THE ECONOMY OF NATURE

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A Textbook in Basic Ecology

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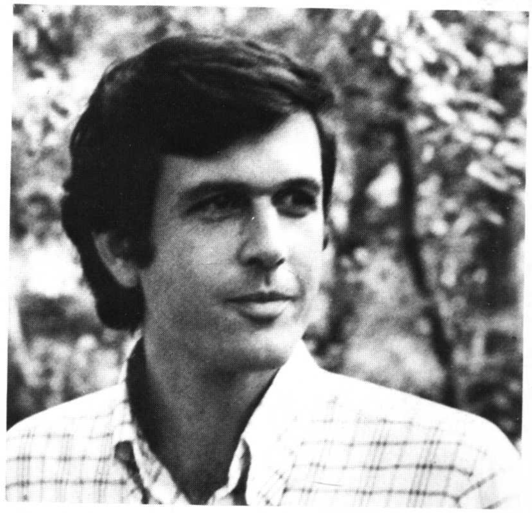

Robert E. Ricklefs was born in San Francisco in 1943. He graduated from Stanford University in 1963 and received a Ph.D. from the University of Pennsylvania in 1967. After a year of post-doctoral study at the Smithsonian Tropical Research Institute, he joined the faculty of the University of Pennsylvania, where he is Professor of Biology. His interests in research include the ecology and evolution of island populations and the organization of biological communities. He is also the author of *Ecology,* the second edition of which Chiron Press published in 1979. The critical praise of that book included:

"Ricklefs writes with authority on the broadest range of ecologically relevant subject matter so far published in one book. What more can one ask?" — Peter Price in *Ecology.*

"Ricklefs has provided an excellent synthesis of modern ecological thought and a strong foundation for future work."

— Robert Cook in *American Scientist.*

"Ricklefs has now produced the book for which [teachers] and their students have been waiting . . . This book should do a great deal to restore some meaning to the widely abused word which serves as its title."

— *Times Literary Supplement.*

"[Ricklefs] reveals not only an impressive array of scientific information, but a gift for turning it into lucid, attractive, and apparently effortless prose." — V. C. Wynne-Edwards in *Times Higher Education Supplement.*

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A Textbook in Basic Ecology

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"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 relations 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 interrelations referred to by Darwin as the conditions of the struggle for existence."
— Ernst Haeckel, 1870

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Preface

The recent proliferation of books in ecology still leaves a gap between long texts that are more or less comprehensive and short books, usually paperbacks, that are inadequate even for beginning courses lasting a quarter or a semester. I have written *The Economy of Nature* to provide a broad, integrated treatment of ecological principles in a book of moderate length.

I have emphasized the dynamics of populations, communities, and ecosystems while keeping sight of the organism as the basic unit of the biological community. I have tried to balance ideas and principles on the one hand with examples of structure and functioning of natural systems on the other. I believe such balance makes clear the complementary roles of theory and observation in the development of science. I have also tried to convey the diversity of biological communities and the remarkable manifestation of basic principles under different environmental conditions.

I have deliberately avoided the problem of man's ecological crisis. One could not hope to do justice to a topic of such importance and complexity in a chapter or two tacked on to the end of a text whose subject is the basic principles of ecology. Where that problem can be understood or solved, students will readily discern applications of the principles discovered in the study of natural systems. I have omitted descriptions of mathematical and statistical techniques in ecology because they do not so much aid our understanding of principles as they provide useful tools for the professional ecologist.

The Economy of Nature is meant to be a basic exposition of ecology, not a source book for advanced students and professional ecologists. I have accordingly omitted literature references and, wherever possible, scientific names in the text so as to give force to the narrative itself. References, selected readings, and source books are listed by chapter at the back of the book.

Philadelphia R.E.R.

