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## Biological Diversity in an Ecological Context

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### INTRODUCTION

The most common definitions of biological diversity focus on state variables, such as genes, species, and communities, but processes, such as gene flow, survivorship, competition, and energy flow, ultimately determine the nature of these state variables and are critical to the survival of biological diversity itself (Noss 1990). The relationship between biological diversity, ecological process, and human activities is now a critical concern for scientists and policy makers (Lubchenco et al. 1991).

In this chapter, we will discuss the history of the biological diversity issue, elaborate more fully on a definition, and briefly describe the value of and threats to diversity. We will then address the general linkage between ecological processes and biological diversity. Because detecting change in diversity is critical to understanding human effects, we will turn to a discussion of major issues in the measurement of biological diversity.

### THE BIOLOGICAL DIVERSITY ISSUE

#### A Historical Perspective

Although conservationists have been concerned with the survival of the individual species for more than 100 years, the goal of conserving “biological diversity” represents a shifted conservation focus that has occurred during the past two decades. The past emphasis has been on three separate goals. We will illustrate these with examples from the United States, although the three categories are universal elements of conservation philosophies.

The first of these conservation goals was the protection of pristine natural areas, with the implicit assumption that this would result in the survival of the species found there. In the United States, this philosophy had its roots in the mid-1800’s through the writings of individuals like John Muir and Henry David Thoreau. The grounds for preservation in these early years were usually aesthetic, rather than biological, and a scientific understanding of such issues as minimum viable populations and ecosystem dynamics was

lacking (Nash 1976). Today, conservationists continue to place emphasis on protecting large wilderness areas, but cite scientific, as well as aesthetic, criteria.

A second emphasis in conservation has been on the survival of particular species groups perceived to be valuable (e.g., wildlife, fisheries, and forest trees, dating from the mid-1800's in the United States), vulnerable (e.g., endangered species, dating from the mid-1950's), or aesthetically pleasing (e.g., wildflowers and the charismatic megavertebrates, dating from the early 1900's). Legislation in the United States to protect fisheries and wildlife dates from the late 1800's and early 1900's, but the culmination of the species-oriented approach at the Federal level was the passage of the Endangered Species Act in 1973. Interest in endangered species also heightened the awareness of the importance of genetic diversity and minimum viable population sizes (Frankel and Soule 1981; Soule and Simberloff 1986; Burgman, Akcakaya, and Loew 1988). Conservation of endangered species has also introduced the idea that *ex situ* management, intensive management in artificial systems, and direct human intervention in natural populations were legitimate conservation means to insure endangered species survival (Templeton and Read 1983; Falk and McMahan 1988; Jordan, Peters, and Allen 1988).

Protection of endangered species has mostly focused on larger animals and higher plants, with less attention to more obscure groups, such as soil insects and fungi, which may be critical to ecological function. Proponents have argued that protection of large, wide-ranging animals would insure, through habitat protection, the survival of these more obscure species, a suggestion that has not been critically investigated. Some have argued that species with key ecosystem roles should be the highest priority for conservation efforts (e.g., Terborgh 1988).

A third conservation emphasis has been on the use of resources in a way that could be continued with no long-term decline in the productivity, thus producing a "sustained yield" of renewable resources (Nash 1976). In the United States, this form of conservation was formulated by individuals who supported resource use, but saw the exploitive and destructive "mining" of natural resources of the late 1800's as eroding the resource base. Conservation in this sense has often resulted in some level of regulation for use of wildlife, fisheries, and forests.

Current interest in biological diversity is, however, more than the sum of interest in pristine natural areas, special groups of species, and sustained productivity of natural resources. Since 1980, awareness of the biological diversity issue has been heightened by increased threats to tropical ecosystems. More than 50 percent of all terrestrial species are found in the tropics, with the rate of habitat loss being estimated at greater than 1 percent per year (Myers 1988). It has been estimated that this habitat loss is causing 1,500-10,000 species to become extinct per year (Wilson 1987; Myers 1988). The rate of species loss is currently much faster than the rate at which new species are discovered and described (Wilson 1987; Ehrlich and Wilson 1991).

The current era of air pollution and global climate change has further brought into question historical conservation emphases. The number of remaining pristine areas is becoming ever fewer, and even those that are fully protected from direct human disturbance will see major changes if global warming occurs (Peters 1988). A host of other direct and indirect human impacts also permeate wilderness areas (White and Bratton 1980). In addition, we have learned that some biological diversity can be protected in the midst of human activity and that biological diversity can be reintroduced to damaged lands in ecological restoration (Jordan, Peters, and Allen 1988). Further, a narrow focus on legally endangered species, including the use of such methods as *ex situ* conservation and

the protection of small areas of critical habitat for rare species, would leave much of biological diversity unprotected until individual species approached extinction.

