Biological Diversity

The coexistence of species
on changing landscapes

MICHAEL A. HUSTON
Oak Ridge National Laboratory

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Introduction

The extinctions resulting from human activities throughout the world have caused great concern in the scientific community and among the general public. This disappearance of species has been decried as a loss of plants and animals with potential agricultural and economic value, as a loss of medical cures not yet discovered, as a loss of the Earth's genetic diversity, as a threat to the global climate and the environment for human existence, and as a loss of species that have as much inherent right to exist as does *Homo sapiens*. The attention given this issue has led to the addition of a new word to the English language, biodiversity (a contraction of 'biological diversity', Wilson and Peter (eds.), 1988). Biological diversity is more than a scientific or economic issue. Biological diversity, in all of its manifestations, is an essential component of the quality of human existence, summarized in the ancient aphorism: 'variety is the spice of life.'

Biological diversity encompasses all levels of natural variation from the molecular and genetic levels to the species level, where we have most of our interactions with biological diversity through enjoyment of the common, strange, and beautiful forms of life or through suffering caused by the effects of pests, parasites, and diseases. Beyond the species level, biological diversity includes patterns in nature up to the landscape level. These components of biological diversity are not independent. The many flowers that form spots of color in a meadow, the songbirds that give forests a different music than fields, the various forest types that create zones of color on a mountain that we see from twenty miles away, or the variations in greenness that can be detected from satellites in space, are all ultimately the consequence of genetic diversity interacting with environmental conditions to produce differences between organisms.

There is little hope of understanding any phenomenon with as many

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complex components and scales of spatial and temporal variability as biological diversity, *unless* it can be divided into components within which repeatable patterns and consistent behavior occur. One central premise of this book is that biological diversity can be broken down into components that have consistent and understandable behavior. The other central premise is that the various components of biological diversity are influenced by different processes, to the extent that one component may increase, while another decreases in response to the same change in conditions. If these premises are true, it is impossible to completely understand 'total biodiversity' until the regulation of each of its components is understood.

The subdivision of biological diversity into tractable components is essential for developing and testing hypotheses about its regulation. The focus of this book is on those components of biological diversity that are influenced by the number and identity of species present in a given area. My goal is to explain the regulation of species diversity and why the number of co-occurring species varies under different conditions. I will not deal with the issue of the regulation of genetic or molecular diversity within species or populations, and only note that the total genetic diversity within any area is primarily a consequence of the number and identity of species that are present. This book is about the ecological regulation of species diversity, the interaction of ecological processes with geological and evolutionary processes, and the consequences of these interacting processes for the large-scale spatial and temporal patterns on landscapes that are generally considered to be components of biological diversity.

Functional Classifications of Organisms

To apply the two premises outlined above to understanding the regulation of species diversity, the ideal components would be groups of species within which consistent patterns appear, and within which a given process will always produce the same pattern. Such groups of species could be defined on the basis of properties of the areas in which they occur, which has been a common approach in ecology and biogeography. However, with the goal of developing explanations of species diversity that are as broadly applicable as possible, my approach will be to classify species based on attributes that they have in common, such as size and physiological properties, rather than on the attributes of their environment, such as the successional stage or moisture conditions of the habitat in

which they are usually found. In particular, I attempt to develop classifi-
cations that are based on 'functional' attributes, that is, attributes related
to how organisms interact with each other and with their environment,
rather than on phylogenetic attributes and genetic relatedness.

One very general classification scheme, which applies to many species
is that of species being either 'structural' or 'interstitial'. By structural
species I mean those species that create or provide the physical structure
of the environment. Obvious examples include trees, reef-forming corals,
giant kelp and other multicellular algae, and sessile animals such as
oysters, mussels, barnacles, tubeworms, etc. These organisms create the
physical structure of their environment, produce variability in physical
(e.g., microclimatic) conditions, provide resources, and in general create
the habitat used by many other, generally smaller, 'interstitial' organisms.
Interstitial organisms would include most insects, other arthropods, birds,
mammals and other vertebrates, microbes and fungi, as well as plants
such as epiphytes and understory herbs.

