ECOLOGY

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PREFACE

"Ecology" is designed to be a teaching tool.

My earlier book, *Introduction to Ecology,* was written from 1968 to 1971 to "introduce" the new ideas of evolutionary ecology that occupied us in the sixties but that had not yet permeated textbooks (Orians, 1973). Since then ecology has come to near-maturity. When moral suasion from my publisher eventually put me to textbook writing once again, I decided to abandon that "introduction," compounded as it was of thoughts from the 1960s, a historical approach, and enthusiastic revisionism. Writing from 1981 to 1984, I set out to review all the basic parts of modern ecology in a way suitable for teaching. My object has been both to offer readable reviews and at the same time to give students a manual of ecological information that may add to material covered in lecture courses.

"Ecology" goes from the individual to the community—the quasi levels of integration approach. This arrangement requires less repetition than the reductionist technique of starting with communities and thus working from the big to the small. I now usually give my lectures in integration order also, though sometimes I choose to begin with ecosystems and work backwards for variety. This book can be used either way by altering the order in which chapters are assigned.

I begin the book with a review of ecological concepts of which modern university students certainly will have heard before starting the course. The concepts of niche, ecological pyramids, succession, energetics, and limiting factors are almost part of the vernacular, although possibly not correctly used. Research with my own propagules, for example, shows that something called the "pyramid of life" enters the school system as early as the third grade. Accordingly, I review these ideas at the start, providing definitions and discussions that might otherwise have been deferred until later in the text.

The beginning chapter also includes as succinct a statement of the principle of natural selection, with its companion concept of fitness, as I can manage. After this beginning I found that most of the subdisciplines of ecology fell into a natural order: individual—population and species—community.

Ecosystem processes, however, do not necessarily follow communities as a fourth level of integration. In fact, physical processes in habitats must be studied before the integration of species into communities can be understood. I recognize this truth by discussing ecosystem processes in Part Three of the book, before going to community synthesis in Part Four. Thus my levels of integration approach puts ecosystems before communities.

The chapters of the book can easily be rearranged for use in a course that begins with ecosystem function as follows:

Chapters 1 & 2	Overview and Ecosystem Energetics
14–21	Ecosystem Processes
11	Species Strategies
12	Social Systems
22–25	Community Building
26 (pp. 679–683)	Ecosystem Stability
6–10 & 13	Population Ecology
3–5	Individual Adaptation
26 (pp. 650–674)	Species Diversity

Table I offers reading suggestions for shorter courses. When time limits the material that can be covered it seems to me that the coverage of the text should be as extensive as possible, so that the inquiring student can put the shortened material in a proper context. Instructors design short courses around their own perceptions of what is most useful. But Table I lists subjects most ecologists will think fundamental.

Table I

Short Course: Levels of Integration Approach	
Chapters 1 & 2	Introduction and Overview
3 (pp. 46–53)	Efficiency of Photosynthesis
4 (pp. 74–82)	Consumer Efficiency
6 & 7	Competition and Speciation
10 (in part)	Review of Predation
11	Species Strategies
12	Social Systems
14	Biomes
16 (pp. 392–406)	Production Ecology
17	Review of Ecosystem Process
23	Ecological Succession
24–26	Community Building, Diversity, and Stability
Short Course: Reduction from Ecosystem Approach	
Chapters 1 & 2	Overview and Ecosystem Energetics
14	Biomes
3 (pp. 46–53)	Efficiency of Photosynthesis
16 (pp. 392–406)	Production Ecology
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26 (pp. 679–683)	Ecosystem Stability
6 & 7	Competition and Speciation
10 (in part)	Review of Predation
5	Individual Adaptation
26 (pp. 650–674)	Ecological Diversity

I have avoided chapters or passages explicitly about environmental issues. Acid precipitation, for instance, is not reviewed, nor is there a statement on population problems. I am not untouched by these matters having, in fact, written a book on human population and history (Colinvaux, 1980). But I decided that a thorough survey of the basics of ecology was of value in its own right and should be treated as such in a university course. The essential background data contributed by ecology to environmental debate lie in these basics and will be found throughout the book. An extensive discussion of the atmospheric carbon cycle and the possibility of enriching the atmosphere with anthropogenic carbon dioxide will be found in Chapter 19 (Maintenance of the Air). Eutrophication is discussed at length in Chapter 21 (Limnology). The effects of clear-cutting are discussed in the contexts of the Hubbard Brook watershed study in Chapter 17. Productive limits of the earth are assessed in Chapters 3 and 16. A review of what is meant by ecosystem stability is given in Chapter 26, and so on. The reading schedule given in Table II could accompany a course for which environmental issues were an organizing theme.

