated and maintained quite precisely through selection and is not inherent in the functioning of organisms. It would be interesting to look at cave organisms to see if they still have well-developed circadian rhythms in spite of their mode of life.

Desert annuals show another strategy for predicting about their environment. For any organism the essential aspect of prediction is: can I reproduce before I die or am killed by environmental adversity? In the desert the principal difficulty is with the availability of water. Many desert annuals "predict" the rainfall by waiting until it rains (MacArthur 1972). The real prediction that is made then is whether the rain is sufficient to grow and set seed. Some species do this by letting water leach a germination inhibitor from the seed coat. If it is leached out sufficiently the seed grows. A prediction has been made that if the amount of water present was enough to leach out the germination inhibitor, there is enough water in the soil to grow and set seed. Other species accomplish the prediction by having seeds of which only a fraction germinate after a rain. This fraction is governed (has been selected for) by the relative frequency of sufficient rain, another prediction which skirts the problem of "when there will be rain" and addresses itself to the real problem of now that it has rained, is it enough to reproduce?

The Interpretation of a Successional Sequence
and Community "Maturity"

Margalef (1963, 1968) has suggested that by viewing communities within the framework of a successional sequence, a quite general pattern emerges. He proposes that through succession there is a tendency for communities to increase in what he terms "maturity." Basically maturity is reflected by increases in species diversity and productivity. I think that the ultimate causes of patterns of species diversity and energy utilization (productivity) lie

in the realm of evolutionary time scales. Proximate relations may well exist which are quite useful for characterizing community relations but ultimate causes lie in evolution.

Margalef (1968) and Odum (1971) have observed that through a successional sequence there is a tendency for diversity to increase quite consistently throughout the sequence. There is some evidence that at the end of the sequence, towards climax, the diversity drops off again. Margalef describes this as an increase in maturity and proposes that disturbance factors are more important going from the tropics toward the arctic and hence the tropics exhibit higher maturity than more polar regions. He leaves unexplained the apparent drop off towards climax.

The scheme I am proposing encompasses these patterns. It also suggests the sorts of situations that might give rise to the apparent drop off towards climax. In the early stages of primary succession fundamental nutrients are frequently in short supply. Organisms are poorly pre-adapted to such conditions and hence the low diversity at that stage. Also, once this stage of succession is completed, it rarely occurs again compared to the frequency of occurrence of later stages. Species therefore have less total "experience" of such environments. As succession proceeds, sand is stabilized or rocks get finely divided and the nutrient exchange capacity of the soil increases. An increase in diversity accompanies this process since the environment has become more "favorable." However, these early seral stages rapidly give way to later ones. As a result less time is spent in those stages than in later ones and so the diversity is less than in those stages that follow. This pattern continues all the way to climax.

At climax the disturbance factor enters the picture. If disturbance is fairly common, more time will be spent in seral stages which are just sub-climax. The diversity in those stages would then be higher than in climax itself (see Loucks 1970). This viewpoint also is consistent with the ideas expressed in a paper by Marks and Bormann (1972). They suggest that successional species in essence maintain the integrity of the environment for themselves and all subsequent species to inhabit the area. This is accomplished by nutrient uptake and storage by the species which come in after disturbance. In a sense, if the frequency of disturbance is at all high they would have to--otherwise the climax species would not have evolved to require nutrients to the extent they do.

The latitudinal gradients in species diversity are similarly interpreted. As a reflection of pre-adaptation of organisms to moist, warm conditions, the tropics generally show a high diversity, temperate regions show less while arctic climates tend to have very low diversity. The effect is further compounded by the influence of habitat extent. The arctic regions are not nearly as extensive as the temperate or tropics and their low diversity is also a reflection of this. The relatively high degree of pre-adaptation of organisms to tropical environments, combined with the dissection of the land masses involved (and hence speciation opportunities) has provided opportunities for the development of a great variety of forms. Because of this activity in divergence, it is likely that many more forms have come into existence in the tropics and served as colonists for other regions than vice versa. These forms have spread to other regions, being

more or less pre-adapted for them through accident of evolution and have diversified in their new-found territories. The experience gained in the tropical environment permitted successful invasion of new territories. This pattern is essentially that described by Darlington (1957).

The notion of organisms gaining "experience" and diversifying through time has been documented by Southwood (1961) in his analysis of the number of insect species which fed on various species of tree in Britain compared to the Eurasian continent. He concluded that the number of parasitic insect species a particular tree had in Britain was related to the amount of time the tree species had been present on the island. Using the fossil record he was able to estimate how long particular tree species had been present on the British Isles and this correlated quite nicely with the number of insects it hosted.

These patterns of species diversity fit quite nicely into the scheme I am proposing. I will come back again to these relationships to show in more detail how other theories of species diversity patterns may be seen as particular subsets of this scheme.

Energetics: Species and Community

I have already suggested why energy may be seen as an important variable in the study of communities: its necessity in life processes and its one way flow through the community. I would now like to harvest a few corollaries of this viewpoint since they suggest further relationships of interest.

