only compound confusion. Scientific concepts develop by interaction between (a) applications that indicate directions of greatest usefulness and (b) periodic efforts at formal statement and systematic interrelation of concepts. Our effort had as its purpose strengthening the usefulness of the concepts discussed by clarifying their relations to one another and stating them in ways appropriate for research using measurements of population variables. The best test of what we have written will be its usefulness in application. We hope that application may show that our formulation of three valuable concepts—niche, habitat, and ecotope—will in practice serve well both the field researcher and the ecological and evolutionary theorist.

CHAPTER 8

Biological Diversity in Ecology

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In the field of ecology the term *diversity* is commonly used to describe the assemblage of species that interact . . . and form . . . a community. Species in the complex do not merely respond to a particular environment but create new conditions through their interactions with each other. For example, one species may modify an environmental factor such as light so that another species, or group of species, can live more successfully, or one species may be the food source for another or produce oxygen by photosynthesis, which is necessary for respiration of both. Through such interactions the community develops its identity and carries out its characteristic functions.

Diversity is a generalized term that refers to the structure of the community. In a sense, it expresses the genetic variability existing in the taxa that occur together and, therefore, the adaptive capacity of the assemblage. Thus, the measure of diversity is not merely a count of presence but rather it is a measure of the structural and functional interactions of the community.

When one considers the structure of communities of organisms, the first question that arises after one has the list of species in hand is why are there so many species with such different characteristics? Reasoning from our human experience, we might think that a single-species community structure might be more efficient. However, this is not the case. For example, at the herbivore level of an aquatic community we might find insects and fish of a variety of species, genera, and families feeding upon the plants. In another comparable community we might find protozoa, as well as insects and fish, serving as herbivores. Intuitively one would say that the gene pool present in these herbivore taxa was greater in the second case than in the first. Furthermore, the second set might consume a greater variety in size and taste preference. Its tolerance to natural products produced by various plants also might be broader; therefore, nutrient transfer from the primary production level might be more, not less, efficient (Freeland and Jansen 1974).

In general we find that species seem to prefer a variety of food rather than a

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single species. Of course, a notable exception is parasitism. In the aquatic world, organisms from protozoa to fish generally prefer many species of diatoms as a food source. In contrast, blue-green algae and green algae such as *Cladophora glomerata* are the least preferred food sources. This may be due to lower food value and the presence of toxic chemicals in *Cladophora.* These data indicate that the characteristics of the prey as well as the preferences of the predator determine the efficiency of nutrient transfer in a diverse community.

One might consider diversity of organisms from a functional rather than a taxonomic viewpoint, although usually they go hand in hand. That is, in an environment that is favorable for many species, one will find an association composed of a large number of species each of which can utilize the environment in a somewhat different way and thus they can cosurvive. MacArthur (1969) and others have pointed out that in such a case there may be a large invasion rate of species into the favorable habitat, with the result that more species will become established and will ultimately pack the area with the greatest number of species that can coexist by utilizing the resources in different ways. From this standpoint the number of species gives us the most information about the diversity of the environment. The most diverse environments exposed an adequate time to invasion would be characterized by many species with relatively small populations. The presence of disproportionately large populations might mean that the environment or the multidimensional habitats were not as diverse as they might be if there were more species with smaller populations, and therefore less redundancy. For example, in a riffle of a stream there is a range of size of rocks that will support the greatest number of species if they are distributed so as to produce a large variety of current patterns and protection against predators. Rocks that are too small roll or are shifted too much and are poor habitats. Rocks that are too large will produce a redundancy of habitats and will not support any more species, but may support more individuals of the same species. Thus, the diversity of organisms tells us about the diversity of the environment and vice versa.

In considering diversity of a community it is also relevant to know whether the species are mainly species with high population growth rates and high productivity ("r" selected species) or "K" species, which are more efficient at utilizing resources and have lower rates of population growth and production (MacArthur and Wilson 1967). The "r" species often have short life cycles and may use resources less efficiently than "K" selected species. Most communities have a variety of "r" and "K" species. Areas in which most of the ecological factors are highly variable tend to have mostly "r" selected species, and species replacement is correlated with the shifting environment. Typically the existing species are not eliminated by unfavorable environmental conditions, but are greatly reduced in population size or occur in life-cycle stages that are dormant, cryptic, or are not collectable.

One may also think of diversity of species in the terms of their ability to disperse and invade communities (Diamond 1975). Very stable "S" species are found only in species-rich communities and represent the extreme of "K" selection in MacArthur and Wilson's (1967) terminology. Then follows a series—A-B-C-D tramps—and finally supertramps that are widely distributed, do well in harsh environments, but can maintain themselves in species-rich communities.

