THE ECOLOGICAL REGULATION OF SPECIES DIVERSITY

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INTRODUCTION

It is common observation that some areas support more kinds of organisms than others. Generally speaking, areas with more "rigorous" environmental conditions have a lower diversity of living forms. Several hypotheses have been proposed to account for differences in species diversity; we will discuss these before we advance our own. (In this paper the term "greater diversity" will signify "more species"; other indications of greater diversity, such as more equal abundance per species, will be dealt with in a later paper.)

PREVIOUS HYPOTHESES

The idea most frequently suggested is that there are more species in a region because there are more ecological niches there than in regions with few species. Thus the land is presumed to have more niches than the sea, the tropics more niches than temperate regions, etc., with corresponding differences in species diversity. This hypothesis is based on the idea that an ecological niche is objectively defineable *a priori*, so that one can look at an area and predict how many niches occur there. For example, one may say that a level sandy sea bottom has "fewer *potential* niches" than a broken rocky bottom.

However, when one attempts to partition a given habitat into different niches, it becomes clear that the physical differences provide only a few of the many dimensions which can be thought to bound each "hypervolume," defined as the fundamental niche of each species (Hutchinson, 1958). Although physical dimensions could account for some diversity, the great majority of it is due to biological interactions, which thus constitute most of the dimensions of each niche. If we attempt to take these biotic dimensions into account in delimiting niches *a priori*, we find ourselves in a circular argument, since the number of niches is partially a function of the number and type of species present. We cannot then explain the number of species by the number of "potential" niches. In fact, the hypervolume which constitutes the fundamental niche of a species can only be described *a posteriori*, never *a priori*, since its biotic dimensions have developed as a complex pattern of interactions by a long *random* process of organic evolution.

As an example, let us take Elton's (1927) analogy of an animal's niche as its "profession," and consider a human situation. The profession of a uni-

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versity professor can scarcely have been considered a potential niche which was waiting to be filled by human evolution. Rather, like an ecological niche, it is the end product of a random process about which nothing could have been predicted at the outset. Many habitats with little physical diversification, such as the open sea, or the flat Amazon basin, support a multitude of species. For all these reasons we conclude that the explanation "more niches therefore more species" is a fallacious one.

Another idea often advanced to explain lack of diversity in desert or polar regions, is rigorousness *per se*; presumably, few species have been able to adapt to these rigorous conditions. However, what could be more rigorous than the land environment for organisms evolved in water, composed chiefly of water, supported by it, and physically and chemically buffered by it? Yet the extreme success of the invasion of land is attested by the presence there of over 80 per cent of animal species (Thorson 1957). The ultimate question remains, if a few species have become adapted to any very rigorous habitat, why have not more? We conclude therefore, that rigorousness *per se* cannot be a universal explanation for lack of diversity.

Another hypothesis which has been proposed to explain the greater diversity in the tropics is that only the tropics have reached an equilibrium state, while the temperate and polar regions are "biologically immature" (Wallace, 1878; Fischer, 1960). This hypothesis assumes that the polar and temperate zones have undergone recurrent climatic catastrophes, with periodic extinctions keeping diversity low.

More recent evidence does not support this hypothesis. Newell (1962) has considered the causes of the simultaneous mass extinctions of animals, from a wide variety of environments, at certain eras in geological history. He concludes that "fossil plants, good indicators of past climates, do not record catastrophic changes in temperature at the ends of the eras. Consequently, it appears improbable that significant temperature changes were responsible for the crises in animal life." In any case, temperature changes would have greater effects in tropical or polar regions than in temperate latitudes. "Ecological zones determined by temperature at high and low latitudes might vanish as a result of a drop or rise of a few degrees of temperature. Temperate zones at intermediate latitudes would simply shift laterally without being eliminated" (Newell, 1962, p. 606). From this evidence it appears that the tropics have not necessarily enjoyed a longer undisturbed period of continuous evolution. The greater diversity of the wet tropics cannot be accounted for solely by a closer approach to equilibrium with the temperate latitudes in a less mature state of lower diversity.

Klopfer and MacArthur (1960) have suggested that birds have smaller niches in the tropics and therefore more species can inhabit the same area, with a consequent increase in diversity. Their evidence is the greater relative abundance in the tropics of non-passerine birds which are assumed to be more specialized, with more stereotyped behavior, characteristics which are taken to indicate smaller size of niche. To our knowledge, no relevant comparisons between these groups of birds have yet been published; temperate

passerines are evidently quite stereotyped in their choice of habitat (Crowell, 1962; Klopfer, 1962). Specialization in the feeding behavior of birds may actually be less in the tropics judged by the decreased character displacement in bill size found by Klopfer and MacArthur (1961). They suggest that niches overlap more in the tropics; while this may be so, the absence of an operational definition of niche makes this hypothesis difficult to test.

