The ECONOMY of NATURE

fourth edition

Robert E. Ricklefs

THE ECONOMY OF NATURE

FOURTH EDITION

A Textbook in Basic Ecology

ROBERT E. RICKLEFS *University of Missouri–St. Louis*

W. H. FREEMAN AND COMPANY
New York

Senior Editor: Deborah Allen
Project Editor: Christine Hastings
Text and Cover Designer: Blake Logan
Text Illustration: Network Graphics
Cover Art: Marquetry mural at the Boston University Biological Sciences Center by Lara Hunt and Spider Johnson
Illustration Coordinator: Susan Wein
Production Coordinator: Paul Rohloff
Composition: W. H. Freeman Electronic Publishing Center/Sheridan Sellers
Manufacturing: RR Donnelley & Sons Company

Library of Congress Cataloging-in-Publication Data

Ricklefs, Robert E.
The economy of nature : a textbook in basic ecology / Robert E. Ricklefs. — 4th ed.
p. cm.
Includes index.
ISBN 0-7167-2815-X
1. Ecology. I. Title.
QH541.R54 1996 96-33300
574.5—dc20 CIP

Printed in the United States of America

First printing 1996

PREFACE

Although it has been only four years since the publication of the third edition of *The Economy of Nature*, the fourth edition includes details of many new developments in ecology as well as broader coverage of traditional topics, rearrangement of some material to provide a more logical organization, and changes in the presentation to improve clarity. *The Economy of Nature* remains a basic textbook in ecology for undergraduate students, with explanations of the general principles of ecology and narrative accounts of the lives of organisms and the workings of ecological systems. As in previous editions, I have endeavored to develop topics, including mathematical models of ecological processes, in a clear and logical fashion, and to balance theory with experimental studies and empirical examples of ecological patterns.

More than ever, ecology is a vital and growing discipline, with new concepts, discoveries, and basic information accumulating at a rapid pace. Furthermore, the connections between the basic principles of ecology and the causes of environmental problems are becoming better understood. This provides some hope for solutions to the dilemma of providing for a growing human population within the constraints of limited space and natural resources. This book emphasizes the critical need for basic understanding of ecological principles and the commitment to act on them.

The fourth edition of *The Economy of Nature* has been revised from cover to cover, with substantial changes in many chapters, including updated coverage and editing for clarity. There are some new topics in the fourth edition, such as a treatment of the biome concept in ecology with a detailed comparison of the terrestrial and aquatic biomes of the earth (Chapter 5). You will also find new sections on phenotypic plasticity (reaction norms) (Chapter 11) and phylogenetic reconstruction (cladistic analysis) (Chapter 21), among other subjects. Some examples, such as the obligate mutualistic relationship between the yucca and its moth pollinator, have been expanded considerably to illustrate general principles, in this case that of coevolution.

A major change in the fourth edition is the addition of a two-color art program throughout the book. In addition to making the text more attractive, I hope that the use of a second color will enhance the graphical presentation of data and concepts. The full-color photo essays have also been retained and somewhat revised with a new selection of photographs. I have also increased the use of "Boxes" to set apart from the main text certain statistical or methodological topics.

As in the past, I have been very pleased with the response of teachers and students to the third edition of *The Economy of Nature* and hope that this new edition will serve your needs even better. Many of the changes have been in direct response to comments and suggestions received from those of you who have used the book, and I look forward to hearing from more of you in the future. This book is an important part of my professional life because of the immense amount I learn from working on it and the many personal interactions it has brought. I hope that *The Economy of Nature* will continue to be current, relevant, and engaging for those who study ecology in the future.

Finally, as I wrote in the preface to the third edition, I hope that *The Economy of Nature* will encourage students to appreciate the natural world they live in, and the increasing impact of human activities on the natural world—our world. Progress toward an ecological balance depends on the rational application of knowledge and understanding. We are the technological species; now we must become the ecological species and assume a responsible position in the economy of nature.

