A GENERAL HYPOTHESIS OF SPECIES DIVERSITY

MICHAEL HUSTON

Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109

Many explanations for diversity patterns have been proposed, and there have been several recent reviews of the subject (Pianka 1966, 1974; Ricklefs 1973; Pielou 1975). High diversity has been attributed both to intense competition which forces niche restriction (Dobzhansky 1950; MacArthur and Wilson 1967) and reduced competition resulting from predation (Paine 1966; Harper 1969; Janzen 1970; Connell 1975). Diversity has been positively correlated with productivity (Connell and Orias 1964; Pianka 1966; MacArthur 1969) and negatively correlated with productivity (Yount 1956; Margalef 1969). The question is far from settled.

This paper develops an approach to the problem of species diversity based on the nonequilibrium interactions of competing populations. Under nonequilibrium conditions, differences in diversity are strongly influenced by variations in the rates of competitive displacement between communities, and such factors as relative competitive abilities, niche partitioning, etc., may not be particularly important. This approach deals primarily with the maintenance of diversity, as opposed to the generation of diversity. While most of the current diversity hypotheses have some relation to the evolutionary origin of diversity, this will not be emphasized here.

COMPETITION AND DIVERSITY

Current ecological theory depends heavily on the concept of competitive exclusion and the assumption that communities exist at competitive equilibrium. There has been considerable recent discussion of the assumptions and general validity of the competitive exclusion principle (Ayala 1969; Gilpin and Justice 1972; Koch 1974a, 1974b; Pielou 1975; Armstrong and McGehee 1976a, 1976b; McGehee and Armstrong 1977). However, the general conclusion still seems valid that when the very limiting assumptions of the hypothesis are met (competition occurs in a stable uniform environment for precisely the same limiting resource at the same time, and equilibrium is achieved), competitive exclusion must occur and one species will eliminate the other. Complete exclusion has been obtained in the laboratory (Gause 1934; Crombie 1947), but it seems likely that complete exclusion rarely occurs in nature (Hutchinson 1961; Miller 1967).

While the assumption of equilibrium has made possible the development of a rich body of mathematical theory, it is not necessarily valid to apply the insights gained from equilibrium solutions to natural communities. Since competitive equilibrium requires that the rates of change of all competitors be zero, and since fluctuations in

the physical environment, predation, and other factors are constantly changing population sizes and the nature of competitive interactions, it seems likely that competitive equilibrium must occur rarely, if at all. There is growing evidence that many natural systems are not at competitive equilibrium (Hack and Goodlett 1960; Loucks 1970; Richerson et al. 1970; Auclair and Goff 1971; Grubb 1977; Opler et al. 1977; Sale 1977; Wiens 1977; Connell 1978).

Models based on equilibrium concepts have not proved particularly useful. Many attempts have been made to measure niche breadths (see Miller 1969; Soulé and Stewart 1970) and determine coefficients of competition for populations of birds, mammals, and desert reptiles, but none of this has brought us much closer to a real understanding of what controls diversity in natural communities. The elusive quality of competition results from the constantly changing intensity and focus of competitive interactions. Species may compete for an endless array of resources, but do not compete at all times for all possible resources. In general, competition will be for specific limiting resources, which may change through time and space, as well as through a species' life history stages (Ayala 1971; Ayala and Campbell 1974; Wilbur et al. 1974; Wiens 1977). Cases may even arise in which competition at one stage or place has no effect on the ultimate population size because limiting competition occurs at another stage, place, or time (Fretwell 1972). The size and composition of competitive guilds may change frequently and radically as various resources change in availability, and shifts between limiting resources may result in major changes in the perceived environmental heterogeneity. In addition, genetic changes may be constantly occurring within populations which will change their competitive interactions (Krebs 1971; Hebert 1974a, 1974b), and even differences in age may drastically alter the direction of interactions (Ayala 1971). Constant competitive coefficients may well be meaningless except in uniform stable environments which never exist in nature.

However, even if competitive equilibrium is never achieved, we would still expect the immediate outcome of competition to be expressed by the increase and eventual predominance of one competitor, with a concomitant decrease in the other. The same effect should be observed whether we are looking at the interaction of two species or many species. Increasing intensity of competition should result in a decrease in species evenness and eventually species number (on an ecological, not necessarily an evolutionary timescale). Thus, it seems reasonable to relate competition inversely to diversity. Intense competition should result in low diversity among the competing species, and high diversity might be expected where there is weak competition (Levins 1968; Vandermeer 1970).

AN ALTERNATIVE HYPOTHESIS

I suggest that the most profitable approach to diversity is not through comparing competitive abilities, but through comparing the rates at which differences in competitive abilities are expressed. This may be thought of as the rate of approach to competitive equilibrium, or perhaps better as the rate of competitive displacement. One species may be a much "better" competitor, but if all competing species are increasing at a very low rate, it will be slow to predominate. Similarly, if one species is

only a slightly better competitor, we would still expect it to predominate fairly quickly in a situation of rapidly increasing populations. If all competing species in a community have relatively low rates of increase, the rate of competitive displacement for that community would be lower than in a situation where all rates were increased (either by a constant proportion, or with the highest rates being increased most). A reduced rate of competitive displacement allows a longer period of coexistence among competitors, and thus the maintenance of diversity.

When competitive equilibrium is prevented by fluctuating conditions, population reductions, or other factors, diversity among competitors should be strongly influenced by the rate of competitive displacement. Diversity should be high for communities with a low rate of competitive displacement, since they will generally be far from competitive equilibrium, and lower for communities with a high rate, since they will tend to approach competitive equilibrium more closely. The various measures of diversity and the difficulties involved in dealing with them have been adequately discussed elsewhere (Hurlbert 1971; Peet 1974). For the purposes of this discussion, "diversity" includes both the concepts of species richness and species evenness, and need not be defined further.

The primary assumptions involved in this approach to diversity follow.

1. Most natural communities exist in a state of nonequilibrium where competitive equilibrium is prevented by such factors as periodic population reductions and other forms of density-independent mortality, certain types of predation or herbivory, and fluctuations in the physical and biotic environment. Competition occurs and diversity would be reduced by exclusion at equilibrium, but equilibrium is rarely achieved.

2. In a community of competing species under a specific set of conditions, the different species will have different population growth rates. The population growth rate is the population specific intrinsic rate of increase, or the per capita rate at which a particular population of a species is capable of increasing in numbers and biomass under specific environmental conditions. This rate is an environmentally regulated potential rate of increase, not an instantaneous rate, and is determined by the interaction of environmental variables, such as energy or nutrient availability, with the genetically determined maximum potential rate for the species. This growth rate includes both the factors of physical increase in size of individuals and actual increase in numbers of individuals, either or both of which may be important depending on the biology of the organisms being considered. In general, this rate of increase will be inversely correlated with the maximum size of the population, or the carrying capacity, but this relationship is not essential for the model.

3. Changes in certain environmental variables will affect all competing populations in basically the same way; that is, the population growth rates of all may be increased or decreased by changes in such factors as energy or nutrient availability. In cases in which the carrying capacity is affected by the environmental changes, it should increase or decrease with the growth rate.

