A NEUTRAL MODEL FOR COMMUNITY STRUCTURE

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ABSTRACT

A NEUTRAL MODEL FOR COMMUNITY STRUCTURE

By

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The relation of community structure to community function is the subject of much ecological theorizing. Three approaches to the problem, based on cybernetics, control theory and niche theory, are identified. They concur in giving biological interactions a major role in the determination of community structure in general and species diversity in particular.

To examine this body of theory, I make use of a "neutral" model for community development; a model which eliminates completely the biological interactions in question. Comparison of the patterns of community structure resulting from the model with the structure of natural communities provides an estimate of the effect of the biotic interactions. This can then be compared to the theoretically predicted effects.

The neutral model used was originally developed in population genetics. In the context in which it is used here, it describes the stochastic development of a set of non-interacting populations, which colonize a community, persist temporarily and eventually become extinct. The model predicts the form of the distribution of relative abundances and of species area curves, and values of species diversity.

Comparisons of the model's predictions with actual community structure are made across what are taken to be gradients in the importance of biological interaction (successional vs. climax communities, high variation vs. low variation environments, the temperate zone vs. the tropics), using data on birds, fish, trees and insects.

The results clearly contradict some of the theories of community structure. In those situations where biological interactions are predicted to generate the greatest increase in species diversity, the neutral model analysis shows that diversity is in fact significantly lower than would be expected in the absence of such interactions. Some implications of these findings for community theory are discussed.

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Herbert H. Caswell, III

A DISSERTATION

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Finally, this thesis is dedicated, with respect and affection, to Professor Herbert H. Caswell, Jr. in honor of his fiftieth birthday.

TABLE OF CONTENTS

I. Introduction - Structure and Function. 1
  A. Cybernetic Arguments 3
  B. Control Theoretic Arguments. 7
  C. Niche Theoretic Arguments. 9
  D. The Role of Biological Interactions. 12

II. Neutral Models 14

III. A Neutral Model for Community Structure. 19
  A. Predictions of the Neutral Model 24
    Species Abundances 27
    Species-Area Relations .33
    Species Diversity. 44

IV. Structure of Natural Communities 54
  A. Successional Patterns. 54
    Succession in Bird Communities 57
    Succession in Forest Tree Communities. 62
  B. Patterns Related to Environmental Variability. 69
  C. Tropical Patterns. 75
    Tropical Bird Communities. 77
    Tropical Foliage Insects 80
    Tropical Tree Communities. 84

V. Concluding Remarks 87

Bibliography 90

LIST OF TABLES

TABLE Page

1. Some Neutral Models in Biology 15

2. Expected values of H' (upper figure) and J (lower figure), conditional on the neutral model, in samples of n individuals containing k species 46

3. Stream Order and Fish Communities. 70

4. Temperate and Tropical Bird Communities. 81

5. Tropical Foliage Insects 83

6. Temperate and Tropical Tree Communities. 85

LIST OF FIGURES

Figure 1. (a) The cybernetic or state-theoretic conceptualization of the regulation of community structure. 6

(b) The control-theoretic approach to the regulation of community structure 6

Figure 2. Semilogarithmic "octave" plot of species abundance distributions generated by three different models of community structure; the neutral model (circles), the broken-stick model (triangles) and the canonical log-normal distribution (smooth Gaussian curves). 30

Figure 3. Semilogarithmic (straight) and log-log (curved) species-area relations, both plotted on a semilog basis. 40

Figure 4. Data taken from Diamond (1969) showing the inverse linear relationship between turnover rate (in % per 51 years) and species number for bird communities of the Channel Islands, California. 43

Figure 5. (a) The deviation statistic, V, for the zooplankton community of a single experimental pond in the study of Hall, Cooper and Werner (1970) 53

(b) The deviation statistic as a function of sample size, N, for samples drawn from the broken-stick distribution. 53

Figure 6. The deviation statistic, V, as a function of successional development in temperate bird communities 59

Figure 7. The deviation statistic, V, for forest bird communities of Wisconsin (Bond, 1957), as a function of the continuum index of the forests 61

Figure 8. The deviation statistic as a function of successional development in upland forests of southern Wisconsin. 64

Figure 9. The deviation statistic as a function of successional development in upland forests of northern Wisconsin. 66

Figure 10. The deviation statistic, V, as a function of successional development in the highly disturbed boreal transition forests of northern Minnesota, Wisconsin and Michigan 74

Figure 11. The deviation statistic, V, as a function of successional development in tropical bird communities. 79

I. Introduction - Structure and Function

This paper is an examination of the role of biological interactions in structuring natural communities. Its context is a body of ecological theory which attaches great importance to the species diversity of communities, by relating this aspect of community structure to several important aspects of community function, especially stability and persistence. To estimate the effect of biological interactions I make use of a family of community models which omit entirely the interactions in question. The results of these models can be compared with the structure of natural communities, and from this comparison we can begin to evaluate the effect of the biological interactions.

Function and structure (physiology and morphology, growth and form, operation and pattern) are dual aspects of any system. Any of the commonly encountered definitions of a "system" contains the concepts of (1) a collection of entities which, (2) exert influences on each others' behavior. A structural approach to the study of a system emphasizes the components, examining their nature, number, distribution, arrangement and pattern of interaction. A functional approach, on the other hand, focuses on the dynamics of behavior and development of the system or selected subsystems.

While structural and functional approaches to a system are never totally independent, this is particularly true of biological systems. To use R. Buckminster Fuller's compelling terminology, biological systems are "self-interfering patterned integrities." They would fall apart and lose their structure or pattern, except that their functioning continually interferes with their own collapse. Homogenize an organism to the point where its structure is irrevocably destroyed and it very shortly stops functioning. Stop its functioning and its structure begins to disappear. This mutual dependence of structure and function permeates biological thinking at every level, and much of biology can be viewed as attempts to understand living systems by elucidation of the interdependence of structure and function.

Odum (1962) defined ecology as the study of the structure and function of ecosystems, including structural and functional aspects of the biological community, abiotic material and energy pools and the environment. The focus of this paper is the structure of the biological community. By any definition, a community is at least a collection of co-occurring populations. A variety of structural aspects of such communities have been examined. Some approaches have looked at the composition of the community in terms of components defined in relation to functional aspects (e.g., trophic levels, trophic pyramids and food webs based on energetic function; life-forms and guilds based on resource acquisition functions within a trophic level, etc.). Other approaches have utilized taxonomic groupings as system components and looked at such structural aspects as niche width and overlap, species packing, and species diversity. Although I will examine several aspects of community structure, species diversity will be a primary concern.

The interest in species diversity is connected to a body of ecological theory which explores the relations between this measure of community structure and various aspects of community function. Relating species diversity to the functioning of communities not only justifies its use as a community parameter, but has also produced a hypothetical structure which attempts to explain observed patterns of diversity.

Theorizing about species diversity seems to follow three major arguments. Two of these are based on very general system properties, while the third depends on more specifically biological assumptions. Naturally, the three are not totally independent, but some mixture of them seems to cover the most commonly encountered theorizing about diversity.

A. Cybernetic Arguments

Margalef (1968 and earlier) invoked a set of arguments based on the cybernetic or general system theoretic concept of the <u>state</u> of a system (see Ashby 1956, Zadeh and Desoer 1963, Caswell et al. 1972). Briefly, the state variables of a system encode all the aspects of the system's history that are relevant to its development in the future. They then appear as differential or difference equations, e.g.,:

$$\frac{d\underline{X}(t)}{dt} = F(\underline{X}(t),\underline{E}(t),t), \tag{1}$$

where $\underline{X}(t)$ is a vector of state variables and $\underline{E}(t)$ a vector of environmental stimuli. An equation such as (1) can be solved iteratively to give

$$\underline{X}(t+dt) = G(\underline{X}(t),\underline{E}(t),t). \tag{2}$$

In other words, the state of the system in the future is determined by its state at the present and the stimuli it receives from the environment at the present. It is this ability of the present (and the past, because the value of $\underline{X}(t)$ is influenced by $\underline{X}(t-dt)$, and so on) to influence the course of the future that is responsible for the dynamics of a system. Now when an influence from one entity to another is capable of producing a change in the recipient's behavior, <u>information</u> may be considered to be transmitted (Ashby 1956, Shannon and Weaver 1949). Margalef (1968 and earlier) used this concept to connect species diversity and information theory. He visualized the dynamics of the community as in

Figure 1a, where $\underline{X}(t)$, the vector of state variables, is now a vector of species abundances. There is a communication channel running from the present to the future state of the system. The capacity or width of this channel can be measured by either of two information theoretic formulae

$$H = \frac{1}{N} \log \frac{N!}{N_1!N_2!\ldots N_s!} \qquad \text{or} \qquad (3)$$

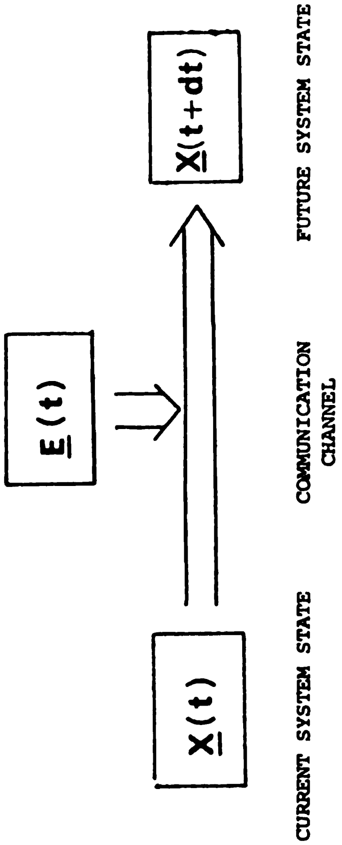
$$H' = \sum_{i=1}^{s} p_i \ln p_i \ , \qquad (4)$$

where N is the total number of individuals in the community, N_i and p_i the number and proportions, respectively, of the i^{th} species, and s is the number of species present. Attempts to tie these formulae too closely to their information-theoretic or thermodynamic roots can lead to problems (see Pielou 1969), and in most cases they are now simply used as indices that have the desirable properties of increasing with the "evenness" of the distribution of species abundances and, for a given evenness, increasing with the number of species. In their original ecological usage, however, they were considered a first approximation to the information capacity of the communication channel in Figure 1a.

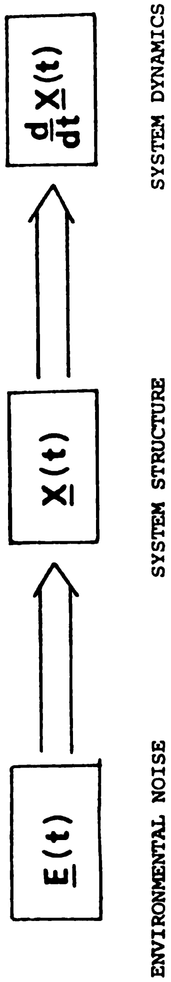
The connection between information transmission and community function followed the following argument. The more the future of the community is influenced by its own internal state, the less it will be influenced by the vagaries of the environment. Such independence of the community from outside disturbance will lead to more and more persistent assemblages of species. Thus there will be a tendency for systems with a lower information content to be replaced by those with a higher one. The limit to this potentially endless increase in diversity is set by the level of

Figure 1. (a) The cybernetic or state-theoretic conceptualization of the regulation of community structure. The capacity of the communication channel from the present to the future state of the system determines the degree of independence of the system's dynamics from the influence of environmental noise. As a first approximation, Margalef equates this capacity with the species diversity of $\underline{X}(t)$.

(b) The control-theoretic approach to the regulation of community structure. The ability of the community to protect its own dynamics from the effects of environmental fluctuation is enhanced by a greater internal complexity and variety of responses. Species diversity is used as a measure of at least the potential for such internal complexity.


E(t)
X(t)
X(t+dt)
CURRENT SYSTEM STATE
COMMUNICATION CHANNEL
FUTURE SYSTEM STATE

(A)


E(t)
X(t)
d/dt X(t)
ENVIRONMENTAL NOISE
SYSTEM STRUCTURE
SYSTEM DYNAMICS

(B)

"noise" inherent in the abiotic environment.[1] In a completely noise-free environment the tendency for diversity to increase should be expressed to its maximum extent. In a wildly fluctuating, unpredictable environment the system will not have time to develop a diverse internal structure before it is perturbed by the next environmental fluke. Such a system would be expected to remain in a state of relatively low diversity.

B. Control Theoretic Arguments

A second very general approach to the theory of species diversity utilizes a set of control theoretic arguments, and a slightly different view of system dynamics (Figure 1b). Referring to (1), we see that the dynamics of the system are a function of the system's current state and the environment in which it finds itself expressed through the function $F(\cdot,\cdot,\cdot)$. In Figure 1b the environment is shown operating on the dynamics of the community <u>through</u> the structure of the community. Using the same arguments about independence of the community from its environment

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[1] In communication theory, "noise" is a component of the transmitted signal which is not usable by the recipient of the message (Shannon and Weaver 1949, Ashby 1956). Thus it is a mistake to include all environmental variation under the heading of noise since the "recipient" of the message (i.e., the dynamics of the community) has "learned" (through evolution) to incorporate many aspects of such variation into the signal, by using them as cues for behavior (e.g., Preston 1969). It is customary among ecologists, when dealing with generalities about this sort of thing, to divide environmental variation into "predictable" and "unpredictable" components, and to equate the former with signal and the latter with noise. While this is probably often accurate, it need not be, especially if the unpredictable environmental fluctuations are of great importance to the community. The unpredictable combinations of desert rainfall and temperature, which are such a strong organizing signal for the community of desert annual plants (Juhren, Went and Phillips 1954) are an excellent example. Throughout this paper, "noise" is defined as variation unusable by the recipient of the signal; it should be kept in mind that the association with environmental unpredictability is less than perfect.

discussed above, we can view the community structure as acting as a control device, attempting to minimize the effect of the environment on the community dynamics (much as an air conditioning system attempts to make the dynamics of room temperature independent of variation in the outside air temperature).

The general theory of such systems has been considered by Ashby (1956). Using information theory, he was able to derive a relation between the amount of fluctuation the environment imposed on the system and the variety of responses required for the controller to protect the dynamics of the controlled system. He formulated this result in the "Law of Requisite Variety," which states that the amount of variation that can be screened out by $\underline{X}(t)$ cannot exceed the variety of $\underline{X}(t)$ considered as an information channel. Again we find that the greater the information content of the community, the greater its independence from the environment.

Equating the variety of responses of $\underline{X}(t)$ with the species diversity of the community is a tricky step. Ideally, we would like to have a measure of the internal complexity of the system, the connectedness, strength and nature of the interactions among components. It is this complexity that is credited with giving the community its ability to absorb environmental perturbations (e.g., the variety of trophic pathways available to absorb a change in the energy input to the community, MacArthur 1955; or the number of feedback loops and interactions through which a perturbation must travel, Margalef 1969). The species diversity of the community can at best be used as a crude measure of the potential complexity of interactions. More feedback loops can certainly be formed from a larger set of species with more equitable relative abundances.

Like the cybernetic ideas discussed earlier, this theory results in the replacement of low diversity communities by high diversity communities. As the diversity increases, changes in community structure slow down, until finally the time between major environmental fluctuations becomes the factor limiting further increases.

C. Niche Theoretic Arguments

The state-theoretic and control theoretic approaches to the regulation of species diversity do not depend on any explicitly biological aspects of the systems under consideration. A third body of theory, however, is based on niche theory, specifically Gause's Law (or Axiom, or Principle, or Theory) of Competitive Exclusion. This states that in order to survive in a community, a species must find "room" in the niche space (see Whittaker, Levin and Root 1973) of that community. This niche space is partly defined by abiotic features of the environment, but a considerable part of it is defined by the other members of the community. The "bottle experiments" of laboratory population ecology have demonstrated the difficulty of maintaining a diverse community in a totally uniform environment. Each species that successfully invades a community makes the niche space of that community more diverse for at least some potential further invaders. Thus as the community becomes more diverse and interactions among the species more complicated, it begins to generate its own "new niches" and species diversity begins to increase in a positive feedback fashion (see e.g., Whittaker 1969, 1972, Hutchinson 1959).

Here again, environmental noise acts to limit the development of diversity. If areas or whole axes of the niche space are available for utilization only temporarily, they cannot support any species that requires a longer period to complete its life cycle. Even if the areas of the niche space in question do not disappear completely, they may shrink to the point where they subject the species occupying them to such an intense competitive squeeze that they may not persist.

Although these three models of community structure follow different theoretical courses, they do have some conclusions in common.

All three models predict that, other things being equal, diversity should increase. They have in common an increasing determination of community function by the community itself (the "biologically accommodated" community of Sanders 1968, 1969, see also Dobahansky 1950). As this insulation of the system from the impacts of its environment increases, more and more species will find the range of conditions tolerable and be able to survive.

