PERSPECTIVES
IN
Ecological Theory

Edited by

JONATHAN ROUGHGARDEN, ROBERT M. MAY

and

SIMON A. LEVIN

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Introduction

JONATHAN ROUGHGARDEN,
ROBERT M. MAY,
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Darwin's views of the role of theory in evolutionary biology will warm any theorist's heart: "let theory guide your observations"; "all observation must be for or against some view if it is to be of any service!" (Gruber and Barrett 1974). In common with physical scientists, Darwin saw theoretical ideas as providing the plans that give shape and coherence to facts and observations that otherwise would lie around like a pile of bricks at a building site.

Ecological theory can, of course, take many forms, many of which are not at all mathematical. Darwin was the most influential ecological and evolutionary theorist, despite his self-acknowledged mathematical incompetence (DeBeer 1964, p. 179, writes that "Darwin himself often regretted that he had never proceeded far enough to understand 'something of the great leading principles of mathematics', for, as he sadly admitted, 'men thus endowed seem to have an extra sense' "). Nevertheless, much of ecological theory today is expressed in largely mathematical terms, if only because (in Joel Cohen's phrase) "mathematics is a way of making commonsense precise." Mathematical formulations force us to make the assumptions clear and unambiguous, and the conclusions are correspondingly unambiguous.

Whether or not in mathematical form, theoretical ideas serve many purposes. They suggest observational protocols and manipulative experiments both in the field and in the laboratory. They provide frameworks around which curricula can be organized, so that the body of facts can be given coherence rather than presented as a jumble. Most important, perhaps, theory can imagine and explore a wider range of worlds than the unique one we inhabit, and by so doing can lead to fresh perceptions and new questions about why our actual world came to be as it is (see, for example, Jacob 1982).

Ecological theory today spans a large range of topics, from the physiology and behavior of individuals or groups of organisms, through population dynamics and community ecology, to the ecology of ecosystems and the geochemical cycles of the entire biosphere. Ecological theory also embraces large parts of evolutionary biology, including paleontology and systematics, and of the earth sciences, especially oceanography and tectonics. Most of this work is, however, scattered among the various subdisciplines; very properly, the theorists are most interested in communicating with the appropriate empiricists, be they physiologists, biogeographers, oceanographers, or whatever.

This book attempts to draw together these contributions into a comprehensive statement of what ecological theory has accomplished over the broad range of its inclusive niche, and of what ecological theory can contribute to defining and to solving the fundamental problems currently facing the discipline of ecology. It aims to outline current accomplishments and current questions, across the panorama of ecological theory. More interestingly, however, the book seeks to air thoughts about likely future directions and about areas in which the dialogue between theorists and empiricists may be enlivened in specific ways.

The book had its origins in a meeting held at Asilomar in 1987, which brought together a group of some forty theoretical and empirical ecologists, representative of the broad sweep of subjects just referred to (see back of book for a complete list of participants). Valuable contributions were also made by representatives of several federal agencies and foundations. Eight general topics were identified, and these topics were discussed against the background of precirculated papers. Hapless chairmen—some of whom did not know what they were getting themselves into—then wrote chapters for the book, based on the discussion. Some of these chapters summarize directions for research and other points of interest that emerged in the discussion, while others take these kinds of ideas as background for their authors' more personal speculations about current and likely future directions; we did not think it a good idea to fit these diverse contributions into some Procrustean conformity.

ORGANIZATION OF THE BOOK

The book is divided into eight sections. The first section deals with the interface between individual organisms and the dynamics of populations. Too often, population biologists must be satisfied with phenomenological descriptions of population processes, without benefit of the understanding that comes from deriving these coefficients from the underlying physiology and behavior of individuals. Such an interplay of individual and population properties allows an explicit consideration of coevolutionary processes, which depend upon variation among individuals within populations and the expressed phenotypic properties of individuals. Conversely, organismal biologists and behavioral ecologists tend to focus on how physiology and behavior are shaped by evolution, and usually give little attention to the consequences at the population level, or to the importance of population interactions in guiding evolution.

In this section Gross gives a theoretician's perspective on plant physiology, particularly as it relates to photosynthesis, and pursues some of the consequences for the population biology of plants. Pulliam gives an overview of work on models that aim to understand the foraging behavior of animals, and shows how these models guide, and are guided by, field and laboratory experiments. Koehl summarizes the discussion, indicating likely growth points in this general area.

