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SYSTEMS ECOLOGY

Edited by

H. H. SHUGART

and

R. V. O'NEILL

Dowden, Hutchinson & Ross, Inc.

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SERIES EDITOR'S FOREWORD

Ecology—the study of interactions and relationships between living systems and environment—is an extremely active and dynamic field of science. The great variety of possible interactions in even the most simple ecological system makes the study of ecology compelling but difficult to discuss in simple terms. Further, living systems include individual organisms, populations, communities, and ultimately the entire biosphere; there are thus numerous subspecialties in ecology. Some ecologists are interested in wildlife and natural history, others are intrigued by the complexity and apparently intractable problems of ecological systems, and still others apply ecological principles to the problems of man and the environment. This means that a Benchmark Series in Ecology could be subdivided into innumerable volumes that represent these diverse interests. However, rather than take this approach, I have tried to focus on general patterns or concepts that are applicable to two particularly important levels of ecological understanding: the population and the community. I have taken the dichotomy between these two as the major organizing concept in the series.

In a field that is rapidly changing and evolving, it is often difficult to chart the transition of single ideas into cohesive theories and principles. In addition, it is not easy to make judgments as to the benchmarks of the subject when the theoretical features of a field are relatively young. These twin problems—the relationship between interweaving ideas and the elucidation of theory, and the youth of the subject itself—make development of a Benchmark series in the field of ecology difficult. Each of the volume editors has recognized this inherent problem, and each has acted to solve it in his or her unique way. Their collective efforts will, we anticipate, provide a survey of the most important concepts in the field.

The Benchmark series is especially designed for libraries of colleges, universities, and research organizations that cannot purchase the older literature of ecology because of cost, lack of staff to select from the hundreds of thousands of journals and volumes, or the unavailability of the reference materials. For example, in developing countries where a science library must be developed *de novo*, I have seen where the Benchmark series can provide the only background literature available to the students and staff. Thus, the intent of the series is to provide an authoritative selection of literature, which can be read in the original form, but that is cast in a matrix of thought provided by the editor. The volumes are designed to explore the historical development of a concept in ecology and point the way toward new developments, without being a historical study. We hope that even though the Benchmark Series in Ecology is a library-oriented series and bears an appropriate cost it will also be of sufficient utility so that many professionals will place it in their personal libraries. In a few cases the volumes have even been used as textbooks for advanced courses. Thus we expect that the Benchmark Series in Ecology will be useful not only to the student who seeks an authoritative selection of original literature but also to the professional who wants to quickly and efficiently expand his or her background in an area of ecology outside his or her special competence.

H. H. Shugart and R. V. O'Neill have developed in *Systems Ecology* a survey of one of the most rapidly developing and newest subdivisions of ecology. The concept of natural systems is old, of course, but the application of mathematics, cybernetic theory, and information theory to ecology is very new. The subject is important yet so recent that the authors must have struggled long for perspective. Fortunately, both authors have deep experience in the subject and both have contributed significantly to it. Shugart and O'Neill are staff members and colleagues at the ecology program of Oak Ridge National Laboratory, Oak Ridge, Tennessee. They were especially active in the modeling work of the United States International Biological Program, and contributed heavily to the development of systems studies at all levels of biological organization in that international effort. Both editors are active contributors to ecological literature.

FRANK B. GOLLEY

PREFACE

Systems ecology is a new and exciting subdiscipline of ecology. The field is characterized by its application of mathematical models to ecosystem dynamics. Although mathematical analysis has long been utilized in ecology, particularly population theory, the first papers in systems ecology appeared in the early 1960s. The field has seen phenomenal growth since then, and literally hundreds of models have been produced. An important factor in this growth was the International Biological Programme, particularly the U.S. Biome Programs. These programs provided substantial support and motivation for modeling activities.

The youth and rapid expansion of systems ecology makes the identification of benchmark papers problematic. It is still difficult to perceive which studies will have the greatest influence on later research. As a result, the selection of papers for this volume has been strongly influenced by the opinions and perceptions of the editors. Readers may well find themselves in disagreement with some of our choices. We have selected early papers that had a significant influence and more recent papers that represent innovative approaches. We have also included several papers that contain information or points of view that are important for understanding systems ecology.

One of the characteristics of systems ecology is the difficulty of communicating results in the traditional journal format. In some cases the models were developed as part of actively evolving IBP programs. The need to make the model available to researchers in the program led to publication in internal reports that are often difficult for nonparticipants to obtain. In other cases, the magnitude of the model made it impossible to condense into a single journal article. The most conspicuous example is the ELM model produced by G. S. Innis and his colleagues at Colorado State University as a part of the Grassland Biome, IBP project. This model is an important development in the field of systems ecology, yet it was not possible to include it in the present volume. The best access to the model is in book form: G. S. Innis, ed., *Grassland Simulation Model* (Springer-Verlag, N.Y., 1978).