Diversity does not increase without limit. A common conclusion of all three models is that a major factor responsible for this limitation is the level of fluctuation inherent in the environment. This variation acts as "noise," limiting the systems' ability to control its own dynamics, it perturbs the niche structure of the community until certain portions of the niche space no longer exist long enough to support species, or it overcomes the ability of the community to transmit information into its own future.

The mechanics underlying this limitation are interesting. In any large collection of species there is a considerable variation in the rate of increase in a non-competitive situation (an "empty" environment). Thus, any occurrence which <u>removes</u> an overall mortality factor will lead to increased dominance by species with quick responses. If the perturbation is repeated, the "slow" species will gradually be forced to extinction.

Several examples of this type of thing can be found in discussions of diversity. One of the classic ways to lower diversity is to apply a burst of resources to a resource limited system. Decreases in diversity due to nutrient input have been noted in a variety of aquatic and terrestrial communities. The question of whether diversity will be regenerated within the community if the nutrient level is maintained at an unvarying high level (the diversity-productivity controversy) is still unresolved.

The removal of a generalist predator from a system can also act to lower diversity (Paine 1966, Harper 1969). This can be particularly striking if there is a positive correlation between predator preference and the ability of certain species to dominate the community in the absence of predation (e.g., size selective feeding by fish on large zooplankton). On the other hand, Harper (1969) reports instances where the species (of plants in this case) capable of dominating the system are avoided by predators. In such cases predation brings about a decrease, not an increase, in diversity.

The occurrence of repeated, unpredictable physical variation in the environment can also act to lower diversity (Dobzhansky 1950, Sanders 1968, 1969) by removing overall mortality factors. It seems that in such situations it is not the stress itself, but rather the periodic removal of the stress that brings about the loss of diversity. For example, Sanders (1968, 1969) found extremely high diversity in the deep sea benthos, which lives in an extremely rigorous, but very constant, environment. Sanders invoked niche theoretic arguments to explain his findings, suggesting that competition had resulted in extensive but subtle niche separation of the many species involved. Recently Dayton and Hessler (1973) have questioned the possibility of such differentiation in this community, and suggested instead that continual mutual grazing was responsible for preventing dominance by any one species.

D. The Role of Biological Interactions

The foundation of all of these theories of diversity regulation is the idea that community structure in general, and diversity in particular, is generated by biological interactions. The network of biotic interactions affects the functioning of the community; the dynamics of community function act to change the structure of the community; the changes in the structure of the community modify the network of interactions among the components. The greater the extent to which biotic interactions, rather than abiotic environmental factors, regulate the dynamics of the system, the greater will be the diversity. An upper limit to the development of diversity is supplied by the level of unpredictable environmental variation imposed by the environment. By disturbing the network of interactions (as, for example, by removing an overall mortality factor, allowing non-interactive growth to occur) such variation keeps community structure from developing.

In this paper I will examine this basic conceptualization of community structure, by applying to communities a model which is "neutral" with respect to biological interactions. The model generates, among other things, a prediction of species diversity (measured by H') under the assumption that the species in the community do not interact by either competition or predation, and do not differ in such intrinsic characteristics as their response to abiotic factors. Comparisons of the model's predictions with patterns of species diversity will estimate the effect of biological interactions on the structure of actual communities.

The theories of diversity regulation suggest that a crucial variable in determining community structure is the degree of internal vs. external control of the community. I will focus on this factor by examining successional gradients and gradients of environmental variability, including comparison of the tropics and temperate zone. A later paper will examine perturbed communities subjected to predation and resource manipulations.

II. Neutral Models

The concept of neutrality, as applied here to theoretical or mathematical models, merits some explanation. The basic activity of scientists is the generation of conceptual schemes that will explain observed patterns in nature. This is accomplished by hypothesizing the existence and mode of operation of certain system properties, and deducing from these hypothetical properties a predicted pattern. By experiment or observation, this predicted pattern is compared with the actual pattern; a severe discrepency leads to rejection and reformulation of the hypotheses. Ideally, this process would result in relatively rapid convergence to a set of hypotheses that cannot be rejected. Actually, for a number of reasons, things often do not work that well. It may not be easy to get enough resolution to distinguish between a number of competing models which all succeed fairly well (or fairly poorly) at explaining the observed pattern.

Often, considerable power can be added to this approach by the use of a "neutral" model. In such a model the entire set of forces competing for a place in the explanation of the pattern are eliminated. The resulting model is neutral with respect to those factors; naturally, it may or may not be neutral with respect to other factors. The neutral model is used to generate a predicted pattern, which is tested against observation.

Table 1 shows a selection of some neutral models that have been applied in biology. In each of these models a set of plausible hypothesized factors have been thrown out, leaving a model that attempts to predict observed patterns in their absence. I have used the term "neutral"

TABLE I

SOME NEUTRAL MODELS IN BIOLOGY

Pattern	Hypothesized Forces	Neutral Model	Agreement
Cyclic fluctuations in animal populations, period ca. 3.5 years.	Weather, sunspots, volcanoes, predator-prey cycles, vegetation changes, epidemics, stress syndrome, genetic changes.....	Sequences of random numbers, subjected to statistical smoothing techniques.	Good (Cole 1951, 1954)
Growth and form in living systems.	Various, limited to living systems and perhaps operating independently of or contrary to the laws of chemistry and physics.	Purely physical models of growth and form.	Good in many cases (Thompson 1917)
Homing ability in untrained birds.	Navigational ability of the birds.	Random wandering.	Good (Wilkinson 1952)
High levels of genetic variation at the biochemical level.	Natural selection.	Selectively neutral allele substitution.	Disputed (e.g., Kimura and Ohta 1971, Johnson and Feldman 1973)
Differences in mean values of sets of experimental units exposed to different conditions.	Treatment effects.	Differences due to underlying random ("error") variation.	Evaluated by statistical significance tests.

rather than "random" to describe these models because randomness is not the only way to achieve neutrality. D'Arcy Thompson's famous studies on growth and form (1917), for example, are neutral with respect to a large set of structuring forces presumed to be unique to living things, but they are based on the very definitely non-random operation of physical forces.

Some care is required in making inferences from the results of neutral model studies. If the neutral model is unable to predict the observed pattern, and must be rejected, there are several possibilities. One or more of the forces included in the structured theory may in fact be operating. The pattern of deviations of the observed pattern from the neutral model's prediction may help to generate new hypotheses about the operation of these forces (as in the estimation of treatment effects following statistical significance tests). Or, of course, there may be another, different neutral model at work. Since there is a potentially infinite set of models capable of generating any given pattern, the only way to explore this possibility is via further hypothesis building and testing. And finally there is the possibility of a Type I error, the rejection of a true neutral model.

The situation is more interesting if the neutral model is _not_ rejected. Clearly this does not "prove" the unimportance of the hypothetical forces. What it does establish is that the observed pattern alone is not sufficient justification to invoke the operation of these forces. The neutral model may in fact be true. Or, there might be a previously unsuspected set of forces at work, which duplicate the neutral model's results insofar as the aspects of pattern used as a test are concerned. This can happen, for example, when a linear regression model is fitted to a set of data generated by a non-linear response. By merely testing the slope of the regression line it may not be possible to reject the null (neutral) hypothesis. And, of course, a Type II error, accepting a false neutral model, may have been committed.

Accepting a neutral model as true is repugnant. After all, the hypothetical forces supposed to be operating in the system usually possess a rich theoretical structure and often seem to be part of the very foundation of the field. Some workers have included disclaimers, leaving themselves an escape from the onerous task of supporting a neutral model. Thus Wilkinson (1952), in discussing his mathematical model for navigational ability in birds, states:

> "In the face of this agreement of experiment with the crudest possible theory, the application of which has usually adopted mathematical devices unfavorable to itself, it seems probable that we should assert that bird 'navigation' does indeed involve nothing but random search. But, as remarked above, we do not wish to do this,but rather reverse the argument, and maintain that nothing about navigational ability can possibly be deduced from experiments of this type so long as they continue to give results such as those which have been forthcoming so far."

Often, neutral models can be investigated further, and other of their properties subjected to testing. This may resolve the problem and provide valuable information about the forces operating within the system, but eventually the neutral model may have to be taken seriously as a hypothesis describing the way things really are. When this happens, it regularly seems to produce a great deal of controversy. As examples, consider Cole's (1951, 1954) random model for cyclic population fluctuations, and more recently, the "neutral allele" hypothesis in population genetics. This latter theory is perhaps the clearest example of the use of a neutral model. A pattern, the large amount of biochemical genetic variability present in many populations, was discovered and begged for explanation. There was both theoretical and empirical disagreement over the ability of the usually invoked forces (selection, particularly balancing selection and/or heterosis) to explain the phenomenon. While some investigators turned to modifications of the structured theory as a way out of the dilemma, others invoked a neutral model. Suppose that evolution, at least of these patterns, proceeded not by the replacement of a given gene by a gene of superior fitness but by the random replacement of selectively neutral genes, no one of them any better than the others? Models were constructed, and the debate over the adequacy of their predictions rages on. It was recognized early on that the neutral model was capable of generating the necessary large numbers of alleles, and now the attempts to reject the neutrality hypothesis are looking at other consequences of the neutral model and comparing them with observed phenomena (e.g., Johnson and Feldman 1973, Bryant 1974).

III. A Neutral Model for Community Structure

The neutral model to be applied here to community structure is actually a family of stochastic models. Among other things, they generate predictions of the distribution of relative abundance, species-area relations, and species diversity. The mathematical properties of the models have been extensively studied by Karlin and MacGregor (1967, 1972), Ewens (1972) and Watterson (1974), in the context of population genetics. Earlier, Kendall (1948), Skellam (1951, personal communication) and Wette (1959) studied some very closely related models in an ecological context. In fact, the formulation of these neutral models is sufficiently general that they can be applied equally well to alleles in a population and species in a community.

Although the three neutral models discussed here are based on very different formulations, they are all completely neutral with respect to

- -- interspecific differences in response to the environment
- -- predator-prey, herbivore-plant and host-parasite interactions
- -- competitive interactions and their effects, including differential population growth and niche and/or habitat expansion/contraction
- -- any other forms of interspecific interaction (symbiosis, allelopathy, etc.).

Thus the meshwork of biotic interactions which is customarily held responsible for structuring the community (and, in theory, for raising its diversity) has been totally eliminated from the model.

Model I (the classification of models follows Watterson (1974)) was discussed extensively by Karlin and MacGregor (1967). In this model, individuals of a new type (new alleles in the original development, new species here) enter the community as a Poisson stochastic process with parameter ν. This is an extremely simple description of immigration,

$$P\text{ (immigration of a new type during time interval dt)} = \nu dt + o(dt)$$

$$P\text{ (no immigration during dt)} = 1 - \nu dt + o(dt).$$

The probability of a colonization event is dependent only on the time available for colonization. It is independent of the identity of the species and the number or identities of the species already present.

Only immigration of new species, not already present in the community, is allowed. This is equivalent to assuming that the net input by colonization to a species still surviving in the community is negligible.

Each new immigrant becomes the founder of a line of descendants generated by a linear birth and death process:

$$P\text{ (transition from N to N + 1 in dt)} = \lambda N dt + o(dt)$$

$$P\text{ (transition from N to N - 1 in dt)} = \mu N dt + o(dt)$$

$$P\text{ (transition from N to N in dt)} = 1 - (\lambda + \mu) N dt + o(dt),$$

where λ and μ measure a per capita birth and death probability, respectively (see Feller 1968 or Karlin 1966 for a thorough discussion of such models). In particular, it is assumed that the birth and death process started by each immigrant has a birth rate which equals the death rate, so that $\mu = \lambda$. This is the stochastic version of the deterministic exponential growth model with $r = 0$. Because zero is an absorbing state in this model, the stochastic version is doomed to eventual extinction with a probability of one. However, the time that it takes to reach extinction can be very long, and when $\mu = \lambda$ the expected time to extinction is infinite.

The important point to note is that each population is completely independent of all the others. There is no replacement of an individual of one type by individuals of another type, as might occur in predator-prey situations. There is no change in growth rate of one species because of the abundance of another, as would happen in competition. And there is no room at all in the model for the development of the networks of intra- and interspecies feedback loops that are supposed by theory to be important in maintaining biological diversity.

Karlin and MacGregor (1967) also studied another model, Model II, which has a rather different structure. Instead of the constantly changing total population size of Model I, Model II deals with a fixed population of size M. At each time increment a randomly chosen individual dies and is replaced by a possibly "mutant" copy; in other words there is the possibility that an individual of a new species will immigrate into the community.

Finally there is Model III, a stochastic model first introduced into population genetics by Sewall Wright (1931), and studied in the context of the neutral allele theory by Ewens (1972). This model also deals with a population of fixed total size M. At each generation the population is replaced by a random sample taken (with replacement) from the individuals in the previous generation, each of which may mutate to a new type not already present in the population. This defines a set of transition probabilities

$$\begin{aligned} P_{a \to b} = P\,(&\text{b individuals of a given type in generation } t + 1 \\ &\mid \text{a individuals of the type in generation } t) \end{aligned}$$

which are given by bionomial sampling probabilities

$$P_{a \to b} = \binom{M}{b} \left[\frac{a(1 - \mu)}{M}\right]^{b} \left[\frac{M - a(1 - \mu)}{M}\right]^{M-b} \qquad (5)$$

where μ is the probability of mutation to a new type. These transitions specify a Markov chain model for the dynamics of community composition.

While these models differ in appearance and structure, they are all satisfyingly neutral with respect to species interactions. Thus it is interesting to compare their predictions regarding community structure. Following the initial work of Ewens (1972) on the sampling properties of Model III, G. A. Waterson (1974, personal communication) and A. J. Trajstman (unpublished) have made extensive studies of the properties of all three models. The results reveal an encouraging robustness to the conclusions drawn from the models.

1) Conditional on populations of the same size, Model I and Model II produce identical results.
2) Model III gives results nearly, although not exactly, identical with Models I and II. The most important properties for our purposes; the distribution of the number of species, the approximate distribution of relative abundances of species, and the sampling properties of the abundance distribution are identical for Models I, II and III.

So these three models provide a set of results which seem to be somehow inherently connected with neutrality. Their predictions will provide a view of what community structure would look like if there were no interactions among the component species.

It is interesting to compare the structure and development of the neutral model with two other commonly used models for community structure, the "broken-stick" model of MacArthur (1957, 1960) and Preston's (1948, 1962) log-normal and canonical log-normal distributions.

The broken-stick model was originally derived as the result of a simple hypothesis concerning community function -- that the competitive interactions between species resulted in contiguous, non-overlapping nich

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niches. The relative abundances of the species were then predicted by the random partitioning of a unit interval, representing the (one-dimensional) niche space. There is unfortunately no corresponding way to randomly subdivide niche spaces of higher dimensionality (Pielou 1969).

There is no need to be concerned here with the history of attempts to compare the broken-stick predictions with natural communities. The results were varied, the arguments heated, and eventually MacArthur himself (1966) expressed a desire to let the model die a natural death. A more interesting weakness of the model is the fact that the same prediction of relative abundance can be derived by at least two other models besides the niche-partitioning one originally used. Cohen (1968) showed that it could be derived from a model which allowed partial niche overlap and from another model which made no reference to niches or competition at all. Thus agreement or disagreement of the model with observed community structure reveals little or nothing about what is going on in the community.

The log-normal distribution was originally proposed as a description of community structure by Preston (1948) on a purely empirical basis. In this model the logarithm of abundance, rather than abundance itself follows a normal distribution. Later (1962) Preston proposed the *canonical* log-normal distribution, a special case of the log-normal in which the parameters are related in a particular way. Again, the justification of the model was empirical rather than theoretical.

There do exist theoretical arguments capable of deriving the log-normal distribution. One of these is closely related to the structure of the broken-stick model, and arises in the study of breakage processes (Epstein 1947, see also Aitchison and Brown 1957). Consider a set of particles subjected to repeated breakage, say by grinding. If the probability that a particle is broken at any step is independent of its size and the size of the other pieces, and if the distribution of pieces obtained from breaking a particle is independent of the size of the particle, then the overall size distribution is asymptotically log-normal.

The size of a particle can be identified with the size of a species niche (no longer restricted to a single dimension) and the breakage process could be generated by speciation or invasion. The broken-stick model seems very close to a biased version of such a breakage process, where the probability that a particle (a segment of the resource axis) is broken at a given step is directly proportional to its size. The differences between the broken-stick and log-normal distributions (Figure 2) are consistent with this interpretation.

