

ume as a whole: James and Boecklen (chapter 26) illustrate the value of considering both the population size of individual species and their morphology in community analysis, though Wiens (chapter 25) warns against naive acceptance of ecomorphological correlates. A warning implicit in many of the studies is the danger of inferring community structure from a study of some part of the community. Biologists, because of their particular taxonomic predilections and because of the difficulty of sampling different types of organisms in the same way, often restrict their study to one taxon such as butterflies, birds, or spiders, yet interactions between, say, wolf spiders (Lycosidae) and certain ground beetles (Carabidae, Cicindellidae) may be far more significant than those between wolf and web-building spiders. Several authors urge, logically, that guilds should be the unit for analysis, and Connor and Simberloff (chapter 18) argue for Root's original definition—a guild exists when there is sufficient resource overlap for competition to be expected. In reality there are few instances where knowledge is adequate to permit the application of such a stringent criterion; also the resources taken into account must include shelter and other spatial requirements, as well as food. There is a case to be made for being flexible in defining guild boundaries; they can, where appropriate, be drawn more widely, usage thus conforming more to the original non-ecological meaning of the term—a group of craftsmen earning their living by the same trade. Lawton (chapter 6, and also in *A New Ecology*) considers all the herbivorous insects on bracken; working with another plant he might have needed to include mites, mollusks, or gall-forming nematodes. Once again the message is, as Wise (chapter 4) states, that one must have knowledge about the natural history of the system. If ecologists realize that they must become familiar with the bionomics of their subjects before they count, calculate, and conceptualize, their conclusions will be on a firmer basis.

Another warning, based on a real knowledge of the organisms, is the potential for predation to interact with competition. Werner (chapter 21) illustrates with fish how predation risk and foraging abilities change with developmental increases in size, so that competition effects may not be simply asymmetric but reversed. Similar considerations apply with many insects, and in partial predators (such as Miridae) the interactions may be particularly complex. Is it biologically meaningful or even possible

in such cases to distinguish competitive displacements from those due to predator pressure? The last general warning is that all nature is not in biological equilibrium all the time (Wiens): Andrewartha and Birch, who have recently published a postscript (*The Ecological Web*; reviewed below), could be forgiven for saying, "This is where we came in."

One can, I believe, conclude from this volume that ecologists must continue to seek patterns in the natural world, but that, having discovered them, they will, thanks to the Tallahassee school, be cautious (as are Grant and Schluter, chapter 13) in their claims concerning the underlying mechanism. As Wise and Werner remind us, one can be confident of this only after a judicious blend of field and laboratory experiments and if the ecologist really knows the system being studied; have we been trying to go too quickly? One can also perceive from this work a distinction between those who are most interested in the commonality in

## A General Theory

**The Ecological Web.** More on the Distribution and Abundance of Animals. H. G. ANDREWARTHA and L. C. BIRCH, University of Chicago Press, Chicago, 1984. xiv, 506 pp., illus. \$35.

In 1954 Andrewartha and Birch published their important book *The Distribution and Abundance of Animals*, which challenged the dominant dogma of population ecology that density-dependent biotic competition regulated the size of natural populations of animals. Their 1954 book had a salutary effect on ecology because they preached rugged empiricism as a philosophy, the importance of weather to population dynamics as a mechanism, and the significance of local populations, their genetics and dispersal, as a new outlook. This book is the authors' attempt to have a fresh look at these problems 30 years later. Andrewartha and Birch are not happy with the present state of population ecology, and many population ecologists will not be happy with the message of this book. Why should this be?

This book is divided into three parts. Part 1 gives Andrewartha and Birch's theory of environment and occupies about a third of the book. The environment of an animal consists of anything that might influence its chance to survive and reproduce. We need to break down the environment into two components: directly acting components (resources,

research findings and those who focus on the differences: progress in science depends on both approaches. For if ecology came to consist entirely of falsifying hypotheses, the total of our collective wisdom would be a sum not significantly different from zero, and ecologists would have no basis from which to claim a role in advising governments and decision-makers on matters of policy. There are therefore practical as well as intellectual reasons for continuing to search for and to understand patterns. Stripped of some of their unnecessarily emotional turns of phrase, the chapters in *Ecological Communities* constitute a valuable guide to an improved methodology for this search. Its publication will surely be seen as a landmark in the early and uncertain progress of the conceptual core of community ecology.

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predators, mates, and "malentities") and indirectly acting components, which form a number of systems of branching chains. These components are put together in a dendrogram whose branches trace causal pathways down to the individual animal. Andrewartha and Birch call these webs "envirograms" and give six examples to illustrate how detailed information on physiology, behavior, and natural history translates into an envirogram. Most of this part of the book is a useful summary of the components of the environment, and there is little of controversy here.