In summary, contemporary developments have served to focus attention on biological diversity as a property to be conserved, whether in pristine natural areas, intensively managed and artificial populations, or areas of human resource use. This new emphasis has served to diversify acceptable conservation tactics (e.g., the “eight paths” of Soule 1991), has raised awareness about the tremendous biological diversity of our planet, and has underscored our poor understanding of both the amount of diversity present and the ecological processes that support or depend upon this diversity. At present, estimates of the total number of species range over an order of magnitude (4-30 million), of which only 1.4 million have been formally described by the scientific community (Ehrlich and Wilson 1991; Erwin 1988). Biologically rich (e.g., the tropics) or remote (e.g., the ocean floor) habitats are poorly known taxonomically (Ehrlich and Wilson 1991; Ray 1988). Ecologically important but obscure groups such as soil insects, fungi, and bacteria are also poorly known.

### **A Working Definition of Biological Diversity**

The phrase “biological diversity” obviously implies enumeration of the variety in living things. However, an account of biological diversity must be more than an enumeration of the living things themselves; it must include the structures and processes that maintain this diversity (Franklin 1988; Noss 1990), as well as levels of organization above and below the species level. Noss (1990) discussed three attributes of biological diversity: composition (the number of “things”—e.g., alleles, species, or ecosystems); structure (the physical arrangement of the “things”—e.g., biomass distribution within a forest or ecosystem arrangement on a landscape); and function (the natural processes). The variety of living things would not exist without a host of ecological processes, such as natural disturbance regimes, nutrient transformations, symbioses, and food webs. Because the species and individuals are obvious, while the natural processes are not, the phrase “biological diversity,” if superficially applied, has the danger of focusing attention away from the underlying processes and dynamics.

The structure of ecosystems and landscapes is critical to the maintenance of biological diversity (Franklin 1988). Two forests may be dominated by the same tree species but have very different structures, with such features as standing dead trees, fallen logs, and soil leaf litter playing a major role in defining animal habitat, nutrient cycling, and the interface with stream ecosystems within riparian ecosystems. The soil compartment of ecosystems, influenced by geology, mineral substrates, the deposition of organic matter, and the subterranean activities of plants and animals, is a key aspect of ecosystem structure and function and one that is potentially influenced by pollutant deposition. On a landscape scale, two areas may possess similar ecosystems and yet be very different in the physical arrangement of those ecosystems, with this physical arrangement influencing ecosystem processes such as animal migration and the spread of disturbance (Gardner et al. 1989). Noss and Harris (1986) have described the effects of landscape structure on ecological function and retention of biological diversity.

Although the species level is often the most obvious element of biological diversity, genetic and ecosystem diversity are also critical. It has been argued that genetic diversity is the foundation of all other aspects of biodiversity; ultimately, it supplies the abilities that produce functioning ecosystems. Small population sizes can result in reduced genetic

diversity, lowered fitness, and increased extinction risk (e.g., Frankel and Soule 1981; Schonewald-Cox et al. 1983), although genetic stochasticity may be outweighed as short-term risks by demographic and environmental stochasticity in many populations (Menges 1986). Further, not all populations of a species are equivalent; the genetic variation among populations can be the basis of both future evolution and response to environmental change. Human impact results in substantial loss in the number of original populations and, presumably, genetic diversity, within a species (Peet, Glenn-Lewin, and Wolf 1983). Loss of alleles can remove variation that is critical in times of change in the physical or biological environment. All of these perspectives suggest that biological impoverishment can proceed on the genetic level in the absence of immediate species extinctions.

Natural variation in ecosystems across a landscape or region is also important. Ignoring for the moment cases of spatial constraint (see below), the distribution of this variation is ultimately controlled by environment, including the dynamics of disturbance regimes. Thus, a wilderness landscape of varying topography and habitats contains ecosystems for a range of environments and, thus, provides for response to environmental change.

Finally, the most efficient way to protect species is through protection of the ecosystems in which they occur.

An undue emphasis on the number of species does not take into account the distinctiveness of biological lineages nor the fact that some groups are rapidly evolving and others are more static. Vane-Wright, Humphries, and Williams (1991) and Erwin (1991) advocate conservation strategies based on information about lineages and evolutionary rate, rather than the equal consideration of all species. A lineage that is monotypic depends on the survival of its one species; a lineage with thousands of species does not depend as greatly on each of its species. Thus, some have argued for the conservation of unique lineages and taxa of higher rank (i.e., making sure each genus, family, order, or taxon of higher rank is conserved). The proposition that the amount of diversity varies with taxonomic level is illustrated by comparisons between marine and terrestrial systems: the oceans possess a greater diversity of higher level animal taxa (e.g., there are more distinct lineages at the phylum level) than do tropical rainforests, where diversity is concentrated at the species level (Ray 1988). However, a greater number of species at lower ranks (within a genus or family) may mean that the group is rapidly evolving and has high evolutionary potential, while monotypic categories may represent “living fossils” with great uniqueness but little potential (Erwin 1991). Arguments based on the uniqueness of a lineage and the conservation of taxa of higher rank and evolutionary potential sometimes conflict, but all support the idea that the number of species need not be the sole conservation goal.

In light of this discussion, we define biological diversity in the broadest sense as the variety of life and life processes at all organizational levels, with usual emphasis on: (1) genetic diversity within species, other taxa, or populations and/or the sum of genetic diversity within a community or geographic area; (2) species or other taxon diversity within a community or geographic area; and (3) community or ecosystem diversity across a landscape or larger region.

