Patterns of species diversity: fact or artifact?

Richard W. Osman and Robert B. Whitlatch

Abstract.—The pattern observed in nature has often served as a compelling motivation for seeking the underlying processes which are assumed to control the pattern. Spatial and temporal patterns of species diversity are the most commonly observed and described from the study of recent and paleocommunities. These patterns include those found within a local or discrete region such as succession and changes along an environmental gradient and inter-regional or global patterns such as latitudinal diversity gradients and comparisons of the deep-sea and the continental shelf faunas. Many hypotheses have been advanced to explain these patterns in terms of differences in the biology of species adapted to different or changing environments. However, a more simple explanation is possible: that these patterns do not result from any specific biologic processes.

We examine this possibility and show that succession can result from probabilistic immigration and local extinction of species, diversity gradients can result from probabilistic disturbance in naturally patchy environments, and that latitudinal gradients can be simply a function of the shape of the earth. As long as such diversity patterns can be explained independent of any specific biologic processes, they offer no test of the importance of these processes, either ecologically or evolutionarily.

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Introduction

A key characteristic of multi-species assemblages of organisms is diversity. Both spatial and temporal patterns of species diversity are easily recognized and these patterns can often be correlated with changes in the physical or biological environment. Such correlations (and often their similarity to one another) have fueled the search for a general process or set of processes whose variability with environmental differences could explain the observed patterns.

In general, diversity has been suggested to vary with one or more "environmental" variables (e.g., temperature, moisture, change in temperature, resource abundance, stability, predictability, time of existence of the environment). Some processes (e.g., competition, predation, reproductive rate) usually are suggested or hypothesized to either vary in intensity with the changing environment or produce differences in second order processes (e.g., speciation rate, degree of specialization, niche breadth, niche overlap, community structure) in different environments. These processes are then proposed to control directly or indirectly the observed diversity patterns.

The question which we address is whether the observed patterns of diversity can result regardless of the processes. We hope to demonstrate that a broad array of diversity patterns can be generated without incorporating spatial or temporal differences in specialization, resource utilization, environmental predictability, niche characteristics, competition, predation, etc. Our objective will be to demonstrate that these processes may be superfluous to many patterns and that the patterns do not justify the existence of the processes. We will examine accepted generalized patterns rather than any specific pattern. These include both local patterns in the realm of ecologic time (i.e., succession and variability along environmental gradients) and global patterns in the realm of evolutionary time

(i.e., latitudinal gradients, and deep-sea-to-shelf comparisons). While the examples we utilize are primarily marine (resulting from our interests) we feel that our discussions can easily encompass diversity patterns in other ecological systems (e.g., recent work of Glenn-Lewin 1977; Whittaker 1972; Grime 1973, Loucks 1970). We will not introduce any new theoretical-mathematical constructions but rather will use a representative dynamic equilibrium equation and the simple logic of such formulations.

Terminology

Diversity.—The simplest measure of diversity, and the one which we will use is number of species. In order to avoid confusion when considering both local and global patterns of diversity it is necessary to recognize at least two types or components of diversity (we will avoid the complications of between habitat differences or β-diversity). The first component is local (or α) diversity, S. It is the number of species found in some discrete unit of habitat (i.e., island, rock, log, sand grain, or any other more or less homogeneous patch of environment). The second or regional component (γ-diversity) can be called species richness, R. It is the number of species available which could potentially immigrate onto or into a unit of habitat. In the MacArthur-Wilson (1967) model, R is equal to the species pool and is usually assumed external to the unit under study. However, if a region is sufficiently distinct, it is the cumulative number of species found on all units composing the region.

Patches and patchiness.—In terms of an individual or population, a patch is that unit of habitat in which the great majority of its interactions with its environment (both biotic and abiotic) take place. It can generally be thought of as some circumscribed area or volume and many populations of many species can share the same patch. The size of a patch will depend on the taxa being considered (i.e., diatom communities may flourish on individual sand grains, elephants obviously cannot). Patches may be and often are continuous. They are, therefore, most easily recognized in discrete habitats (individual rocks or cobbles on a beach) and for certain taxa (particularly sessile organisms). However, all environments are patchy and we assume they can be divided into subunits with a given number of species per patch.

Equilibria: immigration and extinction.—Species equilibrium models (MacArthur and Wilson 1963, 1967; Terborgh 1973; Simberloff 1974) are the simplest formulations for representing the dynamics of multispecies assemblages. The number of species in a patch (S) is simply the sum of the species gained (immigration) minus the species lost (extinction). With R species in a region capable of colonizing the patch, the number of species immigrating must decrease as the number of species in the patch increases (species already present in the patch cannot be "gained" and the number immigrating must decrease to 0 when R species are present). With each individual and thus each species in the patch having some probability of extinction (loss), as more species are added the cumulative probability of any one species being lost should increase. As species are accumulated, immigration decreases and extinction increases and at some $\hat{S}$ (defining the equilibrium number of species) they will balance one another. If S is less than $\hat{S}$, immigration will be greater (more gains than losses) and if S is greater than $\hat{S}$, extinction will be greater (more losses than gains) and S should tend towards $\hat{S}$ from both directions.

Although a patch at times might be represented as having an equilibrium number $\hat{S}$, it is important to remember that this equilibrium is only in terms of number of species. Nothing is inferred about population sizes, species composition, etc. The dynamics of gains and losses (measured in species, not individuals) still continue. Neither is it necessary to treat $\hat{S}$ or R as constants. In fact, our objective is to examine under what conditions and in what ways these may be expected to vary.