Although the log-normal distribution can be arrived at by use of a theoretical model, I know of no such model for the canonical log-normal distribution. Thus in its most fully developed form, in which it makes impressively accurate predictions about community structure (Preston 1962a, 1962b), the log-normal remains an empirical rather than a theoretical description of communities. From a purely philosophical standpoint, the neutral model is more satisfying than either the broken-stick or the canonical log-normal, since it has a theoretical basis, and that basis is robust with respect to neutrality.

A. Predictions of the Neutral Model

Although the following results can be obtained from all three of the neutral models presented above, I will discuss them in terms of Model I, since it so closely resembles certain of the constructs of the theory of biogeography (MacArthur and Wilson 1967). In the context of Model I we will need the following terms:

ν = the instantaneous rate of arrival of new species into the community

λ = the birth rate, which equals the death rate, of a population established by the colonization process

K = the number of species in the community

M = the number of individuals in the community

$\beta(j)$ = the number of species in the community that have exactly j members

t = time

Note that

$$K = \sum_j \beta(j)$$

$$M = \sum_j j\beta(j)$$

and

$$\beta(j) = 0 \text{ for } j > M.$$

The results and terminology presented here are taken from Watterson (1974).

The total community size, M, is a negative binomial random variable with mean and variance

$$\begin{aligned} E(M) &= t \\ V(M) &= t(1 + t). \end{aligned} \tag{6}$$

The number of species in the community, K, is a Poisson distributed random variable with mean and variance

$$E(K) = V(K) = \nu\log(1 + t). \tag{7}$$

The distribution of relative abundance in the population is given by specifying the distribution of the $\beta(j)$. Under the conditions of Model I, the $\beta(j)$ are independent Poisson variables with mean

$$E(\beta(j)) = \frac{\nu}{j\lambda}\left(\frac{\lambda t}{1 + \lambda t}\right)^{j} . \qquad (8)$$

This formula is simplified by Watterson by rescaling time so that $\lambda = 1$. (We will have reason to refer to this rescaling later when discussing species area curves.) Such a change makes

$$E(\beta(j)) = \frac{\nu}{j}\left(\frac{t}{1 + t}\right)^{j} , \qquad (9)$$

which, as t becomes large, goes to

$$\lim_{t\to\infty} E(\beta(j)) = \frac{\nu}{j} . \qquad (10)$$

These results, particularly those for K and $\beta(j)$, are dependent on t, the length of time that the community has been operating. Since this quantity is usually unknown (and even in cases where it is known it will not usually be known in the rescaled time units that make $\lambda = 1$), it is of interest to compute results conditional on values of M, the total community size. Some of these follow.

The complete conditional distribution of the number of species, K, depends on the relation holding between ν and M, but its expectation is given by

$$E(K|M) = \nu \log M.$$

The distribution of relative abundance is given by

$$E(\beta(j))\ M) = \frac{\nu}{j}\,\frac{\binom{\nu + M - j - 1}{M - j}}{\binom{\nu + M - 1}{M}} \sim \frac{\nu}{j}\left(1 - \frac{j}{J}\right)^{\nu-1} \qquad (11)$$

as $M \to \infty$ for $j << M$.

By investigating the sampling properties of the neutral model, Ewens (1972, see also Karlin and McGregor 1972, Watterson 1974) was able to derive an expected value and variance for the diversity statistic H'.

In the ecological context with which we are concerned here, this means that the neutral model can be used as a yardstick with which to evaluate the effect of biological interactions on species diversity, and thus to examine the theoretical basis of the theories relating community structure and function.

Before investigating diversity patterns in actual communities, I want to examine two general aspects of the neutral model, its predictions concerning species abundance distributions and species-area curves. In a way this will help evaluate the validity of using the neutral model as a yardstick for assessing diversity. If its general predictions should appear absurd in relation to observed patterns, inferences made from its specific predictions of diversity would be considerably weakened. On the other hand, if these predictions are at all reasonable, the neutral model should be that much more powerful a tool in the investigation of species diversity.

Species Abundances

The expression above for the expectation of $\beta(j)$, the number of species represented by j individuals, is exactly equivalent to the logarithmic series distribution proposed by Fisher et al. (1943) as a universally applicable species abundance distribution. The terms of the logarithmic series are usually expressed as

$$E(\beta(j)) = \frac{\alpha\theta^j}{j}, \ \theta \leq 1, \tag{12}$$

where α is an inherent property of the community, used by Fisher et al. (1943) and Williams (1964 and earlier) as an index of diversity, and θ is a function of the sample size, approaching 1 as the number of individuals becomes infinite. (See Nelson and David 1967 or Pielou 1969 for discussion.)

Although the logarithmic series form can be derived directly from Model I (Karlin and MacGregor 1967, Watterson 1974), it also arises in a relatively straightforward fashion from the results on the distributions of K and M, using the theory of compound distributions.

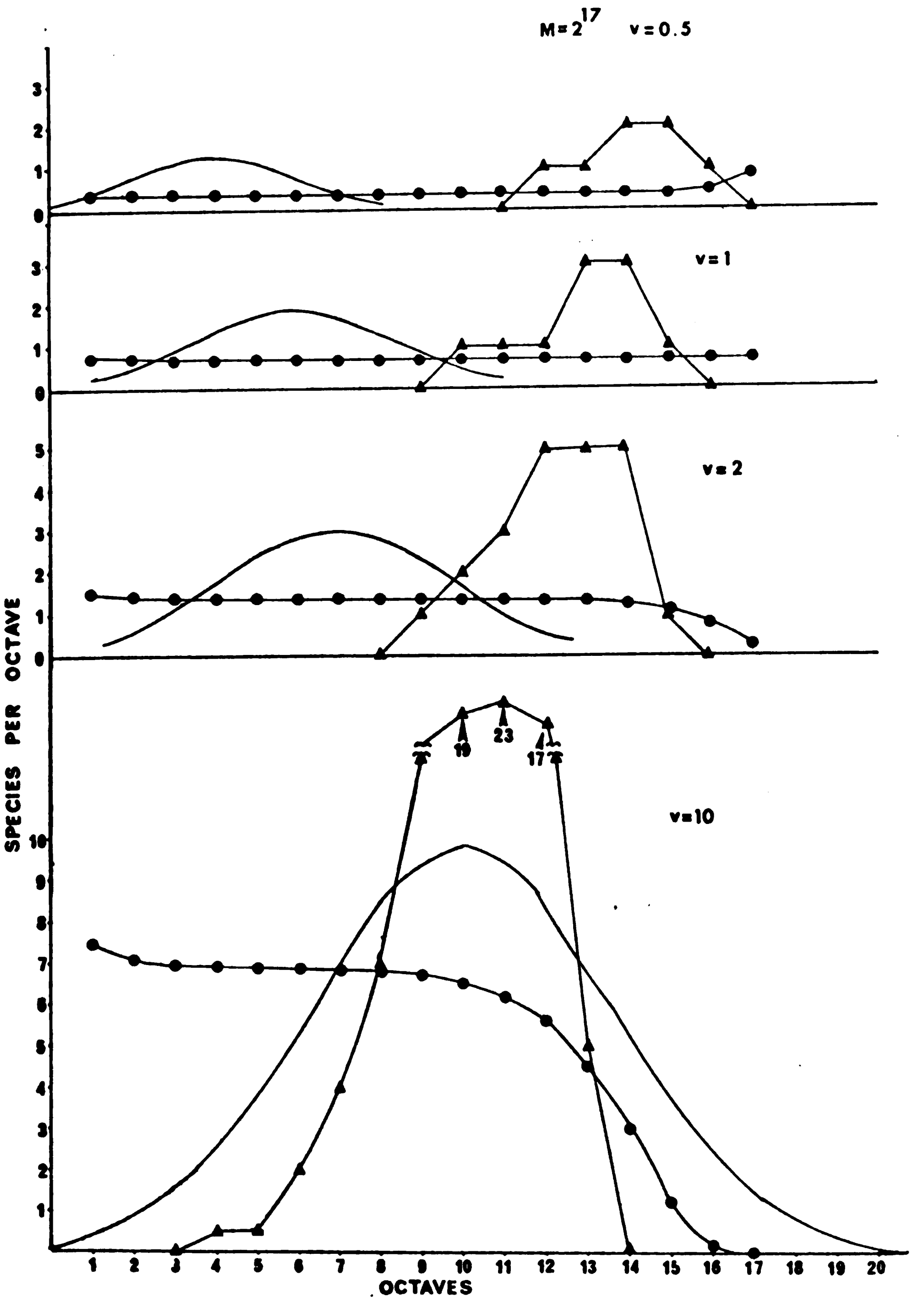
Compound distributions (see Feller 1968) arise in the study of the distribution of sums of random variables, when the number of terms in the summation is itself a random variable. If the variables being summed have probability generating function (pgf), f(s) and the number of terms in the summation has pgf g(s), then the new random variable, defined by the summation, has a compound distribution with pgf

$$h(s) = g(f(s)). \tag{13}$$

In the case of our community model, M, the total number of individuals is the sum of the number of individuals in K species, where K itself is a random variable. So we know two of the three terms in (13) above -- h(s) is the pgf of the negative binomial distribution for M, and g(s) is the pgf of the Poisson distribution for K. This information suffices to determine that f(s), the pgf for the probability distribution of population sizes is the pgf of the logarithmic series distribution (Quenouille 1949), which in turn generates the expression (9) for $\beta(j)$, the expected frequency of populations of size j (Pielou 1969).

By using the results (11) for $E(\beta(j)|M)$ we can compare the pattern of relative abundances generated by Model I with those generated by other models of community structure. Figure 2 shows such a comparison with the canonical log-normal distribution and the broken-stick distribution. The value of ν, the instantaneous colonization rate, is varied from 0.5 to 10, for $M = 2^{17} = 131{,}072$. The integral power of two was chosen to facilitate expression of the results in octaves for comparison with the log-normal distribution. Similar results were obtained for $M = 2^{15}$.

Figure 2. Semilogarithmic "octave" plot of species abundance distributions generated by three different models of community structure; the neutral model (circles), the broken-stick model (triangles) and the canonical log-normal distribution (smooth Gaussian curves). The broken-stick and canonical log-normal distributions are defined to contain the same total number of species as the corresponding neutral model curves. The total community size, M, for the neutral model is 2^{17}, and the colonization rate, ν, varies from 0.5 to 10.


M=2^17 v=0.5
v=1
v=2
v=10
SPECIES PER OCTAVE
OCTAVES
0
1
2
3
4
5
6
7
8
9
10
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17

For small values of ν, the neutral model produces nearly straight lines on the semi-logarithmic octave plotting, as noted by Preston (1948) for the log series distribution with $\theta = 1$. However, as ν becomes larger, the right hand end of the curve falls off, eventually becoming remarkably similar to a log-normal curve up to the mode. Since sampling from such a community progressively "uncovers" the distribution from its right hand end, only in samples large enough to reach the mode of the log-normal curve (and such samples have to be very large, Preston 1948, 1962), would it be possible to distinguish the two types of curves (see also Brian 1953; Figure 2).

The broken stick distribution, as discussed by Preston (1962), is skewed to the right when plotted on an octave scale, and has a much lower variance than the canonical log-normal. Thus it produces much less variation in species abundance and a higher equitability than either the log-normal or the neutral model. The absence of a right-hand "tail" of abundant species is consistent with the interpretation of the broken stick model as a biased breakage process, discussed above.

The question of the magnitude of ν arises, since a reasonable shape of the species abundance distribution requires a sufficiently large value. The recent work on colonization and extinction in island populations (e.g., MacArthur and Wilson 1967, Simberloff and Wilson 1969, Diamond 1969) indicates that immigration rates into communities are higher than had previously been believed. However, there is another factor in Model I operating to insure large values for ν. The results used to obtain Figure 2, particularly equation (11), follow a step in Watterson's (1974) derivation where he rescales time so that the birth rate $\lambda = 1$. Hence ν is the colonization rate expressed in this new time scale, and we need to e

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to evaluate the effect of this change on the probable magnitude of ν. This can be done by considering extinction probabilities.

The extinction probability for a linear birth and death process, with birth rate and death rate equal to λ and starting with a single individual, is

$$P \text{ (extinction at time } t) = P_o(t) = \frac{\lambda t}{1 + \lambda t}$$

(Feller 1968). Thus $P_o(t)$ reaches a value of 0.5 when $t = \frac{1}{\lambda}$. Rescaling time so that $\lambda = 1$ is equivalent to choosing as a time unit the length of time required for the probability of extinction to reach 0.5.

Published estimates of extinction rates (Diamond 1969, Simberloff and Wilson 1969, Terborgh and Faaborg 1973) put the values of this 50% extinction time at 10 to 250 years for birds and 10 to 50 days for arthropods on mangrove islands. Although these estimates are based on the assumption of species equilibrium, while the neutral model predicts a continual increase in the number of species (see equation (7)), the use of the equilibrium assumption will result in an underestimate of ν. At any rate, the rescaling of time in "50% extinction" units assures the reasonableness of large values for ν.

Since the neutral models generate the logarithmic series distribution of species abundances, it is interesting to compare them with other models that have been used in the past to generate that distribution. It turns out that several authors, in deriving the log-series distribution, constructured models that are remarkably similar to Model I, in particular, retaining the essential element of neutrality with respect to biological interactions (see Boswell and Patil 1971 for a review).

Kendall (1948) studied a linear birth and death process, with immigration, for a single species rather than an entire community. He derived the negative binomial distribution of total population size, equivalent to (6), for M. Then, by allowing the immigration rate to go to zero he obtained the logarithmic series distribution. The effect of taking this limit was to assure that the population consisted solely of the descendants of a single immigration event. Model I differs only in considering a set of species following such a model, since all the species are independent and since colonization occurs only by species new to the community. Wette (1954) obtained the logarithmic series in a similar fashion from a linear birth and death model in which he allowed immigration to act only when the population size reached zero. Thus he also assured that the population was descended from a single colonizing event without having to take the limit as the immigration rate goes to zero. Skellam (1951, personal communication) studied a similar model of the number of species in a genus. At each time interval each species may remain the same, may reproduce by splitting in two, may become extinct, or may become the starting point of a new genus. From this model he was able to obtain the logarithmic series as the distribution of the number of species per genus.

Clearly these models are closely related to Model I; they all follow non-interacting lines of descent of random colonization events, and none of them contain any hint of population limitation or interaction. The fact that they all arrive at an identical pattern of relative abundance is encouraging.

Species-Area Relations

The neutral models, like other models proposed for community structure, make predictions concerning the relation between the number of species and the number of individuals in the community. These are most often interpreted as "species-area" relations, since increasing the area of investigation is one of the most straightforward ways of changing the number of individuals present in the community. There are two fundamentally different situations covered by such theories, the problems of different sized samples from a given community and of distinct communities of different sizes.

The problem of sampling within a given community is the less interesting of the two. The neutral Model I predicts, for samples not too small, a linear relation between the numbers of species and the logarithm of sample size (Watterson 1974).

$$E(k|m) = \nu \sum_{i=1}^{m-1} \frac{1}{\nu + i} \rightarrow \nu \log m \text{ as } m \rightarrow \infty, \qquad (14)$$

where k and m are the number of species and the number of individuals in the sample, respectively. The log series, obviously, also predicts such a semi-logarithmic relation. To see this, we let

$$E(\beta(j)) = \frac{\alpha\theta^j}{j},$$

N be the density of individuals per unit area and k_1 and k_q the number of species per unit area and per q units area respectively. In a sample from a unit area, the number of individuals and species are given by (see Pielou 1969)

$$N = \frac{\alpha\theta}{1 - \theta}$$

$$k_1 = - \alpha \ln(1 - \theta).$$

Eliminating θ from the equations yields

$$k_1 = \alpha \ln (I + \frac{N}{\alpha}),$$

from which

$$k_q = \alpha \ln (1 + \frac{Nq}{\alpha}) .$$

Now if q is large, so that $\frac{Nq}{\alpha} >> 1$, this becomes approximately

$$k_q \simeq \alpha \ln (\frac{Nq}{\alpha}) = \alpha \ln \frac{N}{\alpha} + \alpha \ln q.$$

Both the canonical log-normal and the broken stick distributions contain a finite number of species, so an increasing sample size must eventually asymptotically approach this number. Preston (1948) presented a sigmoid curve relating number of species to the log of sample size in the log-normal distribution, but noted that the results would be indistinguishable from a straight line over some eight orders of magnitude in the central part of the graph. My own computer simulated sampling studies of the broken stick distribution similarly reveal nearly linear semilog species area curves up to the point where nearly all the species have been included in the sample.