'Structural' organisms have a major influence on the diversity of 'in-
terstitial' organisms: in most cases the interstitial organisms would not
be present in a particular area without the structural organisms. The di-
rect influence of interstitial organisms on structural organisms and their
diversity is usually minor, although the indirect effects of interstitial or-
ganisms through evolutionary and biogeochemical processes can be very
important. While this size-based functional classification could be used
to further subdivide interstitial organisms into smaller structural organ-
isms and their interstitial dependents, the main point I wish to make is
that the diversity of these two general types of organisms is likely to be
influenced by different factors and processes.

Although the effect of structural species on the diversity of interstitial
species is a major contributor to the total species diversity of virtually
all communities, this explanation does not address the critical issue
of the diversity of the structural species. A second and more general
classification scheme provides a framework for dealing with the diversity
of both structural and interstitial species, and also allows total species
diversity to be broken into two components that (I will argue) operate
according to different rules, and/or according to the same rules at very
different temporal and spatial scales.

The total diversity of any community, or any subset of a community,
can be broken into two hierarchical components: 1. the number of
different *functional types* of organisms (i.e., 'guilds', Root, 1967); and 2.
the number of *functionally analogous species* within each functional type

(cf. Smith and Huston, 1989). Different functional types of organisms use different resources or otherwise interact with their environment in such a way that competitive interactions are minimized. Species of the same functional type use the same resources in such a way that they could *potentially* compete intensely with one another.

The critical idea behind the use of the functional type approach to species diversity is that the mechanisms that influence the number of functional types in a community are almost always different from the mechanisms that influence the number of functionally analogous species within a functional type. In addition, not all functional types respond the same way to a given change in environmental conditions. For example, competition may be important for explaining the diversity within a functional type under one set of conditions, but have no effect under other conditions. Likewise, within a community, the diversity of one functional type may be regulated by competitive interactions, while the diversity of other functional types is uninfluenced by competition, and regulated instead by immigration rates, spatial heterogeneity, evolutionary history, or other factors.

The total species diversity of a community is described by the number of functional types multiplied by the average number of species per functional type (Fig. 1.1). Clearly, the same total number of species can result from many functional types with relatively few functionally analogous species in each type or from few functional types with many functional analogues in each. In spite of the similarity in number of species, these differences in structure imply that the two communities are influenced by very different processes. These differences in functional organization have major implications for the stability and continued functioning of these communities. A large number of functionally analogous species may contribute to high stability and continuity of ecological and ecosystem function in the face of disturbances or environmental change.

This is a very flexible dichotomization, the value of which depends on having sufficient information about the organisms of interest to classify them into functional types. While a useful functional classification may require at least as much information as an accurate phylogenetic classification, the net result is likely to be of more use for understanding the regulation of species diversity. In many cases there will not be clear breaks between different functional types, and functional types will be subsets of species from a continuum or multidimensional cloud of functional combinations. The discrimination of functional types may be subjective and arbitrary, subject to as many problems and differences of