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Introduction

Ecology is the study of plants and animals, as individuals and together in populations and biological communities, in relation to their environments — the physical, chemical, and biological characteristics of their surroundings. Ecology has recently been expanded in concept by the awakening perception in many of us that man, like all other creatures, also dwells in an environment with which he must come to terms to ensure his survival. To be sure, man can, like no other animal, modify his surroundings according to his own design. Yet blight, plague, and pollution constantly remind us of mankind's fallibility. If we are going to come to terms with Nature, it will have to be on her terms for the most part. These conditions of Nature, the bounds beyond which man cannot step, are the subject of this book. It is to these basic laws, obeyed by all other organisms, that man must eventually bow.

Ecology has become enough of a popular catchall to include the likes of sanitary engineering, regional planning, paper recycling, and organic gardening. Most of these endeavors are merely attempts, however necessary, to soften the blow of Nature's verdict on our flagrant violations of her laws — our unwillingness to play the game by the old and tried rules — and to delay the sentencing a little while. But as surely as there are no superficial remedies, so the case against man's environmental policy does not lie in superficial evidence: not in the sewage dumped into rivers, or the pesticides sprayed on crops, or the guns and harpoons of the hunters, or the exhausts of our cars, or suburban sprawl. It has grown out of man's failure to heed basic economic principles of nature.

We are all aware, consciously or not, of our environmental predicament. To emphasize its symptoms here would only add to the confusion, indignation, frustration, gloom, despair, or perhaps even apathy in reaction to the unfolding catastrophe we view each day through newspapers, television, and direct contact with our surroundings.

Technological, economic, and political remedies are outside the scope of this book. My aim in writing is to show how natural assemblages of animals and plants are put together and how these assemblages function. I should hope that man's general place in this scheme — how, like other organisms, he is a part of the natural world and how his activities influence the natural world — will be obvious despite my failure to consider his specific case at length in the pages that follow.

The Realm of Ecology: History

The word ecology is derived from the Greek *oikos* meaning house, man's immediate surroundings. The origin of the word in the middle of the last century is obscure, but its general usage can be traced to the definition given by the influential German biologist, Ernst Haeckel, in 1870. "By ecology," he wrote, "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 interrelations referred to by Darwin as the conditions of the struggle for existence."

The period in which Haeckel and Darwin worked was a period of exploration. Naturalists were just beginning to discover the bewildering variety of plants and animals and their peculiar ways of life. Charles Darwin's theory of evolution by natural selection had placed the organism in the context of the environment: form and behavior were adapted to the particular environment in which the organism dwelled. Ecology first flourished as the study of natural histories of organisms, the life stories of animals and plants: where and when they were found, what they ate, what ate them, and how they responded to changes in their surroundings. This narrow view of ecology gave way, towards the end of the nineteenth century, to a broader perception of the interrelationships of all plants and animals. Whereas *autecology* related the organism to its surroundings, *synecology*, as this broader view has been called, recognized that assemblages of plants and animals had characteristic properties of structure and function shaped by the environment. Does a grassland not differ from a forest, and can these differences not be related to temperature, rainfall, and soils?

Synecology, and its inherent treatment of all animals and plants together as a biological unit, the *community*, achieved its extreme expression in conceiving the community as a superorganism. The parallels between community and organism are obvious. Each is made up of distinctive subunits. The organism has its liver, muscle, and heart; the community its green plants, predators, and decomposers. A forest community grows on cleared land, progressing through field and shrub stages of succession to its mature form, just as the organism progresses through its developmental stages.

Ecologists have always viewed organisms and communities in the context of their physical environments. Evolutionary adaptations and developmental responses enable plants and animals to respond to variation in the environment. Biological structure and function are molded by their physical surroundings. As recently as the 1940's, ecologists began to realize that the biological community and its environment could be considered together as a single unit. The physical and biological worlds form a larger system — the *ecosystem* — within which the material substances of life are continually passed back and forth between the earth, air, and water on one hand and plants and animals on the other.