So all of the models under consideration here result in similar species-area curves resulting from increasing sampling of a given community. Semilog species-area curves have in fact often been reported from natural situations (e.g., Williams 1964), but there have also been exceptions. These deviations are hard to interpret. On the one hand there is the problem with very small samples of deciding if the spatial distribution of the species involved is such that the sampling technique (e.g., quadrats) is in fact obtaining a random sample from the community. At the other extreme comes the problem of deciding when progressively larger samples cease to be taken from the "same" community. It is unlikely that such species-area results will help to discriminate among various models of community organization, but it is worth noting that the results predicted by the neutral model are not at all outlandish, when compared either with the real world or with other models.

More interesting is the problem of the number of species present in total communities of different sizes ("isolates" of Preston 1962). This has been approached by the study of island communities of different size, on the supposition that such communities are truly distinct entities, rather than increasing portions of some larger community.

Neither the log-series distribution nor the broken stick model make any predictions concerning such species area relations; the former because such a prediction would require a theory for the distribution of α and the latter because the number of species is the only free parameter in the distribution.

The canonical log-normal distribution of Preston (1962) contains a fixed relation between the number of individuals and the number of species present, and thus does make species-area predictions. It predicts a linear relation between the logarithm of the number of species and the logarithm of the number of individuals. This log-log relation contrasts with the semi-log relation found in within-community samples. Not only is the form of the relation predicted, but the slope of the curve is predicted to be approximately 0.27. This prediction has been tested with a number of island floras and faunas, and in general the agreement has been found to be good (Preston 1962, MacArthur and Wilson 1967). Several authors (Hamilton et al. 1964, Johnson et al. 1968, Johnson and Raven 1970) have used multiple regression techniques to examine the importance of variables other than area in explaining species number, including elevation, distance from mainland and latitude. Typically, these studies show area to be the most important independent variable in the log-log model, but with other variables making significant contributions.

There are few deviations from the straight log-log relation predicted by the log-normal theory. On very small islands (MacArthur and Wilson 1967 , Whitehead and Jones 1969) there is typically no relation of species number to area at all, but in these cases it appears that there is so much catastrophic mortality that the communities involved never have a chance to develop such a relation. In a few cases (Johnson et al. 1968, Hamilton et al. 1964, Whitehead and Jones 1969) there seems to be a distinct negative curvature in log-log plots of species number versus area. In most cases, though (Preston 1962, MacArthur and Wilson 1967), it would be hard to imagine closer fits to a straight line.

There seems to be no body of biological theory to explain this relation. As pointed out earlier, the canonical log-normal (although not perhaps the log-normal itself) distribution is a strictly empirical distribution. It is possible to justify some sort of a fractional power increase of species number with area, on the grounds that if each increment in area contained all new species, species number would be directly proportional to area (to the first power)

$$K = cA.$$

On the other hand, if there were <u>no</u> new species added with an increase in area, then species number would be constant, i.e., proportional to area to the zeroth power.

$$K = cA^0 = c.$$

Obviously neither extreme is plausible, and as a first approximation we could look for a relation of the form

$$K = cA^z \qquad 0 < z < 1.$$

But this justification is not a theoretical one, and we could just as well expect some other relation that increased more slowly than linearly with area.

What, then, does the neutral model predict? Equating, for our current purposes, area with the number of individuals, the predicted relation is of the same form as (14) for species number in different sized samples:

$$E(K|M) = \nu \sum_{i=1}^{M-1} \frac{1}{\nu + 1} \rightarrow \nu \log M \quad \text{as } M \rightarrow \infty \qquad (17)$$

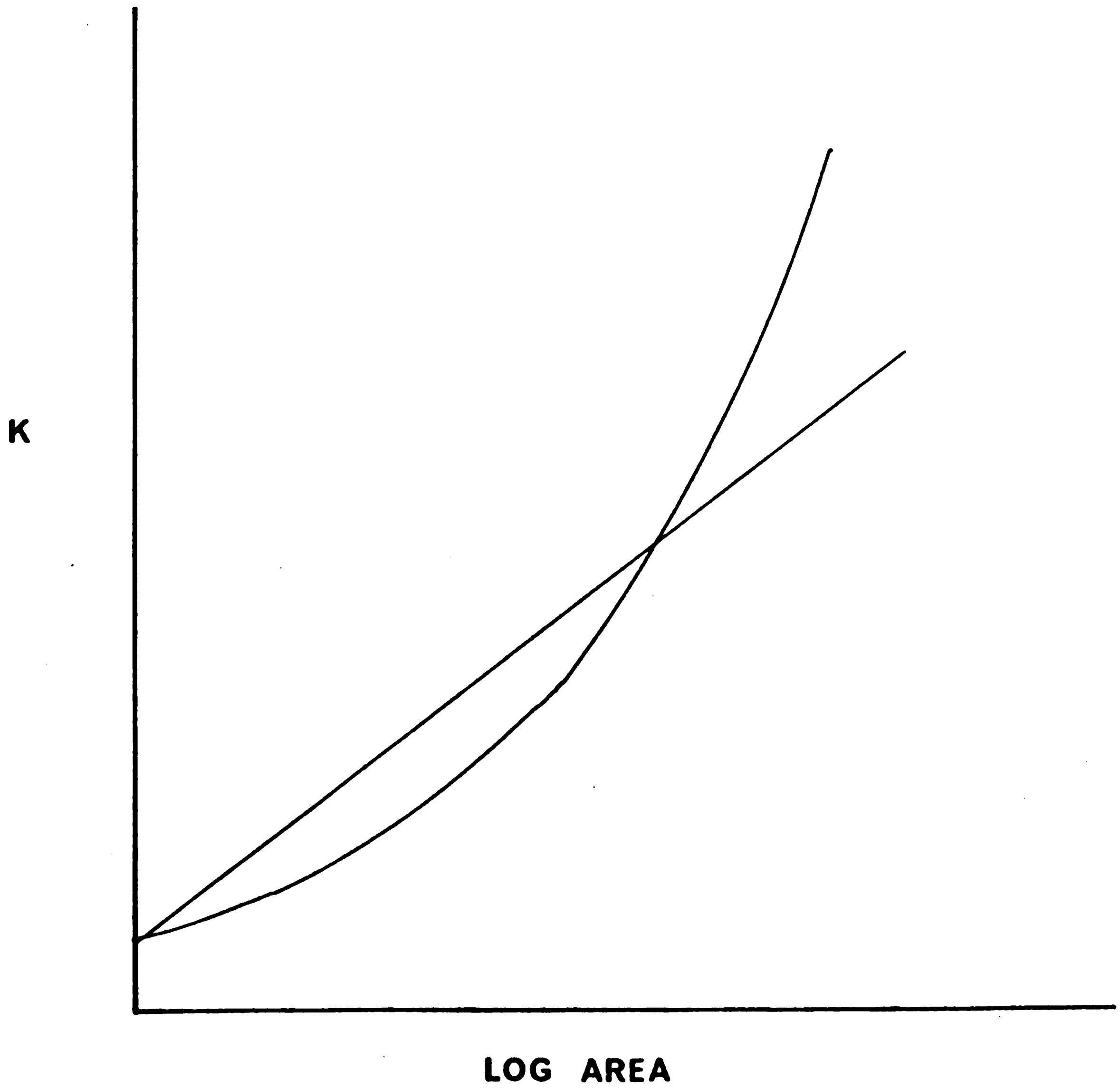
(Watterson, 1974). Thus the neutral model predicts semilog, rather than log-log, species area relations. Is there any way for the neutral model to generate the commonly observed log-log relation between species and area?

It turns out that there is. Figure 3 shows the two types of curves plotted on a semilogarithmic scale. A straight line implies a constant slope for such a curve, while the log-log relation generates a slope that increases linearly with K. In order to obtain log-log species-area curves from the neutral model, then, we need only find a justification for an increase in ν with species number.

The easiest way to do this is to note that ν is measured on a time scale defined by the extinction rate of the species in the community. So even if the colonization rate per unit of "real" time were independent of species number or island area (and it might well increase slightly with the latter), ν would increase if the extinction rate were to decrease with increasing species number or island area. This is because such a decrease would make the "50% extinction" time unit in which ν is measured longer and longer.

A decrease in extinction rate with increasing island size has been suggested by a number of authors (Mayr 1965, MacArthur and Wilson 1967), but for our specific purposes we would like a relation with species number. Diamond (1969) has provided the data for just such a comparison in his study of the birds of the Channel Islands in California. Figure 4 is calculated from his results for percent turnover (T) per 51 years in this

Figure 3. Semilogarithmic (straight) and log-log (curved) species-area relations, both plotted on a semilog basis. The log-log relation exhibits a slope that increases linearly with K, while the slope of the semi-log relation is constant.


K
LOG AREA

avifauna as a function of species number. Now if the percent turnover is T, the time for the probability of extinction to reach 0.5 is given by

$$t_{0.5} = \frac{0.5}{T} ,$$

and if $\hat{\nu}$ is the "real time" immigration rate, the rescaled rate, ν, is given by

$$\nu = (t_{0.5})\ (\hat{\nu}) = \frac{0.5\hat{\nu}}{T} .$$

If T varies inversely with K, as it does in Diamond's data, then ν will vary directly with K. In particular, if

$$T = \frac{c}{K} ,$$

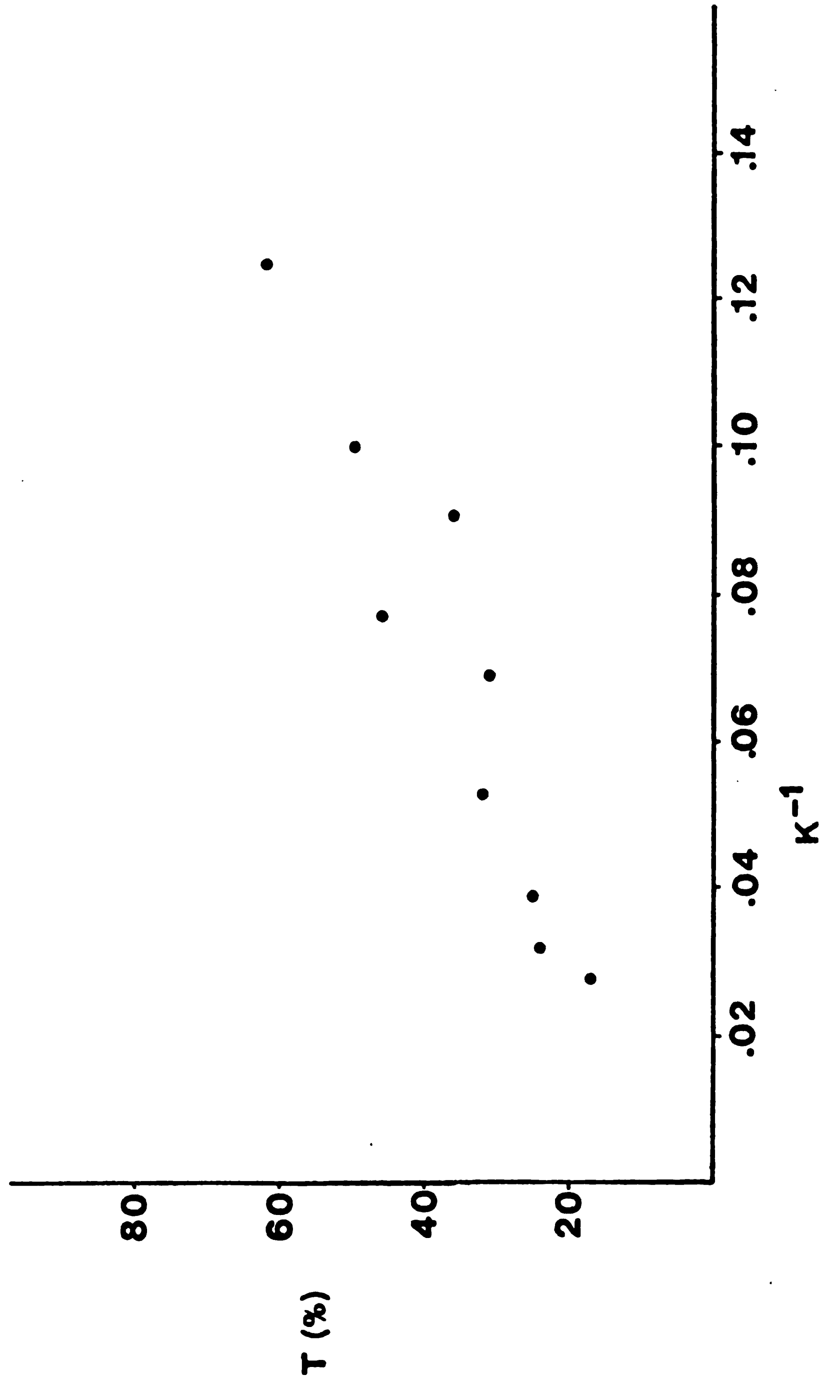
where c is some constant, then

$$\nu = \frac{0.5\hat{\nu}}{T} = \frac{0.5K\hat{\nu}}{c}$$

which gives just the linear relation between ν and K required to generate log-log species area curves. And, as shown in Figure 4, the relation between T and K in Diamond's data is of just this form!

In this section, then, we have examined some of the predictions made by the neutral model. It generates numbers of species and species abundance distributions that are non-trivial. These patterns require large values for the immigration parameter, but because of the time-scaling involved these values are not at all unreasonable. The species-area relations predicted by the model seem surprisingly accurate. On the basis of these comparisons there is no reason yet to reject the neutral model, and in the next section we will use its sampling properties to investigate a theoretically crucial element of community structure: species diversity. Here our interest will focus on patterns of deviation of natural communities from the neutral model's prediction, and the relation of these deviations to theories of diversity regulation.

Figure 4. Data taken from Diamond (1969) showing the inverse linear relationship between turnover rate (in % per 51 years) and species number for bird communities of the Channel Islands, California.


T (%)
80
60
40
20
.02
.04
.06
.08
.10
.12
.14
K^{-1}

Species Diversity

The neutral model is a particularly powerful tool for the investigation of communities because it has a well-developed sampling theory. It is possible to compare samples taken from a community with neutral model predictions for such samples. Both the broken-stick and the log-normal distributions specify species diversity values (measured by H') for the entire community (Lloyd and Ghelardi 1964, Longuet-Higgins 1971), but these results cannot legitimately be used with samples taken from the community. Specification of the broken-stick distribution requires an estimate of the total number of species in the community, while the canonical log-normal requires either this number or the total number of individuals. If this information were available, which it usually is not, the distribution could be specified and the expected diversity for a given sample size computed. As it is, the usual approach is to assume that the samples, rather than the community, follow a particular distribution and then compare the observed sample diversity with a calculated value.

As far as the estimation of parameters in the neutral model is concerned, a sample contains three pieces of information, the number of species, k, the number of individuals, n, and the relative abundances of the species. Ewens (1972, see also Watterson 1974) has shown that n and k are sufficient statistics for the estimation of ν. If n and k are known, no other information, including the distribution of abundances, will improve the estimation of ν. Using this fact, Ewens goes on to show that if the sample is small enough, relative to the total size of the population, to ignore the fact that it is sampling without replacement, one can calculate the probability distribution of the relative abundances in the sample, conditional on n and k and on the hypothesis of neutrality. Thus it is possible to use the relative abundances, or a statistic calculated from them, to test the neutral model, since they were not used in estimation of any of the parameters in the model.

Ewens (1972) proposed the use of the diversity measure H' as a test statistic for the selective neutrality model in genetics. In our ecological applications, however, H' is itself an item of considerable interest. He derives formulae for the expected value and the variance of H' conditional on the observed values of n and k and on the hypothesis of neutrality. The calculations are cumbersome, consisting of a set of recursion relations involving logarithms and Stirling numbers, but they are embedded in a computer program provided in Ewens' paper. A modification of that program was used in performing the calculations discussed later. Table 2 shows selected values of $E(H'|n, k, \text{neutrality})$. Overall, these values are surprisingly high, another indication that the neutral model is capable of producing realistic predictions of community structure.

To make the prediction of H' by the neutral model more useful, consider the types and causes of the deviations that might be observed in a set of samples. There might be factors operating to increase the dominance of one or a few species at the expense of all the rest, leading to a very uneven distribution of abundances and a lowered value of H'. Or, on the other hand, there might be a set of factors operating to eliminate dominance, maintaining a large number of species at reasonable levels of abundance and thus increasing the diversity. In population genetics, these deviations can be ascribed to directional and to balancing or heterotic selection, respectively (Ewens 1972). In the theory of community structure the latter type of deviation is identified with the result of the undisturbed operation of biological interactions. Deviations in the direction

TABLE 2

Expected values of H' (upper figure) and J (lower figure), conditional on the neutral model, in samples of n individuals containing k species.

n	25	50	100	200	400	800
k						
5	1.217 .756	1.084 .673	0.973 .604	0.880 .547	0.802 .499	0.737 .458
10	2.016 .876	1.825 .793	1.660 .721	1.520 .660	1.402 .609	1.301 .565
20	2.917 .974	2.681 .895	2.469 .824	2.285 .763	2.127 .710	1.992 .665
30	-----	3.217 .946	2.982 .887	2.774 .816	2.594 .763	2.440 .717
40	-----	3.607 .978	3.359 .911	3.135 .850	2.940 .797	2.773 .752
50	-----	-----	3.657 .935	3.423 .875	3.216 .822	3.038 .777

of increased dominance are attributed to the action of disturbance, upsetting the internal balance attained by the community.