Disturbance.—Disturbance is a mechanism or category of mechanisms which controls the age of a patch. In terms of the biota of a patch, a disturbance may be defined as an unpredictable event (to the organisms) that results in total or partial extinction in that patch. A disturbance agent will have two components, frequency and magnitude. Both of these affect the probability of a patch having been disturbed in some arbitrary period of time. A high magnitude disturbance agent

can be characterized as one affecting many patches. A high frequency disturbance agent would be one which occurred many times during the time period considered. As either frequency or magnitude increase the probability of a particular patch having been disturbed will increase. For simplicity, we will generally consider the variability in only one of these components, frequency.

Although disturbances can be physical or biological, the frequency or magnitude of a biological disturbance may have some dependency on the species composition or abundance within a patch. A predator might possibly consume organisms in different patches at random, but it is more likely that it will be affected by the abundances within the patch or its population size will be regulated by the abundance of prey. Since additional assumptions would be required for biological disturbances (e.g., see Levin and Paine 1974, 1975), we will assume that disturbance agents are physical and their frequency and magnitude independent of the patches.

Assumptions

In attempting to examine common diversity patterns we will make the following assumptions:

1. Environments are patchy. Patches may form an integrating pattern, but for simplicity, we will assume that all patches are identical in size, resource availability, etc.

2. The frequency of disturbance controls the age of patches. Each patch, independent of its present age, has an equal probability of being disturbed, and if disturbed, we assume that all species are eliminated.

3. The number of species in a region, R, is the sum for all patches.

4. The number of species in patch$_x$ is S_x and with sufficient time will approach $\hat{S}$.

Formulation

Immigration/extinction models provide a simple, convenient, and we believe, logical way to relate the two components of diversity, S and R. Our choice of a specific formulation is somewhat arbitrary, but we feel that Terborgh's (1973) merger-inflow model is qualitatively representative.

After some small interval of time, the number of species in a patch, S can be expressed as:

$$S_{x+1} = S_x + \int_x^{x+1} (dS/dt)\, dt.$$

The change in species number (dS/dt) is simply equal to the rate of gain minus the rate of loss or the immigration rate with S species present (I_S) minus the extinction rate with S species present (E_S). With R species available, the proportion which could potentially immigrate is $(R-S)/R$. Thus, the number immigrating will be $I_S = m(R-S)/R$, where m is the basal immigration rate or the number of species gained per unit time with 0 species present in the patch. Although many factors may be expected to affect m (size of the patch, the distance from a source of immigrants), it is chiefly influenced by the taxa being considered (for a given patch size m would be expected to be much higher for protozoans than for large mammals). Extinction can be expressed as some function of the species present. The simplest form would be to set $E_S = eS$, where e is the specific extinction rate. Terborgh (1973) argued that $E_S = eS^2$ since the number of possible species interactions would increase as the square of S. Because the use of eS or eS^2 will not affect the qualitative results, we will generally use the formulation of Terborgh:

$$dS/dt = m(R - S)/R - eS^2. \qquad (1)$$

However, we will examine the relationship between this equation and the simpler

$$dS/dt = m(R - S)/R - eS \qquad (2)$$

in describing succession.

Local Patterns in Ecologic Time

For local (within a region) patterns over relatively short ecologic time (days, months, years) we can make the restriction that R is constant. This merely recognizes that contributions from other regions will be sufficiently rare and the dynamics within the region will dominate. If we consider a single patch, after some period of time decreasing immigration and increasing extinction will balance ($I_S = E_S$) and by definition, $dS/dt = 0$.

As Terborgh (1973) has shown, equation (1) can be solved for the number of species present when this equilibrium is reached:

$$\hat{S}_1 = R/[1 + (e/m)R\hat{S}]$$

$$= [-m/R \pm (m^2/R^2 + 4em)^{0.5}]/2e . \quad (3)$$

Similarly, equation (2) can also be solved to yield:

$$\hat{S}_2 = R/[1 + (e/m)R]. \quad (4)$$

Since we have made the very restrictive assumption that all patches within the region are identical, each patch would be expected to approach the same $\hat{S}$.

We will now examine the implications of these equations (1–4) to recognized but perhaps overgeneralized, patterns of species diversity. Specifically, these are succession (a representative of temporal pattern) and environmental gradients (a representative of spatial pattern).

Succession.—Succession has been one of the most studied community phenomena, and most temporal changes in community composition or diversity have been labelled as successional. Most studies define succession in terms of changing species composition and concurrently examine diversity patterns. Hypotheses attempting to account for compositional patterns have ranged from the highly deterministic, "one species prepares the way for the next" type (Clements 1916) to the more probabilistic Markovian models of Horn (1975, 1976). Although some general compositional trends appear to exist (Horn 1974), many problems of exact interpretation remain (see Connell and Slatyer 1977 for a discussion of some of these).

If only changes in diversity are considered, patterns are more easily generalized. Starting with some virgin piece of habitat, the common pattern is for diversity to increase with time (usually at a decreasing rate) and then in some "late stage" to decrease somewhat. This late stage is often labelled "climax", giving it an unjustified, non-dynamic stable quality. However, the pattern has been demonstrated or inferred for a wide variety of associations; forests (Auclair and Goff 1971; Horn 1974), coral reefs (Loya 1976), and epifaunal invertebrates (Osman 1977).

In terms of equations (1–4), we can initially view succession as an exclusively within-patch process. Also, because we are only interested in the diversity patterns, we will examine only changes in S. Since we have made

the restrictive assumption that all patches within a region are identical, the trends in S in all patches should be the same (however, species composition may be very different from patch to patch). We will later examine a simple mechanism producing between patch or spatial variability in S.