Under nonequilibrium conditions, a dynamic balance between rate of competitive displacement and the forces that prevent equilibrium can be established that allows the continued coexistence of species that would be extinct at competitive equilibrium. When a community of competitors exists under conditions of rapid population growth, the dominant species (which may have a high growth rate or high carrying
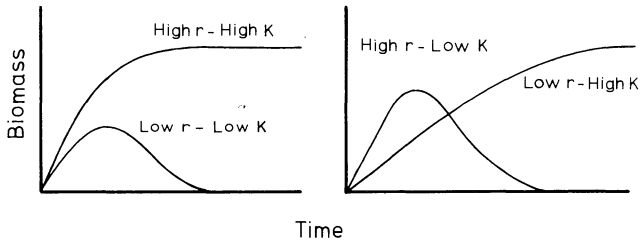
THE AMERICAN NATURALIST

FIG. 1.—Two dynamically different approaches to an equilibrium where only the high K species survives. The only parameters which vary between simulations are the r values.

capacity, depending on the conditions and time scale being considered) would be expected to predominate more rapidly than under conditions where the population growth rates of all species were lower. According to this approach, conditions that increase the growth rates of competing species should generally result in decreased diversity, and any conditions which reduce those rates should maintain or allow an increase of diversity. This model is supported by several lines of reasoning.

TIME-SCALE EFFECTS

The intuitively attractive Lotka-Volterra competition equations form the basis for most of the equilibrium theory of community structure; however, while they have been exhaustively analyzed at equilibrium, their dynamic behavior has been largely ignored. The nonequilibrium behavior of these equations simply illustrates the basic features of the model I am proposing.

Equilibrium solutions are independent of the rate of approach to competitive equilibrium (MacArthur and Wilson 1967; Ricklefs 1973; Pielou 1974; or any recent ecology text), and independent of the pattern of interactions prior to reaching equilibrium, although the relative rates of increase of competitors can determine whether or not they will coexist at equilibrium (Strobeck 1973; Vandermeer 1975). There may be more than one dynamically distinct way to reach the same equilibrium (fig. 1). If competitive equilibrium is prevented by predation or any disturbance which reduces population sizes, the actual outcome of competition may be completely different from that predicted by the equilibrium solution (fig. 2). The nonequilibrium outcome clearly depends on the timing and the magnitude of the population reductions, and on the nature of the competitive interactions, particularly their rate of approach to competitive equilibrium. The frequency of disturbance and the rate of competitive displacement might be expected to reach a dynamic equilibrium, distinct from competitive equilibrium, at which the number of coexisting competitors would remain relatively stable.

Computer simulations of the dynamic behavior of these equations confirm intuitive expectations. Competitive equilibrium may be prevented (and diversity maintained through prevention of competitive exclusion) by periodic population reductions and certain types of predation. "Population reduction" as used in this discussion refers to density-independent, species-independent reductions which affect the entire community being considered, e.g., all populations reduced by half. This is
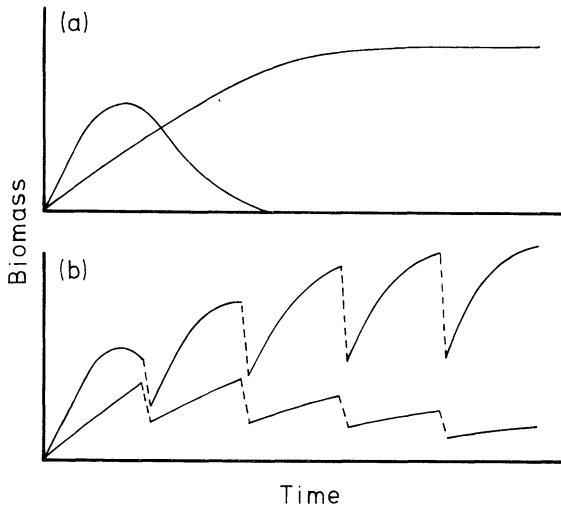
Fig. 2.—Effect of nonequilibrium conditions on the outcome of competition. (*a*) Simulation in which competitive equilibrium is reached, with survival of only the high *K* species. (*b*) Simulation in which competitive equilibrium is prevented by periodic density independent population reductions. Here the low *K*–high *r* species predominates and the high *K* species eventually becomes extinct.

the most conservative type of reduction, and any density-dependent effects which reduce the most abundant competitor more than others (compensatory mortality) will obviously have an even stronger effect in maintaining diversity. This observation has been made by Paine (1966) and many others.

In simulations with intrinsic rates of increase (*r*) held constant, the frequency of population reduction has a major effect on the maintenance of diversity. At low to intermediate rates of increase, diversity is maintained at intermediate frequencies and magnitudes of reduction (fig. 3*b*). Diversity is reduced at high frequencies by reduction or extinction of populations unable to recover from the disturbances (fig. 3*c*), and at low frequencies by competitive displacement and eventually exclusion (fig. 3*a*). The resulting relationship of disturbance and diversity (fig. 4) has been predicted and observed by others (Loucks 1970; Dayton 1971; Grime 1973; Koch 1974*a*; Horn 1975; Connell 1978). Not surprisingly, under nonequilibrium conditions variation in the parameters *K* and α has much less effect on the outcome of competition than at equilibrium.

The intrinsic rate of increase (population growth rate described previously) has a major effect on the maintenance of diversity at a particular frequency of population reduction. This can be seen as a change of the population growth time scale, without a corresponding change of the reduction periodicity. Under conditions of low to intermediate frequency of population reduction (i.e., all populations have sufficient time to recover from the reduction), low values of *r* among a group of competitors allow a longer period of survival for species that would be extinct at equilibrium than do high *r* values. An increase in the *r* values of competitors (either with all being increased proportionately, e.g., doubled, or with a greater increase in the higher *r*
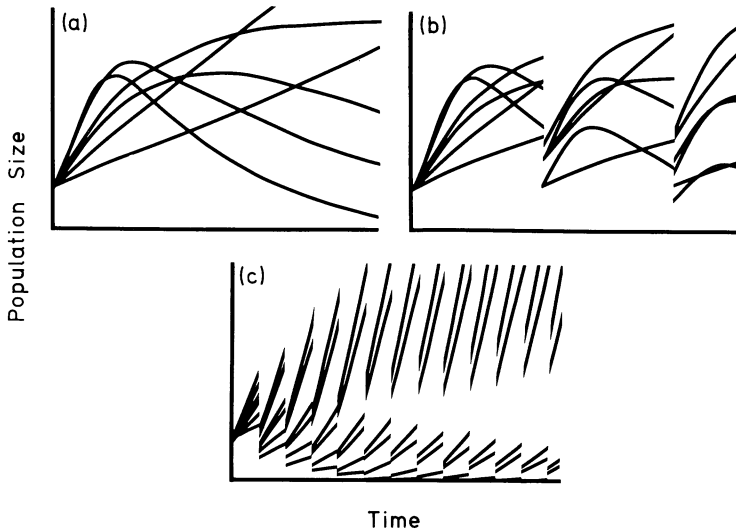
FIG. 3.—Effect of frequency of population reduction on maintenance of diversity, based on computer simulations of Lotka-Volterra competition equations for six species. Values for r's, K's, and α's are identical in all three simulations; all population reductions are .5. (a) No reduction; diversity is reduced as the system approaches competitive equilibrium. (b) Periodic reductions; diversity is maintained for longer time than in a. (c) High frequency of reductions (5 times greater than b); diversity is reduced as low r populations are unable to recover.

values) results in a decrease in diversity in nearly all cases (fig. 5a, b). The major exception is situations where there is high diversity at equilibrium. It should be noted that coexistence at equilibrium requires a very particular balance of parameters (Strobeck 1973; Pielou 1974; Vandermeer 1975), and that exclusion could be expected to result in most cases.