Because of the intimate involvement of energy in life processes, any selective process which expands a species' resource base or

the variety of ways it is using materials is likely to be reflected in an increase in energy utilization. Also, a species can always use less energy than it is currently, until it uses none at all and has gone extinct. Extinction is the reward for a consistent inclination in that direction and so very few (if any) species are around which have that tendency. It seems then that on average a species will tend to use the same amount of energy or increase its energy utilization. Through evolutionary time then, in a particular habitat-type, the energy utilization by a community will tend to increase.

With the possible exception of the Arctic winter within any twenty-four hour period there is nearly always an abundance of raw, high grade energy available in the form of light. The efficiency with which this can be utilized is a limiting factor on its use. This efficiency is a function both of the nature of the process of photosynthesis itself and the availability of necessary nutrients. In view of these facts I think that the availability of usable energy is never an ultimate limiting factor for living organisms. A better use of materials is always a possible means for tapping these energy reserves more efficiently and hence making use of them.

From these relationships it follows that species in competition with one another will tend toward equal energy utilization. Consider two species in competition, for example. Imagine also a set of resources with respect to which they segregate themselves. For those resources for which there is direct competition, a species using less energy is going to be expending proportionally more

energy in competition than one of higher energy utilization (see Fig. 10). As a consequence of this proportional difference in energy used in competition there will tend to be a differential in the selection pressures to resolve this discrepancy. Species of low importance will have a higher "incentive" to find a way out of the problem [Note this suggests that competition matrices may not be symmetric as MacArthur (1970) assumed]. The usual means suggested for resolving this problem among species is a displacement with respect to the resources exploited. This will certainly reduce the intensity of selection but the relationship will be maintained as long as the two species have different energy utilizations. This process is another likely source of a tendency for the lognormal distribution to decrease its variance.

In point of fact species probably never reconcile the sort of differential selection I described above. Changes in the environment or species composition would cause continual changes in the directions of its resolution. Also the diffuse nature of competition with a large number of species could make the resolution of the problem less likely. As a result there exist and probably always will exist species of quite low energy utilization. The resources are sufficient to maintain them and so they persist.

Another problem in describing organisms and their energy utilization is how to incorporate heterotrophs into the analysis. Is their energy utilization to be defined in terms of how much light it takes to support them or how much plant material or how much animal material (in the case of carnivores)? There are quite good arguments either way. In an initial attempt to view this problem I analysed the data Engleman (1961) produced describing

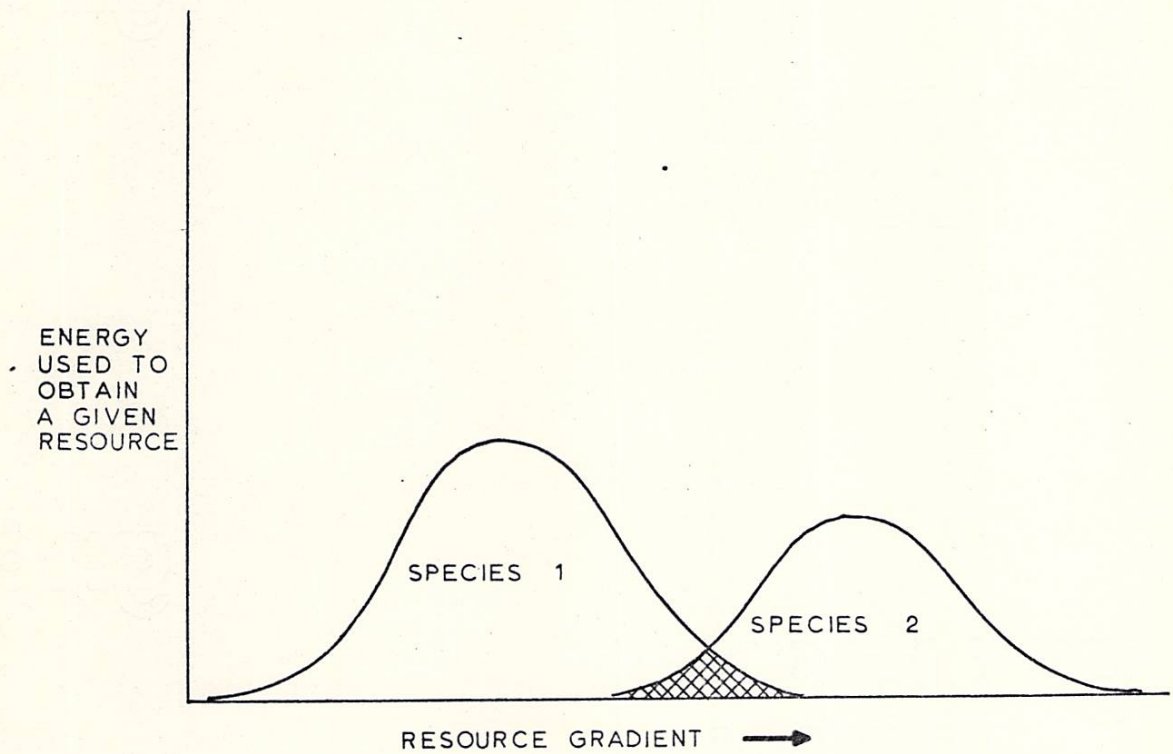


FIGURE 10
SPECIES COMPETING FOR THE
same resource (shaded region)
but having different total energy
utilizations (area under curve).
The amount of energy used to
obtain the common resource is
proportionally greater for the
species of lower energy use.

soil arthropods. The consequences of plotting the two sets of data (herbivores and carnivores) lumped or independently appear in Fig. 11. Although the total number of species is small, it is interesting that when plotted independently the two trophic levels yield curves of approximately equal variance and their means are displaced from one another with the carnivores having a lower modal energy utilization than the herbivores. The poverty of energy analyses for consumers in the literature precludes a decision on the use of such data in examining whole communities.