Starting with a virgin patch (S = 0), both equations (1) and (3) or (2) and (4) would predict an initial rapid increase in S with S eventually approaching $\hat{S}$ at a decreasing rate. However, the increased extinction in (1) because of the inclusion of potential interactions (S^2 term) will cause $\hat{S}_1$ to be less than $\hat{S}_2$. These two values are identical to Wilson's (1969) interactive ($\hat{S}_i$) and non-interactive ($\hat{S}_n$) equilibria ($\hat{S}_1 = \hat{S}_i$; $\hat{S}_2 = \hat{S}_n$). We would expect that in colonization (or succession) there would be some initial period of time when population sizes are low and available area in the patch high such that the probability of interaction would be low. During this phase, S might be expected to approach $\hat{S}_n$. Later, as interactions become more probable, S would approach $\hat{S}_i$. If colonization proceeds more quickly than increases in population size, it is very likely that S will exceed $\hat{S}_i$ (perhaps even equilibrating at $\hat{S}_n$) and then decrease to $\hat{S}_i$. As seen in Fig. 1, the basic successional pattern of an increase in S followed by a later decrease results. Figure 1 also depicts the changes in $\hat{S}$ over longer time periods hypothesized by Wilson (1969). He suggested that with increased time species will "sort out" into stable combinations producing an assortative equilibrium ($\hat{S}_a$) higher than $\hat{S}_i$ and over evolutionary time an even higher evolutionary equilibrium ($\hat{S}_e$) would be attained. Although this idea conforms with the conventional wisdom that with sufficient time biologic processes operate to maximize diversity, no data exist to confirm these ideas (Goodman 1975). We have indicated (Fig. 1) the opposite trend which, without any strong data, is equally as probable.

Even though we have tried to examine only the general diversity pattern, it is interesting to note that specific species compositional patterns are still possible within this general successional pattern. If the taxa being considered present a broad range in the probability of colonizing (wide differences in reproductive rate, dispersal capabilities, or by chance with a large R), immigration may be exponential
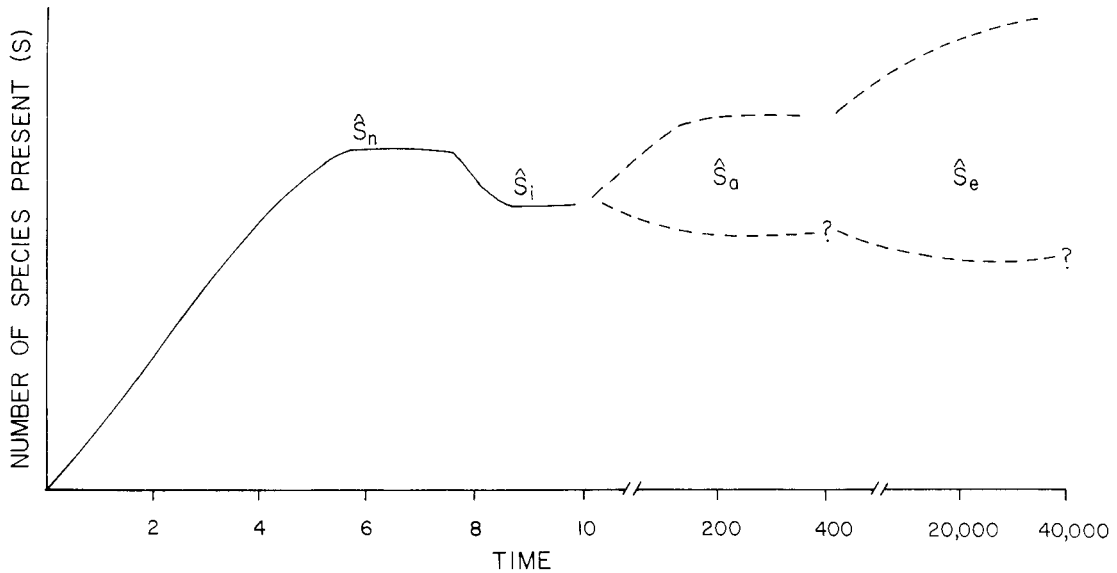
FIGURE 1. The possible temporal or successional changes in diversity (number of species) predicted from a simple equilibrium model. The number of species increase during initial colonization to $\hat{S}_n$ or a non-interactive equilibrium. With increasing species interactions, the number of species decline to $\hat{S}_i$ or an interactive equilibrium. This sequence represents the diversity pattern commonly observed during succession. The long-term increases to assortative ($\hat{S}_a$) and evolutionary ($\hat{S}_e$) equilibria represent the often hypothesized (but unproven) additional increases in diversity. The equally possible decreases in diversity are also shown. Figure modified after Wilson (1969).

rather than linear (as in (1) and (2)) and species would be expected to accumulate in a patch in a specific order (MacArthur and Wilson 1967). Likewise with hierarchical competition or no competition but a wide range in longevity, patches might be expected to converge in terms of species composition. Such differences will separate specific successional patterns, but the overall general pattern in S will remain.

Environmental gradients.—Succession as we have described it allows patches to differ in their species composition, but with time we might expect all patches to have roughly the same number of species. This is generally not the case for most regions. A region is much more likely to be a mosaic of patches having differences in both composition and diversity. Disturbance, as we have defined it, is a simple mechanism which allows patches within a region to vary in S. Given a disturbance agent operating at some frequency, let each patch (independent of its S) have an equal probability of being disturbed. Once disturbed, a patch will have 0 species, but with immigration, it will again begin to accumu-

late species following the successional sequence described above. Disturbance is an additional extinction process controlling the age of a patch or its time since last disturbed, and age will determine how far succession has proceeded. At any frequency (or magnitude) of disturbance, there will be a probability distribution of patch ages. Some patches will be young or recently disturbed and, therefore, will have a low S. Others will be old, having remained undisturbed long enough to have reached $\hat{S}_i = \hat{S}_1$. Last, there will be some patches of intermediate age, old enough to have reached $\hat{S}_n = \hat{S}_2$, but still too young to have declined to $\hat{S}_i$. Thus, a region will be a mosaic of patches of different ages, with the frequency of disturbance determining which age classes will predominate.