Some subjects are given more extended treatment than in other texts. Biogeochemistry is one of these, particularly the maintenance of the ocean as a solution of sodium chloride and of the air as an oxygen–nitrogen mixture (Chapters 18 and 19). Another subject worthy of ecological notice is modern progress in soil classification and in the understanding of soil genesis (Chapter 20). In a one-quarter course these subjects have to be treated only briefly in lecture, but should be accessible to students.

Paleoecology, however, deserves a more central part in ecological teaching. Some of the more important hypothesis testing in ecology can be by appeal to the fossil record, particularly hypotheses about community development. In Chapter 22 I have concentrated on the use of Quaternary records by pollen analysis and paleolimnology, the record of the ice-age earth, and the reconstruction of community changes in the Holocene that led to present patterns of distribution and abundance.

Table II
Readings Organized Around an Environmental Theme

Chapter	14	Climate and biomes.
	19	Maintenance of the air. The carbon dioxide enrichment problem.
	17	Habitat steady states. Watershed studies. Nutrients and fertility of terrestrial ecosystems, clear-cutting.
	21 (pp. 506–516)	Water pollution and eutrophication.
	2	Limiting factors, niche, ecosystem energetics.
	16	Productivity. Food limits to the earth.
	20 (pp. 490–499)	Soils of temperate and tropic regions.
	5	Individual adaptations and optimal foraging.
	6–13	Population ecology.
	23–25	Succession and community building.
	26	Diversity and stability of ecosystems.

My long Chapter 21 on limnology perhaps needs defense beyond the statement that it is one of my research areas. Life in aquatic systems often is starkly different from life on land. Community structure in water is most strongly dependent on predation, as predators hunt prey through lighted spaces, and plants are the smallest prey of all. Problems of adaptation or dispersal are quite different in water, and we must stretch our understanding to realize conditions for microscopic life when Reynolds numbers are low. The limnology chapter may seem long, but even this treatment is highly condensed compared with the treatment of terrestrial habitats in this and other textbooks. Far from being defensive about a whole long chapter describing lakes as ecosystems, I feel remorse at having not written a companion piece on oceans.

The book is deliberately not strong on statistical techniques. Elaboration of ordination methods, and of multivariate analyses, does not to my mind make a book or a lecture course more sophisticated; merely uninteresting to the average student. Likewise I have introduced equations only when they are vital to the argument. Words are still our best medium of communication.

In attempting a complete survey of ecology, it has been necessary to include subjects for which I have little enthusiasm, or which are coming under increasing criticism. An example is the Shannon–Wiener information statistic as a measure of diversity. I have disliked and suspected this measure since my first contact with it in the late fifties. My 1973 book expressed my doubts that it told us anything about the stability of ecosystems. One of the first formal criticisms of the measure in stability studies was done in my laboratory (Goodman, 1974). But the measure remains important to ecology for the way it was used; the old controversy about complexity and stability would not have come about without the use of this measure. Thus it needs to be covered in general texts.

Concepts like character displacement, or *r*- and *K*-selection, have their detractors, myself among them on occasion, but they need to be learned before they can be criticized. Thorough historical accounts of these concepts are essential to an understanding of modern ecology. Some of the older ideas of succession theory may seem archaic, but knowledge of them is essential to understanding of present-day attitudes. For these subjects some history is needed, even though history is always, in a sense, archaic.

Ecological succession is a subject over which consensus has changed completely in the last decade. When I wrote "Succession Revisited" in the 1973 book, I felt I was a revolutionary. Contemporary wisdom had it that succession was the ecosystem process *par excellence,* and various writers experimented with ideas of succession maximizing information or order. To submit that the essential process was no more than the inevitable replacement of opportunists with equilibrium species as I did seemed daring in a textbook. When Drury and Nisbet (1973) independently published this same view of succession they noted in their acknowledgments, "We thank three anonymous reviewers whose comments made clear to us that the traditional view of succession is alive and well among our peers." But now the strategic view of succession has become the new conventional wisdom, and the ecosystem view takes second place. Yet ecosystem changes in succession can be directional and are of interest. Even Clements' old remarks about "superorganisms" need to be understood in order to understand the latest group selection arguments of D. S. Wilson (1982) who actually uses the term "superorganism." I have tried, within the limits of space, to review these different contributions to succession theory in Chapter 23, not just to expound the latest consensus.