Our working definition emphasizes state variables (i.e., “things,” such as genes, species, communities, biomass, composition, and structure), but processes (e.g., gene flow, survivorship, reproduction, migration, competition, energy flow, and mineral cycling) provide the critical bases for and are themselves derived from these state variables. Although states and processes are both part of biological diversity, state variables, such as genetic diversity, species richness, and community pattern, are often the easiest elements of diversity to measure, particularly in short-term studies that essentially take a “snap-shot” of

the state of nature. State variables are also usually the focus of concern about biological impoverishment. Variety in genes, species, and ecosystems is threatened; this variety, particularly for genes and species, is the unique product of past evolution and is impossible to recover once lost. Further, as we will discuss later, the exact correspondence between state variables and ecological function remains an area for continued research. This, again, suggests that documenting change in biological diversity centers on the state variables.

### **The Value of Biodiversity**

Utilitarian arguments are those that base the conservation of biological diversity on current or future human benefit. These benefits may be material or nonmaterial, and economic or noneconomic. Material benefits include ones with direct economic value (e.g., genetic resources for crop plants, tourism and nature conservation, and sources of medicines) and ones without economic benefit (e.g., biological diversity as a reservoir of genetic resources for unknown future needs). Some economic benefits are hard to quantify; e.g., the economic value of clean air is difficult to define because it is not “available” in the marketplace. Environmental quality, ecosystem function, and ecological “services” depend on biological variety in the sense that roles such as organic production, decomposition, and chemical transformation depend on biological variety. Nonmaterial benefits, which include the psychological and spiritual benefits of natural beauty and wilderness, may have economic importance (e.g., tourism).

In terms of economic, material benefits, biological diversity provides potentially useful medicines, foods, chemical products, and fuels. Natural compounds have been the template for the synthesis of many medicines; even if we ignore this past use of biological diversity, 25 percent of U.S. prescription drugs (for a value of approximately \$4.5 billion per year) have at least one ingredient that is extracted directly from higher plants (Farnsworth 1988). Only a small percentage of the world’s plant species have been tested for usefulness and are being used at present (Plotkin 1988). Although at least 75,000 higher plants have edible parts (at least 25 percent of all higher plant species), only 7,000 have had recorded use, and the bulk of the human diet today comes from only 20 species (Plotkin 1988; Veitmeyer 1986).

Although utilitarian arguments are often the most politically compelling, there is a danger in basing conservation solely on these grounds because this can wrongly equate the importance of biological diversity with short-term economic benefits, whereas human survival and quality of life also are utilitarian values, albeit ones that require a longer term view. Alternatives to utilitarian arguments are such ideas as species rights (Norton 1988) and the land ethic (Leopold 1949).

### **Threats to Biological Diversity**

Threats to biological diversity are ultimately driven by the growth of human population and by the per capita amount of impact. There are five major categories of threats:

1. Direct species loss (e.g., large predators and herbivores, vulnerable because of low population density and dependence on large areas of undisturbed land or because of unusual behaviors).
2. Habitat loss and fragmentation (Harris 1984), with the loss often being nonrandom—the most productive sites are preferentially used.

3. Exotic species invasions; i.e., the purposeful and accidental release of species from natural barriers (Elton 1958).
4. Change in natural processes; i.e., human control of natural dynamic processes, such as fire, hydrology, and coastal processes (White and Bratton 1980; White 1987).
5. Air and water pollution (alteration of the physical and chemical environment).

Because of the magnitude of these threats, particularly habitat loss in the tropics, contemporary extinction rates are thought to be 2-3 orders of magnitude higher than natural background rates (Raup 1988; see also discussion in Jablonski 1991). Species can be quickly lost due to human influence ( $10^{0-2}$  years) but are generally slow to evolve ( $10^{3-5}$  years). In addition, each species is unique; once lost, that exact configuration of genetic structure is lost forever. This introduces a large risk and an asymmetry into the process: losses cannot be easily reversed. Further, local losses in diversity can either be global or not (that is, the lost species or genotypes may persist in other places); on the other hand, local increases in diversity due to human activities (migration of new species or genotypes due to climatic warming) are almost never global increases in diversity.

The threats listed above combine in nature. In particular, the habitat loss and fragmentation influence make more severe the loss of biological diversity caused by the other four categories of threats. If the time course of environmental change is fast, sensitive species will be lost before tolerant species invade.

## **BIOLOGICAL DIVERSITY IN AN ECOLOGICAL CONTEXT**

### **Species Richness and Ecological Function**

Impacts to biological diversity and ecosystems can consist of any of the following combinations: impacts to diversity may result in a change in ecological function and/or a loss of ecological integrity; impacts to ecosystem function may result in changes to diversity; and changes to diversity, whether or not these affect ecological function, may be viewed as impacts in their own right. These cases overlap when ecological function changes and diversity is lost, but there are important differences in emphasis. The first view places emphasis on the role of diversity in such attributes as ecosystem health and stability, the second view places emphasis on the role of ecosystem function in supporting diversity, and the last simply sees any loss of diversity as a problem in and of itself.

