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SPECIES DIVERSITY

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Communities vary widely in the number of species they support. Some, such as the communities in the Arctic tundra, are extremely simple, being composed of only a few species. Others, such as those of tropical rainforests, are exceedingly complex, supporting thousands of different kinds of plants and animals. Perhaps the most familiar of all communities, those of the various temperate-zone woodlands, are intermediate between arctic tundra and tropical rainforest, consisting of only a few hundred plant and animal species. In general, the diversity of life decreases more or less gradually and continuously as one travels either north or south from the equator. The nearly universal occurrence of such "latitudinal gradients" in diversity makes it likely that there is a general explanation for these global trends. The goal of the study of species diversity is to discover why some communities support more species than others and to derive a general theory explaining community structure.

Ecological communities are highly structured. The radiant energy of the sun is trapped by green plants and used to form energy-rich molecules. All animal life is dependent upon the energy stored in these molecules, which is passed from organism to organism during feeding. Each organism uses up some of the energy it receives as it works to maintain and reproduce itself. Because of this and the fact that the transfer of energy from one organism to another is a relatively inefficient process (only about 5 to 15 percent of an organism's energy is available to the next higher trophic level), the amount of energy flowing through the community decreases rapidly as the food web is ascended. These facts have led to the concept of "pyramids" of energy, biomass, and numbers. Furthermore, the available space, water, and sunlight set limits on the amount of primary production possible at any point in time and space. A finite amount of energy can be divided in only so many ways; as a result, there is an upper limit to the number of individual organisms able to coexist at one spot. When all available energy is being used, a community is said to be ecologically "saturated" with individuals. That many natural communities are saturated in this way is evident in the fact that pyramids of energy and numbers are so frequently observed.

Communities can also be saturated with species. In order for populations to make the most efficient use of the great variety of resources in a given habitat, each must specialize as to where and how it fits into the overall structure of the community. Some of the other species may actively compete with it for resources in short supply. A superior competitor or an efficient predator can greatly affect the role a population plays in its community. The position an organismic unit fills in the community is referred to as its "ecological niche." Corollary to the niche concept is the principle of "competitive exclusion," which states that no two species can have identical ecologies: If their niches overlap completely, one population will always be competitively superior to the other; and whenever shared resources are in short supply, a superior competitor should, by outcompeting them, "exclude" all inferior competitors.

Thus ecologists studying species diversity are interested in discovering (1) the ways in which the organisms in any given community differ, and (2) how different they must be to avoid competitive exclusion. Many of the means by which various organisms divide up environmental resources are strikingly obvious. Some animal species are herbivores, others are primary, secondary, and/or tertiary carnivores. Even within each of these trophic levels, numerous different "food niches" are usually apparent: shrews feed upon insects, weasels prey on mice, bobcats eat rabbits; mountain lions and wolves take prey as large as deer and caribou. Another conspicuous way in which species differ is with respect to *when* they are active; there are diurnal, crepuscular, and nocturnal species. This might be called the "time niche." Still another component of the ecological niche is the "place niche"; different species forage in different ways and in different places. The time, place, and food niches are interrelated and intimately interdependent. Ecologists have found that, in nearly every case which has been thoroughly studied, animals occurring together in the same community differ in one or more of these three fundamental components of the niche.

How different must two populations be to avoid competitive exclusion? Or, to put it another way, how much can niches overlap? These are crucial questions currently being asked by ecologists. There are indications that among coexisting congeneric pairs of ecologically similar species (presumably potential competitors) living in the same place, the feeding parts (i.e., mouthparts, beaks) usually differ in size by a factor of at least 1.3. This phenomenon has been called "character displacement." It may prove to be a measure of how different two organisms need be to coexist. We should note, however, that when an environment is unsaturated with individuals, most resources are not in short supply and competition is reduced; for this reason, unsaturated habitats may allow greater niche overlap than saturated habitats.