The existence of an environmental gradient only recognizes that disturbance may vary predictably within a region. For example, in a nearshore marine area, the probability of a rock being overturned by waves would be expected to decrease with increased depth or rock size (Osman 1977), or for terrestrial areas, the probability of a patch being flooded
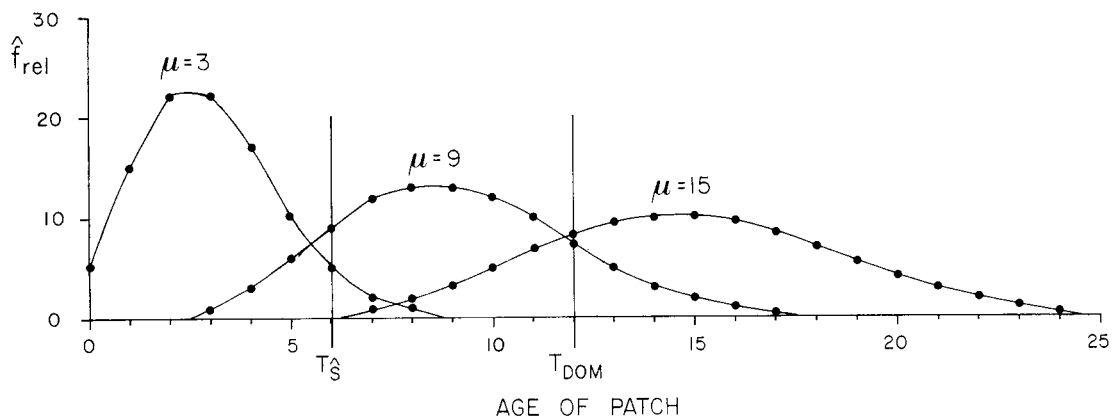
FIGURE 2. Hypothetical age-frequency distributions for three sets of patches resulting from disturbance. Each set has a different average age (μ), and at a high rate of disturbance most patches are relatively young ($\mu = 3$), while at a low rate of disturbance most patches are relatively old ($\mu = 15$). Superimposed is the typical successional sequence. After time $T_\hat{S}$, the average patch reaches $\hat{S}_n$ and after time T_{DOM}, it declines to $\hat{S}_i$. Only when disturbance and age are intermediate ($\mu = 9$) do most patches fall between the ages $T_\hat{S}$ and T_{DOM} and, thus, have the highest average diversity.

would decrease away from a river or the probability of a patch being frozen may increase away from coastal areas or with increasing altitude.

Figure 2 demonstrates the effect of such gradients on S. Shown are three hypothetical frequency (probability) distributions for patches with average ages of 3, 9, and 15 arbitrary time units. Average age will decrease with the frequency of disturbance. Superimposed on these is a probable successional sequence. After a period of time, $T_\hat{S}$, any patch would be expected to approach $\hat{S}_n$ and after a longer period of time, T_{DOM}, it would approach $\hat{S}_i$. (In terms of species-abundance relationships, dominance of one or a few species is often, though not necessarily, a characteristic of late successional stages. To avoid the confusion of subscripts on subscripts, we have chosen to label this time period T_{DOM}.)

In areas with high disturbance ($\mu = 3$), the majority of patches (approximately 92% in this example) would be expected to be younger than $T_\hat{S}$. These will be in some initial stage of colonization and have a low $S < \hat{S}_n$. At the opposite end of the gradient, in areas with low disturbance ($\mu = 15$) approximately 75% of the patches would be older than T_{DOM} with $S = \hat{S}_i$. Last, in the intermediate area ($\mu = 9$) diversity will be greatest. Approximately 65% of the patches will be between $T_\hat{S}$ and T_{DOM} in age, and these would be expected to have $\hat{S}_n \geqslant S > \hat{S}_i$. Although each area would

itself be a mosaic of patches of different ages and S's, the observed trend along a gradient from high to low disturbance would be expected to be for S to increase to some intermediate area and then decrease. Such low-high-low diversity gradients have been demonstrated. For example Grime (1973) found this pattern along a stress gradient, Loya (1976) showed that this type of correlation between diversity and disturbance exists for some coral reefs and Osman (1977) found a similar gradient for marine sessile invertebrates on rocks. The possibility certainly exists for only part of a gradient existing or being observed. For example, Abele (1976) suggested that the diversity of invertebrates on coral heads actually increased with disturbance. Likewise, if the time between $T_\hat{S}$ and T_{DOM} is extremely short, an intermediate peak in S may be transient and diversity may be observed to continue to increase along the gradient.