The Lognormal σ^2 and Niche Overlap

As may have been apparent from the discussion above and Fig. 10, the relationship between a competitive situation and the energy utilization by species may be reflected in the equitability of species. The analysis suggests that the variance of the lognormal distribution, as a measure of the amount of variation in energy utilization by species, is in some way related to the amount of niche overlap among species of the community.

Geographic isolation is a case of zero niche overlap among the species involved. For nearly half the year, migratory birds are geographically isolated from one another compared to their distribution on their breeding grounds. Breeding birds in the temperate zone tend to have high equitability (low σ^2) compared to most other temperate zone organisms. The reduction of competition with one another through the winter could well be involved in this phenomenon.

In contrast, the geometric distribution, as originally postulated, proposed a sequence of species with high degrees of competitive restriction of the subordinate species. This would be

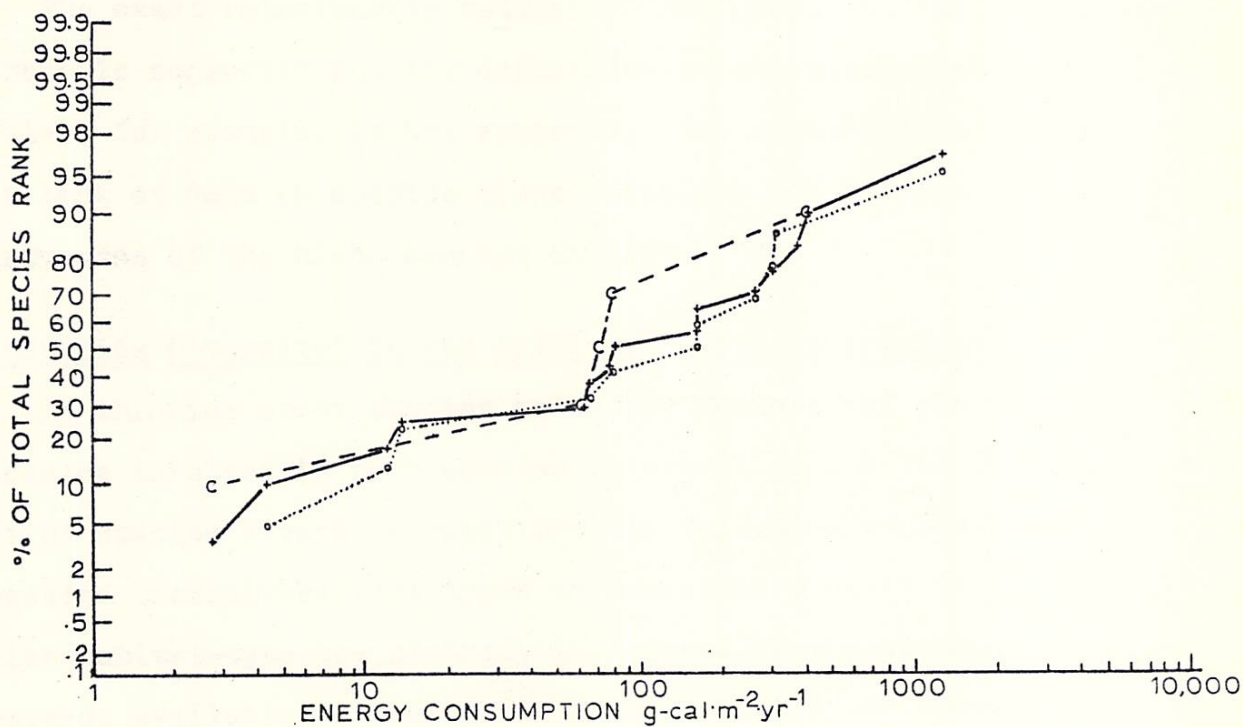


FIGURE 11

RELATIONS BETWEEN TROPHIC LEVELS are unclear. There are good arguments for lumping them (—+—) as well as for treating them separately (—o— carnivores—c— herbivores—c—).

(DATA, FROM ENGELMANN, 1961, ARE FOR SOIL ARTHROPODS.)

equivalent to a situation of very large effective niche overlap because of the high degree of pre-emption of the more dominant species. The variance of the lognormal distribution corresponding to it was likewise large.

The exact relationship between σ^2 and niche overlap is unclear. A trend is suggested but its dependence on the total number of species, for example, is not apparent. The problem lies in part in a lack of data on species niche relations and also in part in the elusiveness of the niche concept itself.