Since diversity will inevitably be low where organisms cannot grow ($r = 0$), there will be a range of extremely low growth rates (perhaps due to severe nutrient or energy limitations, or other extreme conditions) where diversity will be low. Nevertheless, the model clearly predicts that diversity will be highest at low growth rates, and decrease monotonically as r values increase. This suggests that the relationship between growth rate and diversity has a "break point" at very low growth rates (fig. 6) where a slight increase in growth rates will result in a rapid increase in diversity, which will then decrease as growth rates rise.

The population growth rates of competitors in a community will have some sort of distribution over the range found in that community. The discussion so far has considered mainly those situations in which the mean growth rate changed and the distribution remained the same. However, the distribution itself may also change as the mean changes. Just as the variance of the distribution of K, α, and r may affect the equilibrium outcome of competition (Vandermeer 1970, 1975), variance in K, α, and r will affect the rate of displacement in a nonequilibrium situation. The influence of variance in r will have the greatest effect far from equilibrium, and the effect of K and α will increase as equilibrium is approached. These effects may be either compensa-
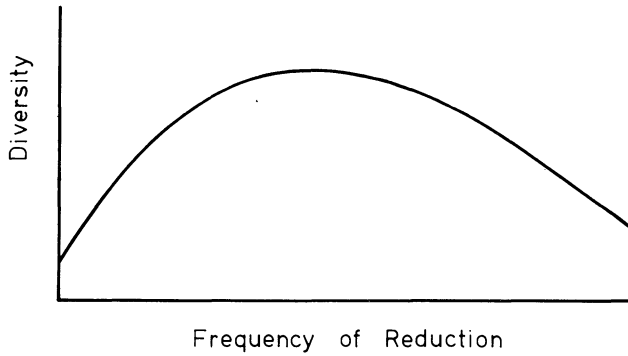
FIG. 4.—Predicted relationship of diversity and frequency of population reduction; the magnitude or intensity of reduction (i.e., whether populations are reduced by .1, .5, or .9) has the same relationship to diversity.
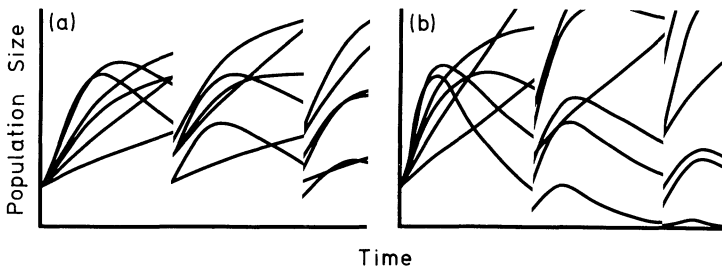
FIG. 5.—Effect of growth rate on maintenance of diversity under nonequilibrium conditions. All parameters are identical in both simulations, except that all r values are doubled in b; Diversity is reduced more rapidly at higher r values.

FIG. 6.—Predicted relationship of diversity and growth rates in nonequilibrium systems with a low to intermediate frequency of population reductions.

tory or depensatory. If all K's and α's are similar, a high variance in r will result in much more rapid competitive displacement than a low variance, since the high r speci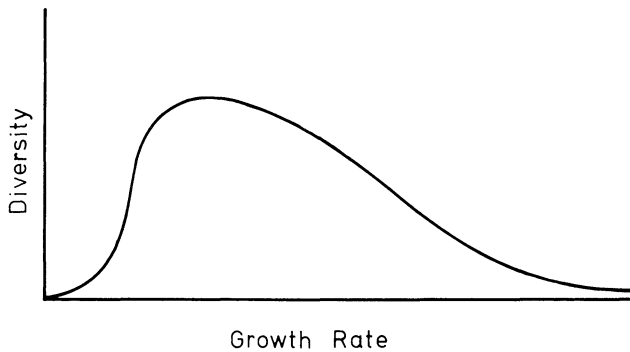es can quickly suppress their slowly growing competitors. Likewise, if all r's are similar, there will be a longer period of coexistence when the variance of K is low than when it is high. It is reasonable to expect that the relative variance (coefficient of variation) of r and K will increase under extreme conditions, e.g., few organisms may be able to survive in the presence of toxic compounds or extremely low nutrient availability; rapidly growing plants show a greater response to fertilization than slowly growing species. This increased variance will tend to reduce diversity both in cases of competitive displacement and lowered diversity due to frequent disturbances.

COMPENSATORY EFFECTS AT LOW GROWTH RATES

Low population growth rates should generally be associated with low densities of individuals. This will be true if both carrying capacity and growth rates are limited by the same resource, such as nutrients or energy. A population may have a low density with a high growth rate if it has a high turnover resulting from predation or some other form of mortality. Low growth rates can only result in high densities over relatively long periods of time under conditions of low mortality.

Low population densities may further increase diversity by increasing the effectiveness of mechanisms which allow coexistence. Low density may reduce the frequency of competitive interactions and change their nature as well. When populations are maintained at low densities by some limiting factor, the intensity of their competitive interactions for other factors should be reduced, since these other factors are nonlimiting. One plant may be a better competitor for space than another, but if both of them occur at such low densities that they do not compete for space, the competitive difference will not be expressed and both will continue to coexist. Also, small environmental differences, both temporal and spatial, that would be insignificant at high population densities, may provide sufficient heterogeneity to avoid competition at low densities. For example, subtle differences in substrate preference may be more effective at separating species at low densities than at high densities, when populations would overflow onto less preferred areas. While some factors, such as the inefficiency of predation at low densities, may act to reduce diversity in some cases, probably the net result of low density would be more likely to augment the effect of mechanisms that maintain diversity than to decrease their effect.

Long periods of time with a low rate of competitive displacement will allow environmental fluctuations to further reduce the rate of displacement by altering competitive interactions. One species may be the best competitor under certain conditions of temperature or precipitation, while under slightly different conditions another species may be better (e.g., Titman 1976). Such reversals of competitive dominance can obviously allow coexistence, as can frequency-dependent competitive differences (Ayala and Campbell 1974; Koch 1974a, 1974b). These factors will only be effective when reversal of competitive dominance occurs prior to competitive

exclusion, which requires low rates of competitive displacement, or population reductions which maintain diversity.

THE DYNAMIC EQUILIBRIUM

Diversity may be maintained by periodic population reductions or a low rate of competitive displacement. The effect of each of these factors is clearly dependent on the other, and they may be expected to interact and reach some sort of dynamic equilibrium, at which point the diversity of a community may remain relatively constant over time. The frequency and intensity of population reduction in a particular community are assumed to have some mean over time; e.g., fires, hurri-canes, treefalls, or spruce budworm outbreaks occur with some predictable frequency over a sufficiently long time period. Likewise, the level of population growth rates of competitors in a community is assumed to remain relatively constant over time, depending on local conditions of energy, nutrients, temperature, etc. An increase in the frequency of population reduction can have an effect similar to a corresponding decrease in the population growth rates, and if both the frequency of reduction and growth rates increase or decrease together, the dynamic balance could remain essentially unchanged. The level of diversity at dynamic equilibrium will vary in its response to changes in growth rates or reduction frequency in different parts of the ranges of these parameters.

