1) in which we learn the long histories of many currently proposed explanations for extinction, including the concept of changing climatic equability (seasonal contrasts). Edouard Lartet first described variations in seasonality in 1867 (*Ann. Sci. Nat. Zool. Paléontol.* ser 5, **8**, 157–194), and the idea was never again discussed at length until D. I. Axelrod published a seminal paper a century later (*Univ. Calif. Publ. Geol. Sci.* **74**, 1–42 [1967]) and brought the concept to its current prominence (see chapters in part 3). Grayson also contributes to the overview section (chapter 37) with an insightful analysis of the structure of the debate between champions of human overkill and supporters of climatic models. He finds that current climatic hypotheses "stand on firm ground as regards their ability to be profitably tested" (p. 820) whereas the overkill hypothesis is "burdened by auxiliary hypotheses that protect it from falsification" (p. 821).

The last paper (chapter 38), by J. M. Diamond, is a fascinating study of historic extinctions and provides generalizations concerning proneness to extinction that could have been helpful to the reader if placed in the opening section of the book. Diamond shows that even some recent extinctions are not understood and that it may never be possible to pin down the causes of prehistoric extinctions. However, he makes some important observations concerning the structure of the fossil record, the need for species-level (rather than genus-level) analysis, and the lessons to be learned from the fossil records of islands. For example, if there were no waves of extinction in the late Pleistocene of New Zealand and Madagascar, it would be hard to attribute continental extinctions to climatic change alone. Here is fertile ground for further research.

There are several respects in which the book might have been improved by discussion in a prior symposium. For example, the interpretation of radiocarbon dates and their meaning for the larger problem receive varied treatment in different papers. Chapters 8 and 19 focus specifically on dates that are taken to indicate the last appearances of species or genera, whereas N. K. Vereshchagin and G. F. Baryshnikov (chapter 22) state that "the latest known record of an extinct species does not record its final extinction, but rather the continued presence of a relatively large population" (p. 483). In the chapters on New Zealand, M. M. Trotter and B. McCulloch (chapter 32) prefer dates on collagen and marine shell over those on charcoal (p. 718), but A. Anderson (chapter 33) prefers the charcoal dates (p. 733). Since chronology is crucial to the demonstration that two events, say extinction and the arrival of humans, are coincident, I would have preferred to see the dates used as a basis for inferring the age of each event with a discussion focused on the reliability of the inference rather than on technical uncertainties of the radiocarbon method.

Another worthwhile symposium theme would have been a comparison of the Sangamon (or any other) interglaciation and the Holocene. R. D. Guthrie (chapter 13; see also chapters 6 and 11) argues strongly that the Holocene is unlike any previous interglacial, whereas P. S. Martin declares that "the only significant difference between the transition to the Sangamon and the transition to the Holocene is the presence of early hunters in North America" (p. 367; see also chapter 16).

The issue of visibility in the fossil record could have been on the symposium agenda, because opinions vary widely in the book. Lack of visibility is one of the auxiliary hypotheses that buttresses the overkill hypothesis, but J. E. Guilday (p. 256) notes that it is "unanswerable and untestable," R. G. Klein (chapter 25) seems to assume that human-linked extinction will be visible in the fossil record, and one of the clearest cases of overkill (the New Zealand moas) is highly visible (chapters 32 through 34).

These matters show merely that more work remains to be done on this fascinating and important subject, and Martin and Klein are to be congratulated on the publication of an attractive, readable compendium. *Quaternary Extinctions* is markedly improved over its parent and reflects the benefit of nearly two decades of vigorous work by numerous researchers. Many of the authors draw heavily upon B. Kurtén and E. Anderson's recent synthesis *Pleistocene Mammals of North America* (Columbia University Press, 1980), a work that clearly aided Anderson's compilation of the bestiary included in this volume (chapter 2, from which hominids are paradoxically omitted). Better geographic coverage is seen in the papers on Africa, China, Australia, New Zealand, and the island Pacific, and better topical coverage is shown by chapters on birds, plants, and longer time spans. Improved theoretical background is reflected in many of the papers. This book should be read by paleobiologists, biologists, wildlife managers, ecologists, archeologists, and anyone concerned about the ongoing extinction of plants and animals.