Hutchinson (1959) has suggested several ideas to account for the differences in diversity shown by animals. He proposed that diversity should increase in the early stages as a self-inducing process due to the increase in community stability conferred by more complex food webs. Diversity would eventually be limited by unfavourable physical factors, by space, by limitations to the length of food chains, by the evolution of large body size and by the fineness of possible subdivisions of niches. In the arctic, organic productivity may limit diversity.

In the remainder of this paper we will describe a model for the development and maintenance of diversity which includes some of Hutchinson's ideas. In essence we propose that the level of diversity of a community is determined by the amount of energy flowing through its food web. The rate of energy flow is determined, not only by various limiting factors, but also by the degree of stability of the environment, by the process which we will discuss next.

THE ALLOCATION OF ENERGY IN LIVING SYSTEMS

Under natural conditions the magnitude of the physical factors of the environment such as heat, moisture, light, etc., fluctuate with time. Within living organisms, however, the amplitude of these fluctuations is almost always reduced by the operation of homeostatic mechanisms, that is, by *regulation*.

The universal occurrence of regulation in living organisms implies that living processes are better carried on under relatively constant conditions. Any random or cyclic variation in environmental conditions is a challenge which must be countered by an appropriate corrective response of the organism. Thus the amount and variety of regulatory activity required for maintenance of the steady state is dictated by the environment. This concept was formalized by Ashby (1958) as the "Law of Requisite Variety," which states that for maximum stability, the variety of homeostatic responses required in any system is equal to the variety of environmental challenges offered to it.

The maintenance of life requires the assimilation of a continual supply of energy. Some of this assimilated energy is used in regulatory activities, of the sort described above, while the remaining portion is used for reproduction, using the term in the broad sense to include growth, regeneration and the production of offspring. The two pathways of energy allocation are usually referred to as "maintenance" energy (Brody, 1945) and "productivity." Productivity, as defined here, is equivalent to the *net* primary productivity of plants or the secondary productivity of consumers in Odum's

(1959) terminology. The energy allocated to maintenance is dissipated as heat to outer space; the energy allocated to productivity is stored in organic matter and becomes available to other organisms in the food web.

These two possible pathways of energy compete for the common supply of assimilated energy. By the law of requisite variety, it follows that in a relatively more stable environment, less energy is needed for regulatory activities, so that a greater proportion of the assimilated energy is available for productivity. For example, Cox (1961) found that tropical finches channelled more of their energy into maintenance ("existence energy"), and less into growth, as temperatures were lowered.

The concept of stability is difficult to define operationally and to measure. (A formal definition can be found in Ashby, 1958, and a promising attempt to measure it in Patten, 1961.) We will use the term as follows. Physiological and biochemical studies have shown that living processes tolerate only a narrow range of variation of the internal environment. The greater the amplitude of fluctuations of the external environment around this range the more unstable we will consider the environment.

The period of the fluctuation is also important. If, for example, the temperature remains continually below (or above) the optimum range for long periods, regulatory mechanisms may be passive (thick pelage, resting stages), in contrast to the active mechanisms (shivering and sweating, etc.) required under short period fluctuation of temperature. The more passive mechanisms probably require less total energy expenditure.

THE DEVELOPMENT AND REGULATION OF SPECIES DIVERSITY

For the purposes of discussion let us consider two similar ecosystems, each with the same energy input. Let us assume that the physical conditions in one are more stable than the other. As we have pointed out, with a more stable physical environment (Step 1, figure 1) fewer or less severe challenges will be presented to the organisms in that ecosystem, and therefore, less regulatory activity will be required of them (Step 2). Therefore, more of the assimilated energy will be channelled into productivity, that is, growth and production of offspring (Step 3).

Increased productivity manifests itself either by the individual organisms growing faster, with a probable lowering of the age of sexual maturity, or by an increase in the rate of production of offspring, or both. In many organisms, larger individuals produce more offspring, so that it seems probable that increased productivity will be translated eventually into a greater production of young.