Diversity may be defined in a number of different ways. The most important element in all definitions is simply the total number of species. Usually diversity indices also take into account the relative abundances of species—diversity being maximal when all species in the community are equally abundant. Another way of saying the same thing is that diversity is high when it is difficult to predict to what species the next individual encountered will belong and low when it is easy to predict what species will be found next. For most of the purposes of our discussion, species diversity may be considered to mean simply *the total number of species in the area under consideration*.

Because species can replace each other in both time and space, there are several distinct components to diversity. For instance, if one habitat contains both a diurnal and a nocturnal fauna and another has only diurnal species, the former should be proportionately more diverse. Thus there is a greater *temporal component* to diversity in the first community. In a similar manner, species often subdivide the environmental mosaic spatially, by living or foraging in different places within it. This is the *spatial component* of diversity. Some organisms, such as birds, separate out into different vertical strata; others, such as ground-dwelling lizards, partition the environment horizontally. Trophic level and food differences afford still another means by which species can sort themselves out. It is no accident that these "components of diversity" correspond respectively to the time, place, and food niches described previously. These three "dimensions" represent fundamental ways in which species have diverged and specialized.

Counts of the number of species are strongly dependent upon the size of the area covered: larger areas almost invariably support more species than smaller ones. However, there is a minimal sample area for every community that will provide a reasonable estimate of the species comprising that community (Fig. 1).

Even when species are counted on areas of equal size, if a sample includes two or more different communities, species diversity will be higher than if it contains only one. Some species are restricted to each community, but usually others are present in both. Because of these shared species, diversity is seldom strictly additive (see Fig. 1). Part of the difference in diversity with change in geographic latitude is due to the existence of more habitats at some localities than at others. Thus there are more different habitat types in Costa Rica than there are in temperate zones. Whereas high mountains in the tropics often support temperate-type communities, true tropical communities can never occur in the colder temperate regions. The presence of more species where there are more habitats is neither surprising nor theoretically very interesting. Latitudinal gradients in community diversity

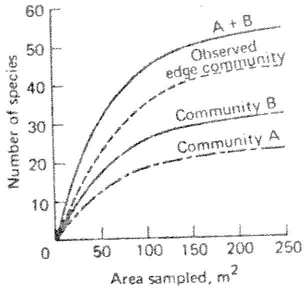

Figure 1 *Some hypothetical "species-area" curves; community A is less diverse than community B. Note that not only are new species added faster as area increases in more diverse communities but also the "minimal area" required to get a reasonable estimate of the community's diversity is larger. Different diversity indices are based upon both the maximal slopes of these curves and on their upper asymptotes. The uppermost curve is the sum of the lower two curves and thus the theoretical maximum species-area curve for an edge community when no species are common to both. Usually some species occur in both communities and sample areas including both fall below this upper limit (dashed line).*

within a given habitat type are inherently more interesting to ecologists, for this is the kind of diversity that is intimately related to community structure.

When communities are truly saturated with species, differences in diversity from place to place can stem from only two factors: (1) One spot could have a greater *variety* of usable resources than another, and/or (2) species might be more similar (i.e., more tightly "packed in") at one place than at another. The former corresponds to the existence of "more niches" and the latter to "smaller niches." On the other hand, when communities are not yet saturated with species, diversity is low because of "empty niches." However, even in the last case it is unlikely that resources will go to waste, since the species which do occur in such a community usually expand their activities to make use of any "empty niche" resources. Finally, a fourth possible way in which diversity can vary from region to region involves a kind of "local oversaturation." This occurs when, for one reason or another, the principle of competitive exclusion fails in one area but not in another. Each of the above influences on diversity has been demonstrated; the problem is to determine their relative importance in nature.

It is often assumed that all communities tend to diversify in time and that, for this reason, older communities support more species than younger ones. Using this argument, the temperate zones are sometimes considered to be impoverished, owing to geologically recent glaciations and other such disturbances. Thus it is often stated that there has not been time enough for species to adapt to temperate zone conditions; neither speciation nor dispersal has been adequate to saturate these habitats with species. If the foregoing were correct, differences in diversity within the temperate zones would be explicable only in terms of the time elapsed since the last disturbance and would therefore be of little ecological interest. However, there is reasonable evidence that many, if not most, habitats are ecologically saturated with species. The dispersal powers of animals and plants appear to be good enough that newly opened habitats seldom exist for very long before appropriate organisms invade.