Diversity may be reduced either by competitive displacement (and eventually exclusion) or by a high frequency of population reduction which does not allow some competitors to recover between disturbances. Organisms must have some minimum growth rate to recover from population reduction and avoid extinction, and this minimum rate must rise as the frequency of reduction increases. This suggests that at high frequencies of population reduction an increase in growth rates can actually increase diversity, in contrast to the effect at lower frequencies of reduction. The level of diversity at dynamic equilibrium can be represented as a three-dimensional surface determined by the interaction of rate of displacement and frequency (and/or magni-tude) of population reduction (fig. 7).

This graphic representation simply illustrates the changes in diversity which may be expected under different conditions. Under conditions where the growth rates of competitors are low (low rate of competitive displacement, fig. 7, transect A), diversity will be low at very low frequencies of disturbance, since this will allow a time period long enough for a close approach to competitive equilibrium. An increase in the frequency sufficient to prevent competitive equilibrium will allow maximum diversity, and the diversity will then decrease as the frequency rises and some competitors are unable to recover. When the growth rates of all competitors are high (high rate of displacement, fig. 7, transect B), diversity will be low at low frequencies of population reduction due to the rapid approach to competitive equilibrium. Diversity will increase as an increasing frequency of disturbance keeps the community further from equilibrium, and diversity may then drop if the frequency becomes sufficiently high that some populations cannot recover. At a low frequency of population reduction (fig. 7, transect C), diversity will be zero where
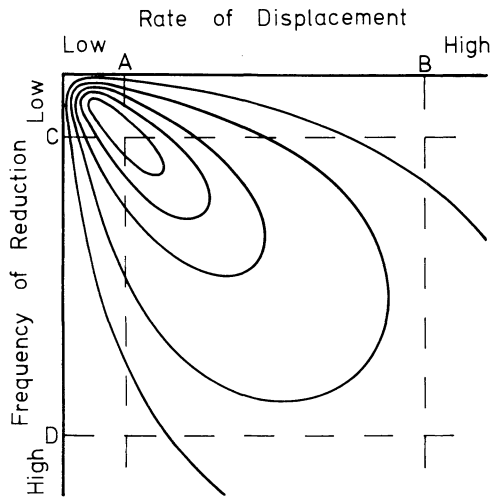
Rate   of   Displacement

FIG. 7.—Generalized contour map of the dynamic equilibria between the rate of competitive displacement and the frequency (or magnitude) of population reduction; diversity is on the axis perpendicular to the page, and is represented by the contour lines, with the highest diversity within the inner ellipsoid (in the upper left corner). The dotted-line transects demonstrate the predicted changes in diversity when one parameter is held constant and the other varied.

growth rates are zero, and low at extremely low growth rates which are not sufficient for recovery and survival of most species. Diversity should increase rapidly with increasing growth rates (the break point) and reach a maximum at low growth rates where the rate of competitive displacement will be low. Further increase in growth rates will increase the rate of competitive displacement, resulting in lower diversity of dynamic equilibria at high growth rates. Finally, at high frequencies of population reduction (fig. 7, transect D), increasing growth rates will allow recovery from disturbances; diversity will increase as growth rates rise, then decrease at sufficiently high growth rates that the system begins to approach competitive equilibrium.

Diversity should be highest at low to intermediate growth rates and frequencies of reduction, since both of these factors allow prolonged coexistence and provide sufficient time for various compensatory factors, such as fluctuating environmental conditions, to be effective. Extinctions should be less likely under conditions where population changes are gradual than when they are rapid and extreme.

The dynamic balance between frequency of reduction and rate of displacement will behave differently in different systems, depending on the relative variability of these two parameters in the type of community being considered and where in the range of each parameter the communities lie. Some types of communities will have a great range in the mean growth rates of competitors between different communities, but only a narrow range of disturbance frequencies. In these cases, variation in growth rates should be most important in determining diversity patterns. In other communities, the frequency of population reduction will vary more and have a greater effect on diversity differences than growth rates. If the communities are characterized by high frequencies of population reduction, increasing growth rates should increase

diversity, whereas if the frequency of reduction is low, the result will be just the opposite.

The growth rates of a single species vary widely in nature, depending on local conditions. Forest conditions can result in a five- or tenfold difference in the vegetative growth rates of rainforest trees (Richards 1952; Schulz 1960), and mussel growth rates vary over five orders of magnitude between southern California and northern Washington (Paine, personal communication). Since the effect of frequency of population reduction is well known (Loucks 1970; Grime 1973; Horn 1975; Connell 1978), the rest of this paper will concentrate on the effect of growth rates.

GENERAL PREDICTIONS

According to the dynamic equilibrium model, a major determinant of diversity in nonequilibrium (referring to competitive equilibrium) situations is the level of population growth rates of competitors. At low to intermediate frequencies of population reduction, low growth rates allow the maintenance of diversity by slowing the approach to competitive equilibrium and enhancing the effect of factors that tend to prevent competitive exclusion.

1. Situations in which competing organisms have high population growth rates will have lower diversity than equivalent situations in which the organisms have low growth rates, unless some species are being eliminated by a high frequency of population reduction. Although it is not always possible to measure population growth rates, any factors which are closely correlated with growth rates should show the same relationship to diversity.

2. Low availability of basic nutrients (as opposed to an extreme deficiency or toxic excess) would be expected to reduce growth rates in communities of organisms requiring these nutrients and result in higher diversity than in a similar situation with high nutrient availability. Increasing the nutrient availability of any environment should tend to reduce diversity, unless diversity is already low due to a nutrient deficiency or a high frequency of population reductions.

3. Since low productivity (biomass/biomass/time) and low density are often the result of low population growth rates, it would be expected that communities with low productivities or densities would have higher diversity than similar communities with high productivity or density.

This approach differs from previous hypotheses in that it provides a simple and intuitive mechanism by which quantitative environmental differences may affect community structure. Diversity is determined not so much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of their interactions. This hypothesis may be applied to diversity variation in terrestrial and aquatic plant and animal communities on a latitudinal gradient as well as a regional level.

RELATIONSHIP TO OTHER HYPOTHESES

Nearly all diversity hypotheses attempt to explain (and derive support from their apparent explanation of) the temperate-tropical increase in diversity. One problem

is that factors such as environmental predictability and stability, productivity, and intensity of competition or predation are difficult to define, measure, and compare in a biologically meaningful way. In addition, these hypotheses may claim credit for changes in diversity which are better ascribed to other causes. For example, productivity may be invoked to explain the fact that grasslands have fewer species of birds than shrublands, which have fewer species than forests, but this change is also correlated with an increase in structural complexity, which has been demonstrated to increase diversity.