Therefore, with increased productivity, greater population size will result. If the greater productivity occurs amongst the green plants at the base of the food web, either the plant population will increase in size or the increased amount of fixed energy will be passed quickly to the consumer levels. The rate of accumulation of organic matter is negligible when compared with that at which energy is being fixed by photosynthesis. This implies that organisms, as a whole, are living to the limit of their energy

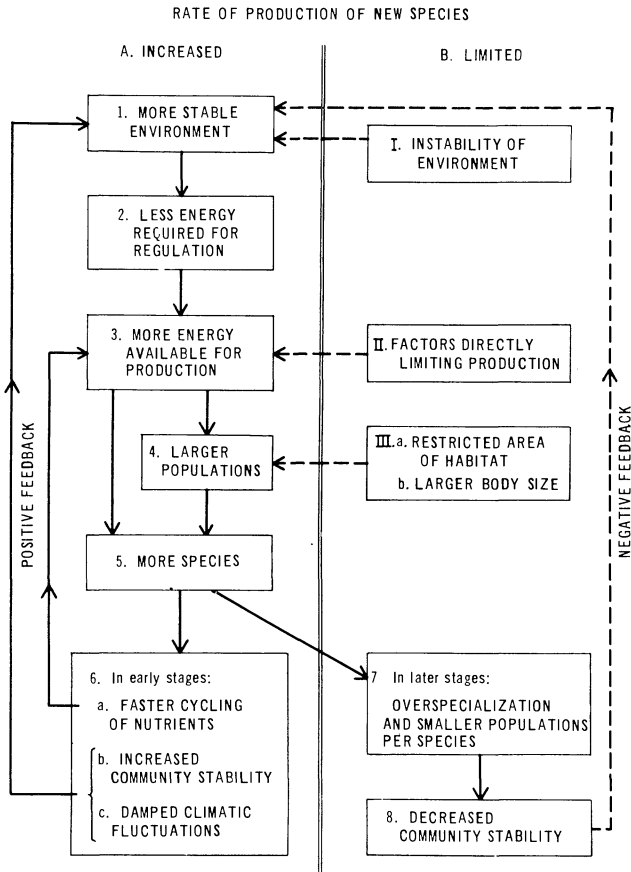RATE OF PRODUCTION OF NEW SPECIES

FIGURE 1. A model for the production and regulation of species diversity in an ecological system. See text for explanation. Solid lines indicate an increase, dashed lines a decrease.

supply (Hairston et al., 1960). Any increase in available energy will result in an increase in abundance of some species somewhere in the food web.

Large populations maintain more genetic variability than smaller populations. Darwin (1859) pointed out that dominant (that is, more abundant) species are more variable than rare ones. Fisher (1958) states that "the number of factorial differences maintained in an abundant species bears a higher ratio to the rate of occurrence of new mutations than does the number maintained in rare species." Given no difference in mutation rates, a more abundant species has more mutations because the gene pool is larger; the chance of gene fixation is also reduced in large populations. Therefore, as a consequence of greater population size, the organisms in the more stable environment possess greater intra-specific genetic variety.

The translation of intraspecific into interspecific variety, that is, the splitting of the species into two or more new species (Step 5), is dependent upon three conditions:

1) Sufficiently great intraspecific genetic variety to allow adaptation to many kinds of new environments.

2) Continual exposure to new environments.

3) Partial or complete spatial isolation from the parental stock in the new environment until sufficient divergence of characteristics has occurred to ensure reproductive isolation.

These conditions are facilitated by Steps 3 and 4 in figure 1. Intraspecific genetic variety is increased by Step 4 as discussed above; this increases the chances that some member of the species will be able to survive and breed if a portion of the population becomes isolated in new environmental conditions.

The second condition, continual exposure to new environments, will also be augmented by Step 4, increased abundance of organisms. This is especially significant when the new environment is created by another species, as where an interspecies association is formed. Such associations are much more characteristic of complex communities than of simpler ones (See Dobzhansky, 1950; Yonge, 1957; Margalef, 1963).

The chance of formation of a new interspecific association is increased if one or both of the partners is abundant. An insect species evolves resistance to an insecticide at a rate proportional to the number of times it is exposed to it. Southwood (1960, 1961) found that the number of species of insects associated with a species of tree was positively correlated with the abundance of that tree. Dogiel et al. (1961) have also found that more abundant species of fish have more species of parasites. Rogers (1962), in discussing the evolution of parasitism, listed frequency of contacts as the first requirement for the formation of an association between species. Thus, as a result of Step 4, increased abundance, the rate of formation of new interspecific associations would be increased. Since a new association with a different species essentially provides a new habitat, this process would tend to increase the number of species.