Functioning ecosystems depend on the presence of a variety of primary producers, decomposers, other heterotrophs, and symbionts. It frequently has been conjectured that variety is necessary within these functional groups, as it conveys a robustness or stability to ecosystems in the face of environmental change. This argument also predicts that monocultures will be more vulnerable to change, with external forces quickly producing instability. Such ideas have a long history in ecology (Odum 1969; Ehrlich and Ehrlich 1981).

While these statements must be true at some level, the exact correspondence between biological diversity and ecological function requires continued research. Part of the problem lies in the definition and quantitative measure of such terms as ecological function, health, stability, balance, and integrity (e.g., Norse 1990). While ecosystems must have organisms that carry out basic processes—carbon fixation, mineralization, and nutrient transformations—no one definition of terms like ecosystem “health” exists (Noss 1990).

Karr (1990) has defined biological integrity as “the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition and functional organization comparable to that of a natural habitat of the region” and further states that “a biological system . . . can be considered healthy when its inherent potential is realized, its condition [relatively] stable, its capacity for self-repair when perturbed is preserved, and minimal external support for management is needed.” The phrases “comparable to that of a natural habitat” and “inherent potential” show that these definitions are based on comparisons to an original or undisturbed condition, rather than on an underlying theory that directly predicts diversity from integrity or vice versa.

Beyond the definition and measurement of ecological function, an additional problem lies in defining the expected relationship between diversity and function. Does the importance of biological diversity to ecosystem function require the demonstration of a one-to-one predictive relationship between diversity and integrity? At what time and space scales should this question be asked? In short-term observations, some species and genotypes may appear redundant or extraneous to immediate ecological function, while these same elements might be critical components of diversity over longer time periods. A final problem is that genetic, species, and ecosystem levels of biological diversity are not necessarily coupled in their responses to human-caused changes. Some may even be negatively correlated. For example, a decrease in species diversity within a community may lead to an increase in genetic diversity within the surviving species if lowered competition favors the survival of additional genotypes.

We summarize these points by saying that while ecological function and diversity are linked and while diversity is required for long-term ecological and evolutionary flexibility, a precise relationship predicting changes in integrity from changes in diversity or vice versa has not yet been shown; this subject remains an exciting area for future research. In the absence of a clearer understanding, an alternative is to follow Karr (1990) by viewing human-caused changes in diversity and ecological function as departures from the original condition.

### **Contingency, Environment, and Biological Diversity**

The amount of biological diversity (e.g., the number of species or the amount of genetic diversity) existing in any area is partially contingent on the past course of evolution. Given the quickness of extinction compared to the origin and spread of new species, the present amount of species and genetic diversity in a given setting is probably not in equilibrium with the present environment. The importance of history may hinder the development of generalities in investigations of both the ecological role of biological diversity and the impacts of pollution because ecosystems, even in similar environmental settings, may have had different amounts of original biological diversity. For example, in the North Temperate zone, diversity (both at the species and genetic level) in many systems may still be recovering from the last advance of glacial ice some 20,000 years ago (Davis 1981). It has been suggested that air pollution impacts on red spruce (*Picea rubens*) in the Appalachians were more severe than on other species because of low genetic diversity in red spruce, a condition that may have resulted from the restriction of this species to a small Pleistocene refugium (Johnson et al., in press).

Below we will develop two contrasting concepts for describing how species richness is distributed spatially, one based on environment-species relations and the other on spatial and temporal constraint.

## The Niche Difference Model

Species have different physiological tolerances to the physical and biological environment and these determine overall distribution and local abundance. Models of this type fall into two subcategories: equilibrium competition-based models and nonequilibrium models (Pickett 1980). In equilibrium models, time is sufficient for species occurrences to reflect niche differences and competitive relations. In nonequilibrium models, time is insufficient for competitive sorting of species, and a component of local diversity (i.e., within communities) is due to the persistence of noncompetitive species or genotypes, and, thus, expansion of species-realized niche space (Peet, Glenn-Lewin, and Wolf 1983).

Among competing organisms, the conjectured basis for niche differences is the idea of evolutionary tradeoffs, which result in species differing in tolerance, competitive ability, and life history strategy (MacArthur and Wilson 1967; Grime 1979; Huston 1979; Tilman 1988). In addition to competition, species occurrence is determined by other biological interactions such as predation and mutualism. Biological interactions also include the influence of community structure on species distributions, e.g., bird species diversity as a function of vegetation structure and prey items (MacArthur 1957), and on the physical environment.

The turnover of species through succession reflects niche differences among these species. Natural processes in ecosystems such as fire, flooding, windfall, and avalanche create successional patches within older vegetation, allowing more species to persist than would if the landscape were either completely undisturbed or entirely within a disturbance patch (White 1979; Denslow 1985). The intermediate disturbance hypothesis predicts that a regime of “intermediate” disturbance will maximize species richness (Connell 1978; Huston 1979). A positive feedback, where the probability of disturbance increases with successional time as a function of the changing structure and age of the patch, can produce a patch dynamic equilibrium in which the locus of disturbance shifts through time but the average area in various patch age classes remains constant (White and Pickett 1985). Shugart (1984) has used simulation models to suggest that the relationship of disturbance patch size to landscape area determines whether a patch dynamic equilibrium occurs or not; the importance of this in conservation and persistence of species is clear (Pickett and Thompson 1978; Romme and Knight 1982).