The environmental heterogeneity hypothesis is the only diversity hypothesis supported by convincing evidence, with the exception of some cases of predation (Paine 1966; Connell 1975). There are sound reasons to expect that increased heterogeneity should increase diversity (Levin 1974) and habitat structural complexity has been correlated with diversity in birds (MacArthur 1957, 1964, 1965; MacArthur and MacArthur 1961; MacArthur et al. 1966; Cody 1968; Karr 1968; 1975; Recher 1969; Karr and Roth 1971), in chydorid cladocera (Whiteside and Harmsworth 1967), in plankton (Richerson et al. 1970), in marine gastropods (Kohn 1967, 1968), in small mammals (Rozenzweig and Winakur 1966), and in lizards (Pianka 1967). In most of these cases the heterogeneity is based on the physical structure of the plant community serving as the substrate for animals. There is some suggestion that the species diversity of the plants themselves may be important, at least for insects (Murdoch et al. 1972), and there is strong evidence for a coevolutionary relationship between the chemical diversity of plants and insect diversity (Ehrlich and Raven 1964; Feeny 1975).

As successful as environmental heterogeneity seems to be in explaining certain patterns of diversity, it is still an extrinsic factor, imposed on the organisms whose diversity is being examined. The complexity and diversity of plants may explain part of the diversity of animals, but this still leaves us with the problem of plant diversity.

Much of the tropical increase in diversity of birds, mammals, insects, and other organisms may be explained by the increased structural complexity and tree species diversity of tropical forests (Richards 1952). However, the high diversity of tropical trees is apparently not explained by edaphic heterogeneity, which shows little relation to tree distribution in tropical forests (Hewetson 1956; Kwan and Whitmore 1970; Webb et al. 1972). Any heterogeneity or niche partitioning argument is further complicated by the convergence of many characters in tropical trees (Richards 1952). Many diversity gradients in aquatic systems have no apparent relation to structural complexity either (Yount 1956; Williams 1964). Any hypothesis which attempts to explain patterns of diversity must deal with diversity gradients which have no component of structural heterogeneity.

Paine (1966) outlined the basic premise of the predation hypothesis, "local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species." This is clearly related to the dynamic equilibrium hypothesis, since predation has the effect of reducing population sizes and hence preventing equilibrium. Predation per se does not have a predictable effect on diversity. Predation can actually reduce diversity if the predator eats certain prey to the exclusion of all others, or if it eats virtually

everything (Jones 1933; Milton 1940, 1947; Jones and Kain 1967; Kitching and Ebling 1961; Southward 1964; Paine and Vadas 1969; Menge and Sutherland 1976). However, the predator which always selects the most abundant prey will inevitably increase diversity, and most of the numerous examples of predation increasing diversity are probably of this type (Connell 1961, 1970, 1971, 1975; Paine 1966; Harper 1969; Paine and Vadas 1969; Janzen 1970; Dayton and Hessler 1972; Porter 1972; Menge and Sutherland 1976).

The predator need not be selective, however. Any type of density-independent mortality applied to a community will tend to prevent competitive exclusion (Hutchinson 1948) and result in higher diversity. An excellent example of this is given by Milton (1940, 1947) who found that mowing pastures for hay increased or maintained the diversity of grasses and forbs in the face of other influences. Charles Darwin (1859, p. 78) made basically the same observation and Harper (1969) cites numerous examples from Great Britain in which diversity of grasses and herbs was reduced when rabbits were prevented from grazing.

The "intermediate disturbance" hypothesis (Grime 1973; Connell 1978) is related to the predation hypothesis, but both are simply population reductions which prevent competitive equilibrium and as such represent only half of the dynamic equilibrium. There is clearly some frequency of disturbance at which diversity will be greatest, but the intermediate frequency can be anywhere in the entire range of frequencies depending on the rate of competitive displacement (fig. 7). Specifically, the intermediate disturbance frequency for any community will be that frequency at which the community can be maintained as far from competitive equilibrium as possible, while allowing the greatest number of species to recover from the reduction. Neither disturbance and predation alone, nor growth rates alone, determine the level of diversity in a community. Community structure is best understood as a dynamic equilibrium.

The environmental stability, predictability, and productivity hypotheses are closely related, since these parameters increase together from temperate to tropical regions (Connell and Orias 1964; Pielou 1975). Predictability and stability in particular are defined in a variety of ways and are difficult to measure, especially on the evolutionary time scale where they are usually invoked. There has been no demonstration that either of these factors regulates diversity. Slobodkin and Sanders (1969) and Pielou (1975) suggest that unpredictable and severe environments have low diversity, based on the argument that unpredictability forces organisms to have broader niches which allow fewer species to be "packed in," as well as causing a greater chance of extinction for marginal populations. However, they present no evidence that cannot be explained just as easily by other hypotheses, e.g., predation (Menge and Sutherland 1976).

A comment might be made here about harsh or restrictive environments. While there are many situations which can barely support life and show a low diversity, this not a satisfactory explanation for all examples of low diversity. Environmental stress or harshness is difficult to define and evaluate, particularly since the inevitable result of natural selection is to minimize the effect of such stress on an organism. If stress is defined as a high frequency of population reduction or conditions resulting in

extremely low growth rates, low diversity under such conditions is completely compatible with the dynamic equilibrium model, although low diversity can occur under very different conditions.

There are numerous examples of low diversity communities in stable environments, such as the coastal redwoods (Whittaker 1966), tropical cativo (*Prioira copaifera*) forests (Holdridge et al. 1971), and freshwater marshes. In general, these environments have high productivities which suggest rapid population growth rates, and both of the forests exist for long periods of time with little or no disturbance. Under these conditions, the dynamic equilibrium model predicts low diversity, while the productivity, stability, and predictability hypotheses predict high diversity.

Examples also exist of communities with high diversity in environments that seem to be severe, unpredictable, or unstable, such as the Sonoran Desert (Whittaker and Niering 1965), some benthic marine communities (Paine 1966), and diatoms in rivers (Patrick 1963). The sclerophyll shrub communities of southern Africa, Australia, and New Caledonia may have a higher diversity than some rain forests (Richards 1969). All of these environments have low population densities and low productivities, suggesting a low rate of competitive displacement. Nonequilibrium conditions are maintained in the sclerophyll shrub communities by periodic fires, and it is likely that the other communities never reach competitive equilibrium either. These are precisely the conditions in which the dynamic equilibrium hypothesis predicts high diversity but the other hypotheses predict low diversity.

The productivity hypothesis (Connell and Orias 1964) has been generally rejected (Margalef 1969; Pielou 1975) because of the numerous examples of an inverse relationship between productivity and diversity (Swingle 1946; Yount 1956; Williams 1964; Whiteside and Harmsworth 1967; McNaughton 1968). This relationship has been called "the paradox of enrichment" and has been discussed for predator-prey (Rosensweig 1971) and competitive (Riebesell 1974) systems. If the interacting species are not equally affected by enrichment, the system may be destabilized and some of the species reduced or eliminated. This approach has been primarily an equilibrium one and has not considered the effects of rate of displacement. The inverse relationship between diversity and productivity is predicted by the dynamic equilibrium hypothesis, since high productivity generally reflects high population growth rates. Even the apparent correlation of high forest diversity and productivity in the tropics is no longer convincing since Willson (1973) has demonstrated that production per day of growing season is no higher in tropical than in temperate forests.