No ecologist doubts the importance of history as a determinant of exactly which kinds of organisms populate a given region—the faunal differences between continents were recognized long ago and have given rise to the notion of biogeographic regions. Even where communities are saturated with species, the geological history of a region determines precisely which biotic stocks reach the area under consideration. Geological history and geographic location also determine, respectively, the parent soil materials (rock types) and the climate at any given spot. The parent soil materials and the climate interact with the biotic stocks that have been able to reach the region to determine the soil type, plant-life form, and vegetative complexity at a given geographic locality. In addition, the climate, soil, and plant types present in a region set limits upon the amount of primary production possible there. Hence history indirectly determines what kinds of communities are built up during evolutionary time.

All plants and animals have had to evolve varying degrees of restrictions on their activities. A fruit fly is more efficient at finding and using small patches of fallen fruit than is an elephant; normally, elephants only eat fruit when it is exceptionally abundant. It is difficult to imagine an animal which could be as efficient as the fruit fly at using small isolated patches of fruit yet still as good as an elephant at eating various tree leaves. Presumably the same kind of considerations are appropriate at a much finer level; even within the fruit flies, different populations and species have their own zones of maximal efficiency (and hence superiority over other groups). A "jack of all trades" is a "master of none."

Extremely constant environments with their dependable and highly predictable resources foster narrower specializations than do the less predictable, climatically more variable, environments. Because organisms must have wider tolerances and more generalized requirements in variable, unpredictable climates than in more constant, more predictable regions, niches are often broader where climatic stability is low.

The major environmental factors affecting plants are temperature, light, water, and nutrients. The first three are directly determined by climate; the last may often be controlled indirectly by climate. Hence plant populations and plant activities might be expected to be more constant in areas of climatic stability than in areas with more variable climates. Increased stability of climate and vegetation also leads to a more constant environment for animal species. It is well known that considerable areas in the tropics have a much more constant climate than do most temperate regions.

Similarly, more productive environments allow greater specialization than less productive environments. In an area where food is scarce, foraging animals can scarcely afford to bypass potential food items; whereas when food is superabundant, individuals can be more choosy and restrict their diets to only the better kinds of food items. Figure 2 demonstrates this diagrammatically; the lower curve is exactly twice the height of the upper one, reflecting a greater food availability in the hypothetical habitat. The range of different kinds of available resources is identical in both; only the amounts differ. The total area in each segment under the curves is constant, meaning that the energy available to populations (or individuals) using the ranges of resources indicated is the same. Whereas the small standing crop in the upper figure will support only 7 fairly generalized species, the higher standing crop in the lower figure supports 11 more specialized

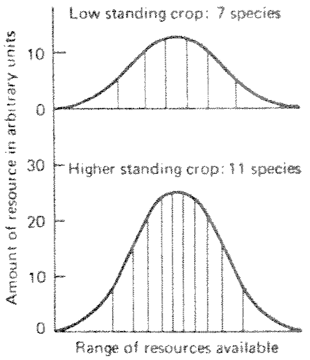

Figure 2 *Graphic portrayal of the way in which more abundant resources support a greater number of species. The horizontal axis represents the different kinds of resources available, ranked in any convenient order (i.e. food items from small to large). The vertical axis is the amount of each type of resource. Both curves cover the same range of available resource types; the lower curve is exactly twice the height of the upper one. All segments marked under both curves (except the tails) include the same absolute amount of resource and therefore contain approximately the same total amount of energy. Where standing crop is low (upper curve), a foraging individual cannot afford to bypass many food objects. However, where standing crop is higher (lower curve), the greater abundance of food items allows individual organisms to be more selective in their feeding. The result is that the same range of resource types will support half again as many species when only the amounts of each resource are doubled.*

species on the same number of different kinds of resources.

Thus both climatic stability and productivity, by allowing component species to reduce their niche size, act to increase the diversity of species. Tropical rainforests are known to be climatically relatively stable and are among the most productive of natural habitats; we have also observed that species which occupy them are often fairly specialized.