"Species Diversity" in the Primitive Earth Environment

In thinking about species as energy funnels and the sort of processes involved in both species interactions and the development of species diversity relations the following generalizations suggested themselves: The types of organisms present in a particular habitat-type are strongly influenced by the elements or compounds available in that environment. What other species are present also influences the composition and structure of the assemblage. Finally, the presence of a particular species and hence strategy for exploiting the environment increases the likelihood of generating new forms through modification of existing forms rather than through spontaneous occurrence of a completely new strategy.

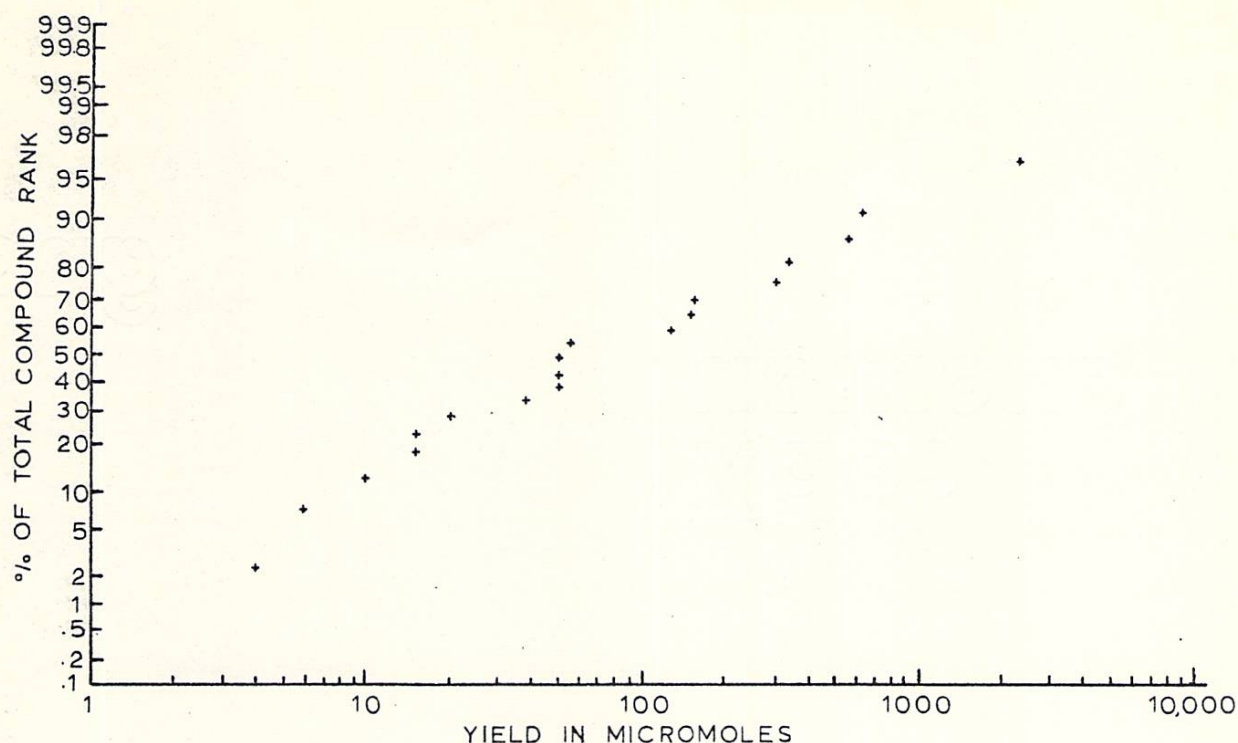
Molecules in a complex mixture and an energetic environment are probably the simplest forms to exhibit these properties. Data from the experiments of Miller (1959) where he subjected simulated primitive earth atmosphere and ocean composition to various forms of energy. This resulted in the formation of a number of

compounds similar to those found in living organisms today. Plotting the concentrations of these molecules on logarithmic probability paper, using concentration in a way equivalent to the use of importance value for organisms (Figure 12) yields a good fit to the lognormal distribution. The use of the amount of energy required for the formation of these compounds from the starting materials is an obvious modification of the use of concentration as a measure of importance. Unfortunately this is not possible because I was unable to find the necessary values tabulated for all the compounds. Those I could find however all have values well within a factor of 2 or 3 of one another so the net effect on the distribution would not be that great (see also on Figure 12).

Several further parallels are suggested by this analogy. In a sense the stability of a compound is equivalent to the fitness of an organism; if a compound is stable, it will persist; if it is unstable, it will not. Likewise with fitness among organisms on the molecular level the production of more molecules of the same type involves the use of pre-formed subunits which react together to form the consequent molecule. It has been suggested that this relationship was elaborated upon by proto-organisms (Cowen 1972, Keosian 1964) as they developed the fine art of heterotrophy. This relationship is preserved to this day although of course the processes involved are far more complex.

Organisms and Information

The branch of mathematics known as information theory (Shanon and Weaver 1949, Weiner 1961) has seen increasing popularity in application by ecologists (Margalef 1958). The particular



<u>COMPOUND</u>	<u>ΔG_f^{298}</u>	<u>ΔG_r^{298}</u>
Acetic acid	-90	+48
Alanine	-89	+65
Aspartic acid	-174	+106
Formic acid	-84	+42
Glutamic acid	-174	+117
Glycine	-89	+104
Lactic acid	-125	+39
Succinic acid	-179	+51
Urea	-47	+21

FIGURE 12

"SPECIES DIVERSITY" OF MOLECULES
 Yields of compounds from simulated primitive earth environments are lognormally distributed.