It would seem that it is possible to account for a broad range of local diversity patterns with a relatively simple immigration/extinction model. We have only included the probability of disturbance. Our arguments have dwelt on its frequency, but similar patterns could be generated by the inclusion of magnitude. For instance, if very low frequency, high magnitude disturbances occur (i.e., hurricanes, abnormally low tides, drought, etc.), a whole region may follow the successional
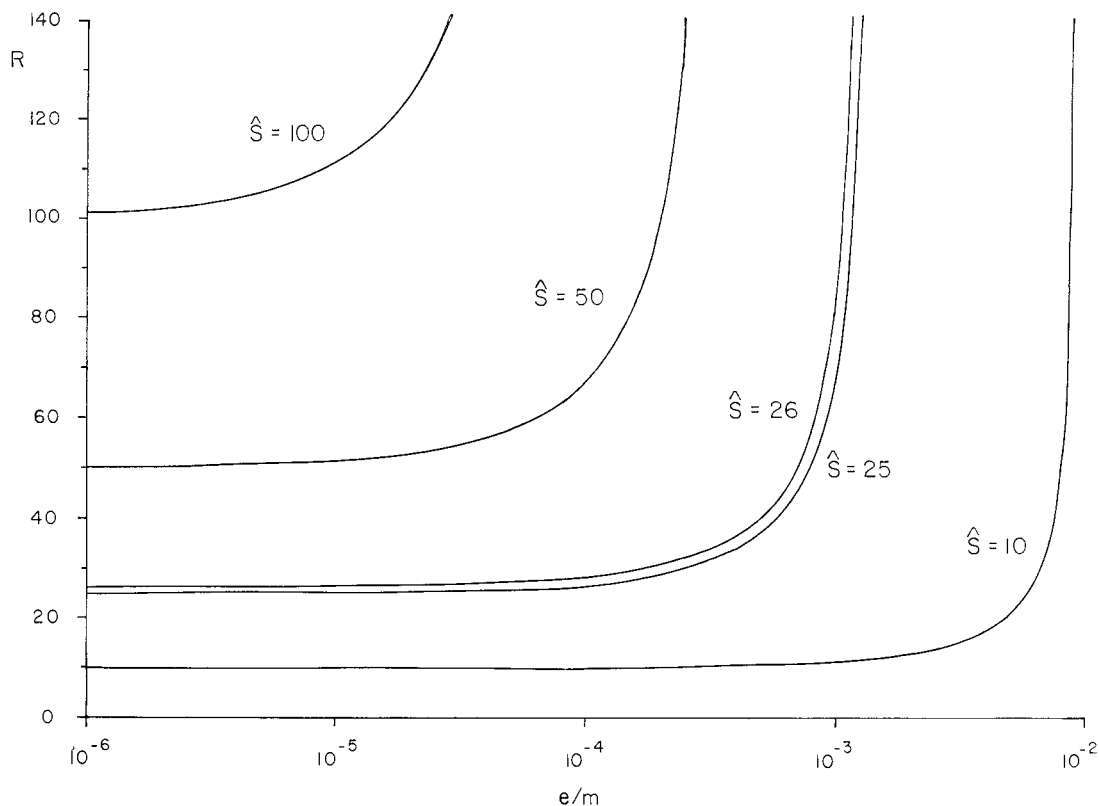
FIGURE 3. Relationship between species richness (R) and the ratio of extinction rate to immigration rate (e/m) for systems with different local diversities $(\hat{S})$.

pattern. Most patches would be "reset" to age 0 and progress in a similar manner. No *specific* biological processes (competitive hierarchies, predation, adaptability to different habitat types, etc.) were assumed. Such processes may enhance a particular pattern, but are not necessary to explain it.

Global Patterns in Evolutionary Time

In examining global patterns, we are interested in comparing different regions in terms of R and $\hat{S}$. Since any region will be a mosaic of patches of different S, the only comparable measure of local diversity on a global scale is $\hat{S}$. We will use $\hat{S}_i$ as a measure and assume that if it changes from region to region or with time, S's for other stages of succession (or $\hat{S}_n$) or for patches of a younger age will change in a similar manner.

Since changes in R are the most easily recognized on a global scale, we will be concerned with the relationship between R and

$\hat{S}$, e and m and how it varies. Equation (1) with $dS/dt = 0$ can be solved for R.

$$R = \hat{S}/[1-(e/m)\hat{S}^2] . \qquad (5)$$

A comparison of (3) and (5) shows that R and $\hat{S}$ are interdependent and both are dependent on e/m. Figure 3 shows the relationship of R to e/m for some representative $\hat{S}$'s. Several features are obvious. 1) For any $\hat{S}$, R can take any value depending on e/m, and greater species packing (the number of species per patch or $\hat{S}$) is not a prerequisite for a high regional diversity. 2) When the immigration rate is much greater than the extinction rate (low e/m) $\hat{S}$ approaches R. Obviously, if, for example, 100 species per patch are possible with $e/m = 10^{-5}$, then all R species in a region might be expected in each patch when R is less than 100. 3) Each curve is asymptotic at $e/m = 1/\hat{S}^2$ (if equation (2) were used, this asymptote would be at $e/m = 1/\hat{S}$). This means that as e/m increases (be-
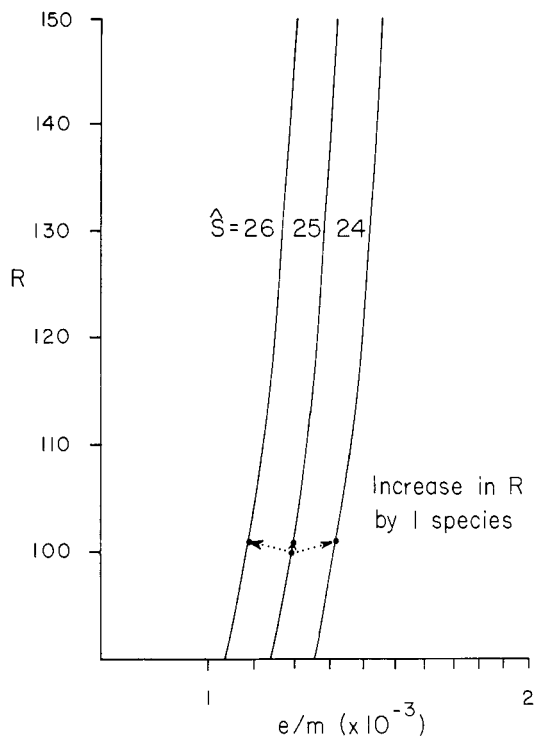
FIGURE 4. A more detailed view of Figure 3, showing the change in e/m (ratio of extinction rate to immigration rate) necessary for R (species richness) to increase by 1. The three most probable cases are when $\hat{S}$ increases, decreases, or remains the same.

yond each $1/\hat{S}^2$), $\hat{S}$ must decrease. However, nothing is implied in terms of R.

