Book Reviews

A Diversity of Textbooks: Ecology Comes of Age

Ecology: An Evolutionary Approach. J. MERRITT EMLEN. Addison-Wesley, Reading, Mass., 1973. xvi, 494 pp., illus. $14.95.

Ecology. ROBERT E. RICKLEFS. Chiron, Newton, Mass., 1973. x, 862 pp., illus. $15.

Introduction to Ecology. PAUL A. COLINVAUX. Wiley, New York, 1973. xii, 622 pp., illus. $12.50.

Ecology: The Experimental Analysis of Distribution and Abundance. CHARLES J. KREBS. Harper and Row, New York, 1972. x, 694 pp., illus. $14.95.

General Ecology. S. J. MCNAUGHTON and LARRY L. WOLF. Holt, Rinehart and Winston, New York, 1973. x, 710 pp., illus. $13.

Dynamic Ecology. BOYD D. COLLIER, GEORGE W. COX, ALBERT W. JOHNSON, and PHILIP C. MILLER. Prentice-Hall, Englewood Cliffs, N.J., 1973. xii, 564 pp., illus. $11.95. Prentice-Hall Biological Science Series.

Until recently, the appropriate unit of measure of ecology texts was the *odum*, and the problem of selection of a text for a course was a simple one. Rather suddenly this situation has changed with the appearance of a diversity of new texts that reflect most of the varied viewpoints ecologists have about their field. On first examination these six books have what appears to be similar coverage of the basics of population and community ecology. Nevertheless, they differ greatly in scope, in their attitudes toward and use of theory, the degree to which the concept of natural selection pervades the text, and the way in which higher levels of ecological organization are approached and conceived.

It is significant that all the books are evolutionary to the extent that they explicitly devote attention to natural selection and adaptation. They differ substantially, however, in the extent to which adaptation is used as an organizing concept, and the authors hold different beliefs concerning the mode of operation of natural selection. Three of the books (Emlen, Ricklefs, and Colinvaux) develop primarily evolutionary approaches to ecology while the other three use the concept of natural selection much more sparingly. Krebs and McNaughton and Wolf do not discuss explicitly the mechanisms of natural selection, perhaps assuming that they are self-evident and familiar to all students, and since some mutually contradictory statements do appear it is difficult to determine how these authors view natural selection. For example, in his chapter 19 Krebs discusses a number of theories of population regulation, some of which require group and population selection, but he never even mentions the selective problems posed by the hypotheses. McNaughton and Wolf at times write about natural selection in the classical Darwinian sense, but at other times they write in such a way as to imply selection at the level of populations and communities, as on page 337:

> The discussion of population regulation so far has concentrated on the ability of populations to respond to approaches to carrying capacity by decreasing the rate of addition of new individuals. For many populations, however, an equally important consideration is to insure that fluctuations in population density do not lead to extinction.

Collier *et al.* are more explicit in their belief that selection does not operate at these levels, but they nonetheless tend to lapse into language that implies the contrary. For example, on page 163 they say,

> Under these conditions, there is no great advantage in being capable of rapid population growth, since the opportunity for such growth rarely exists.

Similarly, on page 385 they discuss what sort of canopy a *forest* ought to have in order to maximize production and on page 434 they treat regulatory controls at the community level as though they were analogous to those operating within organisms to maintain homeostatic conditions.

The best and most thorough treatment of the process of natural selection and the levels of selection is provided by Emlen, but Ricklefs and Colinvaux are both explicit in their view of natural selection and treat it consistently throughout their books. Colinvaux, for example, who has a knack for devising quotable quotes, says on page 233,

> It is a mistake to believe that animals and plants have all evolved primarily as efficient converters of energy. The pressures of natural selection are pressures for survival, and survival may sometimes be more concerned with the efficient use of nutrients, ensuring that individuals mate, safe overwintering, or swift growth and dispersal than with the efficient use, or even collection, of energy. Many choices made by natural selection must compromise food collecting for the safety of the organism and its progeny, so that food is wasted by the herbivores and carnivores of a system, going straight to the decomposers by default.

And on page 577 he says,

> It follows, then, that an ecologist setting out to learn the workings of some part of the natural world must study the strategies of individual species. The question he must ask himself is: What are the tricks used to turn resources into babies? This is the rewarding way to approach autecology. It is also the approach used by those who have made the great advances in ecology in the past few years.

He clearly signals his attitude toward ecosystem structure on page 569:

> But ecosystems are built up by the immigrations and adjustments of the species that are their parts. They do not evolve during the process of succession. Margalef is led to think and to write about ecosystems being selected for. But natural selection does not choose between ecosystems, it chooses between individual living things.

Ricklefs clearly agrees, for on page 728 he says,

> To understand the mechanisms that underlie community patterns, questions that were originally asked about community structure must be rephrased in terms of those mechanisms. Rather than asking what determines the number of species that can coexist in a community, we should ask what determines the outcome of competitive relationships between species and the ability of populations to specialize on different resources.

And on page 746,

> Ecologists usually consider complexity as a community characteristic, but the mechanisms responsible for the generation and maintenance of complexity are based on the adaptations of organisms.