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The State of Ecology

Ecological Communities. Conceptual Issues and the Evidence. DONALD R. STRONG, JR., DANIEL SIMBERLOFF, LAWRENCE G. ABELE, and ANNE B. THISTLE, Eds. Princeton University Press, Princeton, N.J., 1984. xiv, 614 pp., illus. $60; paper, $22.50. From a symposium, Wakulla Springs, Fla., March 1981.

A New Ecology. Novel Approaches to Interactive Systems. PETER W. PRICE, C. N. SLOBODCHIKOFF, and WILLIAM S. GAUD, Eds. Wiley-Interscience, New York, 1984. xii, 515 pp., illus. $59.95. From a conference, Flagstaff, Ariz., Aug. 1982.

Whatever the fate of the theories and hypotheses expanded, exposed, or exorcised in these two volumes, it is likely—as May suggests in his overview chapter in *Ecological Communities*—that the publication of the books will come to be recognized as marking an important stage in the development of ecological theory. That the theoretical core of the subject is still young was brought home to me a few months ago when I saw Charles Elton and G. Evelyn Hutchinson talking together in an Oxford street: virtually all the concepts currently under debate have emerged in their professional lifetimes, often originating from one or the other of them. But, as May also points out, controversy about the related theories of the role of competition in communities and the role of density-dependence in natural populations has been a recurring feature. Does this mean that, in contrast to, say, nuclear physicists, ecologists have totally failed to develop an agreed-upon core of theory? Or if, as I believe to be the case, the conceptual core is merely smaller and relatively less well tested, is this due to some characteristic of the subject and its students, rather than to its youth and comparative underprovision with research funds? Some chapters in both

these volumes are strident in their claims that there has been too much jumping to conclusions and reinforcement of persuasive paradigms and too little testing of theories through attempts to falsify null hypotheses. Indeed, whereas many of the earlier benchmark meetings (to which May refers) were about the validity or lack thereof of the concepts, the real debate in the two conferences reported in these volumes is about the methodology of ecology—the nature of evidence, the role of experiment, and, above all, the place of the null hypothesis.

A variety of views on the philosophy of ecological inquiry were propounded in *Synthèse*, volume 43; I still adhere to the view expressed then that Popperian reductionism is an insufficient tool for ecological inquiry. Having declared my own prejudice, I will attempt to assess that of others, namely the authors of the 46 chapters in these two volumes. There is a large measure of overlap between the volumes: seven of the 17 chapters of *A New Ecology* are by authors who also contribute to *Ecological Communities*. I will brazenly state, without any testing, that the null hypothesis that these "island communities" are random selections from the "species pool" of professional ecologists is false. The "island" of *A New Ecology* has a smaller community, its claims to novelty are advanced in both the title and the subtitle, and in places this attitude permeates the text to the detriment of the work being described. An almost journalistic imperative to be "new" and iconoclastic appears to have run ahead of the "dispassionate approach" the editors commend in their introductory chapter, which itself unfortunately provides some particularly blatant examples of value-loaded phrases (such as "changing ecology for the better"). While applauding the emphasis on objectivity in both these volumes perhaps one should also campaign for the cessation of the use of such language. Like many of the proposals that are made in *A New Ecology*, this would not be new but merely a return to the discipline that prevailed prior to the '60's, when (perhaps in the spirit of love that pervaded that decade) many of us started to lace our descriptions of other studies with laudatory adjectives—"seminal," "elegant," and the like. The appearance of pejorative terms (in the more combative '80's?) does restore the balance, but all such terms are really obtrusions in scientific discussions and militate against a dispassionate approach to the evidence. May I join with Price and his colleagues in urging fellow ecologists to always take such an approach and (except in the privileged forum of a review) to start on this path by eschewing value-laden descriptions. This would be a revival of a helpful discipline for authors and would have kept the editors of both these volumes busy with their blue pencils.