Huston (1979), Grime (1979), and Peet and Christensen (1988) have presented models of community-level plant species richness. In general, these models suggest a unimodal response of richness to both fertility or “rate of replacement” (Huston 1979), and disturbance, or “stress,” (Grime 1979) gradients.

Peet and Christensen (1988) suggest that the descending part of the species richness curve results from a transition from symmetrical (individuals capture resources in proportion to their size) to asymmetrical competition (larger individuals capture resources at a higher rate than is predicted from their size and, thus, increasingly dominate resource use). In forests, they suggest that competition for light during succession follows the full progression from symmetrical to asymmetrical competition (and hence should produce a decline in richness late in succession), but that the use of soil resources is symmetrical throughout (thus, richness increases from the poorest to the richest sites). They also stress the different behavior of various plant guilds and note that published reports of the trajectory of richness through secondary succession to forest showed increases, decreases, and stability. In contrast to forests, species richness in forests almost always declines from the moderately fertile to the most fertile sites (called the “paradox of enrichment” by Peet, Glenn-Lewin, and Wolf 1983). On the most fertile sites, dominant species are able to



competitively exclude other species. Stress, grazing, fire, mowing, or other disturbances in such systems may act in a similar way to keystone predators—that is, they reduce the dominant species and result in increased richness on small scales (Peet, Glenn-Lewin, and Wolf 1983). Presumably, prolonged exposure to these disturbances would result in evolutionary adaptation in the species present; thus, systems that are exposed to novel disturbances would not respond in the same way as systems long exposed to disturbances.

The niche difference model suggests that population and species differences, combined with patterns in the environment, including gradients in physical factors and natural disturbance regimes, explain the original amount and distribution of biological diversity. In general, we would expect that diversity (i.e., genetic diversity among populations within a species, species diversity, and ecosystem variation) would increase with the amount of spatial variation in physical factors, with biological interactions (e.g., those produced by coevolution), with moderate to high resource abundance (where resources are more abundant, a few species dominate their use, according to some models), and with moderate disturbances that prevent a few species from dominating but do not erode site productivity. As an extreme, communities early in primary succession have low productivity, low resources, simple structures, and low diversity. Human activities, including air pollution, sometimes result in parallel changes (Smith 1990). However, the pattern of niche division in more complex communities, and hence the amount of species richness within given environments, has not been yielded to a general model, and attempts to closely correlate diversity with ecosystem processes like productivity or fertility have not yet produced clear patterns.

### **Models of Spatial and Temporal Constraint**

Species and gene occurrences also can be affected by distance and spatial configuration. The theory of island biogeography models species number as a consequence of the processes of immigration and extinction (MacArthur and Wilson 1967). In the simplest situations, immigration rate is determined by distance and extinction rate by island area. Developed to explain species richness patterns of oceanic islands, the theory has also been applied to habitat patches on land. Where the theory holds, spatial configuration, in addition to environment, plays a role in the distribution of species. With the environment held constant, the smaller and more isolated the habitat patch, the lower the expected species richness.

Island biogeography has furnished one of the few predictive models concerning species richness and human effects (Peet, Glenn-Lewin, and Wolf 1983), namely that habitat fragmentation and isolation will result in species loss, called species relaxation, over time (Terborgh 1974; Diamond 1975; Soule, Wilcox, and Holtby 1979; Harris 1984). Once remnants of a formerly contiguous habitat become isolated and reduced in size, they will receive fewer immigrants from the surrounding landscape to balance local extirpations. In the extreme, no source of immigrants remains. Species loss is concentrated in “extinction-prone” species (Terborgh 1974). In addition, edge effects will increase with the increase in the perimeter-to-area ratio, producing environmental change within remnant habitat patches. A substantial literature has developed on design strategies for minimizing the predicted species loss through such features as corridors and networks (e.g., Noss 1983; Noss and Harris 1986). One of the most important considerations with human-caused stresses, such as air pollution, is that they affect natural areas that very often have been fragmented by human activity (Peet, Glenn-Lewin, and Wolf 1983).

Several other mechanisms of spatial constraint also have been proposed. For example, mass effect describes the situation in which species are present on a site because of a high population density nearby and continual immigration (Shmida and Wilson 1985; Shmida and Ellner 1984). At greater time and space scales, the vicariant evolution of several descendant species from a single ancestor species and the convergent evolution of functional equivalents from unrelated ancestors develop through isolation of gene pools and hence are cases of spatial constraint. The apparent commonness of these situations in evolutionary history suggests the importance of spatial constraints at the continental and global scales as mechanisms for increased biological diversity. Preston (1962) suggested that the global diversity of land birds was four times higher than it would be if all of the land were present in a single continental land mass. Local richness may be increased by immigration and subsequent co-occurrence of vicariant and trophically equivalent species, although niche displacement and reproductive isolation may be required for stability of this diversity.

Spatial constraint implies temporal constraint. For example, the probability of dispersal can be described as a decay function of distance. As long as probabilities are above zero, the limit represented by distance and physical barriers can be overcome by long time spans. Given enough time and the lack of absolute barriers, ranges can expand to the full physiological capabilities of the species.

