A NEW ECOLOGY

Novel Approaches to Interactive Systems

Edited by
PETER W. PRICE, C. N. SLOBODCHIKOFF, and WILLIAM S. GAUD

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PREFACE

We designed this volume specifically for students of ecology who are beginning a research career. Here they can find some of the excitement and ferment in this field and readily assess how to make a major contribution to its development. We asked each author to comment specifically on future developments and research needs in the area they address. We anticipate that this volume will be used in undergraduate and graduate ecology seminars, and as a source of discussion topics in general ecology courses. We expect, also, that established researchers will find enough new research, synthesis, and discussion of future ecology to make this a valuable reference volume.

The book is derived from a conference of the same title held at Northern Arizona University, August 11–13, 1982. The conference was organized as a celebration of the increased research capacity on this campus in the form of the new Ralph M. Bilby Research Center building and the establishment of the Center for Ecological Research.

We selected four areas of ecology in which we saw rapid development: the relationship between resources and populations; life history strategies; ecology of social behavior; organization of communities. The need for synthesis among these areas resulted in a fifth part to the book. We do not pretend to cover the full range of exciting areas in ecology, and the topics we chose reflect our personal interests, as well as those of a large body of researchers in the ecological community. Authors were chosen as much for their demonstrated ability for integration and synthesis as for their expertise in the particular area of ecology they addressed. At the conference in which these topics were presented there was much lively discussion and a refreshing sense of rediscovery of areas and points of view resulting from interaction between scientists working in disparate subdisciplines of ecology. We resisted the temptation to publish the discussions because of their volume, both in decibels and length, but they remain for many participants a part of a new ecology that will bear fruit in years to come.

We are very grateful to several people who made the conference and this book possible. Eugene Hughes, President, and Joseph Cox, Vice President for Academic Affairs, of Northern Arizona University have most effectively fostered the development of research personnel and resources on this campus. We were supported in spirit and in substance by Henry Hooper, Dean of Graduate Studies, who allocated funds to cover all conference expenses.

The Director of the Bilby Research Center, Richard Foust, provided advice, organizational expertise, secretarial help, and many other indispensable services. Dr. James Wick, Chair, Department of Biological Sciences, has overseen the department's development for more than 20 years, and without his commitment to creative scholarship neither conference nor book would have materialized.

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Flagstaff, Arizona
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CHAPTER 1

Introduction: Is There a New Ecology?

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CONTENTS

1 A NEW ECOLOGY

Much of the work discussed in this book illustrates developments in ecology that have gained impetus within the last 10 years. It is new to this extent. Some areas are much younger. Many of the approaches taken here and the conceptual bases for them are presently not widely used but deserve to influence a wider range of ecologists. In the future, we believe that the areas discussed herein will flourish and result in major developments in ecological thought and practice.

There is certainly a new realization that plant populations provide a very heterogeneous environment for herbivores, contrasting sharply with a large literature on population dynamics that regards plants as homogeneous resources (Price, 1983a). This new attention to the detailed understanding of patterns of resource availability was sharply focused by Edmunds and Alstad (1978), Whitham (1978), and Whitham and Slobodchikoff (1981), and is discussed in Chapters 2 and 4. Resources also act as central themes in other chapters (3, 8, 13, 15) reflecting a realization of the need in population and community studies to work from the bottom up rather than from the top down. Looking at patterns and trying to guess the mechanisms have been unprofitable, producing a literature that is rapidly being forgotten on such topics as species-per-genus ratios, dominance–diversity curves, and diversity–stability relationships. Resources form the starting points of food webs to which populations and communities respond, and the patterns of resource availability and use need to be understood in detail before ecological mechanisms, which are the basis of ecological organization, can be described adequately. Connell (1980, p. 133) asked the question: *Can ecologists judge availability [of resources] as the organisms do*? We must be able to answer in the positive to this question and the chapters in this book approach that answer. A new ecology must continue to give this question a central place.

The rich possibilities for mutualistic interactions among plants, animals, and microorganisms will eventually lead to a burgeoning literature in major ecological journals. Conventional "wisdom" presently holds that mutualism's "importance in populations in general is small" (Williamson, 1972, p. 95) and that such relationships are "relatively uncommon in many natural ecosystems" (May, 1973, p. 4, but see May, 1981, for signs of change in opinion). The growing emphasis on mutualism as an ecological phenomenon fully as important as the phenomena of competition and predation is illustrated by a recent review (Boucher et al., 1982) in which microbes figure prominently. Resources are also profoundly modified by microorganisms, a subject addressed in Chapter 3, needing much more attention in ecology. The importance of mutualism is discussed also in Chapter 16. As Boucher et al. observe (1982, p. 337), "the study of mutualism has made major advances in just the past decade."