St. Louis
August 1996

ACKNOWLEDGMENTS

I have received much help in preparing this edition. A large part of the credit belongs to my editor at W. H. Freeman and Company, Deborah Allen, who was a constant source of encouragement, gentle prodding, and good advice. The production staff at W. H. Freeman, particularly Christine Hastings, were wholly professional, proficient, and personable. I am grateful for the hard work and interest that they have contributed to this edition. Norma Roche undertook the task of copyediting with thoroughness, precision, and insight.

Of particular importance to me were the many useful comments of individuals who critically read parts of the revised manuscript: Martin B. Berg, Robert Curry, Robert Holt, Michael Mazurkiewicz, Wayne F. McDiffett, Laszlo J. Szijj, Stefan Sommer, and David C. Wartinbee. Helpful suggestions on particular topics came from Robert Curry, Tom Getty, Jon E. Keeley, Olle Pellmyr, and Truman P. Young. One of the strongest elements of *The Economy of Nature* are the photographs, many of which were generously provided by colleagues. My thanks for this to D. N. Alstad, A. Basolo, R. Boonstra, O. Brown, D. H. Clayton, H. Cogger, P. Dayton, G. F. Edmunds, J. R. Ehleringer, T. Eisner, Z. Glowacinski, M. A. Guerra, E. Hanauer, C. C. Hansen, W. H. Haseler, D. H. Janzen, H. B. D. Kettlewell, J. A. McGowan, C. H. Mueller, O. Pellmyr, M. V. Parthasarathy, D. Pimentel, J. W. Porter, D. W. Schindler, P. W. Sherman, W. J. Smith, W. P. Sousa, D. G. Sprugel, K. Vepsalainen, L. T. Wasserthal, and R. H. Whittaker. In addition, I obtained many fine photographs from various agencies of the United States government, including the Bureau of Sport Fisheries and Wildlife, Department of Agriculture, Department of the Interior, Fish and Wildlife Service, Forest Service, National Park Service, Smithsonian Tropical Research Institute, and the Soil Conservation Service.

CONTENTS

CHAPTER 1

INTRODUCTION

The English word *ecology* is taken from the Greek *oikos,* meaning "house," our immediate environment. In 1870, the German zoologist Ernst Haeckel gave the word a broader meaning: the study of the natural environment and of the relations of organisms to one another and to their surroundings. Haeckel wrote:

> *By ecology, we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its organic and to its inorganic environment; including above all, its friendly and inimical relation with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all the complex interrelationships referred to by Darwin as the conditions of the struggle for existence.*

Thus **ecology** is the science by which we study how organisms (animals, plants, and microbes) interact in and with the natural world.

The word *ecology* came into general use only in the late 1800s, when European and American scientists began to call themselves ecologists. The first societies and journals devoted to ecology appeared in the early decades of the twentieth century. Since that time, ecology has undergone immense growth and diversification, and professional ecologists now number in the tens of thousands.

With the rapid growth of the human population and the quickening deterioration of the earth's environment, ecological understanding is now urgently needed to maintain the condition of the environmental support systems upon which humanity depends for food, water, protection against natural catastrophes, and public health. Management of biotic resources in a way that sustains a reasonable quality of human life depends on the wise application of ecological principles to solve or prevent environmental problems and to inform our economic, political, and social thought and practice.

This text, *The Economy of Nature,* presents the basic principles of the scientific discipline of ecology. These principles have been defined through more than a century of observation, experimentation, and theoretical exploration of natural systems. They explain the processes that maintain the structure and function of these systems; they tell us how each part fits into the whole, emphasizing the interrelatedness of all of nature; and they help us to understand why the functioning of natural systems can break down under certain stresses. In this way, ecological principles offer guidelines for the preservation of biodiversity and management of the environment for sustained use.

To begin with, this chapter outlines a general framework for the study of ecology to start you on the road to ecological thinking. We shall first discuss several vantage points from which ecological knowledge and insight can be viewed—for example, as different levels of complexity, varieties of organism, types of habitat, and dimensions in time and space. We shall see how we can regard many different entities as **ecological systems,** by which we mean any organism or assemblage of organisms, including their surroundings, united by some form of regular interaction or interdependence. While the extent and complexity of ecological systems varies from the single microbe to the entire biosphere blanketing the surface of the earth, all obey similar principles of ecological functioning. Some of the most important of these principles are taken up next: these concern physical and chemical attributes of ecological systems, regulation of structure and function in ecological systems, and evolutionary change in ecological systems. Finally, a few examples will illustrate how an understanding of ecology can help us to meet the challenge of maintaining a healthy environment for natural systems and for ourselves in the face of increasing ecological stresses.