The third condition, complete or partial isolation of local populations, is facilitated by Step 3, increased organic productivity per unit area. This is due to the decreased mobility of animals in more productive areas. McNab (1963) has shown that mammals which graze or browse on leafy vegetation have smaller home ranges than do mammals of the same body size which feed on seeds, fruits or animals; the amount of energy available per unit area is obviously much greater in the former case. Home ranges of mammals in wetter regions are smaller than those of mammals in deserts where productivity is less. Therefore, given the same absolute distances between separate local populations, the less mobile animals of highly productive communities will exchange fewer genes than those in less productive communities. For the same reason, dispersal by animals agents of the pollen and seeds of plants would be reduced in more productive communities. Dispersal by animals is more common in the tropics, by wind in higher latitudes. Thus flowers are mainly hermaphrodite and polygamous in tropical rain forests, monoecious and dioecious in temperate woodlands (Baker, 1959).

The massive production of flowers on a single rain forest tree may occupy an entire hive of insects, resulting in much self-fertilization (Corner, 1954). Thus lower mobility of animals in more productive habitats will produce many small partially isolated local populations of both animals and plants; such conditions provide the ideal conditions for speciation (Wright, 1940). For all these reasons, therefore, we propose that Step 5, the formation of new species, will follow in time.

Before continuing our argument, let us characterize these new species evolved under the assumed conditions of greater stability.

a) The new species, having adapted to environmental conditions more restricted than those of the original single species, tend to be more specialized.

b) The population size of the new species will initially be smaller than that of the parental one from which it was split off. Klopfer and MacArthur (1960) found that the population size per species of passerine birds decreased toward the tropics. They interpreted this to indicate a greater degree of specialization in more stable environments.

Two sets of consequences will follow from this. In the early stages of speciation, as ecological communities develop, a set of positive feedback mechanisms will operate with the result that stability and diversity increase without bound. Later on, negative feedback mechanisms will regulate the amount of diversity which any ecosystem can maintain.

The positive feedback mechanisms are shown as Step 6 in figure 1. The first consists in a speeding up of the cycling of mineral nutrients through the food web. In the early stages of evolution we may assume that only autotrophs (mainly green plants) and decomposers were required for the cycling of mineral nutrients. The lag between production of autotroph tissue and its availability to decomposers set the limit to the rate of cycling. Any heterotroph which could attack this plant material at an earlier stage would be selected for. Its attributes would be larger size, mobility, and an apparatus for breaking apart plant tissue. Thus large mobile herbivorous animals and, later, carnivores, would evolve, with a resultant increase in the rate both of nutrient cycling and of plant productivity (Step 6a increases Step 3, figure 1).

Another positive feedback mechanism results from the increased numbers of links in the food web. Many observers have noted that in diverse communities, violent fluctuations in numbers are rare (Elton, 1958; Pimentel, 1961). This is probably because, in diverse communities, "there are many species of enemies and parasites ready to turn on any species that starts being unusually numerous, and by a complex system of checks and buffers, keep them down" (Elton, 1958, p. 148-9).

This concept of "community stability" (MacArthur, 1955), represents a different aspect of environmental stability from that given in Step 1. Yet to organisms dependent upon other organisms for food (all consumers) or for nutrient substances (plants dependent upon consumers), such stability is just as important as the stability of purely physical factors. Hutchinson

(1959) first proposed that the increased community stability of complex food webs would result in ever-increasing diversity of animal species.

MacArthur (1955) has suggested that the number of possible pathways of energy flow through a food web is a good measure of its stability. Therefore a small number of species, each eating a wide variety of other species, could have the same community stability as a large number of species each with a fairly restricted diet. Since new species tend to be more specialized, an increase in diversity would not necessarily mean an increase in community stability. However, most species retain some flexibility in their choice of food; the important idea in the previous quotation from Elton (1958) is the ability of predators to "turn on" any temporarily abundant species, one which they do not ordinarily feed upon. Thus the number of possible pathways of energy flow through a food web would be increased if the new animal species, though more specialized, remained flexible in their feeding behavior. In any self-regulating system, the quicker the homeostatic mechanism responds to a fluctuation in the variable being controlled, the smaller the amplitude of the fluctuation. The greater total number of animals of many species in highly productive communities should ensure the prompt detection of any temporary increase in abundance, with a consequent increase in community stability.

Another mechanism which increases environmental stability is shown in Step 6c. As more species evolve (Step 5), a greater proportion of the globe will be clothed with living organisms. The presence of populations of plants or animals almost always decreases the amplitude of fluctuations in physical factors. In the sea, kelp beds offshore or clumps of mussels attached to rocks reduce the turbulence of waves and so provide shelter for many more delicate species (Hewatt, 1935). On land, vegetation reduces climatic instability; Hursh (1948) found that where all living things had been removed from a large forested area by copper smelting fumes, the amplitude of fluctuations in all meteorological conditions was greater than in the adjoining undisturbed areas. The average annual rainfall was reduced in the bare area, suggesting that the cycling of matter (in this instance, water) was slowed down in the absence of vegetation.