A gradually enlarging view has not been the only contributor to the maturity of ecology. Since the first part of this century, ecology has been a meeting ground for ideas from genetics, physiology, mathematics, agriculture, and animal husbandry. Indeed, for many years the infusion of ideas and approaches from other areas of endeavor had diverted the central movement of ecology to many seemingly divergent paths. One led to population biology, another to physiological ecology, a third to the study of community energetics, and so on. We now seem to be on the threshold of a period of coalescence, a recognition of the ties between the separate disciplines of ecology and an achievement of unity.

The Realm of Ecology: Organization

I cannot imagine the form of the ultimate unification of ecology as a science, nor, indeed, be certain whether it shall ever take a form as well ordered as the structure given by theorems to mathematics and by laws to physics. There is a principle that prevents a scientific discipline from gelling prematurely into a mold shaped by misconception and ignorance. I shall, however, try to provide a basic organization, or plan, of the realm of ecology. I do not mean to describe all the conceptual, often semantic, pigeonholes into which ecologists stuff their observations of nature. To keep these distinctions to a minimum is to hasten progress toward understanding nature which, except for rather restricted use by pigeons, has no pigeonholes. Organizations, plans, schemes of classification, are like the crampon, alpenstock, and piton that help the mountaineer on his way to the summit. We take what help we can find, and this book is in part a catalogue, an encyclopedia, of devices, useful now, but to be put aside along the way as the terrain changes and the path to understanding grows more gentle.

Ecology is a three-dimensional construction of horizontal layers stacked on top of each other, representing a hierarchy of biological organization from the individual through the population and community to the ecosystem, and of vertical sections cutting through all layers, representing form, function, development, regulation, and adaptation. If we follow the community layer across its sections, we find a form section with the numbers and relative abundances of species; a function section with the interaction between predator and prey populations and the mutually depressing influences of competitors; a development section with plant succession, as in the reversion of cleared land to forest; a regulation section with the elusive property of inherent community stability hiding in a corner; and an adaptation section with the evolution of antipredator adaptations. Taking a particular stack of sections, that representing function, for example, we find energy flow and nutrient cycles in the ecosystem layer; predator–prey interactions and competition between species in the community layer; birth, death, immigration, and emigration in the population layer; physiology and behavior of individuals in the organism layer.

Each layer of ecological organization has unique properties of structure and function. Each section in each layer of the construction represents a unique constellation of observed phenomena, perceived patterns, and abstracted concepts. Yet all are presumably governed by a fundamental set of natural laws. Such laws are the quest of ecology the science.

The Need for Ecology

One may wonder where this view of ecology as a science fits into the far vaster construction that is human civilization. How can abstract concepts deduced from observations of unspoiled nature fit next to the realities of corn blight and eutrophication? Ecology is, of course, of dual nature. There is the desire for knowledge for its own sake, a kind of perversity limited, as far as I know, to the human species. But an active science searching out patterns and explanations must be placed with the arts and letters in any definition of civilization. And there is the application of knowledge and understanding to solutions of environmental problems.

The two natures of ecology go hand in hand, because the basic principles found in the study of natural communities ought to pertain to disturbed communities as well. The physical and chemical principles of mineral solubility, chemical reaction, surface tension, and change of state are all pertinent to the management of soils. When desert soils are irrigated for crops, for example, water dissolves salts from the soil particles. Rather than being washed out of the surface layers of the soil, the salts are deposited at the surface as water is drawn upward by rapid evaporation from the ground under the hot desert sun. That irrigation would eventually turn thousands of acres of desert into salt flats unfit for growing crops could have been predicted from general principles of chemistry and physics.

The mathematics of population ecology tells us that populations decline when removal of individuals by predators exceeds recruitment through reproduction. Applied to game species, principles of demography show that harvest rates are greatest when hunting effort is adjusted to maintain game populations at levels that are low enough to ensure sufficient food for vigorous reproduction but high enough to provide a high sustained yield. Effective game management is achieved by regulating the hunting season, the daily bag limits, the type of weapon used, and even the price of licenses. Wildlife biologists follow ecological principles when they flood areas to encourage waterfowl and burn shrublands to encourage the new plant growth on which deer thrive. If game management is one's concern, basic ecological principles point the way to sound practice.