Ecology provides a framework for interpreting the flood of information that comes our way about the natural environment. It also gives us the insight we need to envision the consequences of our activities for natural systems. Haeckel's analogy of the economy of nature emphasizes the interconnectedness of everything on the surface of the earth, just as human ventures are interrelated and defined by economic principles. We and our enterprises directly affect natural processes. Humankind itself is an important part of the economy of nature.

Levels of ecological organization

The organism is the most fundamental unit of ecology, the elemental ecological system. No smaller unit in biology, such as the organ, cell, or molecule, has a separate life in the environment (although, in the case of single-celled protoctists and bacteria, cell and organism are synonymous). The structure and functioning of the organism—whether it is a plant, animal, or microbe—are determined by a set of genetic instructions inherited from its parents and by the influence of many factors in its environment. Every organism is bounded by a membrane or other covering across which it exchanges energy and materials with its surroundings. To be successful as an ecological entity, the organism must have a positive balance of energy and materials to support its maintenance, growth, and reproduction. In Part 1 of this book, we will examine factors that influence exchanges between the organism and the physical environment, and we will see how organisms solve problems involving temperature, water loss, salt balance, and other environmental challenges. We shall return to these themes again in Part 3 to consider how organisms cope with life in heterogeneous and varying environments.

In the course of their lives, organisms transform energy and process materials as they metabolize, grow, and reproduce. In doing so, they modify the conditions of the environment and the amounts of resources available for other organisms, and they contribute to energy fluxes and the cycling of elements in the natural world. Assemblages of organisms together with their physical and chemical environments make up an **ecosystem.** Ecosystems are immensely large and complex ecological systems, including up to many thousands of different kinds of organisms living in a great variety of individual surroundings. A warbler overhead searching for caterpillars, and a bacterium helping to decompose the organic soil underfoot are both part of the same ecosystem. Because of this complexity, the **ecosystem approach** to ecology describes organisms and their activities in terms of common "currencies," which are amounts of energy and chemical elements, by which the activities of organisms as different as bacteria and birds can be compared. Thus, the ecosystem approach provides a framework for studying the transformation of energy and the cycling of elements within ecological systems.

We may speak of a forest ecosystem, a prairie ecosystem, and an estuarine ecosystem as distinct units because relatively little exchange of energy or substances occurs *between* these units compared with the innumerable transformations going on *within* each of them. Ultimately, however, all ecosystems are linked together in a single **biosphere** that includes all the environments and organisms at the surface of the earth. The far-flung parts of the biosphere are linked together by the energy and nutrients carried by currents of wind and water and the movements of organisms. Water flowing from a headwater to an estuary connects the terrestrial and aquatic ecosystems of the watershed to those of the marine realm. The migrations of gray whales link the ecosystems of the Bering Sea and the Gulf of California. The importance of movement of materials between ecosystems within the biosphere is underscored by the global consequences of human activities. Industrial and agricultural wastes spread far from their points of origin, inflicting harm on all regions of the earth. Ecosystem processes are the subject of Part 2 of this book.

Many organisms of the same kind together constitute a **population.** Populations differ from organisms in that they are potentially immortal, their numbers being maintained over time by the birth of new individuals that replace those that die. Birth and death within populations depend on how well organisms function in their environments, as we shall see in Part 3. Populations also have collective properties, such as geographic boundaries, densities (number of individuals per unit of area), and variations in size or composition (for example, evolutionary responses to environmental change and periodic cycles of numbers in some cases) that are not exhibited by individual organisms. The population approach to ecology, the subject of Part 4, is concerned with numbers of individuals and their variations through time, including evolutionary changes within populations.