These aspects of Step 6 will tend to increase diversity without bounds. However, there exist various mechanisms which limit the diversity. The first constitutes a negative feedback mechanism which regulates the amount of diversity any ecosystem can maintain. This mechanism operates by virtue of the well recognized danger in over-specialization. As visualized by MacArthur (1955), community stability would be at a minimum if each species had just one predator and one prey species, so that fluctuations in any one would be transmitted undamped through the food chain. As new, more specialized species are formed the degree of specialization approaches this limit. This, together with smaller populations per species, would decrease the community stability and act as a negative feedback control as shown in Steps 7 and 8.

In summary, positive feedback mechanisms would operate in the early stages of the evolution of a community, ever-increasing its stability, productivity and diversity. Later, the negative feedback mechanism would regulate the amount of diversity being maintained, through the instability which is the price of increased specialization and efficiency.

Up to this point we have used stability as the main determinant of diversity. However, it is possible to envision situations of great stability of physical factors in which the processes of Steps 3 and 4 are directly limited, with low diversity as a result (II and III, figure 1). Productivity may be limited directly by a low rate of energy supply. With increasing depth, algal and coral diversity decrease with light intensity; for the few species at the bottom of deep oceans energy in the form of organic matter arrives at a very slow rate from above. Productivity may also be limited by a low supply of water in deserts, or of mineral nutrients, as at the surface of the deep oceans, both areas of low species diversity.

With both great stability and high productivity per unit area, population size (Step 4) may be limited directly where there is not enough absolute space to allow large populations to exist. Hutchinson (1959) has suggested that space may have limited the number of species of voles in Britain, and Wilson (1961) has found that the number of species of endemic ants on Melanesian islands is directly proportional to the area of the island and independent of the distance from the "source" areas in Australasia. In Australia, the number of species of birds in rain forest may be limited by its small area. The sclerophyll forest, with less productivity than rain forest, has the same number of species of birds; however, sclerophyll forest covers seven per cent of the area of Australia whereas rain forest covers less than one per cent (Keast, 1959).

Another factor affecting the size of a population is body size. For the same energy supply, large-sized plants and animals necessarily have smaller populations than those of smaller body size. Since in addition, larger animals are also more mobile, our model would predict fewer species of large organisms, as is commonly observed. Therefore, in comparing the diversity of two communities, only organisms of similar size can be used. Hutchinson and MacArthur (1959) have suggested that the small diversified elements of the environmental mosaic permit a greater species diversity of small than large animals. This is undoubtedly true to some extent, especially when the diversification is due to other organisms, such as in vegetation structure. However, the diversified elements of the physical environmental mosaic account for only a few of the dimensions of ecological niches.

LIMITATIONS OF THE HYPOTHESIS

In this discussion it has been assumed that enough time has elapsed for ecological communities to come into a steady state in the maintenance of the particular relative abundances of species composing them. Thus com-

munities in early stages of succession or in highly disturbed situations were not considered in this argument. It may be asked whether many ecological communities have arrived at a steady state; MacArthur (1957) and Slobodkin (1961) have considered the problem and concluded that many present-day ecosystems are in a near-equilibrium state. For example, organic matter appears to be decomposed at about the same rate as it is formed by green plants, so that it does not appear to be accumulating at present. While it would be very interesting to consider ecological succession in regard to diversity, our model deals only with equilibrium states.

When non-equilibrium situations are considered, apparent exceptions to our hypothesis may be found. Yount (1956) concluded that the variety of species of diatoms which attached to glass slides immersed in a spring was inversely correlated with productivity. However, it is evident from his figures that the diversity was the same at first and then decreased faster at the more productive station (that which produced the greater standing crop of chlorophyll per unit time). At the end of the experiment equilibrium had been reached at the more productive station whereas the diversity had reached the same level and was still decreasing at the less productive one. We conclude that since the filling-out of niches takes time, any experimental test of our ideas must allow enough time for new niches to be sorted out. For example, when the possibility of a new niche opens in the course of succession, migration may bring many potential occupants of the new niche, and until the successful organisms have sorted themselves out by competitive exclusion, a spuriously high degree of variety will probably be observed, as in Yount's work.

Productivity as discussed in this paper refers to average annual rate of net production of organic matter. The rate of production may be high in polar regions during the growing season, but under the same conditions of nutrient supply, we would predict a greater *annual* rate of production in wet tropical regions. Also, standing crop biomass may be a very poor indication of productivity; Thorson (1957) pointed out that the arctic marine bottom fauna had a high standing crop, owing to a virtual absence of predators, but the productivity was very low.