Ecology is the mistress of much unheeded advice. Plant geneticists have been trying for years to breed *the* perfect strain of wheat, resistant to all pests and diseases. Even while man applies artificial selection to obtain a breed with superior characteristics, he also applies selection to beetles and viruses and fungi, and so obtains the superior characteristic (for the pest, at least) of their being able to eat and infect man's superior wheat. This kind of evolutionary cat-and-mouse game could, in a less demanding world, lead to a harmless stalemate, while providing employment for many plant geneticists. But nature is not so forgiving. Pushing a strain of wheat towards greater pest resistance might reduce its ability to compete with weeds or resist drought. The adaptations of an organism together are like a ball of clay. It can be pinched out in one place only if it is pinched in somewhere else. There is only so much clay in the ball.

Herbicides and irrigation can balance losses in competitive ability and drought tolerance incurred for the sake of gains in pest resistance, but the costs of chemicals and of irrigation systems may more than offset the gains. I am reminded of the attempt to introduce cotton into Costa Rica. In its drier regions, this tropical country offers an ideal climate and in the beginning cotton crops flourished. As with cotton crops everywhere, insect damage can cause great economic loss. At first, insecticides kept the insect damage under control, but as pest populations evolved resistance to the chemicals, greater and greater quantities of poisons had to be applied. The cotton boom in Costa Rica ended when the cost of pesticides ate up the profits from growing cotton. All that remain are rusting tractors and weed-covered fields. That cotton could have been profitable in Costa Rica without pecticides is doubtful.

That the economic and ecologic cost of the pesticides would be unbearable is, in the wisdom of the hindsight, certain.

I am also reminded of a complex case study of the direct and indirect efforts of man's disturbance to natural communities that points to the need for fundamental understanding of ecosystem function. Clear Lake, California, is a beautiful body of water twenty miles long, once providing idyllic vacations and well-known for its fishing and water skiing. In fact, the only drawback to this earthly paradise was the summer swarming of small gnatlike flies, known as midges, around the edges of the lake. The midges, which passed their larval stage in bottom sediments of shallow parts of the lake, posed no threat to health and did not bite. But their great numbers, congregating around the lights of houses in the evening, were a nuisance.

Suitable control programs eluded the efforts of researchers until the end of World War II, when pesticides such as DDD and DDT became widely available. In 1949, DDD was applied to the entire lake at a level of less than two-hundredths of a part per million of insecticide in the water. This measure was so successful that few midges were found near the lake shore over the next two or three years. After 1951, however, the number of midges began to increase. DDD was again applied in 1954, again resulting in substantial killing off of the bothersome insects. Later that year, residents began to find dead waterbirds washed up on the shore of the lake. No one connected these deaths with the midge control program.

The midge population recovered more rapidly after the second application of DDD than after the first. A third treatment, tried in 1957, was less successful, and biologists began to suspect that the midges had become resistant to the insecticide. That year, large numbers of water birds, mostly western grebes, were found dead along the shore. This time, two dying birds were sent to the Bureau of Chemistry of the California Department of Agriculture. Analyses showed that the midge control program had been a death warrant for Clear Lake. The concentration of DDD residues in the fat of the dead grebes was almost one hundred thousand times greater than the concentration of the original application of insecticide to the lake. It was later discovered that fish had also assimilated and concentrated the poison to levels that made many species unsafe to eat.

The effects of the midge control program had been to breed a DDD-resistant strain of midge that is still a local nuisance, to eliminate the western grebe from the lake and reduce populations of other water birds, and to place in jeopardy the lake's most important asset, its fishery. It is ironic that human activities precipitated the pest problem to begin with: nutrients draining into the lake from fertilized croplands and in the form of raw sewage had enriched the bottom sediments of the lake to favor the growth of midge larvae.