Many populations of different kinds living in the same place constitute an **ecological community.** The populations within a community interact in various ways, as explained in Part 5. Many species are predators that eat other kinds of organisms. Almost all are themselves prey. Some—such as bees and the plants whose flowers they pollinate, and many microbes living together with plants and animals—enter into cooperative arrangements, called **mutualisms,** in which both parties benefit from the interaction. All these interactions influence the numbers of individuals in populations—that is, the **dynamics** of populations. The **community approach** to ecology differs from the ecosystem approach in that the units of measurement are population sizes and the focus is on interactions between populations: predation, competition, mutualism.

Unlike organisms, communities have no rigidly defined boundaries; no skin separates a community from what surrounds it. The total interconnectedness of ecological systems means that interactions between populations spread across the globe as individuals and materials move between habitats and regions. Thus, the community is an abstraction representing a level of organization rather than a discrete unit of structure in ecology, as explained in Part 6.

Community and ecosystem approaches to ecology provide different ways of looking at the natural world. We may speak of a forest ecosystem, or we may speak of the community of animals and plants that live in the forest, using different jargon and referring to different facets of the same ecological system. The study of ecosystems deals with movements of energy and materials within the environment, which result from activities of organisms and from physical and chemical transformations in the soil, atmosphere, and water. The study of populations and communities is concerned with the development of ecological structures and with the regulation of ecological processes by means of population growth and the interaction of populations with their environments and with each other. These processes also reflect the activities of organisms going about their everyday lives.

The kinds of organisms

From the standpoint of ecosystem function, organisms play a great many distinct roles. Characteristic differences in structure and function between plants, animals, fungi, protoctists, and bacteria (prokaryotes) have important ecological implications. All ecological systems depend on transformations of energy to function. For most systems, the ultimate source of that energy is sunlight. On land, plants capture the energy of sunlight and use it to synthesize carbon dioxide and water into carbohydrates and other organic molecules. In aquatic systems, photosynthesis is accomplished mostly by various protoctists (algae) and bacteria. The organic carbon produced by photosynthetic organisms provides food, either directly or indirectly, for the rest of the ecological community. Some animals consume plants; others consume animals that have eaten plants. Many fungi and bacteria feed on the dead remains of plants and animals, which are called **detritus;** others feed on living individuals, in which case we refer to them as parasites or pathogens.

Animals and plants differ in many important ways besides their sources of energy (Figure 1.1). Plants expose large surfaces to capture the energy of sunlight, and they feature thin leaves and stiff, supportive stems. Plants also need enormous quantities of water to replace water lost by evaporation from leaf surfaces; not surprisingly, most plants are firmly rooted in the ground, in constant touch with supplies of water and nutrients. Those that are not, such as orchids and other tropical "air plants" (epiphytes), can survive only in humid environments bathed in cloud mists much of the year.

Animals also need large surfaces to exchange energy and materials with the environment, but because animals do not require light, their exchange surfaces can be enclosed within the body. A modest pair of human lungs has a surface area of about 100 square meters, which is close to the size of a tennis court. The gut also presents a large surface across which nutrients are assimilated into the body. For example, the intestine of a robin is about 30 centimeters long and has an absorptive surface area of over 200 square centimeters, or about half the size of this page. By internalizing exchange