Everything else being equal, complex (spatially heterogeneous) habitats should support more species of plants and animals than less complicated (more homogeneous) habitats. This is true simply because there are more different places for species to live in the more highly structured habitats. However, spatial heterogeneity increases species diversity through an increase in the *number* of different resources rather than by a reduction in the average niche size, as with climatic stability and productivity. Figure 3 diagrams the ways in which these and other factors influence species diversity.

There are more species of birds in a forest than in a grassland; furthermore, good bird watchers know that certain kinds of forests have characteristic bird species and that some forests predictably have more species than others. Animal species diversity is often found to be correlated with habitat diversity. This has been nicely demonstrated for birds by R. H. MacArthur and his colleagues. They first measured the leaf surface in three different layers corresponding to grasses and small shrubs (0 to 2 ft), large shrubs and small trees (2 to 25 ft), and large trees (over 25 ft). From these data, they computed an index of habitat complexity which they called "foliage height diversity" [$-\Sigma p_i \log (p_i)$, where p_i is the proportion of the vegetation in each of the three layers]. A convenient

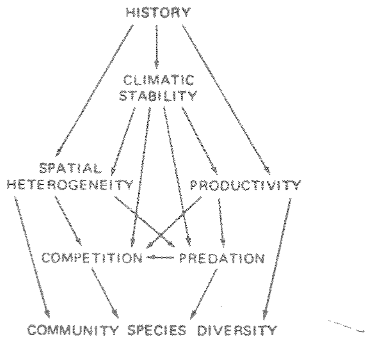

Figure 3 *Schematic diagram illustrating ways in which various factors may influence species diversity (explained more fully in the text). Some of the causal pathways indicated are more important than others, and their relative importance varies from community to community.*

aspect of this index is that it is maximal when the proportion of the vegetation in each of the three layers is the same; that is, foliage height diversity is greatest when exactly one-third of the leaf surface is in each layer. When all the leaf surface is in one layer (as in a meadow or a tall forest with no understory), foliage height diversity is zero. MacArthur then used the same index method to compute bird species diversity. His data are plotted in Figure 4 as solid circles.

H. F. Recher performed the same kind of analysis on five forested areas in eastern Australia (diamonds in Fig. 4) and found that bird species diversity in Australia was correlated with foliage height diversity in almost exactly the same way as in North America. Because the Australian birds and plants have evolved completely independently of the North American ones, Recher's results strongly support the notion that both continents are saturated with species. Moreover, his data suggest that the total "bird niche space" and the average niche size are probably similar on the two continents, even though the "niche

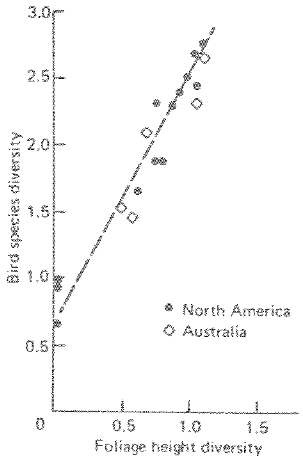

Figure 4 *Correlation between foliage height diversity and bird species diversity. MacArthur's North American habitats are shown as circles, Recher's Australian ones as diamonds. This is perhaps the best evidence that communities are sometimes saturated with species. See the text for a discussion. (Adapted from H. F. Recher,* Am. Naturalist 103: *75–80 (1969).)*

space" is fragmented in a fundamentally different way in Australia, where, for example, parrots and honeyeaters are conspicuous elements of the avifauna, whereas woodpeckers and hummingbirds are completely absent. The "total bird niche space" may be compared to a deck of cards; there are only a certain number of ways in which this space can be exploited. Each bird species or population has its own way of doing things, or its own "hand" of cards, determined in part by what the other bird populations in its community are doing. Many different combinations of the various avian ecological activities are possible; an Australian honeyeater might combine aspects of the food and place niches used in North America by both hummingbirds and warblers. Indeed, the geological history of an area, by determining which plant and animal stocks have reached the region, often has pronounced effects upon community structure.