How new are the themes of *A New Ecology*? They are certainly not as new as the swashing style of the editorial introduction might suggest. Some statements that are true are trivial—for example, "Young ecologists have much more potential for changing ecology for the better than anyone established in the field" makes a point that would be equally true for all sciences, its truth stemming from the greater scientific life-expectancy of the young and the high level of creativity of young scientists (Elton wrote *Animal Ecology* in his 20's). More substantially, there are other themes, such as the need to consider population dynamics and to assess both resource availability and the role of natural enemies in a meaningful way, that have long pedigrees in ecology. One may be forgiven for wondering if the editors' attitudes, expressed in their references to a whole swath of ecological literature as "rapidly being forgotten," predispose them to rediscovery. Nevertheless, it is timely that these aspects be brought more sharply into focus. To mention but three examples, this is well achieved by chapter 2, on individual plants as temporal and spatial mosaics (by Whitham *et al.*), by results-packed chapter 4, on host-plant quality and gall formers (by Frankie and Morgan), and by chapter 12, on herbivore community organization on bracken (by Lawton). Other chapters (5, 6, 7, 8, 13, and 17) point out how features of the environment, its variation on temporal and spatial scales, may be related to life history strategies but that underlying these relationships will be a genetic mechanism. It is true that ecologists have paid less attention to population genetics than they should, and the emphasis in several of these chapters should be a corrective, but Istock (chapter 5), whose citations extend back to 1760, makes it clear that this objective is not new. What is new and encouraging is that quantitative genetic measurements are increasingly being related to evolutionary models and viewed against the habitat templet, and in chapter 13 Price makes a helpful categorization of resources for defining a habitat templet.

The most original aspects of *A New Ecology* are the exploration of the roles of microorganisms in herbivory (Jones, chapter 3) and of mutualistic interactions in communities (Addicott, chapter 16); both aspects have been neglected or damned by faint mention in most recent textbooks. Like genetic variation in natural populations, they are no less important for being difficult to measure and study. Notwithstanding that *A New Ecology* is (fortunately) not what it claims in terms of novelty and is certainly not, as the dust jacket claims, "an invaluable guide" for students, it is a useful and stimulating, if somewhat patchy, resource for practicing ecologists.

The more modest subtitle of *Ecological Communities* is more precise. The island represented by this volume has a more limited resource base than *A New Ecology* but more species (authors). It will not surprise the adherents of so-called orthodoxy to discover that there is clear evidence for interauthor competition in the form of aggressive interactions. Although these occur in several patches, the most intense contest occurs in chapters 17, 18, and 19, where Gilpin and Diamond dispute Connor and Simberloff on the evidence or lack of it for interspecific competition provided by the species lists of birds on Pacific islands. The relatively objective tones of the first two of these chapters are unfortunately lost in the third, entitled "Rejoinders," where the exchanges do less than justice to the issues raised on both sides. The same themes appear in a less strident form throughout the volume. Taken as a whole the volume provides valuable insights into the questions and methods of community ecology and in particular into the assessment of community structure and the utility of the null hypothesis approach, pioneered by the "Tallahassee school," who organized the conference and edited the volume. They are to be congratulated on this well-balanced account that on the one hand shows the value of their critical challenge but on the other reveals new approaches that bypass the original arguments.

It is clear from *Ecological Communities* that the mechanisms underlying the structure of animal communities will not be easily revealed. Given that we cannot get into a time machine, appropriate null hypotheses with neutral models are themselves difficult to construct; Colwell and Winkler (chapter 20) simulate evolution (with a program entitled GOD) and show how sampling (as is unavoidable) from post-competition and post-colonization species pools poses general methodological difficulties for the construction of appropriate null models.

The biological requirements of future investigations are pointed up by the vol-

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 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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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 salutory 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, 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