During short favorable periods, as during the summer in boreal regions or during wet periods in deserts, the animal diversity may be temporarily increased, especially by migratory birds or insects. If it were possible to calculate an average diversity over the year, however, it would undoubtedly be lower. Calculations of diversity based on migratory species during their breeding seasons in these short favorable periods may be misleading if they are then compared with the diversity maintained over the year in more stable habitats. Thus Brereton and Kikkawa (1963) found a greater diversity of birds during the breeding season in the semi-arid savannah woodland than in rain forest in Australia. Since birds in semi-arid areas are often nomadic, one particular area will not maintain the same diversity all year, in contrast to the rain forest where birds are less mobile. Since most observations of bird diversity have been made (like most other ecological studies) at the

higher latitudes where migratory species predominate, great care must be taken to insure that a representative sample is secured of the diversity throughout the year.

DISCUSSION

In our model we have considered whole ecosystems which are not in successional stages and which are not limited by absolute physical space (that is, are not on small islands, etc.). With these restrictions we predict that greater species diversity will accompany greater rate of production of organic matter and/or greater environmental stability.

In regard to the former, some data are available to test our predictions. Ovington (1962) has pointed out that annual net primary productivity of forests is greatest in tropical rain forests. The rate of decomposition of litter and the weight of chemical nutrient elements per unit area are both highest in tropical rain forests. This suggests that the rate of nutrient cycling is fastest in these forests, whose species diversity is also maximum. Both the diversity of marine epifauna (Thorson, 1957) and its rate of growth on buoys (Woods Hole Ocean. Inst., 1952, p. 86, 90) increased at lower latitudes.

Margalef (1963) has pointed out that more complex ecosystems, with greater species diversity, have a lower ratio of primary production/total biomass than do simpler ecosystems. (This production is the *gross* primary production, the total photosynthetic input of energy to the ecosystem which, at equilibrium, is equal to "total respiration and other losses" (Margalef, 1963, p. 359); biomass includes that of both producers and consumers).

In our model, given the same gross primary production, a community in a more stable environment will channel a greater proportion of this energy into "net" production, that is, into either more plant biomass or into a greater consumer biomass. Thus Margalef's ratio will be lower under more stable conditions. Since our model predicts greater diversity and complexity under these conditions, it provides a mechanism to account for his observation. In regard to Margalef's statement that "the energy required to maintain an ecosystem is inversely related to complexity" (p. 373), it is important to emphasize that this refers to the energy *per unit biomass*. In complex natural communities such as tropical rain forests or coral reefs the absolute amounts of both energy flow and biomass are greater than in simpler communities.

The rate of flow of energy and matter through the food web determines the abundance and, in our model, the diversity of organisms in a community. If much of the energy or matter fixed by the plants is removed from the community, few consumers can be supported. Thus in a salt marsh studied by Teal (1962), although the plants fixed a great amount of energy, most of it was dissipated in plant maintenance; of the remaining net primary productivity, almost half was exported from the marsh. The diversity of the consumers was very low. Margalef (1963) has pointed out that many simpler ecosystems export much of their energy and matter to more complex ones.

Two examples are migratory tropical birds rearing young in the arctic and the benthos feeding on the plankton.

Increased environmental stability also accompanies increased species diversity. Seasonal stability of temperature and light are greater in the low altitude tropics where communities of great diversity exist. Within the tropics, species diversity in rain forest is greater where rainfall is evenly distributed throughout the year; in monsoon areas, diversity of these forests is reduced (Richards, 1952).

In the sea, a paradoxical situation appears to exist; although physical factors such as temperature and salinity are very stable only about 16 per cent of animal species are found there (Thorson, 1957). In addition, about three-quarters of these occur on the few hard substrates, whereas only one-fifth are in the extensive soft substrates and the remainder are in the plankton, which occupies most of the oceanic space.

The paradox vanishes when one considers the other challenges offered to aquatic organisms. The greater density of water means that turbulence of the medium imposes much greater stresses on aquatic than land organisms. In the shallow areas where the greatest productivity and fastest nutrient cycling occur the turbulence is greatest. A great proportion of the energy supply of organisms in this region is used in structures and activities which counter the challenge of massive instability of the medium.