Species (Functional Analogues)
per Functional Type
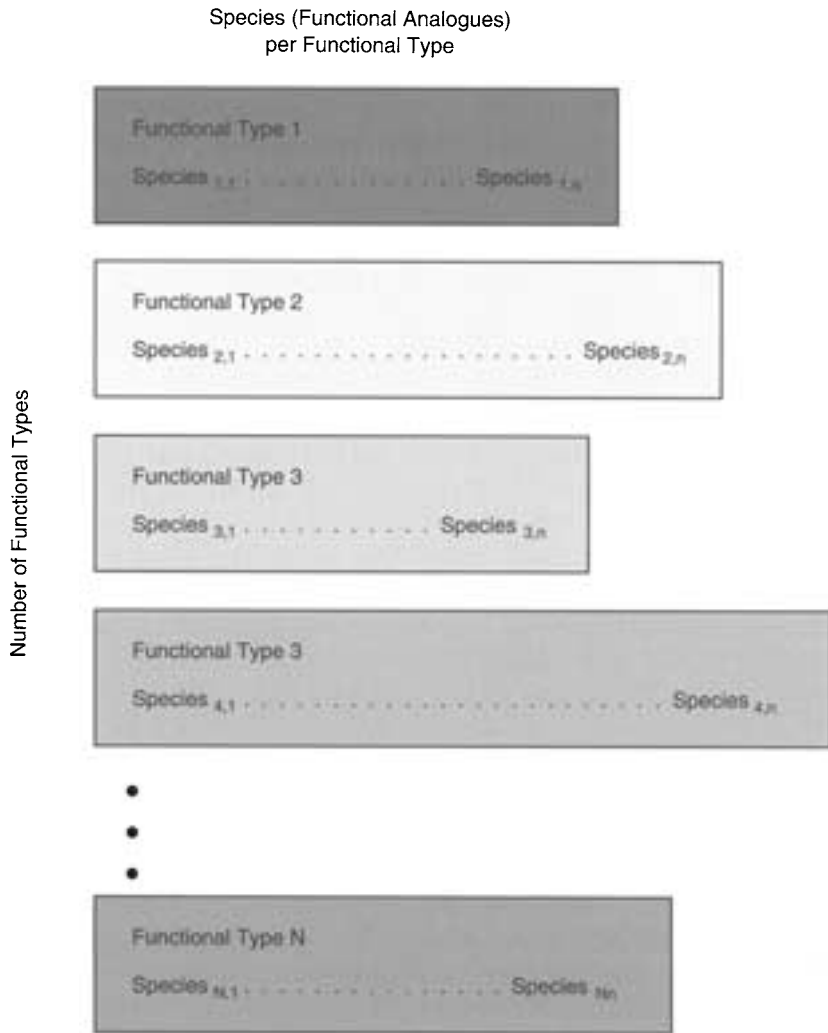
Fig. 1.1 The two components of total species diversity. The number of functional types is illustrated by the horizontal rectangles labeled 1 through N. The number of functionally analogous species within each functional type is indicated by the length of the rectangle and the species labeled $i,1$ through i,n. The total species diversity of a community is the product of the number of functional types and the average number of species per functional type. Not all functional types will have the same number of species. Because functional types are defined on the basis of resource use, competitive interactions are potentially intense among organisms of the same functional type, but very weak between organisms of different functional types.

opinion as the classification of organisms into species. The concept is useful only to the extent that it helps us to understand species diversity by resolving mechanisms that operate at different levels.

The resolution with which functional types must be classified depends on the specific component of diversity being addressed. If the object is to explain differences in the total number of animal species among several communities, the definition of functional type could be broader than if the object were to explain differences in the number of insectivorous animals among the same communities (e.g., Feinsinger and Colwell, 1978). Examples of functional classifications include 1. trophic levels (e.g., Cummins, 1973; Cummins and Klug, 1979); 2. guilds of organisms that use the same resources (Root, 1967); 3. plant life forms (e.g., tree, shrub, herb, or therophyte, cryptophyte, hemicryptophyte, chamaephyte, and phanerophyte; Raunkier, 1934); and 4. shade tolerance classes of trees.

The generality of the concept of functional types is illustrated by the presence of a limited number of general types of organism in floras and faunas that are physically separated and evolutionarily distinct. This phenomenon, known as evolutionary convergence, is one of the best known examples of the functioning of natural selection. In particular, it illustrates that natural selection tends to select for similar features in similar environments. Consequently, unrelated (or slightly related, depending on the scale at which one views the 'evolutionary tree') organisms in similar environments on different continents often are physically very similar, that is, they are the same functional type (cf. Orians and Paine, 1983).

There are many example of evolutionary convergence that illustrate the concept of functional type. Succulent stems that store water are an adaptation in plants for survival in desert conditions. This functional type has evolved independently in several unrelated groups of plants, including the Cactaceae in the New World, and the Euphorbiaceae in the Old World. To the untrained eye, a euphorb 'cactus' from Africa is indistinguishable from a true cactus from Mexico. Unrelated plants from similar environments show convergence in leaf size, shape, and structure, branching pattern, seed size and dispersal mechanism, and many other traits (Raunkier, 1934; Richards, 1952; Cody and Mooney, 1978; Smith and Young, 1987).

Among birds some examples of convergence are the toucans (Rhamphastidae) of South American and the hornbills (Bucerotidae) of Africa; the hummingbirds (Trochilidae) of South America and the sunbirds (Nectariniidae) of Africa and Asia; the meadowlarks (Icteridae) of the Amer-

icas and the yellow-throated longclaw (Motacillidae) of Africa (Cody, 1974). Many of the best known examples of convergence are from the evolutionarily isolated flora and fauna of Australia, where the marsupials have evolved into functional counterparts of the more familiar placental mammals (Keast, 1969). Striking examples of convergence are found in grassland areas around the world, which have morphologically and functionally similar, but phylogenetically distinct, subterranean mammals (Nevo, 1979).