Auerbach and Shmida (1987) have linked models of niche difference and spatial and temporal constraint. As a function of scale, they rank the determinants of species richness as niche relations (important from  $10^{-1}$  to  $10^3$  m<sup>2</sup>), habitat heterogeneity (important from  $10^0$  to  $10^9$  m<sup>2</sup>), mass effects (important from  $10^1$  to  $10^7$  m<sup>2</sup>), and trophic equivalence (important at  $>10^9$  m<sup>2</sup>). The first two of these fall under niche difference models and the second two under models of spatial and temporal constraint.

## MEASURING BIOLOGICAL DIVERSITY

Measurement and monitoring of biological diversity is made challenging because the state variables (composition and structure) are much easier to measure and understand than the function variables (ecological processes), although the latter are critical to the existence of the former. Essentially, we must often take “snap-shot pictures” of the state variables at several points in time and then use the data to describe change, infer cause, and determine what processes should be studied in detail. However, the organizing concept for any research in this area must be the relationship between state variables and function.

While a catalogue of methods for measuring and monitoring biological diversity is beyond the scope of this chapter, several key issues must be addressed because the chances for spurious results are great. Because all measures of the state variables of biological diversity produce different results at different scales, we will end with a discussion of the issue of scale dependence. The emphasis will be on the species level because that has been the most generally studied. However, the general comments apply to genetic and ecosystem levels as well.

### Continuous Variation

Change in some aspects of biological diversity within a study area is continuous. For example, the unambiguous classification of variety in communities and ecosystems may be impossible. In these cases, classification is an inappropriate technique for describing

biological diversity and methods for describing continuous variation, such as ordination, should be employed.

### **Richness and the Distribution of Abundances**

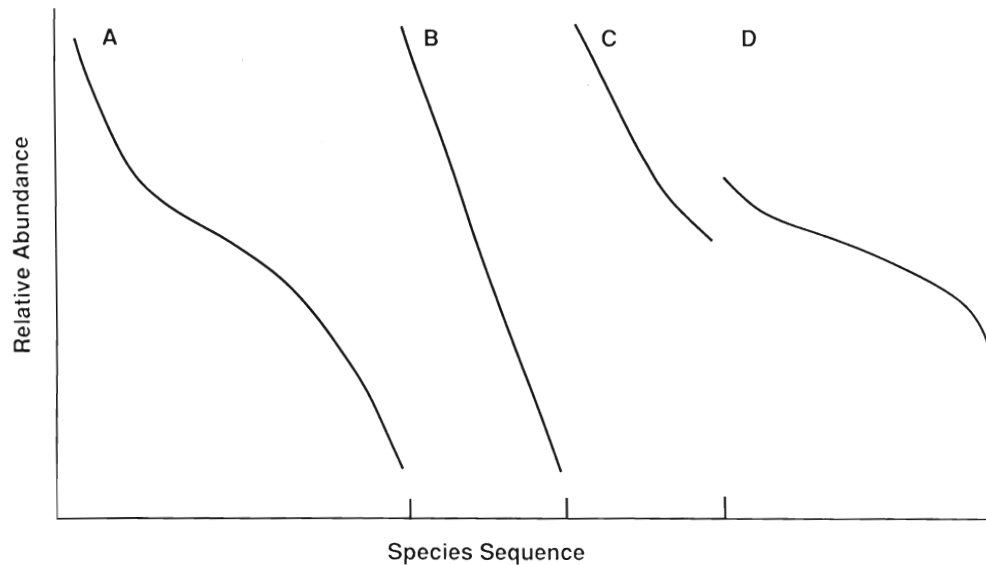
Some kinds of biological diversity are best represented through assessments of the number of “kinds” present (see discussion in Peet 1974). Classifications require that the variation within a class is less than the variation between classes. The classes present may be alleles, species, or ecosystem types. Even when classification is appropriate, it may be practically impossible to enumerate all classes and a representative sample may be required (e.g., the alleles of only some genes, rather than the structure of whole genomes, or the enumeration of only higher plants, rather than all species of all kingdoms). Diversity at any of these levels of organization includes two components: the number of classes and the distribution of abundances across those classes.

Given appropriate classification, the simplest and most widely used measure of diversity is the number of kinds or classes present, a property called richness (e.g., species richness). The number of classes present is, in addition to being a consequence of the ecological setting of the investigation, a function of the size of the sample. This can be stated either as the number of individuals examined or the area inventoried.

In addition to richness or the number of classes present, a second component of diversity consists of the distribution of abundances (e.g., biomass or the number of individuals) across the classes. For example, a community of 10 species in which dominance (e.g., the number of individuals or biomass) is highly concentrated in one species has a lower “apparent” diversity because samples of that community are likely to contain the dominant species only or the dominant and only a few additional species (Peet 1974). On the other hand, a community with the same species richness (10 species) in which abundance is evenly distributed among the species will have a higher “apparent” diversity because samples are more likely to contain more of the species. This may have ecological consequences in the sense that species interactions are likely to increase as evenness increases. The distribution of abundances has also been taken as a reflection of niche division or the way in which the species divide the functional roles in the community (MacArthur 1957; Whittaker 1975).