The study of life history traits, the subject of Part II of this volume, is a rapidly growing field in ecology (Stearns, 1982). Variation in life-history traits shows the diverse ways in which organisms have solved a complex array of problems including resource availability and habitat variability. Of course the idea that environmental variation resulted in variation in populations and species was Darwin's (1859) empirical observation, but since then we have passed through a bottleneck of typological thinking in ecology, typified by *r* and *K* selection theory, in which there is one solution to a given selective regime. Since that time there has been a growing sophistication of experimental analysis in ecology and the realization that alternative solutions to any problem exist in many species. We see in Chapters 5, 6, and 7 some of the major new approaches to life history studies: careful experimental analysis of mechanisms; recognition of a diverse array of solutions for organisms living in variable, unpredictable environments; and a broad comparative basis, both taxonomic and geographical, revealing the full range of variation in life history mechanisms.

The ecology and evolution of one specific life history trait, social behavior, has recently generated considerable debate. The seminal papers of Hamilton (1964, 1972) suggested kin selection as an elegant answer to the question of why animals are social. This answer, however, has not proved to be sufficient in explaining the diversity of social behaviors seen in animal groups, and ecological mechanisms relating to resource availability (Jarman, 1974) and antipredator defense (Triesman, 1975) have been suggested. A new approach has emphasized cooperative behavior (Axelrod and Hamilton, 1981). This approach, inspired by game theory (Maynard Smith, 1976, 1982), suggests that cooperative behavior may arise in response to a number of factors, including kin selection, resource abundance, and antipredator defense, as long as there is a net benefit to the individual to cooperate in a social group. Chapters 8, 9, and 10 reflect this novel approach and a primer on game theory is provided in Chapter 10.

Any textbook on general ecology may be consulted to perceive the importance ascribed to interspecific competition in universally influencing populations and communities. The alternative view that interspecific competition may be unimportant, or only one of several equally important ecological processes, raised many times (e.g., Gleason, 1926; Ramensky, 1926; Andrewartha and Birch, 1954; Whittaker, 1967) was never given much credence until the last decade. Since the early 1970s a growing volume of literature has recognized the commonness of nonequilibrium conditions in which interspecific competition is unlikely to be influential (see Pickett, 1980; Price, 1980, 1983b, for summaries), and the importance of patchiness, disturbance, and other factors (e.g., Dayton, 1971; Wiens, 1973; Connell, 1978; Lawton and Strong, 1981; Strong et al., 1983). We regard this as a healthy, desirable development in which alternative hypotheses on the development and dynamics of community organization are gaining equal plausibility. Part IV in this volume is devoted to this change in perspective in community ecology.

The chapters of synthesis in Part V pick out many themes linking the major areas treated in this volume.

2 THE SCIENTIFIC METHOD AND COMMUNICATION IN ECOLOGY

There are few graduate programs in ecology that deal specifically with the scientific method. This is unfortunate at a time when there is growing dissatisfaction in some sectors of the scientific community about evolutionary biology and ecology in relation to what is and what is not proper science (e.g., Peters, 1976; Brady, 1979, 1982; Bondi, 1980; Halstead, 1980; Popper, 1980). An additional problem is communication. Brady (1982, p. 79) has recognized a deficiency in communication between critics and defenders of evolutionary and ecological theory: "The critics . . . have not been exacting enough with their formulations. The defenders . . . have spent little or no effort finding out what the critics might actually have in mind." This pinpoints a second major failing in the training of ecologists today, that is, the meager emphasis on communication in science as a form of art. The two problems, the application of the scientific method and communication, are coupled and their correction represents a major challenge to ecologists in the future.

In their writing, scientists would profit from Joseph Pulitzer's admonition to writers: "Put it before them briefly so they will read it, clearly so they will appreciate it, picturesquely so they will remember it and, above all, accurately so they will be guided by its light." Few ecologists can claim these attributes for each or any of their scientific communications.

And yet the scientific method incorporates the clarity and precision Pulitzer demanded, if only ecologists would use it. Clarity comes from an explicit hypothesis posed about a certain question, stated early in a communication. Accuracy comes from the fact that the hypothesis is falsifiable: it is accepted or rejected on the basis of observations and experiments (type I and type II errors considered).