Proponents of group selection may call me conservative. The possibilities of structured demes are reviewed in pages 643–644, and of superpredators in pages 301–302. Group evolution is an attractive explanation for curious communities like those surrounding beetles in dung or under bark. But simple natural selection can explain so much more, or many things so easily, that conservatism seems proper in a textbook.

I have curbed my temptations to literary expression, while attempting to retain clarity and readability. Orians (1973) said of my *Introduction to Ecology* that it was "full of quotable quotes," apparently intending that this should be taken as praise for the book. Others found quotable language unsuitable in a science text. In this book I have removed the more colorful products of first draft writing. An attempt to describe ecology in more literary language can be found in my *Why Big Fierce Animals Are Rare* (Colinvaux, 1978).

Columbus, Ohio **Paul Colinvaux**

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CONTENTS

PART ONE

ENERGY AND THE INDIVIDUAL

PREVIEW TO CHAPTER 1

Ecology is the science that seeks to understand the distribution and abundance of life on earth. It is both an environmental science and an evolutionary science, since it works to discover the ways in which environmental resources are divided among individuals of different species. In this process species are forged and kept distinct, males are separated from females, and numbers are so regulated that the common stay common and the rare stay rare. Evolutionary ecology constantly tests the hypothesis that every individual organism acts to leave behind the largest possible number of surviving offspring, and our measure of an organism's success at doing this we call "fitness." Fitness may be increased by more births, better survival of the young, or when close relatives survive to transfer copies of an individual's genes to the next generation. Patterns as different as foraging behavior or systems of sex can be shown to maximize fitness for the individuals using them. The seeming paradox that elegant designs of plants and animals result from basically random processes is resolved because selection works non-randomly on the endless variety provided by genetic recombination in sexual systems. A greater paradox of apparent design is the way communities appear to work as complex entities, but this paradox also is resolved by ecological theory. All community members are fitted by selection to the shared reality of a physical habitat, and to the presence of each other, giving a spurious impression of true community design. Individual plants in communities act selfishly to maximize fitness, but the summed effects of plants in vegetation impose structure on habitat and community alike. Replacement series of colonizing plants, called "ecological successions," proceed as soil forms and nutrients collect, but this appearance of increasing order during succession also can be understood as a consequence of individuals behaving in ways likely to maximize immediate fitness. It was the discovery of how plant communities are regulated by habitats which were themselves influenced by vegetation that was recognized when the term "ecosystem" was first coined. A basic hypothesis of community ecology is thus that natural selection coadapts individuals of different lineages to shared environmental constraints and to the presence of each other. Ecology explores this process of adaptation, finding in it the mechanism that fashions species in the first place. But this study requires that physical processes in the habitat be understood also. Physical process in the environment fashions habitats, setting the ground rules in which the game of speciation and community building is played. Ecologists study these ground rules. Necessarily this takes them all the way from studies of process in habitats to the physics and chemistry of the biosphere, as they seek to understand what regulates the composition of the air, the salinity of the oceans, or the working of the weather.

CHAPTER 1

OVERVIEW: THE ECOLOGICAL INQUIRY

The most widely used definition of ecology is THE STUDY OF ANIMALS AND PLANTS IN RELATION TO THEIR HABITS AND HABITATS (Elton, 1927). This describes ecology as the study of how the ways of life of a place depend upon the local environment and how the environment is changed by life. It is this emphasis on environment that has given ecology its popular image of an environmental science. Yet ecology is more than an environmental science.

Ecology is also a branch of evolutionary biology. It seeks to explain how many different kinds of plants and animals can live together in the same place for many generations. Animals and plants share habitat. Sometimes they can only share for so long before some locally go extinct, but there are other circumstances when many different kinds persist in a habitat indefinitely.