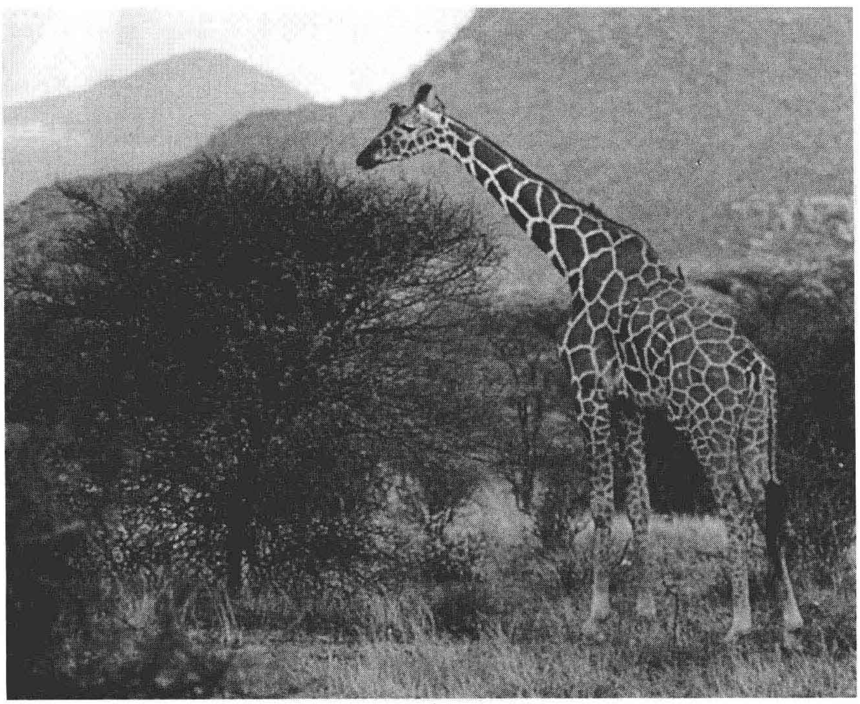


Figure 1.1 This photo of a giraffe browsing on a tree in eastern Africa emphasizes the fundamental differences between plants, which assimilate the energy of light and convert carbon dioxide to organic carbon compounds, and animals, which derive their energy from the production of plants.

surfaces, animals can achieve bulk and streamlined body shapes, and they can develop the skeletal and muscular systems that make mobility possible. In terrestrial environments, the internalized surfaces of animals also are protected from evaporative water loss, so land animals don't need roots to keep them continuously supplied with water.

Although plants and animals are similar in having organized, complex body plans with diverse, interconnected parts, they have contrasting mechanisms of growth and reproduction. Animals grow predominantly by the multiplication of cells in many tissues and organs throughout their bodies. During growth, the size of each part of an animal is precisely regulated in proportion to the rest of the body, and most animals have a characteristic adult size. In contrast, most plants grow in a modular fashion from many independent growth centers, which are called **meristems,** located at the tips of branches and roots (Figure 1.2). This modular organization enables plants to withstand loss of tissue to grazers and yet continue to grow and reproduce. Each meristem can produce a precisely regulated structure, such as a leaf or a flower, but the form of the whole plant may vary depending on which of the shoot tips receive the most light or nutrients from the roots, or escape being eaten.

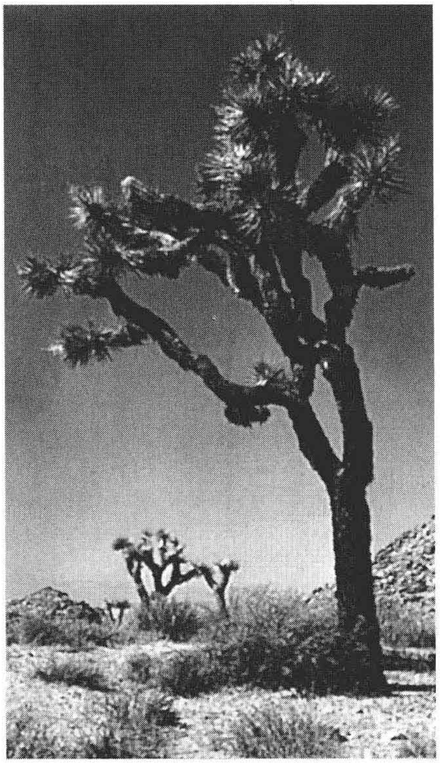


Figure 1.2 Each of the growing tips of this Joshua tree can produce reproductive structures and, potentially, an entire tree. The death of one or more of the branches does not directly affect the others. Joshua trees are native to the Mojave Desert of southern California. Photograph by J. Boucher, courtesy of the U.S. National Park Service.

Any one growing shoot can also reproduce the entire structure of the plant. Thus a branch cut from a tree may take root when placed in soil and become a separate tree (Figure 1.3). This ability allows most plants to reproduce asexually—to engage in what biologists often refer to as **vegetative reproduction,** or **cloning.** Most animals reproduce by means of specialized sexual cells (eggs and sperm) formed in the sexual organs, or gonads. Despite this general difference between plants and animals, most plants also employ sexual reproduction in their life cycles, and many animals have the capacity to clone themselves, either by modifying the sexual process to eliminate fertilization or by mechanisms resembling vegetative growth. The so-called clonal animals—hydroids and corals are familiar examples—illustrate the difficulty of drawing sharp lines between animal function and plant function (Figure 1.4; Figure 1.6d).