Emlen's is the most thoroughly evolutionary book, as it was intended to be, and strategy models, models that predict attributes of organisms from considerations of fitness, pervade every chapter. He includes a rigorous and extremely concise discussion of popula-

tion genetics and the genetic basis of evolution, covering in a couple of chapters material that normally occupies the major portion of an introductory course in the subject. I judge the book to be too difficult for students in an introductory course, but it should be well suited for advanced ecology courses.

Ricklefs has also written an evolutionarily oriented book, but he develops a mix of proximate and strategy models for most topics and has the broadest conception of the domain of ecology. In my opinion he achieves the best balance of theory and examples of all the books. It is difficult to imagine students not being stimulated by many of the interesting examples of adaptations, many of which are illustrated with good line drawings or photographs. Colinvaux usually introduces an aspect of theory with some observed patterns in nature, but takes a much more strongly historical approach, leading the reader through the development of the ideas and explaining where and why investigators went wrong. At times the discourse may seem to border on disrespect for earlier workers, but in general he succeeds in painting a picture that makes their conclusions seem reasonable given the knowledge and intellectual setting within which they worked. The real value of some of these discussions may be lost on beginning students who lack the perspective really to appreciate them, but then one has to begin somewhere.

At the opposite extreme, Collier *et al.* and Krebs make little use of strategy or optimality models and focus their attention on the proximate factors affecting changes in the parameters they discuss. Of the six, Krebs's book is the narrowest in scope, and deliberately so. Krebs follows the ecological tradition of the 1950's championed by H. G. Andrewartha and L. C. Birch by restricting his focus primarily to the limitation of the distribution and abundance of populations. Indeed, the subtitle of the book, "The Experimental Analysis of Distribution and Abundance," clearly signals its scope and its prime message, which is that

> Progress in answering ecological questions comes when experimental techniques are used. The habit of asking *What experiment could answer this question?* is the most basic aspect of scientific method that students should learn to cultivate.

Within this restricted framework Krebs has produced an excellent book that thoroughly reviews evidence and gives good summaries of key experimental studies. Nevertheless, the reader will look in vain for any discussion of the problems associated with short-term manipulative experiments of systems whose components are coevolved and whose properties take long times to respond to changes. Also, the value of "natural experiments" tends to be underemphasized. So consistently does Krebs confine himself to his chosen focus that the chapters on evolutionary ecology are appendices that bear almost no relation to the remainder of the text. In fact, Krebs appears uncomfortable with evolutionary concepts in ecology, as indicated by a telling statement on page 134:

> When we conclude that factor x limits the distribution of a species at point y, we must enquire further to find why adaptation has not overcome this limitation. This meeting ground between ecology and genetics has been explored hardly at all.

Reading of several other of the books reviewed here shows that the exploration has in fact been substantial and fruitful.

Those books that focus their attention on proximate mechanisms also tend to adopt the "limiting factor approach" to population dynamics. The concept of limiting factors has a long history in ecology, but it is an approach that tends to be abandoned when an investigator develops a strategy model approach to adaptations and population characteristics. With his usual flair, Colinvaux poses the perspective in the following way (page 276):

> It is sound ecological thinking to ask, "What are the things of the environment which limit this organism?" It is perhaps not so interesting a question as, "Why has this organism been adapted to this set of limits?" but it is a valid question all the same

and (page 278):

> The real question for ecology is: Why have animals and plants evolved the particular sets of tolerances to which they do own? Measuring tolerances takes ecology no way at all on the road to answering this question.

It is, of course, unfair to criticize a person for using methods that do not answer someone else's questions, but these quotations point to the transition of viewpoint that accompanies the adoption of the evolutionary approach to ecological problems.

Perhaps the greatest challenge for contemporary ecology is the development of theories about the properties of communities on the basis of selection for the attributes of their component individuals. Not surprisingly, it is here that the more evolutionarily oriented books run into their greatest difficulties. Emlen's text loses much of its earlier crispness and Colinvaux can mostly only point to the problem and offer some tentative suggestions. Ricklefs assembles the best account I have found of the ways in which individual strategies might be combined to yield communities, but he would be among the first to admit the preliminary nature of his suggestions.

For the most part the books are all carefully written and edited. Errors are minimal and for the most part not consequential. Only McNaughton and Wolf's text shows major signs of hasty preparation and inadequate editorial attention by the publisher. For example, I found about eight text figures repeated exactly or nearly so in various places in the text and I also encountered more phrases that suffered from vagueness of meaning or triteness than in the other books. In particular, chapter 2, which covers too much too superficially, is the source of much of the repetition, and it should be an unusually difficult chapter for a beginning student.

The teacher of ecology now has an array of excellent books from which to select a treatment that is compatible with his or her views on the subject and how it ought to be taught. A book with a true group-selection orientation is missing from the list, but otherwise the spectrum of current ecological thought is generally well represented. All the books reflect, through their own perspectives, the many exciting advances in ecological thought that have characterized the past decade. It was not to be expected that there would be agreement about the kinds of theories that are most useful to employ, because scientists in other fields of biology are not in agreement either. Nevertheless, inductive and deductive theory, whether mathematical or qualitative, is well represented, and the next generation of students can scarcely avoid picking up a theoretical perspective. Pressing environmental problems are discussed where appropriate, but all the texts avoid giving implications that ecology can be a savior for our society. Taken together they provide a good selection of the ferment and diversity of viewpoints that characterize contemporary ecology.

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