In the more livable parts of the earth, in what an ecologist would call A MESIC HABITAT, there are always many species living together. A prime question of evolutionary ecology is how it came about that so many species should be present to coexist. Consider the plant species of a thickly vegetated place like a meadow. Many kinds of meadow plant get their energy from the sun by photosynthesis, their carbon from the air, and their water and minerals from the soil that they share. Evolutionary biology concludes that these many different species are the product of selection of the best adapted individuals. But the meadow shows that selection has produced many different solutions to the problem of living in a meadow. It is necessary for evolutionary biology to explain why there should be so many different kinds of plant in a meadow rather than one or a few perfectly adapted species. This is an ecological question as well as an evolutionary question, since the answers must be found in the ways in which the many species share the resources of the habitat.

A related purpose of ecology is to explain how, or to what extent, populations are regulated in nature. Wild populations certainly fluctuate but usually only within perceived limits. This fundamental fact is revealed most clearly with the everyday observation that some species are common but others rare. The common stay relatively common and the rare stay relatively rare over many consecutive generations. RELATIVE ABUNDANCE, as well as total population, therefore, must be under control.

Allied to the problem of population regulation is that of species distribution. A species that may be rare in one place often turns out to be common in another. It follows that any attempt to identify those interactions between species or the environment that, regulate number must also identify processes that limit distribution. For this reason ecology is sometimes defined as THE STUDY OF THE DISTRIBUTION AND ABUNDANCE OF SPECIES.

The word "ECOLOGY" is taken from the Greek word "oikos," which means "home," or "house," or "household," or something like that, and "logos," which means "knowledge." Ecology, therefore, literally means "the study of the household," it being implied that the "household of nature" is meant. Haeckel (1866), who is generally credited with coining the word ecology more than a century ago, defined it as "the domestic side of organic life." The modern subject includes all phenomena that result from the interaction of organisms with their environment and with other organisms. Among these phenomena are the dispersal of species, the speciation mechanism itself, population regulation, life in communities, modification of the habitat, soil formation, nutrient cycling, the sources of energy used by organisms, the efficiency with which organisms use resources or energy, and the maintenance of the earth as a life support system. Some of the questions that ecologists try to answer are given in Table 1.1.

NATURAL SELECTION AND FITNESS IN ECOLOGY

Modern ecology developed after the discovery of the process of evolution by natural selection. Natural selection works by destruction; it kills individuals or it stops individuals from breeding. Change comes about because the culling process of natural selection hits some varieties harder than others. It is this endless sifting out of arrays of chance or contrived variety that ensures that existing species are suited to the environment in which they live.

An inevitable consequence of the process of natural selection is that all individuals of all living species must breed to the uttermost. Success is measured by offspring thrust into the next generation through the meshes of natural selection's net. This means that the more eggs or young an individual makes, or the more effort it puts into care of young, the more chances there are of its having survivors. The outcome of natural selection depends not only on the rate at which individuals are removed (selected against) but also on the rate at which their replacements are made (reproduction). A good working definition of the process may be written NATURAL SELECTION IS THE DIFFERENTIAL REPRODUCTION AND SURVIVAL OF INDIVIDUALS CARRYING ALTERNATIVE INHERITED TRAITS.

Charles Darwin spoke of natural selection as promoting "the survival of the fittest." He did not, by "fit," mean those who did calisthenics, or those who were clever fighters or big bullies. Being "fit" in a Darwinian world simply means escaping removal by untimely death or from failing to reproduce more successfully than others do. Fitness is a measure of success at both survival and reproduction.

Both geneticists and ecologists talk of fitness but each adapts the concept to special interests. Geneticists think of fitness in terms of *gene frequencies* and give definitions like *fitness is a measure of the relative change in the frequency of an allele owing to selection* (Valentine and Campbell, 1975). But ecologists follow more closely to Darwin's usage and think of numbers of surviving offspring rather than surviving genes. Ecologists may define FITNESS as THE INDIVIDUAL'S RELATIVE CONTRIBUTION OF PROGENY TO THE POPULATION. Fitness so defined is easy to measure, being simply the number of offspring that themselves live to reproductive age. This meaning of the word "fitness" is not the meaning of everyday speech. Ecological fitness is described as a number. If the Joneses raise four children, all of whom grow up to marry and have children of their own, then Mr. and Mrs. Jones each have a fitness of 4 (or 2 if the context suggests allowing for the fact that each parent has only a half interest in each child).

Fitness is sometimes also conveniently measured as the number of copies of a gene that appears in the next generation, regardless of which organism carries them. This is INCLUSIVE FITNESS. The usefulness of the definition is that it

Table 1.1
The Major Questions of Ecology
Ecology is an analytical, question-asking science. The questions in this list include aspects of all the major problems studied by ecologists. It should be possible to answer all these questions by application of the physical sciences and the principle of evolution by natural selection.

