



Ecology 2

Paul Colinvaux

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Paul Colinvaux

*Center of Tropical Paleoecology
Smithsonian Tropical Research Institute
Balboa, Republic of Panama*



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Preface

I like writing. Among the most treasured happenings of the quarter century I spent as a professor were the times, five of them now, when extracts from my scientific writings were used in readings meant for English classes. I see no reason why a textbook on so rich a subject as ecology should not give pleasure in the reading. To be comprehensible is not to lack rigor. I have tried to be comprehensible.

Ecology2 is actually the third incarnation of my ecology text, the first appearing in 1973 (under the title *Introduction to Ecology*) and the second in 1986. I had much new material to add to the present edition: several chapters are entirely new, and several more overlap only partly with their predecessors. This meant that the old material needed pruning, for I was determined that the book of 1993 should be no longer than that of 1986. The best way to prune is to write more concisely.

Where old material has been retained, I reviewed every paragraph, often rewriting entirely as I went. Usually I found myself recasting the entire chapter. I reordered chapters, with the aim of making the four parts of the book independent entities, each with its own beginning and ending. An extra benefit of this is that the parts of

the book (Energy, Diversity, Community, System) can be shuffled more easily, so that the grander subdivisions of ecology can be read and taught in any order.

Every chapter preview has been entirely rewritten. The new versions are not summaries of what follows, nor do they refer to all the issues to be taken up. Instead they are meant as diminutive essays that tell of the more important or interesting ideas and phenomena discussed in the chapter.

In the new organization, climate is disentangled from biogeography and brought toward the front of the book, rounding out a study of the consequence of energy flows for life on earth that is the subject of the new Part I. The larger change in substance is in the treatment of population biology and speciation, the subject of the new Part II (Diversity). I have recast the ancient debate on the causes of the balance of nature in the ways suggested by the work of Robert May and the others working with difference equations and approximations to chaos. I persist in my habit of keeping math to a minimum, intending the book to be read by the literate as well as the numerate.

I review contemporary ideas of cascades in food webs in a new chapter, and I have

attempted a summary of the ecological properties of oceans in another. The ecological basis for some of the ideas of environmentalism will be found in a number of chapters, in the discussions of diversity and population regulation, and in most of the chapters of Part IV (System). My new chapter on the human impact (Chapter 29) is not a tale of pollution, such as can be found in environmental science books, but rather looks at humans, and the human condition, as they are consequences of choices made by natural selection in evolving populations of hominids long ago. The consequences of our ancient traits are with us yet.

I stress the findings of my own specialty, paleoecology, without apology. Understanding the diversity of life on earth requires that we master the time-scales on which evolution happens. The end of the last ice-age was roughly 40 tree life-times ago, and nearly all contemporary plants and animals have passed most of their existence as species under conditions of the ice-age earth, rather than in the odd climates of short interglacials like the present. The time-scales of evolutionary ecology are those of millennia, or tens of millennia, more than they are those of generation change. Thus a student of evolutionary ecology needs a paleoecological perspective as much as does a student of global change. I have used paleoecological data throughout the book, not just in the review chapter called "The Ecologist's Time Machine."

The new introductory chapter, "The Science of the Universe" echoes one of G. E. Hutchinson's more grandiloquent phrases, but I use the title as an excuse for writing a preview of the whole book, and, of course, of ecology as I know it. Thence the organization is a version of the "levels of integration" approach, though the first emphasis is on energy as much as on the

individual. The partitioning of energy between the quick and the dead, as it were, and the necessary adaptations of individuals to the results of that partitioning, give structure to life.

The behavior, and diversity, of species populations make up the second part, the whole naturally falling together as an inquiry into the causes of diversity. Building and persistence of communities is the natural next part, and one in which Pleistocene time-scales are crucially important. Accordingly, I begin Part III with a review of paleoecological methods, though it is a shorter review than in the 1986 book. The final part on systems is an analysis of the biospheric process, ending with a discussion of the origin and control of the earth's peculiar atmosphere.

I have kept the number of references to a minimum. Textbook writers face a dreadful temptation to pile in references; 'tis so easily done, and the result is a swelling bibliography adequate for the most rigorous graduate student. The references I have left in the text were meant to pass the test: Is this necessary to guide the student to the primary studies, to back up what I say, or to help the captivated student who wants to read more or find the latest work?

THE BOOK AS A TEACHING TOOL

There must be nearly as many ways of teaching ecology as there are teachers of the subject. An "integration" approach, working from individual to ecosystem, as pioneered by E. P. Odum in his classic books of the 1950s, remains one of the more popular, and *Ecology2* follows roughly this format. If time is pressing, or one is impatient to get to the big questions of diversity and community, I recommend

deleting chapters 4–6 on individual energetics from course requirements. Chapter 12 on the origin of sex is also removable, and I admit, with reluctance, that the Chapter 17 review of paleoecology could be omitted in many treatments. And when time is running out at the end of a course, soil, lakes, and oceans can go easily enough. With this stratagem of judicious deletion, *Ecology2* can fit the Procrustean requirements of most courses set to the “levels of integration” approach.

Because each of the four parts of the book is designed to stand on its own, they can easily be reshuffled. The introductory chapter will work for any reordering of the four parts. A common alternative to the “levels of integration” approach is to follow deductive logic from the complex to the simple, starting with ecosystems and ending with populations. I have frequently done this myself, so that my writing reflects this possible need. I suggest the following:

For ecosystem to population approach

- Introduction
- Part I: Energy
- Part IV: System
- Part III: Community
- Part II: Diversity
- Postscript

The parts also lend themselves to an early emphasis on populations or ethology as follows:

For population or behavioral approach

- Introduction
- Part II: Diversity
- Postscript
- Part III: Community
- Part I: Energy
- Part IV: System

In Tables 1–3, I suggest reading outlines for shorter courses organized from alternative population, behavioral, or environmental points of view. Because the chapters are written with the idea that each should be an independent essay, these various organizations should let the subjects flow well enough.