To measure deviations from the neutral prediction, Ewens (1972) suggests the use of the following deviation statistic:

$$V = \frac{H' - E(H' | n, k, \text{neutrality})}{\sigma(H' | n, k, \text{neutrality})} .$$

Clearly V is a random variable with an expected value of zero and unit variance. Patterns of V values can be interpreted in terms of deviation from the neutral model:

$V > 0$: excess equitability

$V = 0$: neutrality

$V < 0$: excess dominance.

Moreover, V provides a statistical test of the deviation from neutrality, either by an approximate two standard deviation test or an equivalent approximate F-test provided by Ewens program. However, this test is limited to single samples, and the most interesting results come from <u>patterns</u> of V values obtained in different situations. To analyze these patterns, I will here simply use V as a measure of community structure and treat it as a variable in standard statistical tests. This is equivalent to using the neutral model as a yardstick with which to measure the diversity of a community. V is thus closely related to other scaled diversity measures that have been proposed in the past.

One such measure is <u>evenness</u> (Pielou 1969), defined by

$$J = \frac{H'}{H'_{max}} ,$$

where H'_{max} is the maximum value possible in a sample containing the given number of species. J ranges from near zero (when there is extreme dominance by a single species) to one (when all species are equally abundant).

Other measures are redundancy

$$R = \frac{H'_{max} - H'}{H'_{max} - H'_{min}}$$

and the scaled diversity proposed by Fager (1972)

$$H'_s = \frac{H' - H'_{min}}{H'_{max} - H'_{min}} \quad .$$

Redundancy measures the extent to which H' is less than its possible maximum, and H'_s the extent to which H' exceeds its minimum, all on a scale defined by $H'_{max} - H'_{min}$, the maximum possible range of variation. A fourth scaled measure of diversity is the equitability of Lloyd and Chelardi (1964). This is given by

$$\varepsilon = \frac{k^*}{k} ,$$

where k is the number of species in the sample and k* is the number of species that would generate the same value of H' if they were distributed in broken stick fashion within the sample. Although this latter measure is a scaled diversity measure (using the broken stick distribution as its yardstick) it differs from the other indices in comparing numbers of species rather than H' values directly.

Values of J, R and H'_s are predicted immediately by the neutral model, because conditioning on n and k suffices to determine H'_{max} and H'_{min}. Thus, a set of deviation statistics for these indices could be defined, as

$$V_J = \frac{J - E(J|n, k, \text{neutrality})}{\sigma(J|n, k, \text{neutrality})}$$

and similarly for V_R and V'_{H_s}. Simple algebraic manipulation and the rules of expected values and variances show that

$$V = V_J = V_{H'_s} = V_R .$$

The deviation statistic V, then, is clearly measuring deviations in community structure, as measured by the evenness of the distribution of relative abundances, from the predictions of the neutral model.

There are some important assumptions concerning the data to which this neutral model analysis is applied. The data are assumed to consist of a random sample from a community that has been operating for a long time. Even in a community governed by the neutral model, a transient response following a severe perturbation or a change in external conditions might result in disagreement with the neutral model predictions. There is clearly no good way to be sure that a given community has had time to settle down into its long-term behavior, so this assumption must be kept in mind in interpreting results.

The data must consist of counts of discrete individuals. This unfortunately eliminates from consideration data using continuous abundance measures, such as biomass. Applying the model to the same set of data with abundances expressed in, say, milligrams, grams and kilograms would give three very different sets of results. There is a fundamental theoretical reason underlying this limitation. The dynamics of the species in the neutral model are described by a discrete state Markov chain, and such models unfortunately cannot be aggregated or disaggregated and still remain Markovian. While the limitation to discrete data might be surmountable, it seems likely to require an extensive reworking of the theory.

The final requirement, one that is violated in many otherwise excellent data sets available in the literature, is that the data cannot have been "compressed" or "expanded." These are commonly used techniques which have the effect of changing the size of the sample in artificial ways. Sampling data are compressed in situations where very large samples are expressed on the basis of a much smaller sample by simple division (e.g., plankton samples expressed as number/liter or number/milliliter). Sample expansion, on the other hand, occurs when sample sizes are increased, as when bird censuses are expressed on a pairs/100 acre basis.

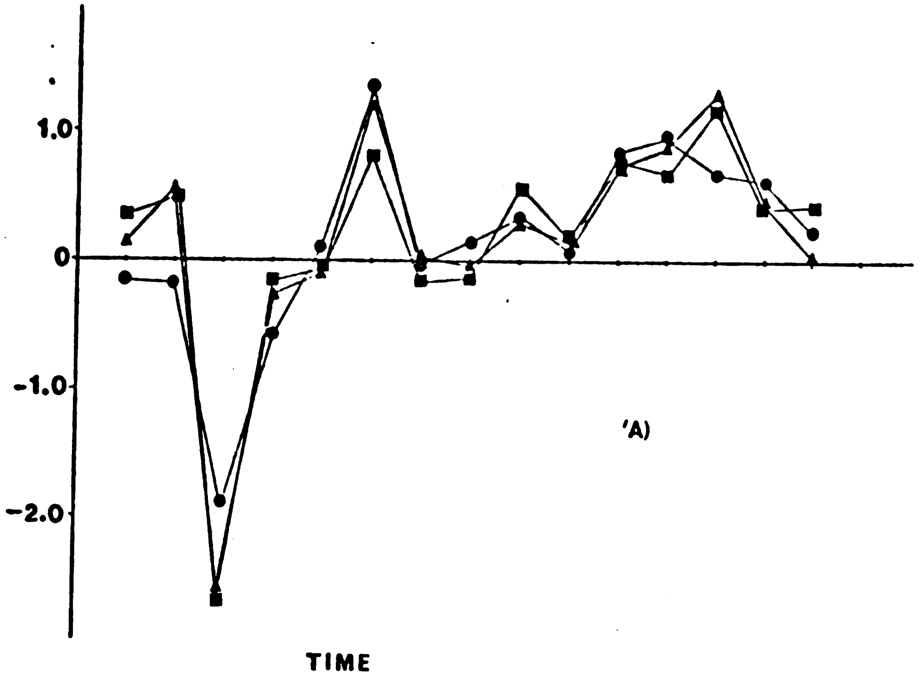
For most applications compression and expansion of samples cause no problems, and they are useful in standardizing scales for density comparisons. The neutral model, however, requires as input the results of a genuine sample. To give it a set of zooplankton data expressed on a number/liter basis is to confront it with an artificially inflated number of species relative to the number of individuals. In fact there are often more species than individuals present in such data -- clearly an impossibility in any real sample. Expanded samples have the opposite effect of decreasing the number of species relative to the number of individuals.

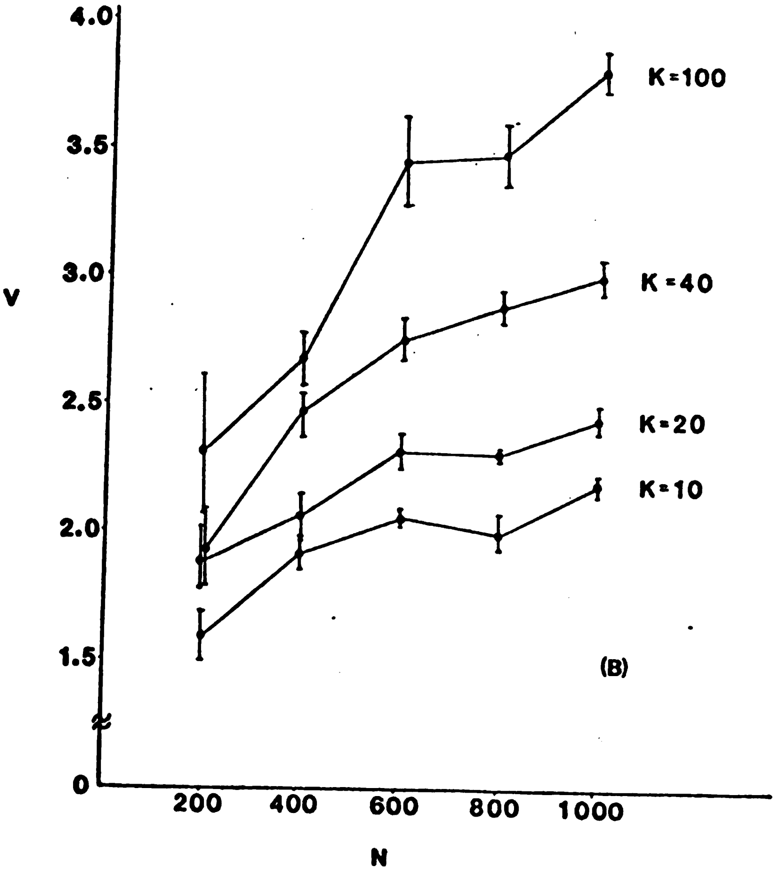
There is an acceptable method of modifying sample size, however. The trick is to generate the samples not by merely dividing the number of individuals by some factor, but by actually drawing a random "artificial" sample from the distribution defined by the relative proportions in the entire sample. This is easily done by computer; the technique is related to Sanders (1968) rarefaction method for analyzing species numbers (see Simberloff 1972). This procedure reduces both the number of individuals and the number of species present in the sample. Thus it provides to the neutral model a sample that might actually have occurred, which simple compression of samples does not. Artificial samples generated in this fashion are useful in cases where the original data contain very large numbers of individuals. The portion of the computer program which calculates $\sigma(H')$ contains a loop which is iterated on the order of n^4 times; for very large n this results in prohibitively long computation time.

One of the important properties of any measure of community structure is its dependence on sample size. While there are no measures that are completely independent of sample size, some behave more consistently than others. Perhaps because its calculation is conditional on both n and k, the deviation statistic is reasonably independent of sample size. Figure 5 shows the results of a set of artificial samples of different sizes drawn by computer from two distributions. Figure 5a is calculated from the zooplankton community of a single experimental pond in the study of Hall, Cooper and Werner (1970). Clearly, the same pattern of V values is demonstrated by samples ranging in size over an order of magnitude. Figure 5b shows the results of artificial samples drawn from a broken-stick distribution with different numbers of species. This is probably as equitable a distribution as any likely to be encountered, and it results in significantly positive values of V. The sensitivity of V to changes in the size of samples drawn from this distribution increases with K. For reasonable values of K ($\leq$ 40) doubling the sample size from 500 to 1000 individuals changes V by a maximum of 0.4, from 2.6 to 3.0.

Figure 5. (a) The deviation statistic, V, for the zooplankton community of a single experimental pond in the study of Hall, Cooper and Werner (1970). Points are the means of five computer-generated samples equivalent to 1 liter (squares), 0.5 liters (triangles) and 0.1 liters (circles).

(b) The deviation statistic as a function of sample size, N, for samples drawn from the broken-stick distribution. Points are means (± S.E.) of five computer-generated samples. The total number of species in the distributions from which the samples were drawn ranged from K = 10 to K = 100.


1.0
V
0
-1.0
-2.0
TIME
(A)


4.0
3.5
3.0
V
2.5
2.0
1.5
0
K=100
K=40
K=20
K=10
(B)
200
400
600
800
1000
N

IV. Structure of Natural Communities

The structure of natural communities, as measured by their species diversity, has been theoretically related to the nature, complexity and strength of the biotic interactions between community components. Now I want to use the neutral model, which excludes all of these interactions, as a background against which to evaluate some patterns of species diversity found in natural communities.

The situations to be examined were selected with their relevance to diversity theory in mind. Basically, they contrast the degree to which the community is free to regulate its own internal dynamics, first by examining successional sequences, and then by contrasting communities in environments with different levels of temporal variability.

A. Successional Patterns

Succession is the process of community development, and as such it should reveal the results of the internal and external factors acting on the community. In particular, successional sequences should present changes in community structure arising from an increasingly important network of biological interactions. The cybernetic, control-theoretic, and niche-theoretic approaches to community structure all make similar prediction about successional trends, based on the operation of these interactions.

Odum (1969) has summarized these trends. The foundation of his argument is that succession represents a "strategy" of ecosystem development; a strategy of increasing homeostasis for the biotic community, and decreasing sensitivity to fluctuations in the abiotic environment. The tactics which carry out this strategy are generated by the pattern of interactions which hold the functioning system together. Thus, along a successional sequence there is a tendency to hold materials and energy more closely within the community, a shift from simple linear food chains to more reticulated food webs, an increase in the subtlety and complexity of competitive and symbiotic interactions and increases in the diversity (and a decrease in dominance) of species present in the system. Odum cites the possibility of some loss of species at the climax, as competitive exclusion of pre-climax species is completed.

Odum's viewpoint is a synthesis of two complementary sets of ideas developed during the 1960's. Margalef (1963a, 1963b, 1968) presented a general systems view of community development, containing various mixtures of the cybernetic and control theoretic viewpoints. In an early paper (1963a, see also 1968) he developed the notion of an increase in complexity of community structure as the system matured and gained more control over its own dynamics. This complexity would increase until limited by environmental noise. Species diversity, measured by information content, was proposed as a first approximation to a measure of this complexity. In another paper, however, Margalef (1963b) used niche theoretic arguments and pointed out the opposing forces of niche differentiation and competitive exclusion. The balance between these forces will determine whether diversity increases throughout succession or whether it reaches a maximum at some midpoint. He cited data from marine phytoplankton communities to suggest that the latter pattern might be the most frequent. Until recently, this possibility was usually mentioned only as an aside in discussions of diversity. We will return to it later.

Whittaker (1965, 1969, 1972) developed a niche theoretic view of succession, in which biotic interactions generate increasing diversity in a positive feedback fashion through competitive interplay and niche differentiation. Again, environmental instability is presented as the chief limiting factor to the increase in diversity through succession, with the possibility of a competition-generated decrease in climax communities.

An interesting alternative to these views on succession has been proposed by Loucks (1970) and Auclair and Goff (1971). Loucks, studying forest succession in Wisconsin, found "wave-like" patterns of diversity and productivity. The maxima were not in climax stands, but midway along the successional sequence. He suggested this as a general pattern, proposing that in true climax situations the dominant species (in this case sugar maple) could exclude most or all other species, thus lowering the diversity of the stand. Community development, then, would consist of a series of these waves, triggered by randomly occurring catastrophies (fire, wind damage, etc.). In terms of diversity there would be an optimum level of environmental disturbance which would maintain the community at the peak of the diversity curve.

Auclair and Goff (1971), also working in the forests of Wisconsin, modify this concept slightly by limiting the climax decrease in diversity to stands located in the middle of environmental gradients (e.g., moisture). They seem to be suggesting that if light becomes the limiting factor for the community, then complete dominance will develop. If other factors are limiting, as they would be in extreme situations, then dominance will not develop.

At any rate, the general theories of community all concur in predicting an increased level of internal homeostasis as communities develop, leading to an increased degree of community structure. The eventual loss of remnant pre-climax species may cause a decrease in species number in climax communities, but is not expected to alter the overall pattern of community structure. When compared to the neutral model, this course of development should, theoretically, exhibit an increase in the value of V, eventually plateauing in climax situation at some positive value. What, then, do actual successional sequences look like?

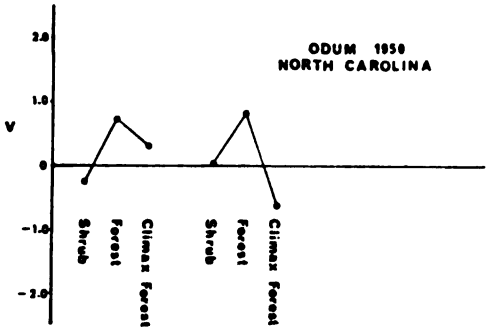
Succession in Bird Communities

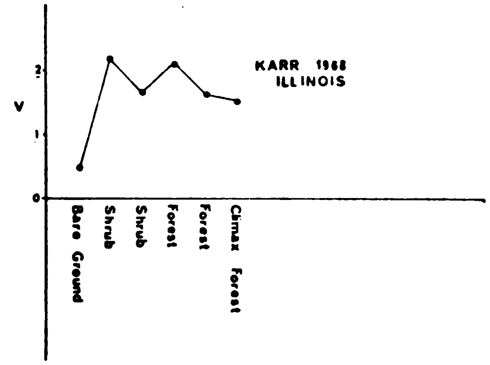
Figures 6, 7 and 11 show patterns of the deviation statistic V over 10 temperate and two tropical successional sequences. These data were obtained from the literature, and used in their original, rather than expanded form. All the data except the Wisconsin forest succession sequence are based on counts of breeding pairs of birds rather than individuals. Thus, for this data the neutral model must be interpreted in terms of immigration of pairs, rather than of single individuals. The Wisconsin data in Figure 10 are counts of individuals, but the results show no particular difference from the data based on breeding pairs, and so are included.