ADDITIONAL EVIDENCE

Aquatic systems are particularly suitable for examining the basic determinants of diversity, since variations in habitat complexity and environmental fluctuations can be minimized. The diversity of diatoms and algae responds dramatically to changes in water quality, particularly enrichment (increased nutrient availability). Natural "clean" rivers generally have low total population densities with high species diversity (Patrick 1963; Williams 1964). However, when these rivers are enriched by land runoff or pollution, the population densities become very high and diversities

much lower (Patten 1962; Williams 1964). It was found that no particular species invariably predominates in enriched situations, but rather that different species are responsible for the high densities in different situations (Williams 1964). The high density and low diversity are apparently not the result of any species being more "pollution tolerant" than other species, but are merely the result of differences in growth rates under conditions of rapid growth.

Similar patterns are found in marine systems. Open oceans, particularly in the tropics, show a low productivity (Russell-Hunter 1970; Bunt 1975; Crisp 1975) and low density of individuals (Hentschel and Wattenberg 1930), but a high species diversity (Russell-Hunter 1970). Areas of high nutrient availability, such as upwellings, lagoons, and shallow coastal areas tend to have high productivity (Russell 1934; Bunt 1975) with a high density of organisms (Hentschel and Wattenberg 1930; Russell-Hunter 1970) and a low species diversity (Russell 1934; Dakin and Colefax 1940; Russell-Hunter 1970; Sanders 1969).

One striking temperate-tropical gradient is the increase in diversity of marine plankton from temperate to tropical waters. This is the inverse of the well-documented decrease in productivity of tropical oceans (Steemann-Nielson 1954; Harvey 1955). The density of calanoid copepods varies on a regular latitudinal gradient from nearly $3000/m^3$ in the North Bering Sea, to about $100/m^3$ in the open tropical ocean. However, the number of species varies in the opposite manner. The dense northern population is composed of only about 10 species, whereas the diffuse southern population is composed of about 80 species (Brodskji, quoted in Fischer 1960).

Detailed information about marine benthic gastropod diversity is provided by Rex (1973, 1976). Changes in diversity are not only related to depth, but also to the density of individuals, which is believed to closely reflect local productivity (Sanders et al. 1965) and is probably related to growth rates. Numerous studies show a pronounced decrease of density of the total benthic fauna from the continental shelf to the abyssal depths (Sanders et al. 1965; Sanders and Hessler 1969). Gastropod diversity is low on the continental shelf, rises at greater depths (lower density of individuals), and finally drops at extremely low densities on the abyssal plain. This pattern has been explained by instability on the continental shelf decreasing diversity, stability and predation increasing diversity on the slope, and limiting productivity reducing diversity in the abyss (Rex 1976). However, this complex scheme may not be necessary, since the pattern correlates well with the predictions of the dynamic equilibrium model, including the breakpoint at low densities. The earlier conclusions that "the effect of abundance of food is minor and is easily masked by differences in both short- and long-term 'climatic' stability" (Hessler and Sanders 1967), is based on the predictions of the productivity hypothesis, which are opposite to those of dynamic equilibrium.

A final comparative study of diversity in aquatic systems is the work of Yount (1956) at Silver Springs, Florida. Silver Springs was selected because of its unusually constant conditions, and two stations were chosen based on apparent differences in productivity. One station was near the main boil of the spring under conditions of high light intensity, and the other was in a side pool under vegetation which cut out most of the light. Slides were suspended in the water at each station and the density

and composition of the diatom populations observed through time. Productivity was determined using the quantity of chlorophyll produced on slides at each station as a measure of primary productivity, and, as expected, the production of chlorophyll was higher at the central site than in the side pool. Succession took place on the slides in the course of the experiment, illustrating the effect of differences in the rate of competitive displacement. The high productivity station reached an "apparent climax" much more rapidly than did the low productivity station. Densities of individuals were much higher and the species diversity much lower at the high productivity station.

Few appropriate data, which include measures of population growth rates, schedules of age-specific fecundity and mortality, and measures of productivity, nutrient availability, and diversity for each community, are presently available for comparative testing of this model in terrestrial systems. Patterns consistent with this hypothesis might be expected to appear in life history strategies, since these strategies reflect constraints imposed by the environment on organisms both on a phenotypic and a genetic level (Wilbur et al. 1974). Organisms in high diversity communities would be expected to have life histories reflecting lower population growth than similar organisms in low diversity communities. An apparent example of this is given by MacArthur (1972). Small birds in temperate areas generally lay four to five eggs per clutch, while small tropical birds average two eggs per clutch. The apparent correlation of this with the burst of high food abundance in the temperate spring, a phenomenon not found in the tropics, is strengthened by the fact that birds dependent on outbreaks of superabundant food have even larger clutches. As might be expected from these differences, diversity among these birds is higher in the tropics.

An example of the effect of nutrient availability on the composition of terrestrial plant communities is found in the work of Milton (1940, 1947). In a series of experiments lasting 16 yr, the effects of varying types of fertilizer applications and different schedules and intensities of grazing and mowing were observed on the yield and botanical composition of pastures in central Wales. The important result here is that application of fertilizer increased the rate at which changes in botanical composition occurred and resulted in a decrease in the number of species present, with the eventual dominance of one or two species of grass. It is significant that the original diversity was maintained for a long period when the fertilized fields were periodically mowed for hay, which suggests that the dynamic equilibrium level of diversity remained essentially unchanged when both growth rates and the frequency of population reduction were increased.

Similar results have been obtained in many other experiments involving fertilization of terrestrial plants (Lawes et al. 1882; Davies and Jones 1932; Murphy 1960; Willis 1963; Thurston 1969; Jeffrey 1971; Stephenson 1973; Bazzaz and Harper 1976).

The dynamic equilibrium model may explain at least part of the temperate-tropical increase in tree diversity, since reduced soil nutrients and increased rates of respiration may result in lower population growth rates in the tropics. This hypothesis is potentially applicable to the increase in diversity found in successions where nutrient availability is decreased or growth rates are reduced through the course of succession.

This model also has significant evolutionary implications, since the survival and accumulation of new varieties or species should be favored in situations where the rates of increase of all competitors are low and competitive equilibrium is prevented. Under such conditions, speciation may require only simple reproductive isolating mechanisms, and extensive niche differentiation may not be necessary for survival.

SUMMARY

A new hypothesis, based on differences in the rates at which populations of competing species approach competitive equilibrium (reduction or exclusion of some species), is proposed to explain patterns of species diversity. The hypothesis assumes that most communities exist in a state of nonequilibrium where competitive equilibrium is prevented by periodic population reductions and environmental fluctuations. When competitive equilibrium is prevented, a dynamic balance may be established between the rate of competitive displacement and the frequency of population reduction, which results in a stable level of diversity. Under conditions of infrequent reductions, an increase in the population growth rates of competitors generally results in decreased diversity. This model clarifies an underlying pattern of variation in diversity and points out the common elements of previous hypotheses. Rather than arguing that either competition, predation, or productivity control diversity, it demonstrates that all of these may contribute to the same basic mechanism. In doing so, it not only explains the correlations of the other hypotheses with patterns of diversity, but also explains the exceptions that these hypotheses could not explain. This hypothesis may be applied to variations of diversity both on a latitudinal gradient and within specific regions.

ACKNOWLEDGMENTS

LITERATURE CITED

Armstrong, R. A., and R. McGehee. 1976a. Coexistence of species competing for shared resources. Theor. Popul. Biol. 9:317–328.

———. 1976b. Coexistence of two competitors on one resource. J. Theor. Biol. 56:499–502.