Functional convergence may often confound taxonomic classification based on supposed genetic relatedness. Christensen and Culver (1968) discovered in their taxonomic study of the tiny insects known as Collembola, that one widespread 'species' adapted to caves was actually four separate species that had independently evolved to be virtually identical. From an evolutionary perspective, different functional types result from the effect of natural selection on adaptations to different resource conditions or adaptations to avoid competition (e.g., character displacement). Functionally analogous species may result from convergent evolution in which distantly related organisms become adapted to similar environmental conditions, or they may be related species that have not diverged functionally. From an ecological perspective, interactions such as competition or predation/cannibalism among the very similar species within a functional type are likely to operate differently than the same classes of interactions among species of different functional types.

An Approach to Understanding Biological Diversity

The approach that I will describe for explaining patterns of biological diversity is not based on a single mechanism, such as competition. Rather, it is based on understanding the conditions under which different mechanisms, such as predation, competition, dispersal, or evolutionary history, are likely to be most important in regulating the diversity of a particular group of organisms. The challenge is to identify the conditions (e.g., spatial and temporal scales, evolutionary and geological history, disturbance regime, resource availability, etc.) under which specific mechanisms are likely to have the greatest influence on the diversity of specific functionally-based subsets of organisms. For example, the explanation for short-term fluctuations in the number of bird species in a community is not likely to be the same as the explanation for long-term fluctuations. Likewise, the explanation for the number of tree species found in large areas is likely to differ in the relative importance of fac-

tors and have factors in addition to those that explain the number of tree species in a smaller subset of that area. A particular change in environmental conditions may increase the diversity of one subset of organisms within a community while decreasing the diversity of a different group of organisms. It is virtually impossible to understand variation in the total number of species in a community unless changes in the major functional groups of species can be understood.

The study of species diversity is of necessity based primarily on comparative and correlative research. The spatial area needed to define an ecological community for many organisms of interest (e.g., trees, birds, most mammals) is simply too large (and too difficult to define precisely) to be amenable to replicated experimental manipulations. Appropriately defined comparative studies can be used to identify factors or processes that are correlated with species diversity of specific groups of organisms at specific spatial and temporal scales. Once a correlation has been identified, it is critical to determine whether the correlation is based on an identifiable mechanism, or is just a coincidental, spurious relationship. The determination of whether a correlation represents a causal relationship is a difficult challenge. In most cases the evaluation must be based on strong inference (Platt, 1964) using a combination of criteria (see Weins, 1989, for a discussion of hypothesis testing in community ecology).

Criteria for the evaluation of causal relationships should include both theoretical and empirical tests. Each hypothesized causal relationship must be evaluated in comparison with all other potential causal factors and mechanisms that are correlated with it. The hypothesized causal relationship must be consistent with theoretical predictions based on specific mechanisms and assumptions that can be shown to apply to the data. The hypothesized causal relationship should be supported by data from (smaller-scale) experimental manipulations that can be shown to be relevant to the comparative data. The hypothesized causal relationship should be able to address exceptions to the expected pattern of diversity, either by clarifying why the expectation was wrong or by demonstrating why the causal mechanism should not apply. Meeting all of these criteria is a tall order, one that few hypotheses addressed in this book will completely satisfy.

My own approach to understanding species diversity has been to begin with a theoretical framework general enough to predict the relative importance of many different processes that influence local species diversity over a broad range of communities and environmental conditions, which I have called the *dynamic equilibrium model of species diversity* (Huston,