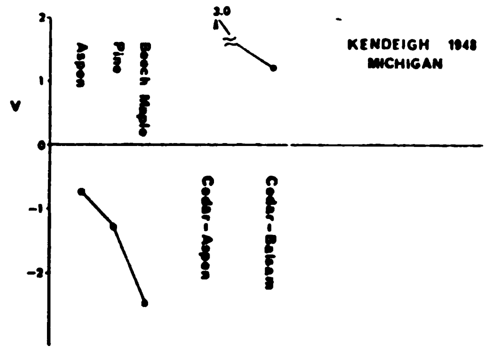
The starting points of these successional sequences vary, some running from bare ground or old-fields all the way through climax forests (e.g., Karr 1968) while others include only different stages of forest development (Bond 1957).

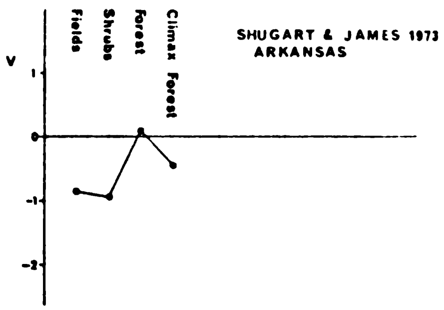
The actual values of V in these data are highly variable. Karr's (1968) series includes the highest values, a fact probably related to the unusually high values of H' he encountered. The brush-conifer site in Beaver's sequence is the single lowest value. This value is probably a result of the mixture of vegetation occurring in this site. Beaver (pers. comm.) describes it as a brush stand with a few isolated conifer clumps in it. These clumps contained a scattering of the conifer bird species in them. The presence of this additional set of rare species produces much more dominance in the sample than can be accounted for by the neutral model, and thus the very low value of V.

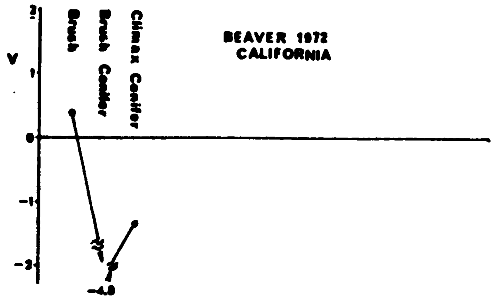
Figure 6. <u>The deviation statistic, V, as a function of successional development in temperate bird communities.</u>

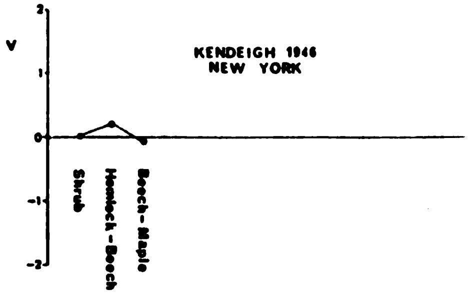

ODUM 1950
NORTH CAROLINA
V
2.0
1.0
0
-1.0
-2.0
Shrub
Forest
Climax Forest
Shrub
Forest
Climax Forest


KARR 1968
ILLINOIS
V
2
1
0
Bare Ground
Shrub
Shrub
Forest
Forest
Climax Forest


KENDEIGH 1948
MICHIGAN
V
2
1
0
-1
-2
3.0
Aspen
Pine
Beech Maple
Cedar-Aspen
Cedar-Balsam


SHUGART & JAMES 1973
ARKANSAS
V
1
0
-1
-2
Fields
Shrubs
Forest
Climax Forest


BEAVER 1972
CALIFORNIA
V
2
1
0
-1
-2
-4.0
Brush
Brush Conifer
Climax Conifer


KENDEIGH 1946
NEW YORK
V
2
1
0
-1
-2
Shrub
Hemlock-Beech
Beech-Maple

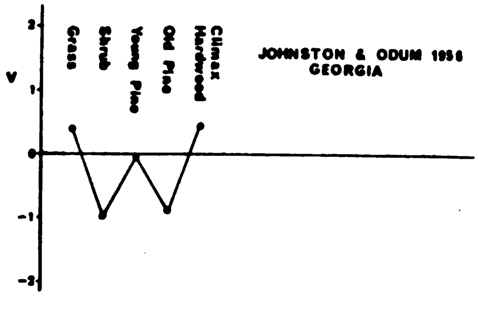
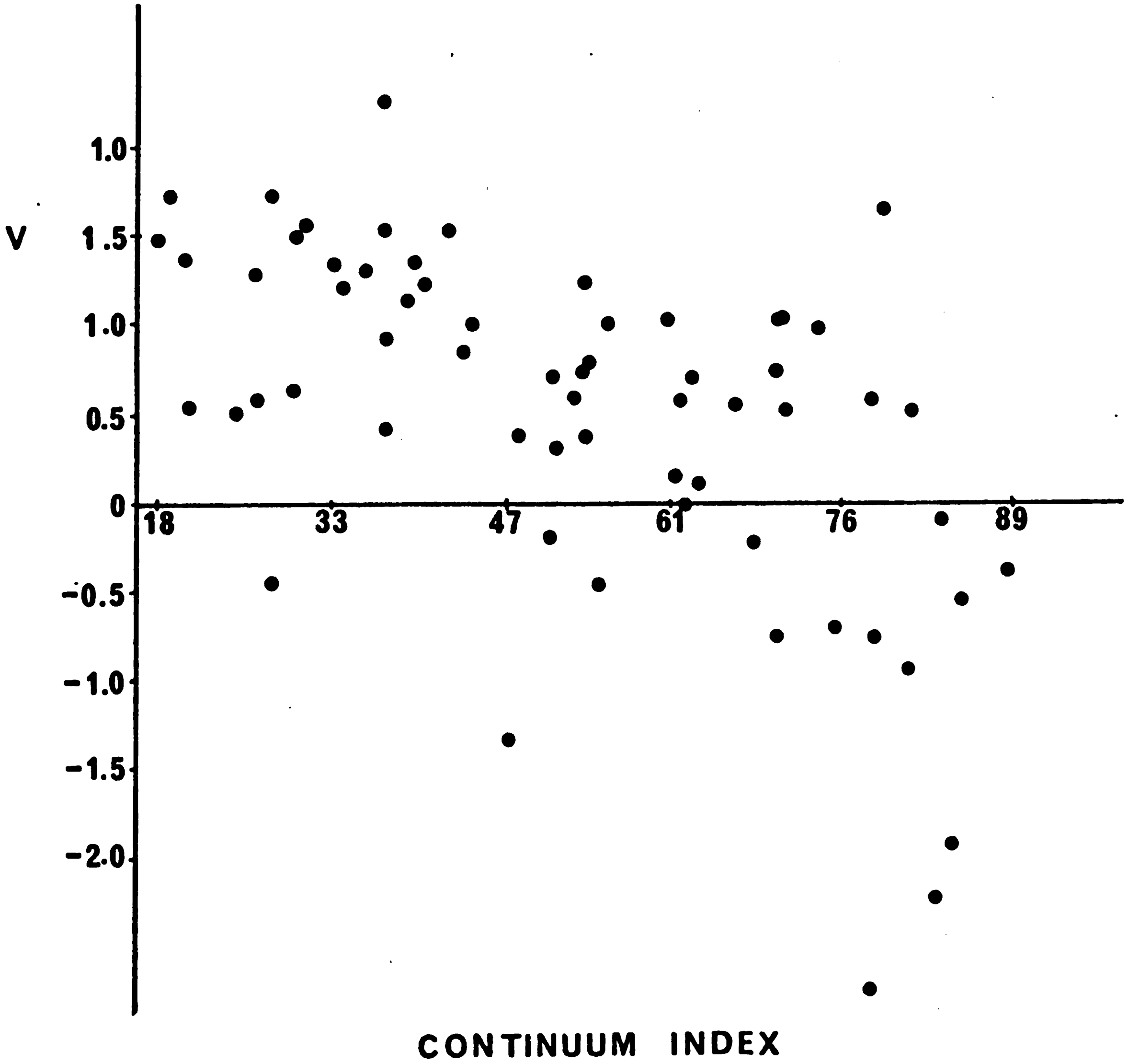

JOHNSTON & ODUM 1956
GEORGIA
V
2
1
0
-1
-2
Grass
Shrub
Young Pine
Old Pine
Climax Hardwood

Figure 7. The deviation statistic, V, for forest bird communities of Wisconsin (Bond 1957), as a function of the continuum index of the forests. For the relation between continuum indices and succession, see text.


V
1.0
1.5
1.0
0.5
0
-0.5
-1.0
-1.5
-2.0
18
33
47
61
76
89
CONTINUUM INDEX

In general, the values of V in these data fluctuate on both sides of zero. It would be hard to support a contention that biological interactions had increased the structure of these communities above the level predicted by the neutral model.

More important to the theory of succession is the pattern of values of V exhibited as the community develops. In the bird data, we find that in all cases but two there is a <u>decrease</u> in the value of V as the climax state is reached rather than the increase predicted by theory. One of the exceptions is in Beaver's (1972) study, in which the extremely low intermediate brush-conifer value is lower than the climax value. However, the climax value itself is lower than the value for the early successional brush stage. The other exception is Johnston and Odum's (1956) data from Georgia, which reveals no particular pattern at all.

Succession in Forest Tree Communities

Figures 8 and 9 show values of V for a successional sequence in the southern upland forests (SUF) and northern upland forests (NUF) of Wisconsin. These data were originally collected in a series of studies by the late J. T. Curtis and his associates at the University of Wisconsin. Auclair and Goff (1971) analyzed the diversity patterns in the data, and A. N. Auclair kindly furnished the data for use in this study.

The data consist of counts of trees ($\geq$ 4" dbh) in stands arranged according to their "continuum index". The calculation of this index is described by Curtis (1959). Each tree species is assigned a "climax adaptation number", describing where it fits in the successional sequence of the area. For each stand, the relative frequency, relative density and relative basal area are measured for each species. The sum of these three numbers gives the importance value (IV) of each species. The continuum

Figure 8. The deviation statistic as a function of successional development in upland forests of southern Wisconsin. The line is a ten-point running average of the data.

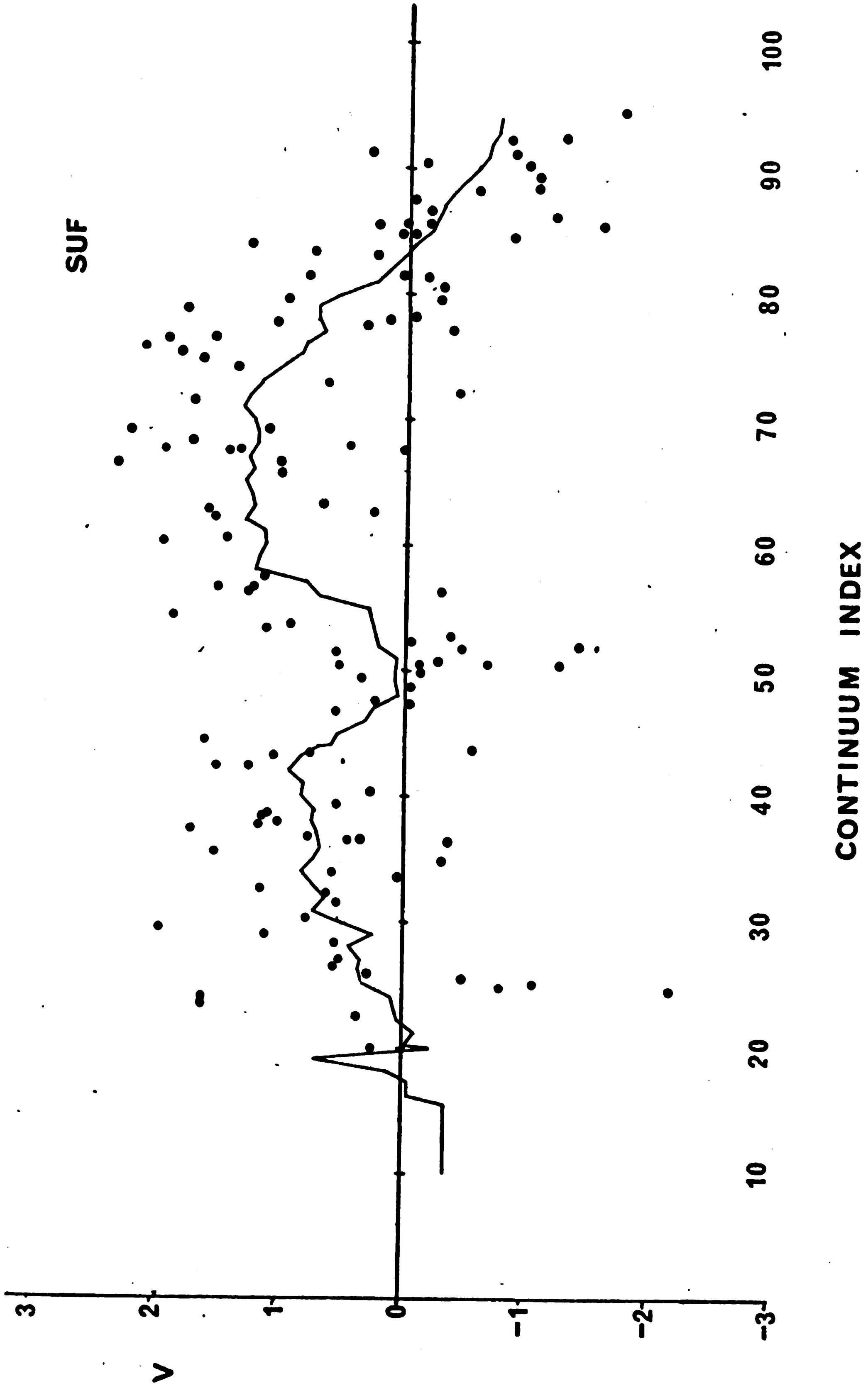
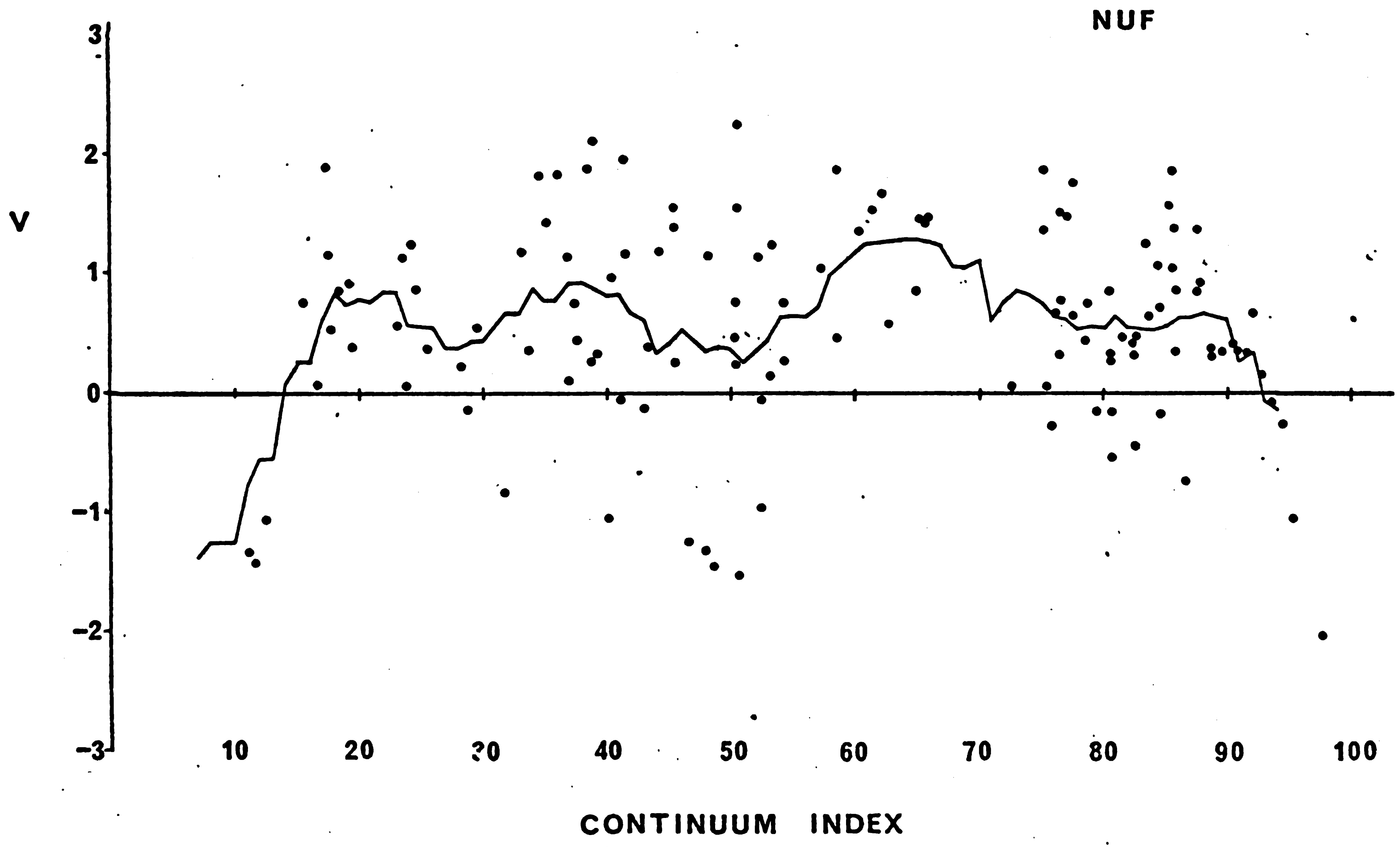

SUF
V
3
2
1
0
-1
-2
-3
10
20
30
40
50
60
70
80
90
100
CONTINUUM INDEX

Figure 9. The deviation statistic as a function of successional development in upland forests of northern Wisconsin. The line is a ten-point running average.