The ultimate results of the midge control program came as a complete surprise. Its designers ignored basic principles of ecology. They did not count on the ability of the midge population to evolve resistance to a toxic insecticide, nor did they foresee that residues of DDD would accumulate in the bodies of animals and be passed from prey to predator up the food chain, concentrated at each step until they became lethal. Unforeseen consequences have plagued nearly all our efforts to bring under control the complicated system of checks and balances that maintains the stability of the natural world. As our activities continue to exert an increasing impact on the environment, control of environmental problems will become more difficult and complex, and recognition and application of basic ecological principles will become all the more crucial to survival of life, including our own.

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Life and the Physical Environment

We often contrast the living and the nonliving as opposites — biological versus physical and chemical, animate versus inanimate, organic versus inorganic, active versus passive, biotic versus abiotic. While these two great realms of the natural world are almost always readily distinguished and separable, they do not exist one apart from the other. The dependence of life upon the physical world is obvious. The impact of living beings on the physical world is more subtle, but this impact is equally important to the continued existence of life on Earth. Soils, the atmosphere, lakes and oceans, and many sediments turned to stone by geological forces owe their characteristics in part to the activities of plants and animals.

The Uniqueness of Life

Many properties held in common by all forms of life set organisms apart from stones and other inanimate objects. Motion and reproduction are the two most obvious of these properties, even though many plants may be said to move very little indeed, and one might describe the growth of crystals as a kind of reproduction. Exceptional cases which appear to fall on the wrong side of the great fence separating the biotic and the abiotic are less worrisome than they seem at first, for motion is a superficial expression of a more fundamental property of life, namely the ability to perform work directed toward a predetermined goal, and reproduction represents, above all, the emancipation of biological structure and function from the direct influence of physical laws. One might compare the genetic material passed from generation to generation by the act of reproduction to language in its abstraction and specificity.

Organisms are like internal combustion engines transforming energy to perform useful work. Whether the organism directs this work toward pursuing prey, producing seeds, keeping warm, or maintaining such basic body functions as breathing, blood circulation, and salt balance, it perpetually strives to maintain itself *out* of equilibrium with the physical forces of gravity, heat flow, diffusion, and chemical reaction. In a sense, this is the secret of life. A boulder rolling down a steep slope releases energy during its descent but no useful work is performed. The source of energy, gravity in this case, is external and as soon as the boulder comes to rest in the valley below, it is once more brought into equilibrium with the forces in its physical environment.

A bird in flight must constantly expend energy to maintain itself aloft against the pull of gravity. The bird's source of energy is internal, being the food which it has assimilated into its body, and the work performed serves a purpose useful to the bird in its pursuit of prey, escape from predators, or migration. To be able to act against external physical forces is the one common property of all living forms, the source of animation that distinguishes the living from the nonliving. Bird flight may be a supreme realization of animation, but plants just as surely perform work to counter physical forces when they absorb soil minerals into their roots or synthesize the highly complex carbohydrates and proteins that provide their structure.

Physical forces in the environment could not be held at bay without the expenditure of energy to perform work. The ultimate source of energy for life is external, the light from the Sun. Plants have evolved special pigments, among them chlorophyll, that absorb light energy. That energy is then converted to food energy in the form of sugars manufactured from simple inorganic compounds — carbon dioxide and water. The energy trapping process is called *photosynthesis,* literally a putting together with light. Energy contained in the chemical bonds of the manufactured sugars, and thence proteins and fats, may then be used by the plant, or by animals that either eat plants or eat other animals that eat plants, and so on, to perform the work required of an animate existence.

The Interaction of Life and the Physical World

Life is totally dependent on the physical world. On one hand, organisms receive their nourishment from the physical world, and on the other, the distributions of plants and animals are limited by their tolerance of the physical environment. The heat and dryness of deserts prevent the occurrence of most life forms, just as the bitter cold of polar regions prevents the establishment of all but the most hardy organisms. Form and function are also brought under the yoke of the physical world. The viscosity and density of water require that fish be streamlined according to rigid hydrodynamic rules if they are to be swift. The concentration of