1979). My ideas were originally motivated by the well-known global patterns of species diversity, and, in particular, the high tree species diversity of tropical rain forests (Huston, 1980). However, the resulting theory made predictions about the diversity of a variety of ecological communities that contradicted the predictions of several widely accepted alternative hypotheses (e.g., Huston, 1985a). The predicted patterns for some communities were sufficiently 'counter-intuitive' that initial data in support of them were not accepted by some ecologists. In the next stage of my own pursuit of this issue, I used experimental manipulations to address specific mechanisms hypothesized to regulate small-scale, short-term changes in the species diversity of plant communities (Huston, 1982). The hypothesized mechanisms were tested for logical consistency and predictive accuracy using the mathematical formalism of computer simulation models (e.g., Huston and DeAngelis, 1987; Huston and Smith, 1987). Use of computer simulation models has allowed the predictions of mechanisms that operate at experimentally tractable scales to be extrapolated to larger spatial scales where experimental manipulation is not possible (e.g., Huston *et al.*, 1988; Smith and Huston, 1989; Huston, 1991). Understanding multiscale variation in species diversity remains a fascinating challenge, one made more stimulating by the complex feedbacks between ecosystem processes, as well as the potential responses of organisms and ecosystems to disturbances, stresses, and changing climatic conditions.

Overview

The purpose of this book is not to test the hypotheses that I propose for understanding biological diversity. Such a test would require replicated, multi-factorial experiments in many different ecosystems, and detailed comparisons of natural ecosystems over a wide range of conditions. Such data are simply not available, nor are there resources to collect the required new data. Rather, the purpose of this book is to demonstrate how these hypotheses and general framework can provide useful insights into the regulation of biological diversity, using the data and concepts developed by ecologists over the past century.

The important question throughout the book is not which explanation for species diversity is correct, since virtually every explanation that has been proposed is important under some circumstances. The critical questions are which of the many potential explanations apply to a specific diversity pattern, whether any particular mechanism is the dominant

explanation for a specific pattern, and, finally, whether there are any general rules about which mechanisms are likely to be important under particular environmental conditions, among specific groups of organisms, or at particular spatial and temporal scales.

Much of the structure of this book follows the course of my own intellectual journey through the field of community ecology, and the hypotheses and models presented are those that I have found most interesting and useful. The book is divided into four sections. The first section, composed of Chapters 2 and 3, deals with the raw material for the study of biological diversity. Chapter 2 discusses the variety of diversity patterns found in ecosystems around the world at spatial scales ranging from the entire globe to soil particles. Presented along with the somewhat confusing diversity of diversity patterns is the even more confusing diversity of environmental conditions that are correlated with them. Chapter 3 briefly addresses issues related to the measurement and quantification of biological diversity.

The second section, Chapters 4 and 5, reviews the historical development of theories of species diversity, focusing on the importance of equilibrium versus non-equilibrium processes in regulating species diversity. Again, the issue is not whether an equilibrium or a non-equilibrium viewpoint is correct, but which of many potential opposing processes are likely to be in equilibrium at a particular spatial and temporal scale.

The third section, Chapters 6 through 10, addresses mechanisms of intra- and inter-specific competition, particularly among plants, which are the dominant structural organisms in most terrestrial environments and in many aquatic and marine environments. Each chapter deals with the influence of interactions among individual organisms on diversity at a different organizational level or spatiotemporal scale. Chapter 6 deals with the regulation of diversity within populations of single species, manifested primarily as variation in size. Chapter 7 extends the effect of interactions among individual organisms from the population to the community and ecosystem level. Chapters 8, 9 and 10 discuss the major spatial and temporal patterns of the distribution of organisms on landscapes, again in terms of the interactions between individual organisms. In aggregate, these chapters deal with the major components of biological diversity over the range of scales at which they are perceived by humans.

The fourth section, Chapters 11 through 14, applies the concepts developed in Parts two and three to some of the major issues in biological diversity and some of the major ecosystems in which species diversity shows the most variability. Endemism and invasions, discussed in Chap-

ter 11, are two of the most dramatic manifestations of variation in the equilibrium between speciation and extinction. Chapter 12 discusses marine systems, ranging from the intertidal to the mid-oceanic benthos, that span the range from low to high species diversity, and illustrate the influence of virtually all the factors that are known to influence species diversity. Chapter 13 deals with a range of terrestrial plant ecosystems in which diversity is regulated by a single type of major disturbance, fire. The diversity of fire-dominated ecosystems ranges from virtually monospecific stands to ecosystems with some of the highest plant diversity found on Earth. Finally, Chapter 14 deals with the *sine qua non* of biodiversity, tropical rain forests, and comes to what may be perceived by some to be the most counterintuitive conclusion in the entire book.

I conclude with a brief discussion of some of the economic and conservation implications of the counterintuitive regulation of global diversity gradients.