Sometimes, on the other hand, a particular niche appears to be determined in a more or less discrete rather than continuous way. We sometimes see this when the stocks which have invaded two different areas and the environment of the areas are comparable; under such circumstances, natural selection seems to have followed a similar path in independently evolved organisms. Many specific instances of such "convergent evolution" are known, some of them quite remarkable (Fig. 5). The most striking examples of evolutionary convergence usually occur either in (1) relatively simple communities where biotic interactions are simple and the number of different ways of exploiting the environment are few, or (2) under conditions where the selective pressures for the achievement of a particular mode of existence appear to be exceptionally strong. The end products of both kinds of forces, which may of course act together in some situations, are shown in Figure 5. Such convergent species pairs, occupants of roughly similar niches in different parts of the world, have been called *ecologic equivalents*.

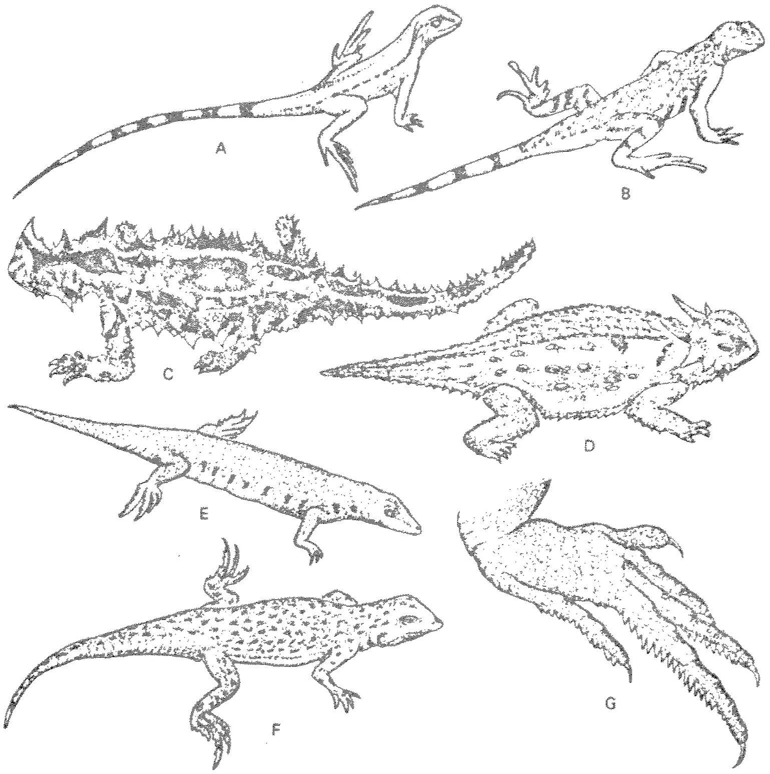

Figure 5 *Several examples of evolutionary convergence in desert lizards. A, an Australian agamid,* Amphibolurus cristatus*; B, the North American iguanid,* Callisaurus draconoides. *Both forage in the open sun between shrubs and eat similar foods; the stance shown, with the head and body elevated on the front legs, is characteristic and presumably related to foraging in the open. Both have long hind legs and are very fast runners. C, the Australian agamid,* Moloch horridus*; D, a North American iguanid,* Phrynosoma coronatum. *Both have specialized diets consisting mostly of ants, are cryptically colored and spiny, and are fairly slow-moving. E, the African skink* Scincus scincus*; F, the North American iguanid,* Uma scoparia. *Both are adapted to live in sandy desert areas, with their flattened heads and bodies and enlarged scales fringing the toes on their hind feet. These lizards forage above ground but quickly "dive" into the sand when danger threatens. G, An enlarged view of the hind foot of* Uma. *Toe lamellae have been similarly lengthened independently in at least four different families of lizards, the members of which invariably live on loose sandy soils.*

The extent to which predators reduce competition between their various prey species by cropping prey populations is an intriguing question, for the effect should be a greater niche overlap between prey species and hence greater community species diversity. Such "predator-induced" diversity was demonstrated by R. T. Paine in a simple ecological experiment. Paine removed all individuals of the top predator, a starfish, from a rocky intertidal seashore community, and observed a drastic reduction (from 15 to 8) in the number of species remaining. Paine noted that a slow-growing mussel species crowded out and excluded several other, faster-growing invertebrate species. He suggested that the starfish kept down the slow-growing mussel's population size and left open space for colonization by faster-growing invertebrates, thereby preventing competitive exclusion and enhancing species diversity.