NUF
V
3
2
1
0
-1
-2
-3
10
20
30
40
50
60
70
80
90
100
CONTINUUM INDEX

index (CI) of the stand is calculated as the summation, over all species, of the importance value times the adaptation number. Calculated in this way, CI has a range of 300-3000. In the figures this has been rescaled by dividing by 300, thus giving a range from CI=1 (a stand composed completely of pioneer species) to CI = 100 (a stand composed completely of the climax species). This same CI is used in Figure 7, showing bird communities on the same gradient.

These continuum studies differ from the other successional sequences in several ways. In its original development, the relation between the continuum sequence and succession was not clearly defined. The climax adaptation numbers assigned to the tree species define an idealized theoretical successional sequence (Curtis 1959), since they are calculated from observed co-occurence of species and from observations on the reproductive physiology of the species. But in any large collection of stands, the theoretical sequence of succession will not always be followed, and local environmental conditions such as soil type and moisture will exert varying degrees of influence on community composition. Curtis himself tended to use the adaptation numbers primarily as measures of species response to environmental gradients, thinking of community development in his stands not in terms of succession but of longer term geoseral phenomena. Several later studies, however, have indicated that succession is far more important in these continuum studies than was originally realized. Buell et al. (1966) combined a continuum approach with a study of vegetation dynamics in upland New Jersey forests. Fifty-five of the sixty stands they examined had higher continuum indices for saplings than for trees, indicating that successional development was in fact tending toward higher values for CI. Examination of particular early successional species supported this conclusion. Langford and Buell (1969) used these results to question the support provided by such continuum studies for Gleason's individualistic hypothesis, suggesting that "in large measure" such continua express successional development.

Zedler and Goff (1973) studied successional relations in northern upland forests of Wisconsin, using size-association analysis to examine patterns of species replacement. They determined an order of replacement that was highly correlated with the climax adaptation numbers for the species involved. Their study was restricted to a very undisturbed portion of the Wisconsin forest in a single county. The original studies of Curtis and his associates used stands throughout the whole state, which suggests that disturbance, and hence successional development, is likely to be of even more importance in their data.

So, while the continuum index sequence is closely related to succession, environmental variation is also important. This is one reason for the wide scatter of points in Figures 8 and 9. Also contributing to this variation is the fact that the continuum index, like any weighted average, is a many-to-one mapping of community composition. Thus communities of widely different species composition can and do generate nearly identical continuum indices (Buell et al. 1966). To identify trends in this data ten-point running averages are presented in the figures.

These averages reveal a pattern similar to that shown in the bird succession data. There is some evidence of an initial increase in V, and a distinct decrease, beginning at a CI of about 70, in the climax stands. This part of the pattern follows closely the results of Auclair and Goff (1971), who found that diversity (measured by H') also reached a maximum at CI ≃ 70 and decreased in the more developed stands. There is also a distinct decrease in V at CI ≃ 50 in both sets of data, the reason for which is unclear.

These successional sequences reveal some interesting patterns of community development. There is some indication of a rise in V during the early stages of succession, indicating an increase in diversity relative to the expectation from the neutral model. In contrast to the predictions of most community theories, however, there is a distinct tendency for decreases in V to occur as succession reaches a climax. In many cases (10/14 of those examined), the climax values of V are zero or less. For these climax communities, diversity has not been elevated above the level that could be maintained if the community were neutral, and has sometimes been depressed below that level.

B. Patterns Related to Environmental Variability

One of the correlates of successional development is an amelioration of environmental variability. Fluctuations of light, temperature, moisture and nutrients tend to be less in climax than in successional communities. This decrease in environmental fluctuation is postulated to act as both cause and effect, in a feedback fashion, of the increase in diversity predicted by the cybernetic, control theoretic and niche theoretic theories of succession (e.g., Margalef 1963a, 1968, Whittaker 1969, 1972, Sanders 1968, 1969).

Since succession has been seen to have a different effect on community structure than has been theoretically predicted, I now want to examine patterns related to environmental fluctuation per se.

The first of these sets of data is taken from Harrel et al. (1969) and relates fish community structure to stream order in an intermittent Oklahoma watershed (Table 3). Stream order is a method of stream classification based on the number of tributaries entering the stream. The smallest streams in the watershed are classified as 1st order; when two first order

TABLE 3

STREAM ORDER AND FISH COMMUNITIES

June (pre-drought)			September (post-drought)		
Order	H'	V	Order	H'	V
4	1.232 ±0.143	-0.355 ±0.443	4	1.464 ±0.258	0.837 ±0.395
5	1.540 ±0.090	-0.473 ±0.563	5	1.749 ±0.049	0.564 ±0.282
6	1.159 ±0.181	-1.118 ±0.545	6	1.821 ±0.155	0.941 ±0.452

streams join the result is a 2nd order stream, and so on. When a low order stream flows directly into a higher order stream (e.g., a 1st order into a 3rd order), the classification of the higher order stream is not changed.

Our interest in stream order here is that it is well correlated with both environmental fluctuation and species diversity. In general, environmental fluctuation decreases with increasing stream order. This has been documented for temperature, pH, dissolved oxygen, total alkalinity and turbidity (Harrel and Dorris 1968, Whiteside and McNatt 1972). In addition, the gradient of the stream decreases, and the drainage area increases, with increasing order (Harrel and Dorris 1968). All of this suggests that higher order streams provide more constant environments than do lower order ones.

As predicted by most theories, there is typically an increase in species diversity with stream order. Harrel, et al. (1967), Whiteside and McNatt (1972) and Lotrich (1973) have documented this for fishes, and Harrel and Dorris (1968) for benthic macroinvertebrates.

The data we will use for a neutral model comparison is taken from Harrel, et al. (1967), for the Otter Creek drainage basin in North Central Oklahoma. This data provides an opportunity to examine two types of environmental fluctuation. First is the continual fluctuation to which the fish are exposed while living in a stream of a given order. Secondly, there is a catastrophic perturbation caused by drying of the drainage basin during the summer. Data were collected before the summer drought and immediately following refilling of the basin in the fall.

Species diversity, as measured by H' increases from 4th to 5th order and decreases to 6th order streams in the spring data, and increases continuously in the fall (Table 3). Harrel et al. (1967) used as a diversity index

$$d = \frac{k-1}{\ell nN}$$

where k = number of species, N = number of individuals, and found a continual increase with stream order in both samples. In addition, the values of d were slightly lower in the fall samples than in the corresponding spring samples, although the values for H' are higher after the drought.

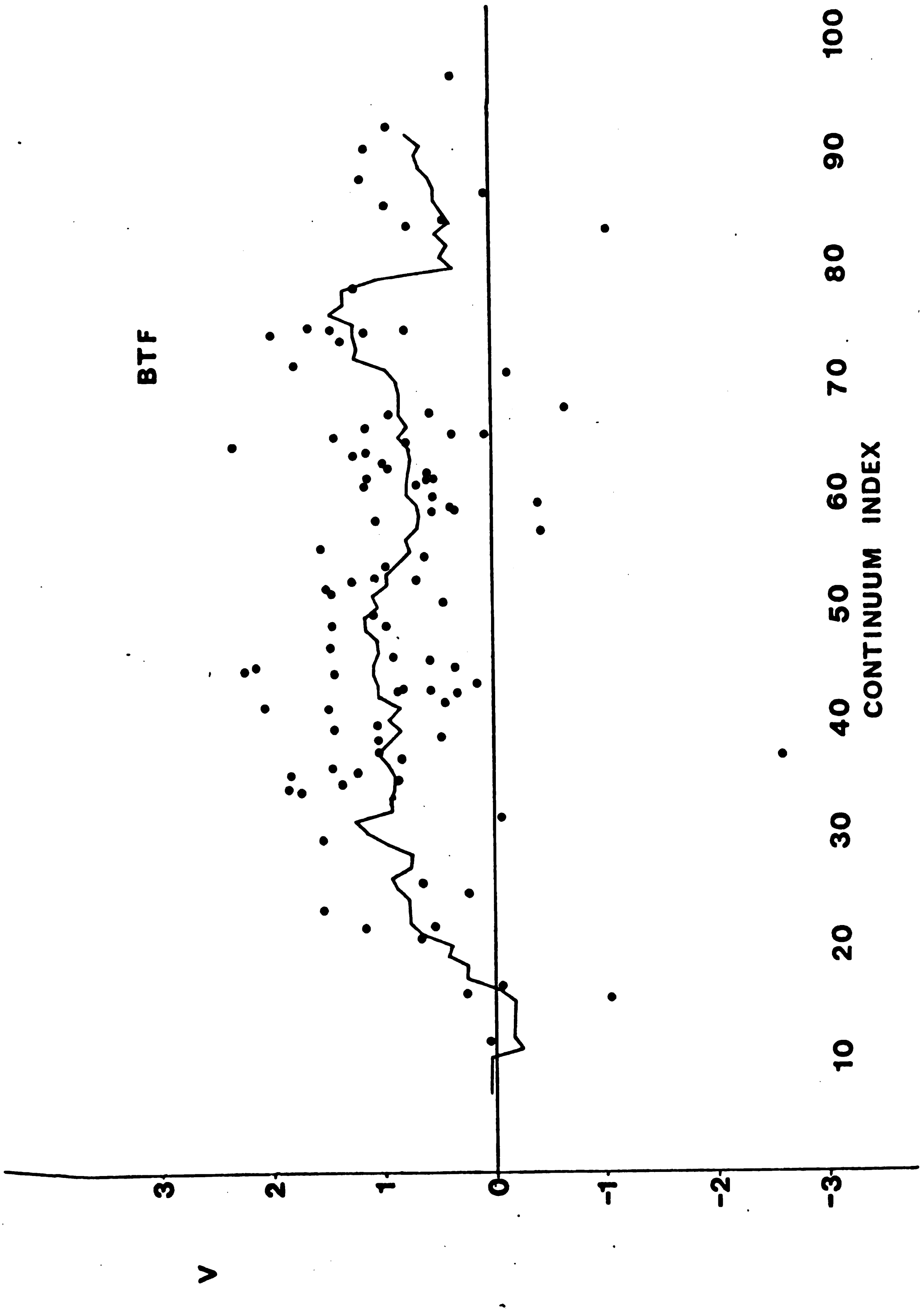
The patterns revealed by the deviation statistic V are interesting. In the spring samples, the values are negative, and <u>decrease</u> distinctly with increasing stream order. After the major perturbation of a summer drought, the pattern of V values is gone, but the actual values have been increased until they are significantly greater than zero. (Note, however, that this latter instance is very likely to violate the equilibrium assumptions of the neutral model.)

Another example relating community structure to environmental variability can be seen by comparing Figure 10 with Figures 8 and 9. Figure 10 shows the relation of V to succession in the boreal transition forests (BTF) of the northern edge of Minnesota, Wisconsin and Michigan (Data from Auclair and Goff 1971, courtesy of A.N. Auclair). Unlike the northern and southern upland forests discussed earlier, this forest is subjected to repeated disturbance by fire, wind damage and the spruce budworm. The perturbation is so severe that Maycock and Curtis (1960), who collected the original data, question the existence of a true climax situation,

> "In northern regions the question of terminal climax becomes highly doubtful, since large scale catastrophe is present and prevents the termination of succession."

It is clear from Figure 10 that this increase in unpredictable environmental fluctuation has greatly decreased, or even eliminated, the decline in V values occurring in the advanced stages of succession.

Figure 10. The deviation statistic, V, as a function of successional development in the highly disturbed boreal transition forests of northern Minnesota, Wisconsin and Michigan. Note the reduction in the depression of V at climax relative to Figures 8 and 9.


BTF
CONTINUUM INDEX
10
20
30
40
50
60
70
80
90
100
V
3
2
1
0
-1
-2
-3

A third set of data is provided by Brown (1973) in a study of the diversity of seed-eating rodents in the southwest. In this area, sand dunes form relatively isolated, well defined communities, and Brown sampled the rodents in a set of the dunes. He found that species number correlated most closely with a measure that included both the amount and the variability of a crucial resource, water. He used the annual mean rainfall minus one or two standard deviations as measures of the predictable rainfall, and found that he could use it to predict the number of species present. Although this is not strictly a measure of environmental variability, I examined patterns of V values in relation to it. The values of V were mostly small and positive (0-2). There was a non-significant but positive correlation between V and $\bar{x} - \sigma$, and a non-significant but negative correlation between V and $^{\sigma}/_{\bar{x}}$. No trend was evident in a graphical analysis of the data, and the figures are not presented here.

In two of these three data sets there is a clear relation between environmental variability and the direction and magnitude of the deviation of community structure from the neutral model. Rather than an increase in interaction-generated diversity as the environment becomes less variable, there is the same loss of community structure exhibited by the climax communities in the succession studies. Again, this relation is the opposite of that predicted by theory.

C. Tropical Patterns

The preceeding sections suggest that communities in more stable environments, rather than becoming more diverse, exhibit increasingly greater degrees of dominance than would be expected from the neutral model. This suggests examination of another contrast associated with a change in environmental variability, the tropics and the temperate zone.

The tropics, especially the moist lowland tropics, seem to be subjected to much less abiotic environmental variability than is the temperate zone. They are also famous for their diversity, exhibiting an increased variety and equitability of almost any taxa one cares to examine (e.g., Fischer 1960, Stelhi 1968, MacArthur 1969, Richards 1966). A number of theories have been proposed to explain this pattern (Pianka 1966). Among the most popular are a number of variants of the niche theoretic arguments discussed earlier, which basically view the diversity as generated by biological interactions (competition and niche diversification) which are able to express themselves fully in the tropics because of the reduced level of abiotic environmental variation (e.g., Dobzhansky 1950, Sanders 1968, Slobodkin and Sanders 1969, MacArthur 1969). In considering the problem, MacArthur (1969) has given as clear a statement as any of this approach

> "The simplest -- in fact the only -- hypothesis I know which can account for all these properties of tropical communities [the diversity patterns under consideration here as well as other properties] is that species interactions are important; both competition and predation influence species existence and abundance. The alternative, with which I cannot account for these data, is that species live their lives independently of one another."

Now, if the tropics truly do exhibit a decreased level of environmental variability, all of the community structure theories concur in predicting the development of a greater species diversity, generated by interactions among the component species. But are the tropics truly less variable? There is no doubt that at least some aspects of the environment fluctuate less in tropical than in temperate areas. Seasonal temperature variation can be so slight that the daily range exceeds the average annual range (MacArthur 1972). However, seasonal variation in rainfall typically exceeds that in many temperate areas. MacArthur (1969, 1972) points out a number of biological indications that the tropics are at least regarded as less seasonal by the species that live there: the absence of tree growth rings, the occurence of some breeding bird species and some fruiting trees at any time of year, and the lack of any migratory bird species in Colombia and Surinam. This kind of evidence is used to suggest (e.g., Orians 1969) that because certain regions of the niche space (e.g., fruit) are present here on a year round basis, they can support a set of species with no ecological counterparts in the temperate zone (e.g., fruit-eating birds). It seems reasonable to accept this sort of bioassay as evidence that the tropics at least seem less variable to their inhabitants than the temperate zone does to its inhabitants, although we note that Dobzhansky (1950) suggested the opposite conclusion after finding the same type of seasonal variation in Drosophila chromosome polymorphisms in Brazil as he found in California.