Ecology has moved from a strongly descriptive discipline to an experimental science. Descriptive studies of vegetation types, animal distributions and communities, food webs, and types of interaction (e.g., Elton, 1927; Tansley, 1939; Shelford, 1963) have been replaced by studies of mechanisms. The transition from description to mechanisms, however, has not been accompanied by a wholesale move to a more rigorous application of the scientific method. Answers have been largely speculative at best. Had the scientific method come into play adequately as the interpretive phase in ecology developed, description would have provided the first link in erecting hypotheses about ecological mechanisms. Tests of these hypotheses would have provided us with some concrete information on the validity of some mechanisms and interpretations. Such an approach applied throughout the field would undoubtedly have carried us beyond the condition we find ourselves in today, where we still debate the roles and influences of even the most obvious kinds of interactions. Even in 1980 Strong asserted that most ecological research "is either phenomenological on the one hand or corroborative on the other" (p. 273), with explicit null hypotheses infrequently used.

Since we believe that the scientific method is integral to ecological research, we would like to summarize the steps of the method, in the sequence appropriate for ecological questions. The elements of the scientific method are

1. Observation and description of a condition in nature.
2. Formulation of an interesting question relating to this condition.
3. Erection of hypotheses.
   (a) Erection of an hypothesis to explain the condition:
      (i) The hypothesis suggests the simplest possible explanation, separating the condition from its hypothetical cause(s); this null hypothesis may invoke nothing but random processes as leading to the observed condition (see Strong, 1980).
      (ii) The hypothesis must be verifiable or falsifiable using observations and experiments.
      (iii) An explicit statement should accompany the hypothesis on how it could be falsified.
   (b) Erection of alternative hypotheses that may account for the condition under study.
4. Tests among hypotheses.
   (a) Observations and experiments are designed to test as directly as possible the hypotheses.
   (b) An explicit method must be devised and stated in order to distinguish among hypotheses.
   (c) Tests among hypotheses must be objective and not biased towards a particular hypothesis.
   (d) Tests must incorporate the potential for falsifying hypotheses.
   (e) The extent to which the real world is modified by such experimental practices must be explicitly addressed and evaluated, and should be minimized with appropriate controls. Testing in the real world changes it, and testing in modified environments may alter reality.
5. Revision of hypotheses and asking new questions.
   (a) Once the original hypotheses have been tested and the results ascertained, they may require revision. Retesting with new data and/or the formulation of deeper, more searching questions may be necessary.
6. Communication of results.
   (a) Specialized terms are defined clearly and briefly.
   (b) Definitions, questions, and hypotheses are explicitly stated and distinguished.

(c) Distinction is made among established fact, extrapolations from fact, possibilities, speculations, guesses, and fresh working hypotheses to be examined later.

Testing hypotheses by the scientific method provides two possible outcomes: (1) accepting the null hypothesis (because it was true, or because the evidence was not sufficient to reject it even though it was false); and (2) rejecting the null hypothesis (because the evidence was sufficient to prove it false, or because the evidence was misleading). The former of these two conclusions constitutes a negative result (see below).

We see in the literature a growing awareness that the scientific method must be applied to ecological questions. As more ecologists apply this method, there will be increased improvement in the scientific rigor with which ecological mechanisms are developed. Much of this rigor will come from the new ecologists being trained today, and from those faculty members and journal editors who are deeply concerned with the proper application of the scientific method and communication in science.

3 THE IMPORTANCE OF NEGATIVE DATA

The scientific method necessarily includes the reporting of negative results. Some biological disciplines, such as biogeography, have taken this for granted. Ecology has not. Researchers and editors have considered it meritorious to publish evidence of interactions such as competition, however poor or misleading the evidence is, whereas a scientifically rigorous demonstration of competition's absence in a certain community is regarded as uninteresting. Whereas a biogeographer can say that a certain animal occurs in one area and not in another, the ecologist cannot say that a certain type of interaction occurs in one type of community and not in another. We have little idea of the relative commonness of interspecific competition, mutualism, parasitism, amensalism, and so on, in different kinds of communities, because we have not paid enough attention to negative evidence. This has allowed our science to become dominated by simple themes with apparently universal application, because the evidence establishing both the presence and absence of a certain phenomenon has not been treated equitably. Part of a new ecology must involve a new appreciation for negative data, as a step in the development of appropriate hypotheses. This requires a new ethic among investigators, authors, reviewers of research proposals and articles, research granting agency personnel, and editors; that is, an ethic that establishes the morality of reporting negative results.