Thermodynamic data was not available for all the compounds produced. That available (listed above) suggests that similar results would apply if energetics were considered.

(DATA ON YIELDS FROM MILLER, 1959 also in KEOSIAN, 1964

THERMODYNAMIC DATA FROM STULL et al.(1969) The chemical thermodynamics of organic compounds John Wiley & Sons, NY. ΔG_r CALCULATED ON THE BASIS OF H_2O , NH_3 , & CH_4 AS REACTANTS.

relationship which has been used is the information index, used to express the species diversity of the community. Unfortunately it seems that as it has been used, species diversity is more a relationship between a sampler and the community he is looking at than a function of genuine community interrelationships. There have been murmurings of more meaningful relationships such as the suggestion (Lloyd 1964) that individuals^{within a} species be weighted by their reproductive value (Slobodkin 1961, p. 50) in calculating species diversity but not much has ever come of them. In my mind, in describing a significant aspect of a community, the information index as currently employed falls far short of the ideal since it would give the same evaluation to a pure stand of cattails in a marsh as a barren rock surface without even a lichen to adorn it. Clearly there is a substantial difference in terms of the adaptations of life to those environments. One has 0 productivity while the other is one of the most productive communities in the world.

It is with trepidation that I propose yet another measure related to species diversity. It seems as though virtually every paper on the subject has its new measure to propose which usually is then shown to be nearly equivalent to some subset of the old familiar measures complete with regression equations and graphs of one plotted against the other. Perhaps this is a reflection of a dissatisfaction with current forms of diversity measurement. In my case it certainly is, although the measure I propose here is in the general case decidedly different from any other I have seen. It is designed that way and so I will not give regressions or graphs which relate it directly to other diversity measures.

Strictly speaking it is not even diversity in the usual sense. Diversity involves principally a sampler and his community of interest, describing something about a sampler's uncertainty of the identity of, say, an individual picked at random from the community. It is intended that my measure indicate the amount of knowledge organisms possess for exploiting the energy available in their habitat.

If energy utilization is taken as a measure of species success, the ratio of the energy used by the species per unit time to the total available energy per unit time represents the partition of the total available energy which goes through the species in a given time interval. The total available energy per unit time is taken as the total amount of thermodynamically useful energy which is present in the environment. This value must be used since some sort of time average of energy fluxes is misleading. The overall yearly energy budget of the earth's surface shows a net loss of radiant energy at latitudes above about 38° , because the earth radiates heat as a black body continuously and if solar influx is not sufficiently great, the losses due to black body radiation will exceed them. Relative to such an analysis any organism which survived in latitudes above 38° would be making an energy profit. While correct within the context of that analysis, such a statement is superficially misleading and so a more appropriate analysis is in order. The amount of thermodynamically useful energy is a more appropriate measure. It measures the total amount of energy which is available to do work. It is in this that any energy consumer is interested.

The measure I propose uses the information index $(-\sum p_i \log p_i)$

in a new way. Always before the values of p_i used in the expression have been relative to the whole organic community. p_i has been the fraction of all individuals sampled which were of a particular species or the fraction of total productivity of the community which was contributed by a particular species. What I propose is that p_i represent the absolute energetic efficiency of the species or to rewrite the expression:

$$CI = -\sum_i E_i \log E_i$$

where CI = Community Information

and $E_i = \frac{\text{energy used by species } i \text{ per unit time}}{\text{total available energy in the community per unit time}}$

This measure has a number of properties which parallel those developed on the lognormal distribution. Moving the mode of the lognormal distribution to the right corresponds to an increase in productivity. An increase in productivity will tend to increase the value of CI since the energy utilization by species must be increased to increase productivity. An increase in the number of species will explicitly increase the value of CI . It did not have an explicit expression in the lognormal distribution but was present in the interpretation of the curve. An increase in equitability (reduction in variance of the lognormal) will also increase the value of CI , even if total productivity remains constant. The influence of habitat extent is also present in the measure although not explicitly. If successively larger areas are examined, a species which maintains a high value of $-E \log E$ has more information on survival under general earthnormal conditions than one which does not. The evolutionary time perspective is also preserved in that

major changes in a species' energy utilization on a large scale are apt to be of evolutionary significance.

Pielou (1966, 1969) has argued that the use of the statistic-- $-\sum p_i \log p_i$ is legitimate only when the system being sampled is very large. When counting individuals in a small area the validity of its use becomes questionable. Because my measure is related to the information content of the community with respect to the total energy environment, the larger system of total available energy being sampled is many orders of magnitude larger than the energy used by species under scrutiny and so the application is fully justified in that regard.

Another advantage of the measure is that it is fully additive. That is, a community may be analysed with respect to subgroups, guilds (Root 1967) or component communities (Root 1973) and their separate CI values calculated and then the total community may be viewed by merely adding up the component parts (without repetition of species which might be present in more than one component).