The fungi, which like plants and animals are multicellular organisms, assume unique roles in the ecosystem because of their distinctive growth form. Unlike plants and animals, the fungus grows from a microscopic spore without passing through an embryonic stage. The fungal organism is made up of threadlike structures called **hyphae** (singular, **hypha**). These hyphae may form a loose network, called a **mycelium,** which can invade plant tissues or dead leaves and wood on the soil surface, or grow together into the reproductive structures that we recognize as mushrooms (Figure 1.5). Because fungal hyphae can penetrate deeply, fungi readily decompose dead plant material, recycling many of the nutrients in detritus. Fungi digest their foods externally, secreting acids and enzymes into their immediate surroundings, cutting through dead wood like biochemical blowtorches and dissolving recalcitrant nutrients from soil minerals. Fungi are the primary agents of rot—unpleasant to our senses and sensibilities, perhaps, but very important to ecosystem function.

The protoctists are a highly diverse group of mostly single-celled organisms that includes the algae, slime molds, and protozoa. Algae can form large structures—some seaweeds can be up to 100 meters in length (see, for example, Figure 1.12)—but their cells lack the organization into specialized components—tissues and organs—that one sees in plants and animals. Algae, including diatoms, are the primary photosynthetic organisms in most aquatic systems. Foraminifera and radiolarians feed on tiny particles of organic matter or absorb small dissolved organic molecules. Some of the ciliates are effective predators—on other microorganisms, of course.

Bacteria, or prokaryotes, are the biochemical specialists of the ecosystem. Their structure is a simple, single cell, lacking a proper nucleus and chromosomes to organize their DNA; however, their enormous range of metabolic capabilities enables them to accomplish many unique biochemical transformations essential to the ecosystem. These transformations include the assimilation of molecular nitrogen (the common form found in the atmosphere), which is used to synthesize proteins and nucleic acids, and the use of inorganic compounds such as hydrogen sulfide as sources of energy. Plants, animals, fungi, and most protoctists cannot accomplish these feats. Furthermore, many bacteria live under anaerobic conditions (lacking free oxygen) in mucky soils and sediments, where their metabolic activities regenerate nutrients and make them available for plants. We will have much more to say in later chapters about the special place of microorganisms in the functioning of the ecosystem.

Because each type of organism is specialized to a particular way of life, it is not surprising that there are many examples of different types of organisms joining together to their mutual benefit, each partner in the symbiosis providing something that the other lacks. For example, the specialized organelles so characteristic of the eukaryotic cell—chloroplasts for photosynthesis, mitochondria for various oxidative energy transformations—originated as symbiotic prokaryotes (bacteria) living within the cytoplasm. Other familiar examples include lichens, which comprise a fungus and an alga in one organism; bacteria that ferment plant material in the guts of