Auclair, A. N., and F. G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. Am. Nat. 105:499–528.

Ayala, F. J. 1969. Experimental invalidation of the principle of competitive exclusion. Nature 224:1076–1079.

———. 1971. Competition between species: frequency dependence. Science 171:820–824.

Ayala, F. J., and C. A. Campbell. 1974. Frequency dependent selection. Annu. Rev. Ecol. Syst. 5:115–138.

Bazzaz, F. A., and J. L. Harper. 1976. Relationship between plant weight and numbers in mixed populations of Sinapsis alba (L.) Rabenh. and Lepidium sativum L. J. Appl. Ecol. 13:211–216.

Bunt, J. S. 1975. Primary productivity of marine ecosystems. Pages 169–183 in H. Leith and R. H. Whittaker, eds. Primary productivity of the biosphere. Springer-Verlag, New York.

Cody, M. L. 1968. On methods of resource division in grassland bird communities. Am. Nat. 102:107–147.
Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the
         barnacle *Chthamalus stellatus*. Ecology 42:710–723.
———. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several
         predatory species of *Thais*. Ecol. Monogr. 40:49–78.
———. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals
         and in rainforest trees. Pages 298–312 *in* P. J. Den Boer and G. R. Gradwell, eds. Dynamics of
         populations. Proceedings of the Advanced Study Institute on dynamics of numbers in popula-
         tions, Oosterbeck, September 7–18, 1970. Centre for Agricultural Publishing and Documenta-
         tion, Wageningen.
———. 1975. Producing structure in natural communities. Pages 460–491 *in* M. L. Cody and J. M.
         Diamond, eds. Ecology and evolution of communities. Belknap, Cambridge, Mass.
———. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302–1310.
Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. Am. Nat. 98:399–441.
Crisp, D. J. 1975. Secondary productivity in the sea. Pages 71–89 *in* Productivity of world ecosystems.
         National Academy of Science, Washington, D.C.
Crombie, A. C. 1947. Interspecific competition. J. Anim. Ecol. 16:44–73.
Dakin, W. J., and A. N. Colefax. 1940. The plankton of the Australian coastal waters off New South Wales.
         Univ. Sidney Dep. Zool. Publ. Monogr. 1:1–215.
Darwin, C. 1859. The origin of the species. 1972 Mentor ed. New American Library, New York.
Davies, W., and T. E. Jones. 1932. The yield and response to manures of contrasting pasture types. Welsh
         J. Agric. 8:170–192.
Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and sub-
         sequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351–389.
Dayton, P. K., and R. R. Hessler. 1972. The role of biological disturbance in maintaining diversity in the
         deep sea. Deep-Sea Res. 19:199–208.
Dobzhansky, Th. 1950. Evolution in the tropics. Am. Sci. 38:209–221.
Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution
         18:586–608.
Feeny, P. 1975. Biochemical coevolution between plants and their insect herbivores. Pages 3–19 *in* L. E.
         Gilbert and P. H. Raven, eds. Coevolution in animals and plants. University of Texas Press,
         Austin.
Fischer, A. G. 1960. Latitudinal variation in organic diversity. Evolution 14:64–81.
Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, N.J.
Gause, G. F. 1934. The struggle for existence. Williams & Wilkins, Baltimore.
Gilpin, M. E., and K. E. Justice. 1972. Reinterpretation of the invalidation of the principle of competitive
         exclusion. Nature 236:273–274, 299–301.
Grime, J. P. 1973. Control of species density in herbaceous vegetation. J. Environ. Manage. 1:151–167.
Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the
         regeneration niche. Biol. Rev. 52:107–145.
Hack, J. T., and J. C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the
         central Appalachians. U.S. Geol. Surv. Prof. Pap. 347.
Harper, J. L. 1969. The role of predation in vegetational diversity. Brookhaven Symp. Biol. 22:48–62.
Harvey, H. W. 1955. The chemistry and fertility of sea-waters. Cambridge University Press, Cambridge.
Hebert, P. D. N. 1974a. Enzyme variability in natural populations of *Daphnia magna*. II. Genotypic
         frequencies in permanent populations. Genetics. 77:323–334.
———. 1974b. Enzyme variability in natural populations of *Daphnia magna*. III. Genotypic frequencies in
         intermittent populations. Genetics 77:335–341.
Hentschel, E., and H. Wattenberg. 1930. Plankton und Phosphat in der Oberflächenschicht des Südatlan-
         tischen Ozeans. Ann. Hydrogr. Marit. Meteorol. 58:273–310.
Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep-sea. Deep-Sea Res. 14:65–78.
Hewetson, C. E. 1956. A discussion on the climax concept in relation to the tropical rain and deciduous
         forest. Emp. For. Rev. 35:274–291.
Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi. 1971. Forest environments in
         tropical life zones: a pilot study. Pergamon, New York.

Horn, H. S. 1975. Markovian properties of forest succession. Pages 196–211 *in* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities, Belknap, Cambridge, Mass.

Hurlbert, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52:577–586.

Hutchinson, G. E. 1948. Circular causal systems in ecology. Ann. N.Y. Acad. Sci. 50:221–246.

———. 1961. The paradox of the plankton. Am. Nat. 95:137–145.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104:501–528.

Jeffrey, D. W. 1971. The experimental alteration of a Kobresia-rich sward in Upper Teesdale. Pages 79–89 *in* E. Duffy and A. S. Watt, eds. The scientific management of animal and plant communities for conservation. Blackwell, London.

Jones, M. G. 1933. Grassland management and its influence on the sward. Emp. J. Exp. Agric. 1:43–57.

Jones, N. S., and J. M. Kain. 1967. Subtidal algal colonization following removal of *Echinus*. Helgol. Wiss. Meeresunters. 15:460–466.

Karr, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70:348–357.

———. 1975. Production, energy pathways, and community diversity in forest birds. Pages 161–176 *in* F. Golley and E. Medina, eds. Ecological studies. Vol. 11. Springer-Verlag, New York.

Karr, J. B., and R. R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. Am. Nat. 105:423–435.

Kitching, J. A., and F. J. Ebling. 1961. The ecology of Lough Ine. XI: The control of algae by *Paracentrolus lividus* (Echinoidea). J. Anim. Ecol. 30:373–383.

Koch, A. L. 1974*a*. Coexistence resulting from an alteration of density dependent and density independent growth. J. Theor. Biol. 44:373–386.

———. 1974*b*. Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. J. Theor. Biol. 44:387–395.

Kohn, A. J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. Am. Nat. 101:251–260.

———. 1968. Microhabitats, abundance, and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology 49:1046–1062.

Krebs, C. J. 1971. Genetic and behavioral studies on fluctuating vole populations. Pages 243–256 *in* P. J. Den Boer and G. R. Gradwell, eds. Dynamics of populations. Proceedings of the Advanced Study Institute on dynamics of numbers in populations, Oosterbeck, September 7–18, 1970. Centre for Agricultural Publishing and Documentation, Wageningen.

Kwan, W. Y., and T. C. Whitmore. 1970. On the influence of soil properties on species distribution in a Malayan lowland Dipterocarp rain forest. Malay. For. 33:42–54.