The basic assertion is that for a given habitat type, this measure will tend to increase through evolutionary time. This suggests a slight modification of Odum's (Odum and Pinkerton 1955) maximum power hypothesis. His assertion is that a community of greater power (energy use per unit time) will always displace one of less power. The modification proposed here is that while the relationship is a strong function of total community power, that some degree of resistance to displacement may exist as a result of a large number of species in the community or high equitability among them. To the extent that the argument I used above with respect to successional sequence is accepted, the nature of the relationship between this measure and progress

through time is suggested by Fig. 13. For comparison I have also plotted total production and $-\sum p_i \log p_i$ as usually calculated for a successional sequence (data from Whittaker 1972).

Other Relations Suggested by the Energy Funnel Concept

In comparing aquatic and terrestrial systems, there is some evidence that for the lower trophic levels, the trophic-biomass structures are reversed. The biomass of phytoplankton in the water is usually less than that of the zooplankton. On land, the plants have a much higher biomass than the animals. I have already suggested that the oceanic pattern would permit faster cycling of nutrients. Misra (1968) has suggested that these differences could involve the differences in metabolic rates of aquatic vs. terrestrial animals. The metabolic rates of aquatic animals tend to be much lower. This would permit the accumulation of biomass since the energy would not be "burned up" so rapidly by metabolism. This could also help explain the much greater length of food chains in open water systems. Schmitt-Nielsen (1972) has added additional perspective to this picture. He has found that the energy cost swimming is less than that of flying, and running is most inefficient of all, for organisms which are adapted to each of those forms of locomotion. This fact could be involved in food chain length on land also. Long food chains on land nearly always involve birds and insects. Because locomotion is generally of great importance to the survival of a species, the energetics of locomotion could be reflected in species diversity. I consider birds and mammals as roughly comparable groups, with respect to their total geographic ranges, autotroph energy sources, and presumed times^{of} geologic origin. Rough estimates

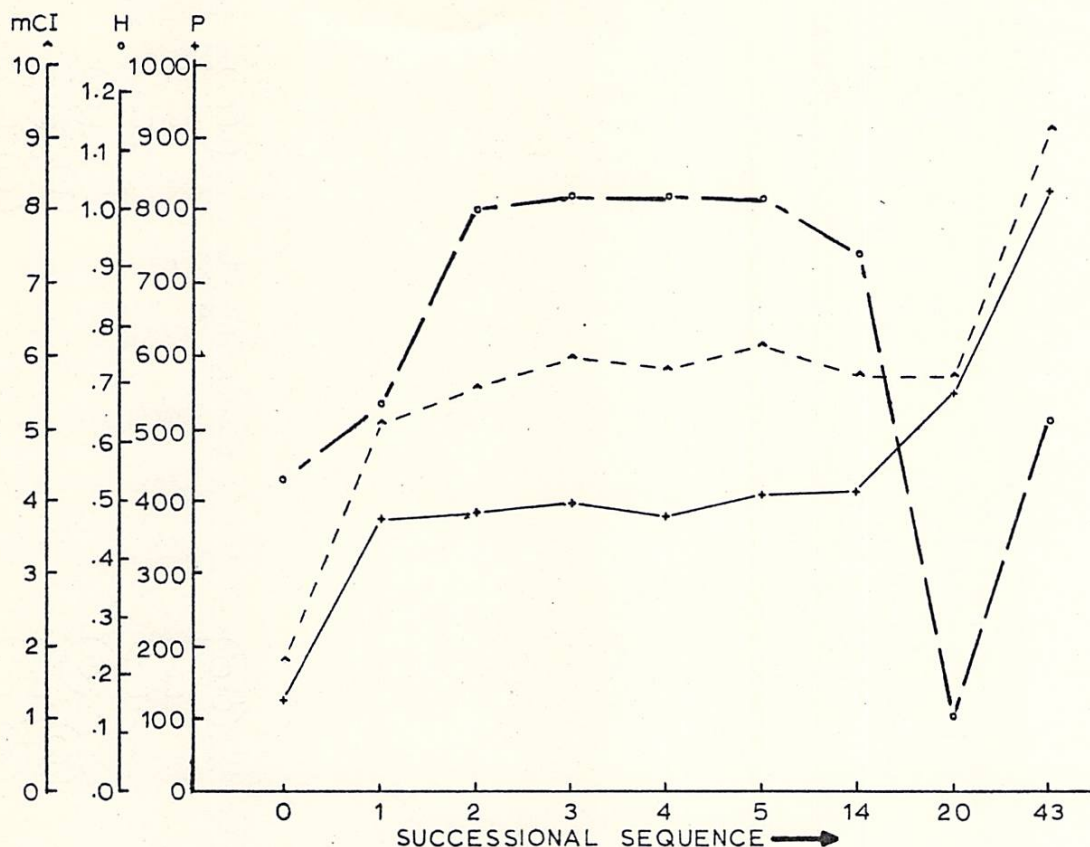


FIGURE 13

PRODUCTION, DIVERSITY, AND
community information along a
successional sequence.