QUESTIONS OF DIVERSITY
Why do living things exist as discrete species?
Why are there so many different species of plants and animals?
Why do so many species divide their resources between males and females?
Why are there more species in some places than others?
Why are some species common, whereas others are rare?

QUESTIONS OF EVERY SPECIES
Why are individuals shaped the way they are?
Why do individuals do the things they do?

QUESTIONS OF BALANCE
Why do the common stay common, whereas the rare stay rare?
Are natural populations normally controlled in systematic ways?
Do predators control their prey?
How often do diseases or hunger regulate populations?
Is it possible for natural populations to have self-regulating mechanisms?
What causes "population explosions" (irruptions, plagues, epidemics)?
Are complex communities of many species more stable than simple communities of few species?

QUESTIONS OF ORGANIZATION
Why are maps of vegetation, soils, and climate similar?
Can communities be identified and described as if they were Linnaean species?
Why is the destruction of mature vegetation nearly always followed by an ecological succession of plant communities, seldom by direct regeneration of the original vegetation?
Why does the pattern of change in natural communities repeat itself to the extent that the course of succession is predictable?
Is the association of many species in a natural area the result of chance, of physical circumstances, or of an organic organizing process?
Are complex communities more efficient at using energy and raw materials than simple communities?

takes into account the copies of genes that may be carried into the next generation through relatives, notably brothers and sisters, called SIBLINGS.

The concept of inclusive fitness allows the parallel concept of KIN SELECTION as an explanation of what would seem to be otherwise altruistic acts. Any action by an individual that helps the relatives of that individual survive and reproduce necessarily gives some reward in *inclusive fitness* because those relatives carry copies of that individual's genes. The closer the relationship, then the higher the probability of sharing genes. Hamilton (1964) showed that an act of helping relatives at cost to the helper (apparent altruism) can be selected for if the gain in inclusive fitness resulting from relatedness outweighs the apparent costs in fitness of the act to the altruist itself.

The concepts of kin selection and inclusive fitness satisfactorily explain social systems where close relatives help care for offspring in circum-

QUESTIONS OF LIFE FORM

Why are there no trees in the arctic?

Why are trees evergreen in equatorial and northern latitudes, but deciduous at in-between latitudes?

Why are the plants of open water microscopic?

Why do some trees have round leaves but others have needles?

Why does a grass have spear-shaped leaves?

QUESTIONS OF PHYSICAL PATTERN

How is the ionic composition of the oceans maintained?

How is the gaseous mixture of the atmosphere maintained?

What proportion of solar energy flux is used to drive the living components of ecosystems?

Why are soils of temperate regions brown, whereas those of the tropics are red?

What sets the limit to the mass of living tissue on the surface of the earth?

What sets the limit to the energy available to life?

QUESTIONS FOR STUDENTS OF THE HUMAN CONDITION

Why does the western-style agriculture of monoculture yield more food than have any attempts at manipulating the original complex wild vegetation?

Why does western agriculture work less well in the tropics?

What sets the upper limits to food production?

How much extra food could be taken from the sea and what would set the eventual limit?

Is life on earth at risk from contamination with radionuclides or novel chemicals?

Can pollution kill a lake?

What will set the limit to the energy flux that societies of the future will be able to release?

Why do human populations continue to grow?

What influence do population growth and human ecological need have on the structure of society and the events of history?

What changes may people expect in themselves from living at high densities?

Can we trigger an ice age, and does it matter?

Is the atmosphere at risk?

stances when they do not breed themselves, particularly if their chance of inclusive fitness is higher in a cooperative breeding effort than if they attempted a family of their own with small chances of success. The concepts are also used to explain sterile castes in insects, or various patterns of warning behavior in birds or mammals that seem to put the warning individual at risk.

An object of evolutionary ecology is to try to explain the grand patterns of the distribution and abundance of life on earth as the outcome of a game of reproduction and survival played on a gaming-board made up of the physical earth. Each roll of the reproductive dice yields new varieties, and natural selection is a universal obstacle that delays some individuals more than others in the reproductive race. The game proceeds at different speeds at different times and different places, depending on the local environment. Ecologists try to understand the rules of the game, asking what gives fitness in different places or to different individuals, and why these local rules