Any discussion of diversity in ecosystems will find itself intertwined with the concept of stability (see Levin 1970; Botkin and Sobel 1975). In the last thirty years the terms *diversity* and *stability* have been the subjects of many scientific papers in response to questions such as: Why are there so many species? (Hutchinson 1958a); to findings by Patrick (1949) that in similar ecological habitats the numbers of species were similar and remained similar over time if severe perturbation did not occur; and to the Odums' (E. Odum 1962; H. Odum 1957) concepts of community homeostasis derived from study of the energy flow through communities and the relationship between community structure and function. It has often been proposed that a direct relationship exists between diversity and stability, and research on this relationship reached a peak with the 1969 Brookhaven Symposium on *Diversity and Stability in Ecological Systems* (Woodwell and Smith, eds.).

Stability has many definitions but the two that pertain to our use are, first, a quality of endurance without alteration and, second, the ability to return to the original form after alteration. It is this double meaning that has contributed to the different interpretations of the meaning of stability in considering community structure.

Stable communities composed of a few species are found in harsh environments such as the *Spartina* marshes of the east coast of the United States. Niering (personal communication) has found by boring these marshes that the same species have been dominant over hundreds of years. There are many reasons why this is true. For example, the concentration of salt in the water and its high variability and the very high evapotranspiration rates in summer limit the number of species that can establish themselves in this environment. A second consideration is the characteristics of the *Spartina* plants. The species are perennials with well-branched rhizomes. In *Spartina alterniflora,* the most common species, the rhizomes are 4–7 mm thick. These rhizomes and roots form a tough mat and thus reduce the invasion of other species. These various factors would tend to mitigate invasion and, coupled with the harsh environment, produce stability of the species over time. This is an example of a highly productive community, in terms of carbon fixed, that is simple and stable.

A similar type of a relatively stable simple community has been observed in polluted streams. In this condition the nutrients may be adequate to support a diversified species community, but the pollutant contains a toxic substance in concentrations that only a few species can tolerate. These grow well and dominate the stream over time. An example is the dominant growth of *Stigeoclonium lubricum* in Lititz Run (Lancaster County, Pennsylvania). The stream receives a variety of toxic materials, particularly heavy metals. The absence of predators, which are killed by the toxic substances, allows the species to develop large standing crops. As long as the pollutant is released this simplified and productive (in terms of ^{14}C fixation) community is stable. Under natural conditions in this drainage basin other species are common and *Stigeoclonium lubricum* does not develop large populations.

These are examples of what might be classed as communities that live in harsh environments where stability is not correlated with diversity. There are, of course, other examples where stability and diversity in the community are highly correlated. Tropical rain forests and coral reefs are often cited as examples.

The other definition of stability—that is, the ability to return to the original state after displacement—is exemplified by communities found in natural streams. These communities are composed of many species forming interlocking chains or nets of nutrient transfer. Typically the species are "r" selection species, although a few may be "K" selection types. The communities are in a quasi-equilibrium state with significant inputs and outputs. The stream is a multidimensional resource area, with the resources fluctuating in an unpredictable manner. The species with short turnover time rapidly adjust to the variable environment. Usually the number of species performing various functions remains fairly similar, although the kinds of species vary greatly in similar ecological habitats at the same time or in the same habitat during the same season over time (Patrick et al., 1969). Furthermore, these stream communities—because of the large available species pool, rapid invasion rates, and inputs and outputs—can recover rather quickly from severe perturbation; whereas smaller perturbations, such as increased nutrients, produce a readjustment in population sizes of the existing species rather than a shift in species.

McNaughton (1977) similarly found in his studies of the grassland of the Serengeti-Mara in Tanzania and Kenya that areas with large numbers of species adjust to the perturbation of chemical fertilization of the vegetation by shifts in the population sizes rather than shifts in species. Such communities were more stable than those with fewer species. It is the natural oscillations of the multidimensional environment that help to maintain the large number of species, which in turn promotes functional stability.

From these comments it is evident that when one talks about species diversity one may be concerned with taxonomic diversity, functional diversity in the community, diversity in autecology of the species, or in reproductive strategy.

In each case the primary datum is a count of species and individuals, and depending upon our knowledge of the taxa these counts may represent any relevant biological or ecological feature of the community.

It is interesting to note that the formation of diverse communities, whether they are bird or diatom communities, involves the same factors—that is, size of species pool, invasion rate, size and diversity of the area to be invaded (MacArthur and Wilson 1963). Furthermore, the maintenance of a diverse community is dependent on density-independent factors, density-dependent factors, and predator pressure. The relative importance of these forces depends on the type of community being studied. A community in or near equilibrium is usually more dependent on density-dependent factors and predator pressure for its maintenance, whereas a quasi-equilibrium community (with substantial inputs and outputs as compared with storage) often is more dependent on the type of oscillation of density-independent factors and on predator pressure for its maintenance.