Although Fig. 3 illustrates the vast array of possible combinations of R, $\hat{S}$, and e/m, it can still be used to examine the most probable ways by which R and $\hat{S}$ may increase. Given a region with an R, $\hat{S}$, and e/m, the addition of at least one new species (to the region) is necessary for R to increase. The source of new species can be treated as external to the region. Over long periods of time, low probability events of invasion from outside the region will gain importance. Plate tectonics provides a mechanism to merge previously isolated regions and increase this probability. Speciation within the region is most likely to occur through the isolation of some peripheral area (Eldridge and Gould 1972) and this isolated area can also be considered external to the remaining region.

Given this new species, we can ask how $\hat{S}$ and e/m must change for this species to be permanently added to the region and thus

for R to increase to $R + 1$. The key to a successful increase in R will be how the ratio e/m changes, however, no systematic or unidirectional change in e/m is evident. It appears that e/m can increase, decrease, or remain the same and a limitless array of patterns of change in R and $\hat{S}$ are possible. Figure 4 illustrates the conditions of a typical region (many more species exist than can be found in any individual patch). It is a detailed section of Fig. 3, depicting for an arbitrary example ($\hat{S} = 25$, $R = 100$) the three most probable ways by which R will increase by one species. (It is important to note that in all cases, e/m must change with the addition of a new species.)

1. For $\hat{S}$ to increase, e/m must decrease, either by a substantial increase in m or a reduction in e. For a new species to substantially increase m its immigration rate must be higher than the rates of the species within the region and such additions must have their limit (Horn and MacArthur 1972). Any set of taxa may present a broad range of reproductive capabilities and thus immigration rates, but there are physiologic limits. To decrease e/m by a reduction in e would require some evolutionary change reducing the extinction rate of at least some of the species. In light of the other ways by which R can increase, such changes are certainly not necessary.

2. The possibility that R can increase with $\hat{S}$ remaining the same demonstrates this. The change in e/m necessary for this to occur is extremely small. With the new species having an immigration rate within the range exhibited by the species of the region, the increase in m by its addition may be small. For $\hat{S}$ to remain the same, the presence of this new species within the region must only increase e slightly. The presence of the new species in a particular patch will increase extinction in that patch, however, it must occur in enough patches of the various ages to cause a significant increase in e.

3. Even if a new species presence causes a substantial increase in e, it is still possible for R to increase. The new species may be a superior competitor or a predator and be found in a sufficient number of patches to decrease $\hat{S}$, but it is still possible that it will not eliminate any existing species from the region and R will increase.

Obviously, there are many circumstances in which the addition of a new species will change e/m such that R will not increase or in which some species are lost and R decreases. Regardless, the point we wish to make is regional diversity can increase under a variety of conditions, and adaptation, changes in niche characteristics, tighter species packing, etc., producing a higher $\hat{S}$ are not prerequisites for global variability in R. In a more deterministic sense, a patch will contain some quantity of resources and the group of taxa being considered will have some limited range of generation times, reproductive capabilities, dispersal capabilities, space requirements, etc. These properties of patches and organisms can determine a particular range of e/m and possibly some unique $\hat{S}$ may still exist for the particular patch type and group of organisms. However, for an open system or patchy region the $\hat{S}$ for each patch does not have to change for the diversity of the region to change. Both laboratory (Huffaker 1958; Pimentel et al. 1963) and mathematical (Caswell 1977) modelling of simple systems have demonstrated how the dynamics of an open system present an exceedingly strong force counteracting the expected results of highly deterministic processes (in this case, predator-prey relationships). The question is, therefore, whether specific global diversity patterns can still be explained without relying on any differences in biological organization between regions.

Latitudinal diversity gradients. — Many groups show latitudinal gradients of regional diversity decrease from the equator to the poles. A few recent explanations for regional differences (not necessarily latitudinal) in diversity are: global environmental gradients (MacArthur 1975), differences in niche characteristics (Pianka 1975; Karr and James 1975; Cody 1975), differences in tropic complexity (Menge and Sutherland 1976), and differences in temporal stability (Sanders 1968, 1969). We characterize these as $\hat{S}$ arguments because the question of regional differences is usually posed as, "How are the species and/or environment different such that more can co-exist?". When patches are more readily defined and R and $\hat{S}$ are separated, the pattern of change between R and $\hat{S}$ may not necessarily be correlated. For example, Stout and Vandermeer (1975), in

studying rheophilic insects on rocks, found a definite increase in R in the tropics. Their diagrams, however, indicate little difference between the temperate and tropics in the number of species on a single rock ($\hat{S}$). If, as we have shown above, R can change without any change in $\hat{S}$, the question becomes whether any simple conditions exist which would produce latitudinal gradients in R regardless of $\hat{S}$.