Tropical Bird Communities

There are a number of problems in collecting data on tropical bird communities comparable with that available for temperate communities. The usual methodology (territory mapping) is hindered by the lack of a clearly defined breeding season, a lower level of vocalization by territorial birds and the decreased visibility of birds in the thick rainforest canopy. The result is that in many of the studies cited here, as many as half of the species found had abundances of less than one territory in the census area. Thus these results may be much less accurate than the temperate data.

Figure 11 shows a successional sequence in sites in Puerto Rico and Panama. There is no sign of the predicted increase in V values compared to the temperate data presented earlier, and in fact the values for climax communities are lower than most of those in the temperate data.

Figure 11. The deviation statistic, V, as a function of successional development in tropical bird communities.

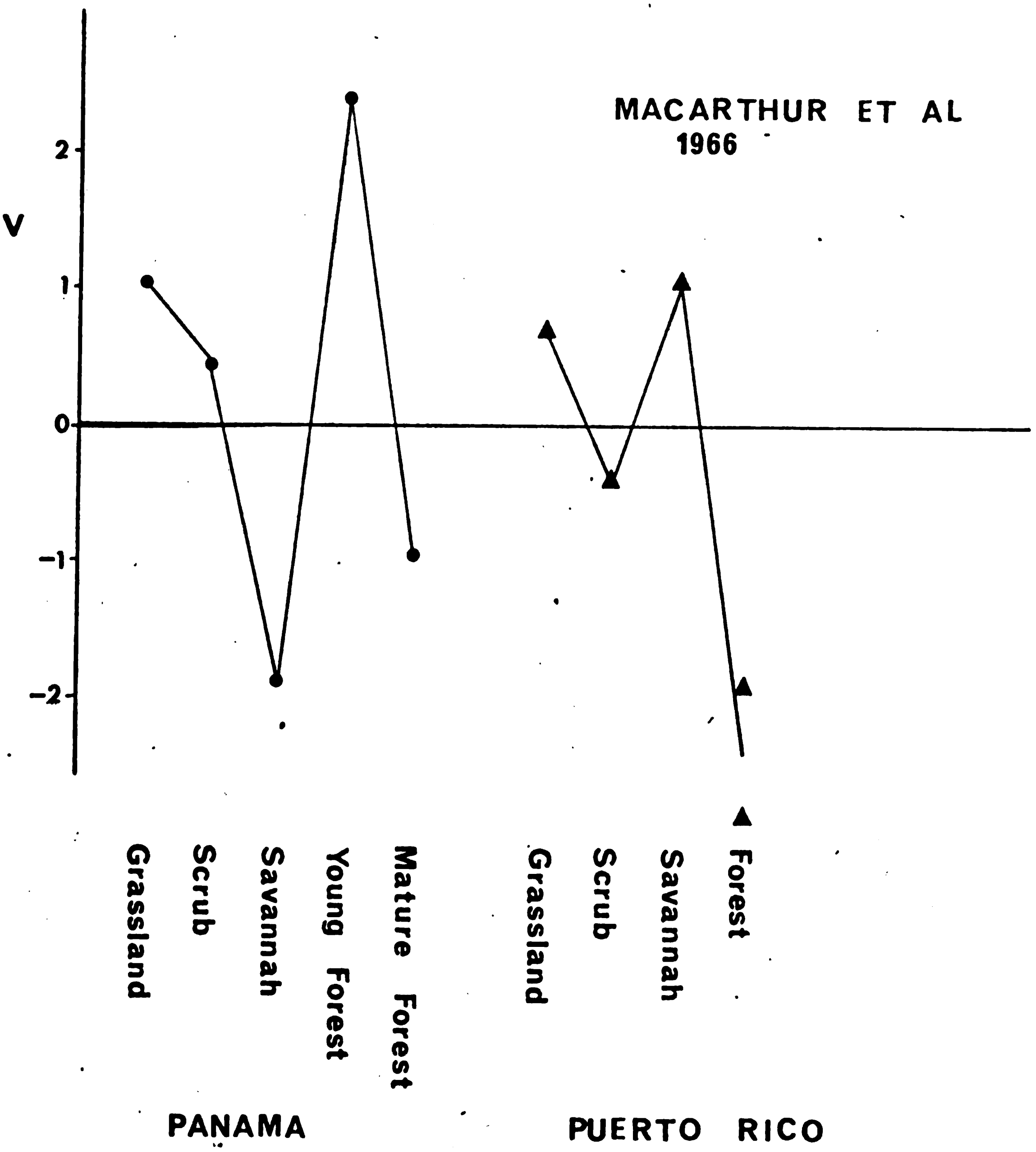

MACARTHUR ET AL
1966
V
2
1
0
-1
-2
Grassland
Scrub
Savannah
Young Forest
Mature Forest
Grassland
Scrub
Savannah
Forest
PANAMA
PUERTO RICO

Table 4 presents some data for tropical-temperate comparison. A selection of six censuses from mature tropical forests in Nicaragua, Panama, Mexico and Puerto Rico all exhibit negative values of V. In contrast, the average value of V for 15 years of data in a thoroughly studied and very mature climax beech-maple forest in Ohio is $V = 0.70 \pm 0.09$. Thus while the mainland tropical diversities (measured by H') are definitely higher than that in the temperate studies, the values of V are significantly lower.

Some data for a tropical community other than the rain forest are also presented in Table 4. The tropical pine savannah has a typically tropical level of climatic variability, but is apparently maintained by periodic burning (Howell 1971). Structurally, this area can be compared with an open pine woods site in Georgia, cited by Howell (1971) as a comparable temperate area. There is no sign of higher V values in the tropical data; if anything they are lower than in the temperate situation.

Tropical Foliage Insects

Janzen (1973a, b) has presented a large set of data on foliage insects in primary forest understory and adjacent secondary vegetation in Central America. The samples were collected by sweep netting, and the insects were sorted into what appeared to be species, but were not identified. Particular attention was paid to beetles (Coleoptera) and bugs (Hemiptera). For these groups the sample size, number of species found, and species diversity were presented for each site. Unfortunately, I have no comparable temperate data available.

In contrast between primary and secondary tropical vegetation is associated with the kinds of environmental differences we are interested in. The primary forest community is a mature association with a long coevolutionary history. On the other hand, the secondary vegetation found on disturbed sites

TABLE 4

TEMPERATE AND TROPICAL BIRD COMMUNITIES

Location	H'	V	Reference
Rain forest, Nicaragua	3.37	-2.15	Howell 1971
Lowland forest, Mexico	4.45	-0.925	Davis & Moroney 1953
	4.47	-4.06	Davis 1955
Mature forest, Panama	3.48	-0.97	MacArthur et al. 1966
Rain forest, Puerto Rico	1.40	-2.88	"
	1.47	-1.88	"
Beech-Maple climax forest, Ohio (15 yrs)	2.72 ± 0.02	0.70 ± 0.09	Williams 1947

Tropical pine savannah, Nicaragua	2.095	-0.347	Howell 1971
	1.73	0.80	"
Open pine woods, Georgia	2.91	1.07	Davenport 1964
	2.77	1.89	Davenport 1965
	2.77	0.68	

has a coevolutionary history dating back no farther than the introduction of European agriculture (Janzen 1973a). Environmental fluctuations of all kinds are likely to be less severe in the forest than in the secondary vegetation. In particular, the response of the plants to the dry season, which is the major seasonal climatic change, will be less in the primary than the secondary vegetation. Since many of the insects involved are herbivorous, the response of their plant resources to the dry season is probably the most important environmental fluctuation they face.

Beetles probably face a very different regime of environmental variability than do bugs (Janzen 1973b). With their sucking mouthparts, bugs are highly sensitive to the physiological activity of their plant hosts. A reduction in plant activity such as occurs in the dry season, with its attendant decrease in phloem transport, could be expected to be a significant factor to a bug. Beetles, on the other hand, can feed on inactive plant tissue as well as on actively growing material, as long as they can chew it. For them the reduction in plant growth during the dry season is probably a much less severe perturbation.

Table 5 shows the results of these comparisons. By and large, the results for H' are in accord with theoretical predictions. The values for beetles are higher than for bugs. For beetles, the values increase from secondary to primary communities. For bugs there is a slight decrease in H' from the secondary to primary communities which is contrary to theoretical expectation.

The results for V, however, are in distinct contradiction to standard theory. The community facing the lowest level of environmental perturbation, primary forest coleopterans, has the lowest values of V. In fact, this group of samples contained the lowest V value encountered in my whole study. The

TABLE 5

TROPICAL FOLIAGE INSECTS

MAINLAND

		Primary, wet	Primary, dry	Secondary, wet	Secondary, dry
Coleoptera	H':	3.81	3.73 ± 0.27	2.98 ± 0.06	2.81 ± 0.37
	V :	-5.35	-6.49 ± 1.31	-4.60 ± 0.87	-4.47 ± 1.35
Hemiptera	H':	-----	2.07 ± 0.20	2.19 ± 0.21	2.42 ± 0.10
	V :	-----	-1.22 ± 0.68	-1.78 ± 0.31	-1.725 ± 0.79

ISLANDS (Secondary vegetation only)

Coleoptera	H':	1.612 ± 0.12
	V :	-1.45 ± 0.46
Hemiptera	H':	1.24 ± 0.16
	V :	-0.42 ± 0.30

secondary beetle community, in spite of its decreased diversity, has a less negative value of V than does the primary community. And the hemipterans, facing the most variable environment, exhibit the highest values of V. In samples taken from secondary vegetation on Caribbean islands, the same pattern of H' and V values appears.

While these data don't permit a direct temperate-tropical comparison, they are yet another example of extremely negative V values from tropical communities, and of an apparent inverse, rather than the predicted direct relation between environmental stability and community structure.

Tropical Tree Communities

The incredible richness of the tropical rainforest is legendary. It has inspired attempts at explanation at least since the time of Wallace, and has been influential in the development of some of the theories currently in use (Dobzhansky 1950). A comparison of the structure of this community with that of temperate forest communities should be informative.

Table 6 presents a set of data on rainforest tree communities from the major rainforest areas of the world -- Malaysia, Africa and South America, (Richards 1966) as well as from Australia. These data are direct counts of individual trees over a certain diameter (usually 8 inches, sometimes 4 or 16 inches).

The diversity values for these stands are of course all strikingly high. However, only one of the 18 sets of data exhibits a positive V value, while all the others are negative. The average value for V is significantly less than zero.

The Mixed Mesophytic Deciduous Forest of eastern North America provides a suitable temperate comparison. This is geologically the oldest forest

TABLE 6

TEMPERATE AND TROPICAL TREE COMMUNITIES

Location	H'	V	Reference
Sarawak			
Mixed forest	4.28	1.12	Richards 1936
Heath forest	3.31	-0.49	"
Forest reserve	3.34	-0.29	"
Nigeria			
Mixed primary rain forest	2.33	-1.67	Richards 1939
	2.63	-1.36	"
	3.07	-4.01	"
Swamp forest	2.70	-0.60	"
British Guiana			
Tropical forest	3.07	-2.62	Davis & Richards 1934
	3.28	-2.81	"
	3.61	-2.05	"
	3.64	-1.67	"
	3.09	-2.61	"
Brazil			
Igapo rain forest	2.63	-5.60	Black et al. 1950
Rain forest	3.72	-2.25	"
	3.86	-1.86	"
Australia			
Rain forest	3.79	-2.66	Connell 1970
Puerto Rico			
Rain forest	3.01	-1.06	Odum 1970
	3.00	-0.61	"
Mean for tropical trees	3.242 ± 0.119	-1.839 ± 0.356	
Eastern North America			
Mixed Mesophytic Deciduous Forest	2.27 ± 0.036	0.72 ± 0.16	Braun 1950

association in North America (Braun 1950) and has been cited by Richards (1966) as possessing a structure comparable to that of the rainforest. It has the highest species diversity of any of the eastern U. S. forests (Monk 1967). Thus it should provide a contrast with the tropical forest emphasizing the differences in environmental stability between the two communities. Data for stands in this association were taken from Braun (1950). The results appear at the bottom of Table 6. The species diversity, as expected, is significantly lower than the tropical forest stands. The deviation statistic, however, is significantly greater than zero, and certainly more positive than that for the tropical communities.

The data on the southern and northern upland forests of Wisconsin (Figures 8 and 9) can also be compared with the tropical data. Only a handful of the most negative V values in climax Wisconsin stands even approach the average value of V for the tropical data. Thus there seems no doubt that tropical forests deviate more, in the direction of increased dominance, from the structure of a neutral community, than do the forests of the temperate United States.

This examination of tropical bird, insect, and tree communities concurs with the pattern observed in the studies of succession and environmental variability. Although the patterns of species diversity follow the theoretical predictions, use of the neutral model as a frame of reference shows that the operation of biological interactions is producing a decrease, not an increase, in community structure.

V. Concluding Remarks

The analyses just completed attempt to estimate the effect of biological interactions on community structure, using the neutral model as a scale of reference.

A logical question arises concerning the validity of the comparison; is the neutral model reasonable, or do its general predictions clash violently with either observed patterns in nature or with accepted ecological theory? If it can be claimed that the model's predictions are absurd, then its use even as a scale of reference could be questioned. Its general predictions, however, seem eminently reasonable. It generates the log-series distribution of relative abundances, which has been proposed as a description of community structure on both theoretical and empirical grounds. It is capable of generating log-log species-area curves, given a relationship between turnover time and species number which is supported, both qualitatively and quantitatively by available data.

Not only does the model produce reasonable results, but it does so in robust fashion. Essentially identical predictions result from at least three different model structures -- all of which share the property of neutrality with respect to biotic interactions.

These general results are free of any connection to a specific community, specifying as they do the <u>form</u> of the relationships in question. But because of the sampling theory developed by Ewens (1972) the neutral model can be applied to actual samples from specific communities. The result is an assessment of the diversity of the community relative to that predicted by the neutral model, and is thus an estimate of the effect, on species diversity, of those aspects of the real community that differ from the neutral model. In particular, it estimates the effects of biological interactions, which gleaning bird guild as opposed to the whole bird community);

-- the results might express themselves in terms of biomass or energy flow instead of numbers of individuals.

It is also possible to question the existence or the nature of the gradients of biological accommodation. That biological interactions should be able to express themselves more fully in climax, or low variation, or tropical situations is itself a theoretical prediction. If it is not true, then the connection of these results to the theories of diversity regulation is weakened or destroyed.

The impact of these findings on the niche-theoretic formulations of community structure is much less severe. This theory was developed primarily around the question of species coexistence, and is much less tightly linked to relative abundances in general and information-theoretic measures in particular. Although increases in evenness of distribution are usually predicted across the kinds of gradients examined here, the predictions are not rigorously derived and not of fundamental importance to the theory.

It is interesting, with regard to niche theory, to note that the patterns of V reveal an increasing amount of dominance (relative to the neutral model, of course) as biotic interactions become more important. This seems closely related to, and in agreement with, the theories of Loucks (1970) and Auclair and Goff (1971), who predicted, in the absence of disturbance, a drop in species diversity at the end of succession in non-extreme situations, where one or a few species could become very dominant.

Unfortunately, the neutral model itself is not sufficient to determine the mechanisms by which the shift towards dominance in biotically accommodated communities occurs. At least two possibilities spring to mind. As the community becomes more and more stable (e.g., in the terminal stages of succession) competitive interactions might finally succeed in squeezing out a set of species which previously had existed only marginally, or temporarily because of disturbance. Alternatively, such stable conditions might allow invasion of the community by new species occupying odd, out-of-the-way corners of the niche space, which were previously not predictable enough to support species. These new species would be rare relative to the majority of the species present, and would thus increase the dominance in the community.

It is entirely possible that the first of these mechanisms operates in successional situations, where climax communities seem to be characterized by a decrease in the number of species and equitability (Loucks 1970, Auclair and Goff 1971), as well as V. The second might operate in temperate-tropical comparisons, where the environmental stability is present over a much longer time scale. In tropical communities, the number of species and the equitability are much increased over temperate communities, but V is dramatically decreased.

All this suggests an approach to the study of community structure, which, when combined with the neutral model approach, may shed more light on the role of biological interactions. It seems desirable to evaluate the manner in which species characteristics (e.g., feeding biology) are related to their entering and leaving communities along gradients such as those examined here. Orians (1969) and Schoener (1971), for example, have applied this technique to tropical birds.

At any rate, the general role of biological interactions in generating community structure clearly needs to be rethought. The results of this study indicate that the diversity of natural communities may be maintained in spite of, rather than because of, such interactions.

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