Within the sea, the epifauna have the greatest stability of position owing to their mainly passive methods of attachment to the substrate. The animals of the infauna must be continually active in the maintenance of their positions as the sediments change in depth and position. Cleaning of respiratory surfaces is also a major activity of infaunal animals. The plankton is in an even more unstable environment, requiring great expenditures of energy in swimming. In addition, only the epifauna (and flora) have developed dense enough aggregations so that they damp the turbulence of the medium. In mussel and algal beds the greatest diversity of marine organisms is found; only where eelgrass or sargassum weed provide an essentially epifaunal habitat do such conditions occur in the infaunal and planktonic habitats. Thus we attribute the greater diversity of the marine epifauna to the lesser requirements for regulatory activity, plus the opportunity of damping the instability of the medium by the formation of dense aggregations.

At this point we will stop listing examples because it is obvious that what is needed next are both more critical observations and experimental tests of our hypothesis. We have tried to link together many scattered ideas into a single operational model whose main purpose is to suggest aspects about which careful observations should be made. By using only ecological processes we hope we have produced an hypothesis which is more readily tested than one based on historical evidence alone.

SUMMARY

A model is proposed to account for the level of diversity supported by any ecological community. If we begin with a hypothetical increase in the sta-

bility of the physical environment, the following consequences ensue. With greater environmental stability less energy is required for regulatory activities, that is, those which counter the challenges offered by the environment. Therefore, more energy is allocated for net productivity, that is, growth and reproduction. With increased net productivity, larger populations are supported.

Larger populations provide more opportunities for the formation of interspecific associations; they also maintain greater genetic variety. Animals in more productive communities are more sedentary so that the species tends to be broken into many semi-isolated populations. As a result, speciation is favored with the interspecies associations providing the new adaptive opportunities. Plants which are pollinated by animals would be in the same situation. The new species tend to be more specialized and to have, initially, smaller populations. These events are shown in Steps 1 to 5 in figure 1.

In the early stages of the evolution of a community, positive feedback mechanisms would operate, ever-increasing the rate of speciation. The evolution of large heterotrophs (animals) would increase the rate of cycling of mineral nutrients, which would augment the net productivity. As more complex food webs developed with the increase in the number of species, community stability would increase, augmenting the stability of the physical environment. The clothing of the earth's surface with larger plants would tend to damp the fluctuations in climate, also increasing stability (Step 6).

In the later stages, the tendency toward overspecialization and smaller populations would decrease community stability and provide a negative feedback control on the whole process (Steps 7 and 8).

Even under very stable conditions, productivity may be limited directly by the short supply of various factors such as light, water, heat, etc. Population size may also be limited directly by a restriction in the area of suitable habitat or by a larger body size. Any such limitations would result in a lower diversity of species.

This model applies only to equilibrium conditions. In certain situations, such as during the short favorable periods in the arctic or desert, diversity may be temporarily increased; care must be exercised in comparing this to the diversity maintained all the year in the wet tropics.

We feel that, although some niches are determined by physical variations in the environment, most of the dimensions of the niche are a result of interaction between organisms. For this reason, it is impossible to predict the number of niches (and therefore species) from environmental complexity alone. We also discard the idea that rigorousness *per se* limits diversity. Lastly, the hypothesis that the tropics are closer to equilibrium while the temperate zone is in a "successional" state of development of diversity is not accepted, for theoretical reasons and for lack of evidence.

LITERATURE CITED

Ashby, W. R., 1958, An introduction to cybernetics. John Wiley and Sons, New York, N. Y. 295 p.

Baker, H. G., 1959, Reproductive methods as factors in speciation in flowering plants. Cold Spring Harbor Symp. Quant. Biol. 24: 177-192.

Brereton, J. Le Gay, and J. Kikkawa, 1963, Diversity of avian species. Australian J. Sci. 26: 12-14.

Brody, S., 1945, Bioenergetics and growth. Reinhold Publ. Co., New York. 1923 p.

Corner, E. J. H., 1954, The evolution of tropical forest, p. 34-46. In J. Huxley, A. C. Hardy and E. B. Ford [eds.], Evolution as a process. George Allen and Unwin Ltd., London, England.

Cox, G. W., 1961, The relation of energy requirements of tropical finches to distribution and migration. Ecology 42: 253-266.

Crowell, K. L., 1962, Reduced interspecific competition among the birds of Bermuda. Ecology 43: 75-88.

Darwin, C., 1859, On the origin of species by means of natural selection. First Ed. John Murray, London.

Dobzhansky, Th., 1950, Evolution in the tropics. Am. Scientist 38: 209-221.

Dogiel, V. A., G. K. Petrushevski and Yu. I. Polyanski, 1961, Parasitology of fishes. Oliver and Boyd Ltd., Edinburgh, Scotland. 384 p.

Elton, C. S., 1927, Animal ecology. Sidgwick and Jackson, Ltd., London. 209 p.