There is further evidence that predators may increase species diversity: frequently, more diverse communities support proportionately more individuals or more species of predatory animals than do less diverse communities. This has been found to be true of marine invertebrate, marine fish, and desert lizard assemblages (portions of communities). Should such shifts in trophic structure prove to be a widespread phenomenon, we would have to conclude that the pyramid of energy would be basically different (steeper) in more diverse communities. However, at present this is still unknown.

In the temperate zones, where climate is usually variable and often unpredictable, large numbers of organisms are frequently killed during catastrophic environmental changes. A good example is the mass die-off of wintering birds during sudden cold snaps. Such mortality is often not very directed; whether an individual lives or dies has relatively little to do with his genotype, the size of his population, or his competitive abilities. Hence natural selection favors high reproductive rates rather than competitive ability. This kind of selective regime, tending to favor accelerated development, earlier reproduction, and/or increased fecundity, has been called "*r* selection" (because it maximizes the intrinsic rate of natural increase, usually designated by *r*).

By way of contrast, in the tropics, where climate is fairly constant and usually predictable, such catastrophic mass mortality is rare. More constant environments lead to more constant population sizes, with the result that both interspecific and intraspecific competition are keener in the tropics than they are in the temperate zones. Mortality is usually more directed, being dependent upon an individual's genotype, competitive ability, and the size of his population. Hence selection works to increase competitive abilities in the tropics; since an organism that can survive and reproduce on a lower threshold amount of any resource is generally a superior competitor, selection tends to increase the efficiency with which individual organisms exploit the environment. Because this type of selection results in more individual organisms per unit of resource, it increases the "carrying capacity" (usually designated by *K*) of the environment. For this reason, it has been called "*K* selection."

The dichotomy between *r* and *K* selection is in some ways artificial, since both must be occurring simultaneously in most populations, but it does serve to emphasize an important latitudinal difference in selective pressures which is related to species diversity. It is noteworthy that *K* selection results in greater specialization; "smaller niches" in turn give rise to more diverse communities. The characteristics of *r* and *K* selection are summarized in Table 1.

Simple communities with only a few species such as the arctic tundra community frequently show marked fluctuations in the population sizes of their component species. More diverse communities such as the tropical rainforests are usually relatively stable in time. Diversity and stability often go hand in hand. The reason for this correlation is simply that in a more complex community there are numerous alternative pathways of energy flow; when any species gets too common, it is likely to be preyed upon by predators that normally do not eat it. Man's traditional method of agriculture, the growing of "pure stands" of one species, may well result in some of the least stable of all possible communities. It is no wonder that pesticides seem to be necessary to prevent mass outbreaks of insect pests!

In brief summary, it has been demonstrated that a wide variety of factors can influence community species diversity. History, climate, spatial heterogeneity, productivity, predation, and competition all work together in a complex and as yet poorly understood way to regulate the number of species and their relative abundances in any community.

TABLE 1. OUTLINE OF THE DIFFERENCES BETWEEN *r* SELECTION AND *K* SELECTION, SHOWING HOW THEY AFFECT COMMUNITY DIVERSITY*

	r selection	*K* selection
Where	Temperate zones	Tropics
Climate	Variable or unpredictable	Fairly constant or predictable
Mortality	Catastrophic, nondirected, density-independent	More directed, density-dependent
Population size	Variable	Constant (equilibrium)
Competition	Variable, often lax	Usually keen
Selection	Favors rapid development, high reproductive rate	Favors competitive ability and increased efficiency (lower resource thresholds)
Niche form	Broader niches	Narrow niches
Community diversity	Low	High

*Usually both kinds of selection occur simultaneously, but the relative importance of each may vary considerably.

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