There are two general conditions which can affect the probability of R increasing: 1) an increase in the probability of new species being "available" to the region, and 2) an increase in the probability that any new species will be successfully added. (1) The probability of new species being available will increase as the number of sources of new species increase. Two factors will affect the number of sources: time and isolation. The longer a region exists, the greater its chances of encountering new species or sources of new species. The greater the isolation between regions, the greater the chances that random drift will allow differentiation of species between the regions. On a global scale, plate tectonics supplies the mechanism for isolation and merger of regions. (2) The probability of successful addition will be related to the number of patches within a region and, therefore, its size. Presumably, as the number of patches increases, the persistence of any species will become less dependent on the outcome of immigration and extinction in any one patch.

If one or more of these factors, age, isolation, or size of regions, can be shown to vary with latitude, then latitudinal gradients in species richness may exist independent of any environmental differences or differences in $\hat{S}$.

1. Time or Age. The importance of time to increase in diversity (e.g., Fischer 1960) has been seriously questioned. Most recently, Strong et al. (1977) in examining the diversity of sugar cane predators found that time of existence had little importance in determining diversity when compared with regional area. Additionally, it can be argued that except for very discrete and usually unique localities (i.e., volcanic islands, Lake Baikal, the Great Salt Lake, the Black Sea, etc.), it is difficult to date a biological region and much more difficult to demonstrate a poleward decrease in age. In terms of the species which inhabit

them, regions do not have to be viewed as existing at some discrete location. For example, the poleward retreat of continental glaciers certainly would expose new shelf areas for polar marine organisms, but equivalent regions of polar climate would have existed towards the equator before this exposure and they can be viewed as moving towards the poles (along with lower latitude temperate and tropical areas). This is similar to having a pile of rocks and picking up one rock on the north side of it and moving it to the south side, repeating this process until the pile is a kilometer farther south. It will be the same rock pile and it will be older, but it will be the same age as a pile that was not moved. Processes such as glaciation do create change, but as Strong et al. (1977) suggested, the associated changes in area may be more important, probably overriding any temporal effect.

2. Area. Because of the subspherical shape of the earth, the surface area of latitudinal bands will definitely decrease towards the poles. Using present conditions, we identify at least five latitudinal zones: one tropical zone extending 20 to 23.5° on either side of the equator, two temperate zones extending to 50 or 60°, and two polar zones. In terms of area, the tropical zone would encompass 33–38% of the total global area, a temperate zone, 18–25%, and a polar zone, 8–13%. It would follow that either regions will be larger towards the tropics or the number of regions within a zone will increase. Certainly other factors, such as exact continental positions placing a disproportionate amount of land in higher latitudes, could equalize or negate this general global pattern. Also, glaciation may be viewed as compressing these zones and the tropical zone could be disproportionately compressed [the temperature data presented by McIntyre et al. (1976) for the last ice age gives the suggestion of greater compression in high latitudes]. Nevertheless, the shape of the earth increases the probability of greater region size or number for low latitude zones, and each of these should favor an increased R.

3. Isolation. As with area, the shape of the earth leads to the prediction that longitudinal isolation between regions in the same zone should vary inversely with latitude. Since the tropical zone girdles the equator, two regions within this zone can be separated by the greatest distance. In the polar zones, the maximum distance between two points will be the least. The opportunity for isolation and endemism should, therefore, follow a latitudinal gradient. With regions separating and merging, this should also increase the opportunities for R to increase in lower latitudes.

To summarize, because of the shape of the earth, the probability of more regions, each with a greater area, and each being more isolated, will increase towards the tropics. A latitudinal gradient in species richness would be expected regardless of any specific biologic processes or environmental gradient.

Deep sea species diversity.—So far we have examined very general and, perhaps, oversimplified diversity patterns and how they can result from probabilistic events in open, dynamic systems rather than from differences in the biologic structure, composition, or order of systems. Certainly specific patterns can be found that result from unique biological events, no matter how low their probability. The deep sea may be such a unique environment and since the discovery of higher species richness, several explanations have been hypothesized to explain this phenomenon (Sanders 1968, 1969; Grassle and Sanders 1973; Dayton and Hessler 1972; Menge and Sutherland 1976).

Before discussing the relationship of the three factors examined above (time, area, and isolation) to deep-sea species richness, R, we feel it is necessary to consider two potential differences between deep-sea organisms and their counterparts on the continental shelf.

1. For the *same* taxonomic groups patch size in the deep-sea may be much smaller. Although gigantism can be found in the deep-sea (Hessler et al. 1972) deep-sea species are generally much smaller than those from similar groups on the shelf (see Thiel 1975 for a review). From a small sample of box cores, Jumars (1975) could not demonstrate the patchiness of infaunal species on the scale one might expect for nearshore infauna (Whitlatch 1976). Because of the small size of deep-sea species rather than their specialization (preliminary data collected by one of us, R. B. W., seems to indicate that deep-sea infauna are less selective in feeding than nearshore species) it seems reasonable to expect smaller rather than larger patch sizes.

2. Biologic processes within the deep-sea

environment seem to occur much more slowly on an absolute scale. Evidence suggests lower metabolic rates (Jannasch et al. 1971; Jannasch and Wirsen 1973), lower respiration rates (Smith and Teal 1973; Smith 1971), reduced number of offspring (Allen and Sanders 1973), low colonization rates (Grassle 1977), and long lifetimes (Turekian et al. 1975). However, it must be noted that not all data indicate universally low rates. Dayton and Hessler (1972) suggested relatively high rates of fish predation. These predators could be accommodated if they were not feeding on the slow-growing benthos but rather on large food particles or carrion from the surface waters.

Although some of the evidence is puzzling (and intriguing), the majority of the information favors small species interacting at very slow rates. Potentially, this presents a situation dramatically different from those normally studied (see Southwood 1976). In terms of ecologic diversity patterns, however, these features may not be that critical. For example, turbidity currents might be expected to cause a gradient in the frequency of disturbance decreasing in areas more distant from the continental slope. The typical low-high-low diversity gradient would still be expected regardless of patch size or the absolute rates of dynamic interactions. However, these two factors must be considered when examining patterns in species richness.