Diversity and community information
are dimensionless quantities; here I
have used \log_{10} for their computation.
Production is in grams of shoot per
square meter per year.

(DATA FROM WHITTAKER, 1972)

for the numbers of bird and mammal species are 12,000 and 4,000 (Jaques 1947), giving a ratio of 3:1 of bird species to mammal species. In the size range of birds and mammals (200g) flight is about 3.5 times as efficient as running. By extrapolating his regression lines to insect size ranges (0.01g) I obtain a factor of about 8.6:1 for the estimated efficiency of flying over walking. Using estimates of 640,000 insect species and 49,000 non-insect terrestrial arthropods (Jaques 1947) a ratio of 13:1 is obtained. While I would not want to say that the cost of locomotion is the determining factor for species diversity I think it is quite likely that it is involved in diversity patterns.

The idea that organisms may be viewed principally as energy funnels suggests a number of other relationships. I suggested that more energetic mileage might be extracted from particular types of materials by faster cycling. The open oceans are notoriously poor in a number of essential nutrients such as phosphorous. It would be interesting to see if this poverty was reflected in the mineral contents of whole organisms from oceanic vs. terrestrial systems. I suggest a pattern of lower content of essential minerals relative to total body weight in situations where these minerals are in short supply. Furthermore, since the holdup of such minerals is not just related to concentration in organisms but also to the total biomass of organisms, different trophic levels may tend to have different mineral concentrations because the biomass at those trophic levels differs. Successive trophic levels might tend to have higher concentrations due to two contributing factors. One factor would be the higher concentrations in the food (plants would concentrate them relative to the concentrations in the water or

soil), and hence potentially larger throughout. The other would be the reduction in total biomass at higher trophic levels which would make such a nutrient holdup of less consequence to other organisms in the community.

The interpretation of increasing energy utilization by the development of new methods of materials utilization has other ramifications. If this is the case, then more advanced forms would tend to come into existence by tuning tighter and tighter to the fine points of earthnormal chemistry. This is seen in the loss of the ability to synthesize various organic compounds or vitamins in higher organisms. This also has implications for man's tendency to pollute his environment. The forms which are most tightly tuned to the normal chemistry of their environment are apt to be the most sensitive to its disruption. Woodwell (pers. comm.) has commented on man's disruption of earth's normal chemistry and its possible consequences. The pattern of destruction at the Brookhaven radiation laboratory experimental forest (Woodwell 1962) is approximately that of loss of more tightly adapted species as the radiation levels increased. The lush growth of blue-green algae in polluted waters is another example.

Relation to Other Concepts of Species Diversity

Clearly, the patterns I have suggested are quite general. A number of other theories have been proposed to explain species diversity patterns. These were reviewed by Pianka (1966) and I would now like to show the relationship between my ideas and those theories.

The time theory or "'history of geological disturbances" assumes that all communities tend to diversify in time, and that older communities therefore have more species than younger ones." Both ecological and evolutionary processes would be involved with evolution providing new species and colonization from elsewhere causing additional increases in species in a particular place. My ideas suggest that time is very important in the development of species diversity, both as an agent for providing colonizing opportunities and for evolution of new species. The effect of time, however, is complex. It seems that time is required for the generation of major types which then undergo rapid radiation and equilibrate until a new "adaptive zone" is entered (see Fig. 14). Simpson (1969) has noted this and also states that the equilibrium number of fossil genera in a group may be the same for long periods of time although a tremendous turnover in particular genera may be involved.

The theory of spatial heterogeneity suggests that species diversity is related to the amount of heterogeneity in topographic features and/or local structure as of vegetation. Topography is certainly involved in speciation relations as is extent of habitat. Micro-spatial relations (e.g. vegetation structural diversity) have been investigated by MacArthur (MacArthur and MacArthur 1961, MacArthur 1964, Pitelka 1943) and others in birds. Such fine grain relations are not present in the perspective I am proposing. Pianka (1966) points out that such analyses really only push back the relations to the question of structural diversity of the vegetation. In this regard Whittaker (1970) has estimated that net primary productivity in forests is higher than in grasslands. Any