A simple graphical way of describing both richness and the distribution of abundances is the dominance-diversity curve (Whittaker 1975; Wilson 1991; Figure 2-1). Species are arranged from left to right from most abundant to least abundant. The length of the sequence is richness; the shape of the curve shows how abundances are distributed. Again there is a sample size effect: the more abundant species will be easy to capture, even in relatively small samples, whereas the rare species will usually be found only in larger samples.

Several indices have been used to represent the length and shape of the dominance-diversity curve. The absolute representation of the distribution of abundances among entities is called evenness (the shape of the dominance-diversity curve); when this quantity is expressed relative to a standard model (e.g., the maximum possible evenness for the sample), the measure is called equitability. Some diversity measures combine richness and evenness in a single measure; Peet (1974) proposed the term heterogeneity for these measures. The several indices of heterogeneity, equitability, and evenness have different sensitivities to sample size, richness, evenness, and kind of temporal trend (Peet 1974; Boyle et al. 1991).



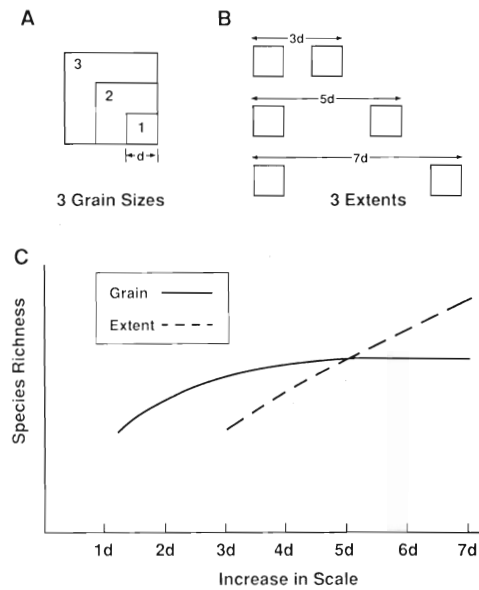
**FIGURE 2-1.** Dominance diversity curves. A. Log-normal distribution of abundance. B. Geometric distribution of abundance, implying strong dominance. C. Log-normal distribution of abundances after reduction of rare species and increases in dominance. D. Log-normal distribution after reductions in dominant species and increases in evenness.

A change in species diversity could include both the length and the shape of the dominance-diversity curve (Figure 2-1). For example, air pollution might eliminate particularly vulnerable species, thus truncating the sequence of species. However, the sequence could also be lengthened, as in the immigration of southern species into an area with climatic warming. Species tolerant of air pollution could also become more dominant, thus steepening the shape of the curve. Alternatively, if air pollution acts on the most dominant species more than others, the dominance-diversity curve would become flatter. Moderate stress that affects dominant species only may, in fact, increase local richness, even though this effect represents only a local, not global, source of richness.

### Scale Dependence

Observed biological diversity is, in part, a function of sample size and the spatial and temporal scale of sample. For example, species richness is a curvilinear function of the area sampled (e.g., Preston 1962). Although the gain of species number often slows as the accumulated area of the sample increases, we cannot a priori assume that an asymptote exists in any particular circumstances. All richness values are contingent on sample size; a corollary is that sample size must be specified in order for any richness value to be useful.

Scale includes two components: grain and extent (Wiens 1989; Figure 2-2). Grain is the size of the unit of observation (e.g., quadrat size). Extent is the distance over which the observations (e.g., individual quadrats) are distributed. The two components of scale can independently influence the levels of diversity measured. Beyond grain and extent, sample number (e.g., the number of quadrats), and the way a given sample is arranged within the



**FIGURE 2-2.** Grain, extent, and species richness. A. Three grain sizes ( $d$ =a unit of distance). B. Three spatial extents. C. Species accumulation as a function of increasing grain and extent. In this hypothetical case, more different kinds of environments are sampled with an increase in extent than an increase in grain; thus, species number (even at lower total area sampled) increases faster with increase in extent than increase in grain.

study area (e.g., random, stratified random, or regular) also influence the observed level of diversity.