TABLE 1
Abridgement with Population Emphasis

- Introduction
- Part II
 - Chapters 8–11
 - Chapters 13–16
- Part III
 - Chapter 17 pages 338–347
 - Chapter 18
 - Chapters 20–22
- Postscript: The Human Impact
- Part I
 - Chapter 2
 - Chapter 3, pages 30–36, 45–49
 - Chapter 7
- Part IV
 - Chapter 23
 - Chapter 28

TABLE 2
Abridgement with Behavioral Ecology Emphasis

- Introduction
- Part II
 - Chapters 8–16
- Postscript: The Human Impact
- Part III
 - Chapter 18
 - Chapters 20–22
 - Chapter 29
- Part I
 - Chapter 2
 - Chapter 3, pages 30–36, 45–49
 - Chapter 7
- Part IV
 - Chapter 23
 - Chapter 28

TABLE 3
Abridgement with Environmental Emphasis

Introduction
 Part I
 Chapter 2
 Chapter 3, pages 30–49
 Chapter 7
 Part IV
 Chapters 23–28
 Part II
 Chapters 8–11
 Chapters 14–16
 Part III
 Chapter 17, pages 338–347, 360–363
 Chapter 18
 Chapters 20–22
 Postscript: The Human Impact

THE ECOLOGIST'S SEVENTH SENSE

Ecology is the most privileged of sciences. We who follow it savor the life of a naturalist while using the methods of chemistry or the philosophy of mathematics. Above all we see the workings of natural selection in the form and function of every living thing. Long ago, Darwin said admiringly of mathematicians that they seemed to have a sixth sense. But ecologists have a seventh sense, even more precious and coming from their gut understanding of natural selection. The shape of a tree as a great light diffuser, the singing of birds in the morning, the puny size of a male black

widow spider beside his fearsome mate, the flash of a firefly and the croaking of a frog: —everything noted by the ecologist as naturalist in a country walk seems right and good and proper before the seventh sense that understands natural selection.

I wrote most of this book in a cottage at Woods Hole, with the waters of Buzzards Bay just visible through the trees and the library of the Marine Biological Laboratory a comfortable walk away. I conclude it looking out over the Bay of Panama, with the soft growling of waves beneath my window and the lights of freighters entering the Panama Canal to my right. Over to the left the English pirate Morgan anchored 300 years ago before storming ashore in one of the most ruthless robberies in history. In the evening, greater ships than Morgan's, with jet engines throttled for their final approach, bank over his old anchorage before landing at the airport near the ruins that are all he left of a city. In my mind's eye I can see Morgan's ship there still; what if his ruffians could have imagined those wonderful crafts that would float above that anchorage on their way to land just three centuries later? But those three centuries are nothing in ecological time. The cormorants and pelicans, and the lone osprey, fish the same waters now as then. Real time is measured in millennia, and tens of millennia, and hundreds of millennia. It is into this real time that our seventh sense grasp of natural selection most easily fits.

Acknowledgments

I have a huge debt to The U.S. National Science Foundation, which has funded my research almost continuously for more than 30 years. The NSF projects grant system, with its forbidding hazards of peer review, is the protector of freedom in science. No better system of seeking out the great questions of science, or of rewarding individual initiative in science has been found by any country. I offer my heartfelt thanks to those who maintain the NSF: its staff, its reviewers, and its defenders in Congress.

This book was written after twenty-five years of teaching ecology. Inevitably I have borrowed from the minds of more than two generations of ecologists, my own and my teachers' generation. Most important to the formation of my thinking have been D. A. Livingstone, E. S. Deevey, and G. E. Hutchinson; my gratitude to the happenstance that placed me in such intellectual descent is not easily expressed. D. A. Livingstone not only guided my thesis long ago but reviewed my earlier texts as well as this one. R. H. Whittaker served as role model and counsellor when I wrote my first text of 1973. Other teachers of my formative years in ecology whose thoughts became embedded in my own were P. H.

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Chapter 1

Introduction : The Science of the Universe

Ecology is the study of how the world works, "the science of the universe" as G. Evelyn Hutchinson, one of the greatest of ecologists, once called it. Most of us working ecologists narrow this definition somewhat, restricting our studies to the planet we live on, and of course its energy supplies. This still leaves us plenty to do.

Our generation knows "ecology" to grapple with pressing questions of public concern: greenhouse warming, pollution, habitat destruction, spreading deserts, feeding the hungry, saving rain forests. This "ecology" fits well in the definition of "how the world works." The public affairs side of ecology thus overlaps geography, climatology, and even economics, in studying the systems that run the earth.

But at its core, ecology is a biological discipline. Ecologists concern themselves first with life on earth, asking how the living part of the earth system works. They see a biosphere in which life is driven by

the energy of the sun. Green plants are staked out under that sun in every part of the earth that is moist, warm, or nutrient-rich enough to let them live, using solar energy to drive a chemical synthesis of carbohydrate fuels. The rest of life (with the exception of remarkable chemists among the bacteria) persists as a tax on the fuel hoards that the green plants make. Animals eat plants; fungi and bacteria rot plant corpses. All give off heat, so that the energy once trapped from the sun by green plants is radiated back to outer space. Elegant in its simplicity is this ecologist's overview of how the world works.

But the details are not simple at all. Consider a meadow or old pasture; a place of moisture, warmth, and good soil where the green plants are indeed staked out under the sun as expected. In keeping with the simplicity of the model, all are synthesizing the same carbohydrate fuel using essentially the same complex chemistry.