For the reader who is interested in further explorations of the systems ecology literature, particularly models available only as internal reports, we recommend R. V. O'Neill, N. Ferguson, and J. A. Watts, eds., *A Bibli-*

ography of Mathematical Modeling in Ecology, EDFB/IBP-75/5 (U.S. Government Printing Office, Washington, D.C., 1977). This report contains over 900 references to the modeling literature.

H. H. SHUGART
R. V. O'NEILL

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INTRODUCTION

Systems ecology is a robust hybrid of engineering, mathematics, operations research, cybernetics, and ecology. Depending on one's point of view, it has either borrowed from or given much to its sister subdisciplines: mathematical ecology and theoretical ecology. In this book we have collected papers that provide a sense of the history of systems ecology, that are important state-of-the-art contributions, or that represent directions the field may take in the future. Taken as a whole, these papers represent the content of systems ecology. Effort has been given to describe why we have chosen the various papers and to explain how the papers fit into the mainstream of the field. Our purpose in this Introduction is to convey something of the *gestalt* of systems ecology.

A decade ago, one of us and a fellow graduate student, George I. Child, developed a computer model of magnesium cycling in a Panamanian tropical moist forest. This model took almost a year to develop. Most of the time was spent debating the proper approach to use in applying systems ecology to the forest. George Child had spent two years in Panama collecting data on the standing crops and transport of several elements, including magnesium, in six different tropical ecosystems. The field work was intense; it included total harvesting of tropical trees, and the data were collected under the most primitive conditions. After two years of living in the wilds of Panama, George spoke Choco Indian dialect and Spanish fluently, had hiked across the Isthmus of Panama through the backcountry, had become an expert on the natural history of the area, and was dedicated to understanding tropical ecosystems. We argued for days.

The model had to fit on a small analog computer. We were limited to four to eight ordinary linear differential equations. We ended up with six. We argued whether one could express anything of interest about a tropical forest ecosystem using such a small number of equations. Since we worked with an analog computing device, analogies between voltage (the commodity of the analog computer), and magnesium rose and fell in importance. We were amazed to find that data that had taken George, Mike Duever, and about sixty Choco Indians almost six months to gather was represented as a single parameter in the model. On the other hand, analysis of the model revealed aspects of system stability that would not have been discovered otherwise (Child and Shugart 1972). We discussed how these model results might actually reflect the true nature of the Panamanian forest.

This anecdote points out two important characteristics of the systems ecologist's experience. First, there is the frustration in forcing the complexity of a real system into a few equations and parameters. As ecologists, we have been trained to deal with complexity and to appreciate the exceptions at least as much as we appreciate the generalities. Second, there is the excitement of hypothesizing new underlying behavior for the total ecosystem as a result of analyzing the model. For most, this excitement more than compensates for the initial frustration.

While the anecdotal account is useful for providing an impression of the working experience, it is also worth noting some of the unique attributes of systems ecology. Studies that make up the body of the field tend to differ from other ecological studies in the following attributes:

1. Consideration of ecological phenomena at large spatial, temporal, or organizational scales
2. Introduction of methodologies from other fields that are traditionally unallied with ecology
3. An emphasis on mathematical models
4. An orientation to computers (both digital and analog devices)
5. A willingness to develop hypotheses about the nature of ecosystems

We will elaborate on each of these five attributes.

Scales

Problems with temporal and spatial scale often plague data collection efforts. Frequently, the system changes more rapidly than one can measure it (e.g., insect populations). In other cases, changes occur so slowly that sampling intervals exceed the investigator's lifespan (e.g., tree populations, particularly in mature forests).

Systems ecologists frequently combine phenomena at glaringly different temporal or spatial scales. In some cases, the process is relatively simple. For example, if one is interested in the dynamics of forest canopy insects during the summer, it may be reasonable to assume that tree biomass is constant. Much of the "art" in modeling concerns which ecosystem attributes of an ecosystem must be considered explicitly and which attributes can be ignored. There is as much creativity in deciding what can be left out of a model as in designing the appropriate mathematical functions to mimic some ecological response. Needless to say, there is also ample opportunity for leaving out important phenomena that will embarrass the systems ecologist later.

Ecologists have only recently begun to work actively on the problem of scale in ecological models. Criteria for adding or leaving out a specific process has been considered part of the "tools of the trade" of the systems ecologist. Bits of information on scale have been passed among modelers largely as informal communications, in discussions at workshops, and, in the case of mistakes, as gossip. Unfortunately, there is no codification of what has been learned to date. Papers that treat the problem of modeling differing scales are Clymer (1969), Clymer and Bledsoe (1970), Zeigler and Weinberg (1970), Overton, (1972), and Overton et al. (1973). Allen and Koonce (1973) have used statistical transformations to determine scales in time and space for which various phenomena are important.