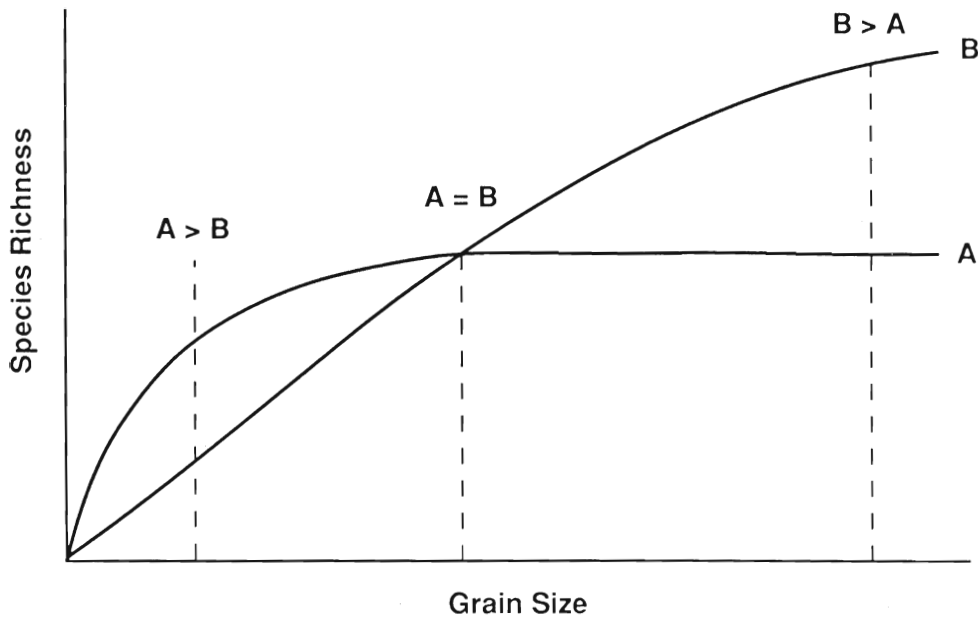
The number of species encountered increases with the grain of the sample, steeply at first, and then with a diminished rate. If two areas (or the same area at two times) are sampled at different grain sizes, the differences in the number of species will be partly an artifact of the sample (Figure 2-3).

Thus, the shape of the relationship between richness and grain size is probably more useful than a single richness value at an arbitrary grain size. Richness will usually increase with an increase in the extent of the sample. Samples of greater extent are likely to encounter more variation in environment or history than the same sample (same grain size and same number of grains) concentrated in a smaller area.

In addition to the importance of spatial grain and extent, scale dependence also occurs with samples that have a temporal dimension. The greater the continuous duration (grain size in time) of the sample and the greater the time over which individual samples are distributed (extent in time), the greater the number of species that will be encountered.

Detected richness will also increase with the number of samples (e.g., the total amount of area or total amount of time sampled at a specific grain size and extent) and will increase faster for samples stratified by change in environment (e.g., positioned along a spatial or temporal gradient in a way that will minimize similarity among samples).

Changes in species richness and in the distribution of abundances among species underscore the potential problems of scale dependence. Species richness could behave differently on different scales. Obviously, local decreases in species richness may not be global losses. Chronic stress (e.g., grazing) increases species richness at small, but not



**FIGURE 2-3.** Species-area curves for two sites, showing the potential importance of grain size and scale dependence in detecting differences.

large grain sizes (Peet, Glenn-Lewin, and Wolf 1983; Van der Maarel 1988). In the absence of this stress, individual plant biomass is higher and dominance may be concentrated in a few species; thus, species richness may decrease in small grains with decrease in stress or disturbance rate. The alpha, beta, gamma, and delta components of diversity (Whittaker 1975; Cody 1986) are related to the phenomenon of scale dependence. Alpha diversity is the diversity within a community; in the extreme this is sometimes called “point diversity” (Cody 1986). Beta diversity is the turnover of species along an environmental gradient; a higher rate of turnover means that more species are present. Gamma diversity is the diversity present within a landscape in which many communities and gradients are often present.

Cody (1986) has used the term delta diversity for the geographic turnover of species, including those caused by climatic gradients and spatial and temporal constraints (e.g., the trophic equivalency of Auerbach and Shmida 1987). At small grain sizes, alpha diversity dominates; as grain size increases, beta and gamma diversity, and finally delta diversity, contribute to the species richness observed. Increase in spatial extent at a fixed grain size and sample number will more quickly detect beta, gamma, and delta diversity compared to an increase in grain size at a fixed spatial extent.

Although this discussion has centered on species richness, there is likely to be a similar scale dependence in the amount of genetic and ecosystem diversity observed as well. Scale dependence means that there is a great danger that sampling designs will introduce artifacts into comparisons of diversity between human-impacted systems and pristine systems or between systems before and after exposure to stress. Quality control and assurance protocols will be essential in assessments of biological diversity and its change. This is important because studies of biological diversity will almost always be conducted with samples due to the impossibility of inventorying large areas.

## SUMMARY

Contemporary efforts to conserve biological diversity represent a shifted conservation focus. The emphasis on biological diversity includes but is more than the conservation of pristine ecosystems, particular species groups, or sustained use of resources. The protection of biological diversity now requires a range of conservation tactics, including protection of natural areas, better management of resource-use areas, and the manipulation of artificial ex situ populations.

Biological diversity implies the enumeration of living "things," but an undue emphasis on "things" can divert attention from the underlying processes that are critical to the survival of biological diversity. The attributes of biological diversity include diversity in composition, structure, and function. These attributes must be investigated at four levels: genetic diversity, species diversity, community or ecosystem diversity, and landscape.

Measuring change in biological diversity is made complex by the phenomenon of scale dependence; reported changes will vary with the scale of observation.

The amount of species diversity present has generally been explained by patterns in the physical environment, including the frequency of disturbances, and by spatial and temporal constraint. Although a general and dependent relationship has been found between diversity and ecological function, the precise formulation of this relationship remains an important area for research. More information is needed on the predictability of biological diversity from environment and history, on the dependence of ecological function on diversity, and on the historic and spatial contingencies present.

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