Part 2 gives a general theory of population ecology and occupies the middle third of the book. The theory rests on three concepts—the concept of the environment just given, the concept of the multipartite population, and the concept of "spreading the risk." Populations are subdivided into many local populations, and the resulting patchiness of populations has implications for demography and genetics. The important idea of "spreading the risk" is due to den Boer and recognizes that local populations can go extinct and their area be recolonized by dispersers. Given these three concepts, Andrewartha and Birch postulate their general theory that the numbers of animals in natural populations may be explained by either a shortage of time or a relative shortage of a resource. This leads into an analysis of some controversies in population ecology. The hypothesis of competitive exclusion is roundly

criticized, and outbreaks and collapses in mammal and insect populations are suggested to be due to changes in food supplies.

Part 3 gives eight examples of population studies to illustrate the theory that has preceded it. The ecology of the rabbit (*Oryctolagus cuniculus*) in Australia is summarized in nearly 60 pages. Briefer analyses are given for the black-backed magpie (*Gymnorhina tibicen*), the gray teal (*Anas gibberifrons*), and marine fish populations in one chapter and for spruce budworm (*Choristoneura fumiferana*) and the fruit flies *Dacus tryoni* and *Dacus oleae* in a second chapter. The ecology of humans is described in a final chapter. These examples are an important part of the book. There is an Australian bias to be sure, but there is in the literature no comparable review and synthesis of all the work that has been done on the rabbit, the magpie, and the teal over the past 40 years. The critique of marine fish population dynamics is well done and is a good example of the utility of the methods discussed in part 1.

In spite of all these good points this book is somehow disappointing. The general theory it contains is too general to be very useful for addressing concrete questions about animal and plant populations. It is perhaps better described as a paradigm or research philosophy than as a general theory. And there is too much left out of the book. Population ecology is exciting now because it is rigorous, quantitative, and experimental, all the virtues espoused by Andrewartha and Birch in 1954 but curiously lacking in this book. The application of mathematical modeling and evolutionary thinking to population questions is almost absent from this book. Too much energy is spent attacking "competition theory" as though it were the only alternative paradigm to the theory of environment championed by Andrewartha and Birch.

In my judgment Andrewartha and Birch try to do too much in this book. There can be no general theory of the numbers of animals in natural populations that can subsume the great diversity of species and local populations without becoming trivial. If we are to find generalizations about population dynamics, it will be at a lower level of generality with much more detail and more restrictive conditions than most of us would prefer. We are reaching now for specific hypotheses, and much of the excitement of modern ecology is in finding the right level of generality to aim for. None of this is easy, and we should all be grateful to Andrewartha and Birch for trying to go so far and do so much.

No one knows what a general theory of population dynamics should look like. Here is one. If you do not like it, be inspired to make a better one.

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## Rain Forests

**Tropical Rain Forests of the Far East.** T. C. WHITMORE. With a chapter by C. P. Burnham. Second edition. Clarendon (Oxford University Press), New York, 1984. xvi, 352 pp., illus. \$64.

Very few ecologists, biologists, or biogeographers have written substantively and at length on the tropical rain forest. Perhaps only P. W. Richards, in *The Tropical Rainforest*, published 33 years ago, has succeeded in presenting a unified ecological account of this complex subject. His book—aside from particular treatments in older works by Schimper, Warming, and more recently Walter—is the only classic in the field. Most tropical ecologists still return to it as an authoritative source and for its disinterested and coherent line.

The paucity of such works in any language—and there appear to be none by indigenous tropical scientists—sug-

gests that the subject may now be too vast and diverse to be grasped in a unified way as it was by Schimper and Richards. Of course there is a fast-growing number of disparate works by specialists in the tropical forest. But it is a chastening thought, despite holism, that the little we know about these complex ecosystems is already too large to apprehend, even with our new computer wisdom.

Given this situation the second edition of Whitmore's *Tropical Rain Forests of the Far East*, providing a timely update and appraisal of ecological information for the Malesian region, is to be welcomed. This is especially so because of the delay in revision of Richards's classic, in whose tradition it follows. Whitmore's book, as in the first edition, emphasizes the ecological basis of forest disturbances, both natural and human, and so is relevant to growing problems of forest regeneration and land rehabilitation in the tropics.

The second edition is rather longer than the first, which was published ten years ago, with 352 pages as against 282. The bibliography has nearly doubled, although one may doubt that the plethora of material listed will be accessible to the general audience, especially in the Far East, to which the book is directed. The extension of the text has enabled some important topics that were virtually unexplored previously to be discussed in



Limestone pinnacles reaching 30 meters in height (altitude 1200 meters) from the island Gunung Api, Sarawak. "Between the pinnacles there is about 0.6 m of peat and a low forest which has distinct similarity to that on the adjacent sandstone mountain Gunung Mulu." [From *Tropical Rain Forests of the Far East*]