Use of Work From Other Sciences

Although most ecologists are willing to use proven techniques from other fields, systems ecologists are unique both in the breadth of other disciplines that they consider and in the fervor with which they search for these techniques. This exploration of other fields has been successful in the past and has become the *modus operandi* of many systems ecologists. Over the past decade, engineers, physicists, and mathematicians have colonized ecology, in part because the explorations of early systems ecologists created an interest in techniques from these disciplines. For example, the group with which we work (the Oak Ridge Systems Ecology Group) is presently composed of individuals with graduate training in astronomy, plasma physics, electrical engineering, zoology, botany, hydrology, and statistics. There is an excitement that is (or at least can be) attendant to crossing into other scientific fields for insights into ecosystem function.

Other sciences share characteristics with ecology that suggest their methodologies might be transferable. For example, like ecologists, astronomers are forced to speculate about their system (the universe) using limited observational data and without recourse to experimentation. Therefore, techniques developed by astonomers, such as spectral analysis using the maximum entrophy technique, may be applicable in ecology. But whether or not maximum entrophy spectral analysis proves to be applicable, the point is that astronomers do not, on a regular basis, go to great lengths to assure that ecologists become aware of their findings. Systems ecologists have had to do the searching. Many systems ecologists feel this is their greatest contribution to ecology and take delight in the intellectual excitement produced in the melding of two otherwise disjunct aspects of science.

Models

If one were to pick the single most reliable fieldmark of the systems ecologist, it would be the use of mathematical models as a tool. However, there have been raging debates among systems ecologists on criteria for choosing types of models. These debates have, in several cases, amounted to divergent views on the fundamental nature of ecosystems. For example, the debate on whether ecosystems were linear or nonlinear has also identified possible dichotomies in management strategies. One might manage nonlinear systems in ways very different from linear systems. It is not clear at present that this debate is heading toward any resolution, nor is such resolution necessarily desirable. Diversity of opinion on appropriate mathematical formulations is healthy and should continue to be so in the future. The papers we have chosen in this book reflect part of the spectrum of the multifaceted argument, "How can one best model an ecosystem?"

Computers

Quantitative ecology was certainly an active field before the advent of the computer. However, the increased availability and reduction in cost (in the sense of cost per arithmetic operation) of computing devices has catalyzed the development of systems ecology over the past twenty years. In the 1950s, systems ecologists (notably H. T. Odum) actually built their own analog computing devices.

For a time, it was not clear whether analog or digital computers were more appropriate for ecological models. Analog computers had several advantages over digital computers until the mid-1960s. They were fast and relatively inexpensive. They allowed the ecologist to work "hands on" with a device that modeled flows directly (using electrical flow as an analog for energy or nutrient flow). Today, digital computers dominate the field because of their availability and the ease of programming. The ability to program an analog computer can be taken as the mark of an "old-timer" in the field.

Digital computers are readily available to ecologists at all major universities in the United States and Europe. Languages (such as IBM's CSMP-III Language) are being developed that greatly simplify the implementation of models and require little knowledge of numerical analysis. These languages promise to make simulation models available to students and working ecologists in the same way that "canned" statistical computer packages (e.g., SAS, SPSS, BMD, and so forth) have made elementary statistical analysis available in the past decade.

Hypothesis Development

Systems ecologists often break from "safe" descriptions of ecological systems to form interesting (and testable) *hypotheses* about system functions. We emphasize "interesting" because the hypothesis most frequently tested in ecological research is the uninteresting statistical null hypothesis: "the data indicate that there is no difference between these things." The hypotheses formulated by systems ecologists result from the juxtaposition of the assumptions and intuitions contained in a model. In fact, the ecosystem model itself can be viewed as a complex hypothesis about system functions.

Systems ecologists are anxious to formulate hypotheses that may someday lead to a theory of ecosystems. Probably most hypotheses developed today will be rejected. It is not the reward to success that stimulates hypothesis generation, it is the zeal for building a theoretical science that is the real motivation. Systems ecologists tend to feel that it is better to offer an hypothesis even though it may be rejected, than not to advance it in the first place. This seems an essential characteristic of systems ecology as it is of any young theoretical field.

In this Introduction, we have sought to provide a feeling for the spirit of a young field in the young science of ecology. This spirit is important to bear in mind while reading the papers that follow. In many respects, systems ecology is developing a theoretical tone to match the historical emphasis on accurate descriptions of ecological phenomena. If ecology develops in a manner analogous to older sciences such as physics, astronomy, and chemistry, it is possible that the spirit of systems ecology may be its most contagious aspect, with the potential to change ecological thought.

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