Considering that the species richness of the deep-sea benthos has been found to be generally within the range of that found on the tropical shelves (Sanders, 1968, 1969), two simultaneous questions arise: why is R this great in the deep sea and why is it not greater? As with latitudinal gradients, we can examine the influence of time, isolation, and area.

1. Time. As we have argued for latitudinal gradients, it is difficult to separate regions on the basis of their time of existence. At least some deep-sea areas are probably as old as their adjoining shelf areas and date to the time when the continents began moving apart. However, in relation to the longer generation times and lower reproductive rates of deep-sea organisms, the relative time scale for the deep-sea may be much shorter. This would favor a higher R for similar shelf regions. However, if the argument of Strong et al. (1977) can be extended to much longer

periods of time, this may not be that important.

2. Area. The area of the deep-sea is much greater than that for the continental shelves. Additionally, if patches are similar but much smaller in the deep-sea (same S/patch, but more patches/unit area), this areal difference would be magnified on a relative scale. Such a difference would favor a higher R in the deep-sea (and could potentially more than counteract any relative time difference).

3. Isolation. Isolation is the key. However, it is difficult to determine, even on a relative scale, what the extent of a region in the deep-sea will be. The small size of the organisms (more patches) plus the low dynamics (reduced exchange between patches) might favor a particular habitat-type in the deep-sea being subdivided into many separate regions, with little interaction, and thus a great deal of endemism. The areal expanse of the deep-sea favors large regions, but the dynamics favors small regions with little interaction between them. The opportunity for isolation through low reproductive rates, long generation times, and perhaps low dispersal capabilities is great, but these same processes may also limit the relative rate of merger of regions and thus their potential to increase in R.

Our unsatisfactory and speculative conclusion for deep-sea richness is that small organism size resulting in small patch size plus a large areal expanse favors a high R, the reduced relative time for regional enrichment favors a low R, and the low rates of various biological processes can favor greater isolation, lower merger rates, and potentially have an important but indeterminate influence on R. In this sense, the diversity of the deep-sea cannot be compared to other systems or be included in any argument on diversity patterns until the question of its biological uniqueness is resolved.

Conclusions

Our purpose has been to demonstrate that common diversity patterns *can* be artifacts of open and dynamic systems. By recognizing the patchiness of environments, the dynamic nature of systems can be artificially ordered through the simple processes of immigration and extinction. On the *first* level is the patch. It is connected to the other patches within the

region through immigration. The majority of short-term interactions will occur within the patch. Immigration of species into it and extinction of species already present will cause its species composition to change, but the rates of immigration and extinction may result in a predictable temporal diversity pattern or succession. On a *second* level is the region or collection of patches. Disturbance represents the power of total local extinction or that patches can "become extinct" or "be created." Patches will be of different ages, be in different stages of succession, and have a variable number of species. If disturbance or patch age structure varies predictably within the region, a gradient in species diversity is possible. On a *third* level, regions are interconnected by low probability inter-regional immigration. Such probabilities can change with isolation and merger of regions. However, the geometry of the earth would seem to impose some simple constraints on regional "connectiveness" resulting in latitudinal gradients. These simple dynamic relationships would be expected to operate for any set of taxa, but for groups with strikingly different rates, or when comparing very different taxa, some scaling would be necessary for legitimate comparisons. The comparison of the deep-sea with the shelf may represent a case where similar scaling is necessary within the *same* set of taxa.

Diversity patterns can exist regardless of any assumptions concerning the importance of competition, predation, species packing, niche characteristics, species ability to adapt, etc., and, in this sense, they do not justify the existence of these processes or any local or global differences in them. Certainly, processes such as competition or predation may be important in determining the co-occurrence of particular suites of species or a particular successional change in species composition, but a diversity pattern could have resulted independent of these. Species richness of a region can increase independent of how many species can coexist within a single patch and is no argument for reduced competition, increased or decreased predation, changed niche characteristics, etc.

We do not wish to argue the importance of biological processes, but merely that diversity is some measurement of their existence. If diversity is excluded as a meaningful param-

eter and the possibility of local extinction operating in an open, dynamic system is accepted as being powerful, then one is free to examine the processes without the encumbrance of diversity. Competitive exclusion again becomes a straightforward process. One species can always eliminate another in a patch, but they can both survive in a patchy region without any finer and finer adaptations. Species can be "sloppy" in how they adapt and can even make the ultimate "mistake" of making their survival solely dependent on the existence of another species [e.g., the reproductive dependence of a tree on the now-extinct dodo (Temple 1977) may represent such a mistake]. Higher trophic levels can be added, but the diversity of lower levels is not contingent upon their addition.

Just as there are alternate views of reality, our present ecologic and evolutionary knowledge is such that it is important to admit alternate views of the biologic world. The importance of considering both probabilistic and deterministic alternatives has been well-illustrated in such areas as phylogeny (Gould 1976; Gould et al. 1977) and the massive extinction associated with the Permo-Triassic boundary (Schopf 1974; Simberloff 1974). We feel that a non-deterministic alternative for diversity patterns is also possible. This in no way denies the evolution of a vast array of intricate biological adaptations, the fine partitioning of resources, or the importance of predation or competition. What is denied is that diversity by itself is a measure of the magnitude of these processes or that it implies any uniqueness to a system. Species diversity does not necessarily imply anything about the biology of the species or of the environment in which they live. These processes, not diversity, are what should be of interest.

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