    1958, The ecology of invasions by animals and plants. Methuen and Co. Ltd., London. 181 p.

Fischer, A. G., 1960, Latitudinal variations in organic diversity. Evolution 14: 64-81.

Fisher, R. A., 1958, The genetical theory of natural selection. 2nd revised ed. Dover Publ., New York, N. Y. 291 p.

Hairston, N. G., F. E. Smith and L. B. Slobodkin, 1960, Community structure, population control, and competition. Am. Naturalist 94: 421-425.

Hewatt, W. G., 1935, Ecological succession in the Mytilus californianus habitat as observed in Monterey Bay, California. Ecology 16: 244-251.

Hursh, C. R., 1948, Local climate in the Copper Basin of Tennessee as modified by the removal of vegetation. U.S. Dept. Ag. Circ. No. 774: 1-38.

Hutchinson, G. E., 1958, Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.

    1959, Homage to Santa Rosalia or Why are there so many kinds of animals? Am. Naturalist 93: 145-159.

Hutchinson, G. E., and R. H. MacArthur, 1959, A theoretical ecological model of size distributions among species of animals. Am. Naturalist 93: 117-125.

Keast, Allen, 1959, Australian birds: their zoogeography and adaptations to an arid continent. In A. Keast, R. Crocker and C. S. Christian

[eds.], Biogeography and ecology in Australia. Monographiae Biologicae VIII: p. 89-114. Dr. W. Junk, Den Haag, Netherlands.

Klopfer, P. H., 1962, Behavioral aspects of ecology. Prentice-Hall Inc., Englewood Cliffs, New Jersey. 173 p.

Klopfer, P. H., and R. H. MacArthur, 1960, Niche size and faunal diversity. Am. Naturalist 94: 293-300.

1961, On the causes of tropical species diversity: niche overlap. Am. Naturalist 95: 223-226.

MacArthur, R. H., 1955, Fluctuations of animal populations, and a measure of community stability. Ecology 36: 533-536.

1957, On the relative abundance of bird species. Proc. Natl. Acad. Sci. U.S. 43: 293-295.

Margalef, R., 1963, On certain unifying principles in ecology. Am. Naturalist 97: 357-374.

McNab, B. K., 1963, Bioenergetics and the determination of home range size. Am. Naturalist 97: 133-140.

Newell, N. D., 1962, Paleontological gaps and geochronology. J. Paleontol. 36: 592-610.

Odum, E. P., 1959, Fundamentals of ecology. 2nd Ed. W. B. Saunders Co., Philadelphia, Pa. 546 p.

Ovington, J. D., 1962, Quantitative ecology and the woodland ecosystem concept. In Advances in ecological research, Vol. 1: 103-192. Academic Press, London.

Patten, B. C., 1961, Preliminary method for estimating stability in plankton. Science 134, No. 3484: 1010-1011.

Pimentel, D., 1961, Species diversity and insect population outbreaks. Annals Entomol. Soc. Am. 54: 76-86.

Richards, P. W., 1952, The tropical rain forest. Cambridge Univ. Press, London, England. 450 p.

Rogers, W. P., 1962, The nature of parasitism. Academic Press, New York. 287 p.

Slobodkin, L. B., 1961, Growth and regulation of animal populations. Holt, Rinehart and Winston, New York.

Southwood, T. R. E., 1960, The abundance of the Hawaiian trees and the number of their associated insect species. Proc. Hawaiian Entomol. Soc. 27: 299-303.

1961, The number of species of insect associated with various trees. J. Animal Ecol. 30: 1-8.

Teal, J. M., 1962, Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614-624.

Thorson, G., 1957, Bottom communities (sublittoral or shallow shelf). In Treatise on marine ecology and paleoecology, Vol. 1. Geol. Soc. Amer. Memoir 67: 461-534.

Wallace, A. R., 1878, Tropical nature and other essays. MacMillan, London. 356 p.

Wilson, E. O., 1961, The nature of the taxon cycle in the Melanesian ant fauna. Am. Naturalist. 95: 169-193.

Woods Hole Oceanographic Institution, 1952, Marine fouling and its prevention. U.S. Naval Institute, Annapolis, Maryland.

Wright, S., 1940, Breeding structure of populations in relation to speciation.
        Am. Naturalist 74: 232-248.
Yonge, C. M., 1957, Symbiosis.   *In* Treatise on marine ecology and paleo-
        ecology, Vol. 1.   Geol. Soc. Amer. Memoir 67: 429-442.
Yount, J. L., 1956, Factors that control species numbers in Silver Springs,
        Florida.   Limnol. Oceanog. 1: 286-295.