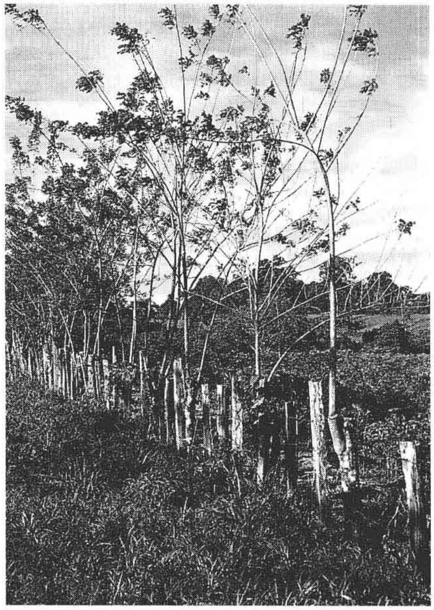
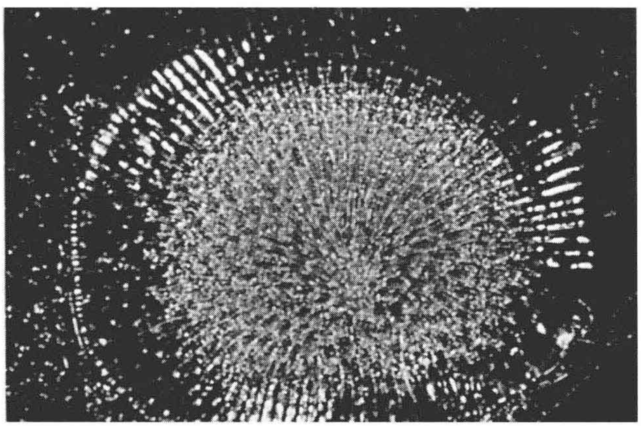
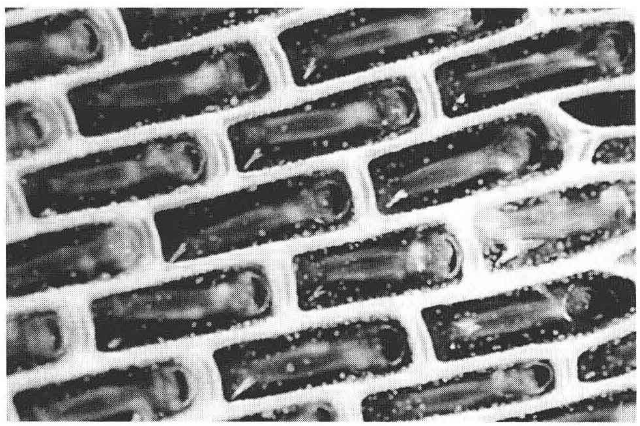


Figure 1.3 A living fence, which results when freshly cut fence posts take root and sprout. Because such fences provide shade and resist termite damage and rot, they are commonly used throughout the Tropics. Courtesy of J. Blake.

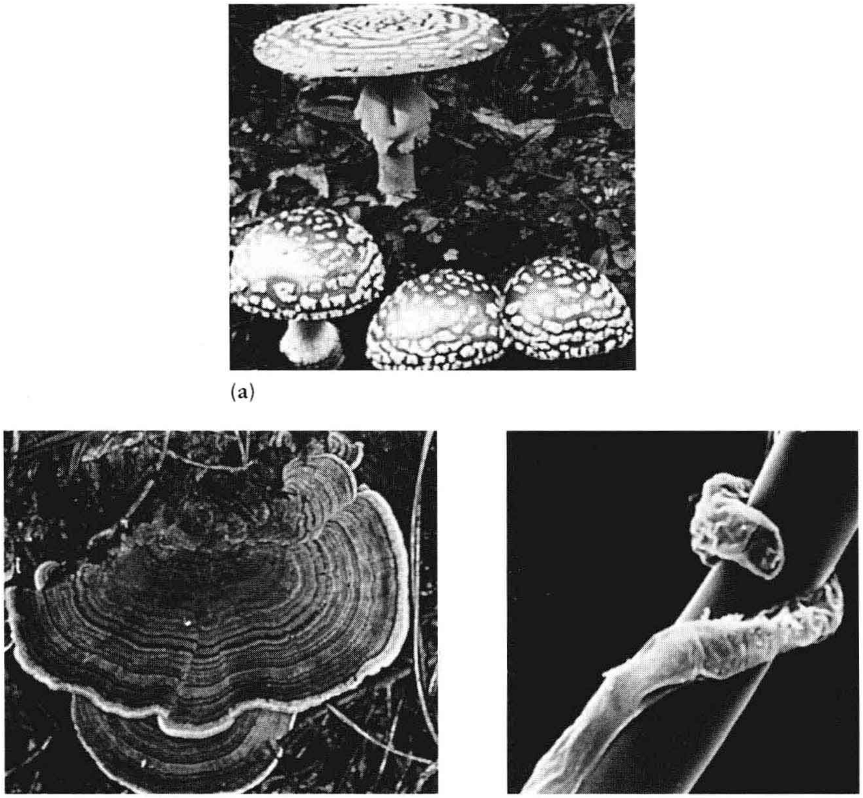
Figure 1.4 (a) Colony of a marine bryozoan. (b) Close-up of individual zooids. Each zooid was produced by asexual reproduction at the edge of the colony, which is about 15 mm in diameter. Courtesy of D. Harvell.