Part of the difficulty in accepting negative data can be ascribed to an incorrect application of the scientific method. As statistics have shown, hypotheses can be accepted or rejected with different levels of confidence. A biogeographer who spends several years trapping and studying the mammal fauna of several mountaintops can say with nearly 100% confidence that a particular mammal is not present. Ecological experiments can rarely approach such confidence levels. The complexity of variation between organisms and their environment leads to much higher levels of uncertainty than a biogeographer would normally face. Such uncertainty allows detractors of negative data to say that the hypotheses producing the negative data were incorrectly stated, and a set of reformulated hypotheses, usually untestable under the particular circumstances, would have produced a positive result that had less associated uncertainty. Without question, the goal of the scientific method is to reduce the uncertainty in accepting or rejecting hypotheses. However, all the hypotheses must be testable. If a testable hypothesis produces negative results, with some degree of uncertainty, then that hypothesis is preferable to an untestable one that fits more closely a current or popular paradigm.

4 SYNTHESIS OF DISCIPLINES

With the increasing interest in mechanisms and processes in ecology, accompanied by a sincere effort to analyze them in detail, there is a new need for collaboration between scientists of divergent backgrounds. Chapter 3 emphasizes the need for understanding the role of microorganisms in plant–microorganism–herbivore interactions. Since microbial techniques and understanding are specialized, adequate study of such interactions requires the collaboration of microbial ecologists with plant–herbivore ecologists. In addition, plant quality and variation within plants need to be understood in more detail (see Chapter 2), not only in a descriptive way but also in terms of the genetic and physiological mechanisms involved. It now seems impossible to understand one trophic level unless the details of the resources that trophic level depends on are understood. Thus, instead of having one investigator studying plant–herbivore interactions it is much more realistic, and more productive, to have an association among a plant physiologist, a phytochemist, a microbiologist, and a person working on the dynamics of the herbivores and their enemies.

Other areas in ecology are also in need of more collaboration than is now apparent. As mutualistic relationships receive the attention they deserve there will be a growing need for understanding both parties in the system (see also Chapters 14 and 16), many of which are microbes. For example, the development of galls by herbivores is not well understood except in the crown gall system (reviewed by Ream and Gordon, 1982), but no doubt similarly complex interactions between vectored plasmids or viruses and the host plant will be involved.

The same broadening of perspective could be justified in any other area of ecology. Unfortunately, the training of ecologists does not seem to be adequate for the task. Ecologists trained in the broad conceptual arena usually do not get an adequate exposure to natural products chemistry, microbiology, plant physiology, or other pertinent fields. Perhaps this is expecting too much, and the answer may lie in more collaboration among researchers. However, there is a challenge in training ecologists to make them fully aware of the need for integrating several disciplines in any realistic study of a natural system.

The other stricture on collaboration is the funding available. Funding agencies have tended to keep grants relatively small, as a way of spreading limited dollars widely. This contributes to a fractionation of effort and is divisive at a time when growing understanding seems to demand a broadening of the ecological base to include other disciplines more intimately. An alternative is to foster more collaborative efforts with some larger grants supporting three or four workers from different disciplines in a tightly integrated research effort. We predict that this approach will advance our understanding of ecology more rapidly. The emphasis should remain on a detailed understanding of mechanisms, and research teams should be small, with each member working on an essential component of the system. The initiative for this development should come from the research community. Graduate students sensitized to the need for a broader yet more detailed approach may well be the ones that establish the more integrated research perspective needed in many areas of ecology. In this way the synthetic and reductionist approaches so necessary in ecology may best be served (see also Bartholomew, 1982).

5 FADS IN ECOLOGY

The strongly reinforcing system in ecology for publishing positive results has delayed progress perhaps by decades. Many scientists feel compelled to fit data into some existing body of theory, and do not feel equally compelled to falsify theory. This bias predisposes ecology to faddishness. Once a theory is established, researchers struggle to fuel it, and confirm its validity. A healthier science would emerge should equal time be devoted to attempts at falsifying the theory.

The most notable case of a fad in ecology is interspecific competition. So dominant has this concept been that its status has reached that of a paradigm, in Kuhn's (1970) sense (Strong, 1980). The body of theory is vast, and yet very little has been tested objectively. Assuming that its construction started with Gause, only after 50 years of building an edifice to competition is serious doubt being cast on the evidence for its foundation (e.g., Connell, 1980; Simberloff, 1980; Strong, 1980; Arthur, 1982; Strong et al., 1983). Connell (1980) could find only one study in which adequate experimentation had been performed to establish that competition played a significant role in the interaction between species. After an extensive review of interspecific competition, Arthur (1982, p. 181) concluded: "However, as regards the relative