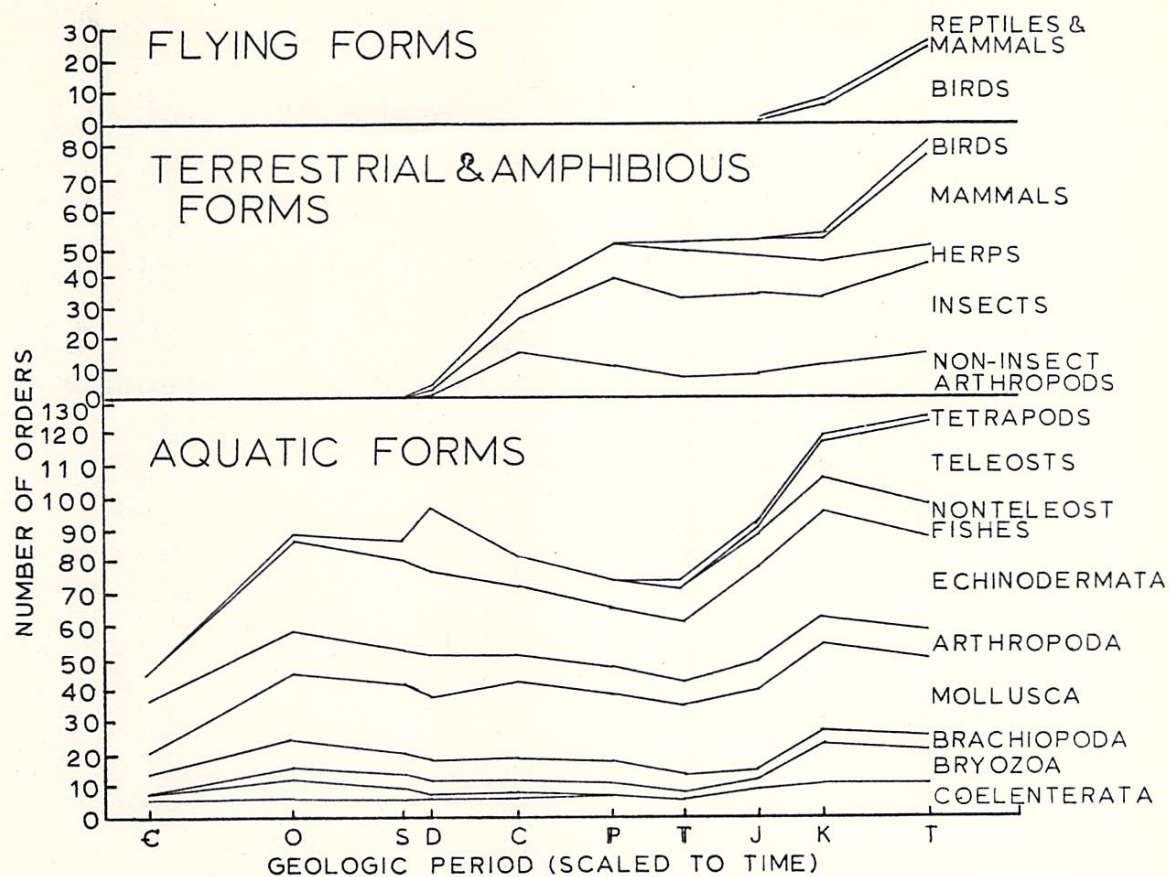


FIGURE 14

AS NEW ADAPTIVE ZONES ARE entered, there seem to be virtual quantum jumps in the total number of forms. Equilibrium numbers of types are reached and approximately maintained in spite of a high turnover rates of types within groups.

(DATA FROM SIMPSON, G.G. 1969. BROOKHAVEN SYMPOSIA IN BIOLOGY No. 22)

heterotroph is going to be reliant on this factor, and so energy availability may be involved. Also more of the earth's land surface is under forest than under grassland so the extent of habitat may also be involved.

Competition and predation have been proposed as mechanisms for increasing or limiting species diversity and Pianka (1966) has also suggested that they may be seen as antithetical to one another. At any one particular time, within a particular group these two relations may well not be operating simultaneously. I think that such relations may well each have some validity (Paine 1966, Dobzhansky 1950). I think the conflict might be resolved by imagining a cycle of predation, invasion by a new species, competition, and then predation again. The predation stage would result in the reduction of the prey species, making "room" for a new species. When a new species invades, it takes off and becomes limited by competitive interaction with other species. A predator then develops a strategy for exploiting this new species and it then becomes limited. This interpretation is essentially a consequence of the time dependence of the development of species exploitation patterns. When it first arrives, the new species is immediately in a selective regime to which it must adapt. The predator on the other hand will not be under a selection pressure to exploit the species until the new species becomes a significant part of its ^{new} environment.

The theory of climatic stability suggests that climatic stability permits the development of diversity. My interpretation places stability and favorability in the plan of the strategist. It permits the notions of stability and predictability as they

usually applied but also allows an interpretation of such otherwise aberrant relationships as the comparatively high diversity of desert annuals.

The productivity hypothesis states that productivity is going to be directly related to species diversity. The argument is analagous to my suggestions about productivity (as energy utilization) and individual species. Instances such as the cattail marsh autotrophs (the cattails) complicate this picture. Species diversity and productivity, while they may often be interrelated, are not directly coupled. Species diversity per se lacks an inherent impetus independent of the energy utilization properties of individual species. As a result there are departures from this pattern.

CONCLUSION

Needless to say the scheme I have proposed here leaves much room for further embellishment and investigation. The suggestions I have made are quite comprehensive in their application to ecological interactions and, I think, internally consistent. They also seem to conform quite well with the limited data available. It is in these factors that the strength of my suggestions may lie.

Root (pers. comm.) has suggested that ecologists should place more emphasis on developing methods of community analysis for which data are readily gathered. In this I can only agree. The problem lies in the development of a useful theoretical structure onto which such observations may be hung. Energy use is a notoriously tedious variable to measure in ecological situations. I am convinced of its essentiality for good understanding of community processes. The challenge that remains is to determine how much of the descriptive information which energy use provides is lost when individuals are counted instead or biomass is substituted for net productivity. Perhaps we can meet happily somewhere in the middle.

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