(a)



(b)



(a)

(b)

(c)

Figure 1.5 Many fungi, such as the *Amanita* mushroom fungus (a) and the shelf fungus (b), obtain nutrients from dead organic material. Others are pathogenic and attack living tissues of plants and animals, or even other fungi. (c) A hypha of one fungus attacks that of a larger plant pathogen. The hypha of the larger fungus has a diameter of about 5 μm. Courtesy of the U.S. Department of Agriculture.

cows; protozoans that digest wood in the guts of termites; fungi associated with the roots of plants that help them to extract mineral nutrients from the soil in return for a carbohydrate energy source from the plant; photosynthetic algae in the flesh of corals and giant clams; and nitrogen-fixing bacteria in the root nodules of legumes.

Habitats and niches

Another way of looking at ecological systems is from the perspective of the organism itself. A **habitat** is the place, or physical setting, in which an organism lives. A **niche** is a representation of the ranges of conditions that an organism can tolerate and the ways of life that an organism can pursue—that is, its role in the ecological system. A simple analogy might help. A worker's habitat could be an office building, and his or her niche in that building could be described in terms of the physical office space (fifth floor, 2 by 3 meters, a long way from the coffee machine), the office furnishings (desk, typewriter, filing cabinet), office hours, the particular task performed, and his or her boss and coworkers. A katydid's "office building"—its habitat—is the forest, but its niche within the forest includes the range of temperatures it can tolerate, the types of plants it can eat, and its enemies. An important principle of ecology is that each species has a distinctive niche: no two are exactly the same, because each species has distinctive attributes of form and function that determine the conditions it can tolerate, how it feeds, and how it escapes its enemies.

Ecologists characterize habitats by their conspicuous physical features, often including the predominant form of plant life or, sometimes, animal life (Figure 1.6). Thus, we speak of forest habitats, desert habitats, and coral reef habitats. How we define a habitat depends on the point of reference: it is strictly a matter of convenience. The habitat of an earthworm is the soil, whereas that of the bear treading on the soil is the forest. The habitat viewpoint differs from the ecosystem and community viewpoints because of this focus on the organism and its way of life rather than on the functioning of the ecological system within which it lives.

Ecologists have devoted much effort to classifying habitats. For example, one may distinguish terrestrial and aquatic habitats; among aquatic habitats, freshwater and marine; among marine habitats, ocean and estuary; among ocean habitats, benthic (on or within the ocean bottom) or pelagic (in the open sea). Such classifications ultimately break down, however, because habitat types overlap broadly and absolute distinctions between them do not exist. The idea of habitat nonetheless emphasizes the variety of conditions to which organisms are exposed at the earth's surface. Inhabitants of abyssal ocean depths and tropical rain forest canopies experience vastly different conditions of light, pressure, temperature, oxygen concentration, moisture, viscosity, and salts, not to mention food resources and enemies. Thus, although the same principles of ecological interaction and evolution apply to both habitats, the expressions of these processes differ utterly. The variety of habitats holds the key to much of the diversity of living organisms. No one organism can live under all the conditions of the earth's different habitats; each must specialize, with respect to both the range of habitats within which it can live and the size of the niche that it can occupy within a habitat.

Scale in time and space

The natural world varies in time and space. We perceive temporal variations in our environment as the alternation of day and night and the seasonal progression of temperature and precipitation. Superimposed on these cycles are irregular and unpredictable variations. Winter weather is generally cold and wet, but the weather at any particular time cannot be predicted much in advance; it varies perceptibly over intervals of a few hours or days as cold fronts and other atmospheric phenomena pass through. Some irregularities in conditions, such as the alternation of series of especially wet and dry years, occur over longer periods. Some events of great ecological consequence, such as fires and tornadoes, strike a particular place only at very long intervals.

Each type of variation in the environment has a characteristic dimension or scale. Variation between night and day has a dimension of 24 hours; seasonal variation has a dimension of 365 days. Waves pound a rocky shore at intervals of seconds; winter storms bringing rain or snow may follow one another at intervals of days or weeks; hurricanes may strike a particular