Lawes, J. B., J. H. Gilbert, and M. T. Masters. 1882. Agricultural, botanical, and chemical results of experiments on the mixed herbage of permanent grassland, conducted for more than twenty years in succession on the same land. II. The botanical results. R. Soc. Lond. Philos. Trans. 173:1181–1413.

Levin, S. A. 1974. Dispersion and population interactions. Am. Nat. 108:207–228.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. Am. Zool. 10:17–25.

MacArthur, R. H. 1957. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

———. 1964. Environmental factors affecting bird diversity. Am. Nat. 98:387–397.

———. 1965. Patterns of species diversity. Biol. Rev. 40:510–533.

———. 1969. Patterns of communities in the tropics. Pages 19–30 *in* R. H. Lowe-McConnell, ed. Speciation in tropical environments. Academic Press, New York.

———. 1972. Geographical ecology: patterns in the distribution of species. Harper & Row, New York.

MacArthur, R. H., and J. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

MacArthur, R. H., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Am. Nat. 100:319–322.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

McGehee, R., and R. A. Armstrong. 1977. Some mathematical problems concerning the ecological principle of competitive exclusion. J. Differential Equations 23:30–52.

McNaughton, S. J. 1968. Structure and function in California grasslands. Ecology 49:962–972.

Margalef, R. 1969. Diversity and stability: a practical proposal and a model of interdependence. Brookhaven Symp. Biol. 22:25–37.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110:351–369.

Miller, R. S. 1967. Pattern and process in competition. Adv. Ecol. Res. 4:1–74.

———. 1969. Competition and species diversity. Brookhaven Symp. Biol. 22:63–70.

Milton, W. E. J. 1940. The effect of manuring, grazing and cutting on the yield, botanical, and chemical composition of natural hill pastures. J. Ecol. 28:326–356.

———. 1947. The yield, botanical, and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. I. Yield and Botanical. J. Ecol. 35:65–89.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53:819–829.

Murphy, W. E. 1960. Ecological changes induced in moorland pastures by different fertilizer treatments. Proc. Int. Grassl. Congr. 8:86–89.

Opler, P. A., H. G. Baker, and G. W. Frankie. 1977. Recovery of tropical lowland forest ecosystems. Pages 379–421 in J. Cairns, K. L. Dickson, and E. E. Herricks, eds. Recovery and restoration of damaged ecosystems. University Press of Virginia, Charlottesville.

Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65–75.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. Oceanogr. 14:710–719.

Patrick, R. 1963. The structure of diatom communities under varying ecological conditions. Ann. N.Y. Acad. Sci. 108:359–365.

Patten, B. D. 1962. Species diversity of net phytoplankton of Raritan Bay. J. Mar. Sci. 20:57–75.

Peet, R. K. 1974. The measurement of species diversity. Annu. Rev. Ecol. Syst. 5:285–308.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100:33–46.

———. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333–351.

———. 1974. Evolutionary ecology. Harper & Row, New York.

Pielou, E. C. 1974. Population and community ecology. Gordon & Breach, New York.

———. 1975. Ecological diversity. Wiley, New York.

Porter, J. 1972. Predation by Acanthaster and its effect on coral species diversity. Am. Nat. 106:487–492.

Recher, H. 1969. Bird species diversity and habitat diversity in Australia and North America. Am. Nat. 103:75–80.

Rex, M. A. 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. Science 181:1051–1053.

———. 1976. Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. Deep-Sea Res. 23:975–987.

Richards, P. W. 1952. The tropical rain forest. Cambridge University Press, Cambridge.

———. 1969. Speciation in the tropical rainforest and the concept of the niche. Pages 149–153 in R. H. Lowe-McConnell, ed. Speciation in tropical environments. Academic Press, New York.

Richerson, P., R. Armstrong, and C. R. Goldman. 1970. Contemporaneous disequilibrium, a new hypothesis to explain the "paradox of the plankton." Proc. Nat. Acad. Sci. 67:1710–1714.

Ricklefs, R. E. 1973. Ecology. Chiron, Newton, Mass.

Riebesell, J. F. 1974. Paradox of enrichment in competitive systems. Ecology 55:183–187.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387.

Rosenzweig, M. L., and J. Winakur. 1966. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50:558–572.

Russell, F. S. 1934. The zooplankton. III. A comparison of the abundance of zooplankton in the Barrier Reef Lagoon with that of some regions in Northern European waters. Great Barrier Reef Expedition Sci. Rep. 2:176–201.

Russell-Hunter, W. D. 1970. Aquatic productivity. Macmillan, New York.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337–359.

Sanders, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. Brookhaven Symp. Biol. 22:71–81.

Sanders, H. L., and R. R. Hessler. 1969. Ecology of the deep sea benthos. Science 163:1419–1424.

Sanders, H. L., R. R. Hessler, and G. R. Hampson. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. Deep-Sea Res. 12:845–867.

Schulz, J. P. 1960. Ecological studies on rain forest in northern Surinam. Verh. K. Ned. Akad. Wet. Afd. Natuurkd. Tweede Reeks. 53:1–367.

Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22:82–93.

Soulé, M., and B. R. Stewart. 1970. The "niche-variation" hypothesis: a test and alternatives. Am. Nat. 104:85–97.

Southward, A. J. 1964. Limpet grazing and the control of vegetation on rocky shores. Pages 265–273 in D. J. Crisp, ed. Grazing in terrestrial and marine environments. Blackwell, Oxford.

Steemann-Nielsen, E. 1954. On organic production in the oceans. J. Int. Counc. Stud. Sea 19:309–328.

Stephenson, S. N. 1973. Fertilization responses in six southern Michigan oldfield communities. Bull. Ecol. Soc. Am. 54:33. (Abstr.)

Strobeck, C. 1973. N species competition. Ecology 54:650–654.

Swingle, H. S. 1946. Experiments with combinations of largemouth black bass, bluegills and minnows in ponds. Trans. Am. Fish. Soc. 76:46–62.

Thurston, J. M. 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the yield of hay. Pages 3–10 in I. H. Rorison, ed. Ecological aspects of the mineral nutrition of plants. Blackwell, Oxford.

Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192:463–465.

Vandermeer, J. H. 1970. The community matrix and the number of species in a community. Am. Nat. 104:73–83.

———. 1975. Interspecific competition: a new approach to classical theory. Science 188:253–255.

Webb, L. J., J. G. Tracy, and W. T. Williams. 1972. Regeneration and pattern in the subtropical rain forest. J. Ecol. 60:675–695.

Whiteside, M. C., and R. V. Harmsworth. 1967. Species diversity in Chydorid (Cladocera) communities. Ecology 48:664–667.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103–121.

Whittaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains. II. A gradient analysis of the south slope. Ecology 46:429–452.

Wiens, J. A. 1977. On competition and variable environments. Am. Sci. 65:592–597.

Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Nat. 108:805–817.

Williams, L. G. 1964. Possible relationships between plankton-diatom species numbers and water-quality estimates. Ecology 45:809–823.

Willis, A. J. 1963. Braunton Burrows: the effect on the vegetation of the addition of mineral nutrients to the dune soils. J. Ecol. 51:353–374.

Willson, M. F. 1973. Tropical plant production and animal species diversity. Trop. Ecol. 14:62–65.

Yount, J. L. 1956. Factors that control species numbers in Silver Springs, Florida. Limnol. Oceanogr. 1:286–295.