The second section deals with the dynamics of populations and with interactions among species. The past decade or so has witnessed the development and experimental testing of "second generation" models of intermediate complexity, which aim to go beyond the very broad generalities of earlier models, to take account of the particular features of specific categories of systems. Pacala reviews mathematical models for the dynamics of plant populations, and discusses their relation to existing and proposed future experiments; he also discusses the relation between these models and the more familiar ones that have been constructed for animal populations. Kareiva surveys models for the dynamics of herbivorous insect populations, emphasizing the role played by dispersal and by the patchy structure of most habitats; he also shows how these models may be combined with manipulative experiments in the field. Tilman's chapter summarizes the current status of theories and experiments concerning the dynamics of interacting populations, and gives suggestions about possible lines of future research.

The third section focuses on the interface between ecological and evolutionary theory. Travis and Mueller give an overview of recent work on ecological genetics, which is leading to a clearer understanding of the adaptive significance of genetic variation within populations. Theoretical advances here include a better understanding of frequency-dependent and density-dependent natural selection (and extensions to coevolution between interacting populations) and of age-specific aspects of selection and applications to the theory of life histories, as well as developments in the theory of quantitative inheritance (and concomitant measurement of the heritability of quantitative traits). Lifting his sights to the broad sweep of the paleontological record, Stanley discusses the significance of differential rates of extinction and their possible explanation in ecological terms; he also speculates on the role of "species selection" as an evolutionary factor. Feldman provides a commentary on a range of topics concerned with the interplay between ecology and evolution, and with mathematical models that combine population ecology with population genetics.

The fourth section wrestles with a difficult set of questions concerning how theoretical and experimental studies of ecosystems are to be structured, when ultimately one is dealing with systems and processes that involve many widely different spatial and temporal scales. How, for instance, does one put bounds on a study of a food web: when studying an intertidal system, does one include the owls that may eat the odd rodent that rarely consumes an item from the seashore? What is the role of "tourist" species (in Southwood's phrase), which occasionally wander into a food web but are not a permanent part of it? How are ecosystem structure and function influenced by the rare but important events that may occur every century or so? When and how is it permissible to deal with species aggregates ("mollusks," "phytoplankton"), rather than individual species? Is a functional classification of species, or, for example, one organized according to body size more appropriate than a taxonomic classification?

In this section O'Neill presents ideas about the possible use of hierarchy theory to organize studies of ecosystems, and to understand the relations among the different kinds of information that are present at different levels in a complex system. Powell shows how different physical and biological processes operate on different spatial and temporal scales in aquatic systems, with special emphasis on plankton patchiness and its connection with hydrodynamic processes. Steele, whose book on the structure of marine ecosystems pioneered explicit consideration of the influence of scale upon ecosystem dynamics, gives a summary of suggestions for further research on the general theme of scaling in space and time.

The fifth section deals with theoretical work on communities and food webs as such. Roughgarden shows how earlier work on conditions for coexistence among competing species and on prey-predator interactions (tracing back to MacArthur in the 1960s and beyond) is being succeeded by more complex studies of multilevel trophic webs and the assembly of communities of interacting species. He illustrates his discussion by reference to the buildup of lizard communities in the Lesser Antilles, a group of islands that also seems to reveal a "disassembly" of larger communities as a result of plate tectonic processes. Cohen summarizes some interesting patterns that have emerged from the analysis of systematic comilations of data about terrestrial and marine food webs, and shows how many of these patterns follow—in a statistically well-defined way—from a few simple assumptions or "rules" (which themselves, however, remain unexplained at this time). Cody's chapter summarizes the discussion that took place on this general theme, to provide an overview of the relations between theoretical and empirical ecology at the community level; his chapter also identifies areas of community ecology that seem in need of fresh ideas.

The sixth section deals with ecosystem structure and function. Levin reviews fundamental and applied aspects of mathematical models addressed to questions of productivity, nutrient cycling, and patterns of succession, with emphasis on how various kinds of environmental stress can affect such processes. Approaching some of the issues of Section IV from a different perspective, Levin argues that our increasing appreciation of local and global problems in the environment makes it necessary to couple biological and physical factors (including the effects of climate change), which inevitably involves the recognition that components of biotic and abiotic systems can operate on vastly different scales of space and time. Horn, Shugart, and Urban review models for forest ecosystems. Schlesinger's overview records suggestions for other ways in which theory may combine with existing and new technology in pursuit of a better understanding of how ecosystems work.

The final two sections focus on applications of ecological theory to resource management, conservation biology, and the control of pests and diseases. The seventh section begins with Clark's review of how population biology and economics interact in the management of what are usually called "renewable resources." Among other things, Clark shows how, even if there is a "sole owner" (thus avoiding the "tragedy of the commons"), narrowly economic considerations can lead to the overexploitation, or even extinction, of a biological resource. This tends to happen if the maximum sustainable biological yield, expressed as a percentage of the "standing crop," is below the inflation-corrected bank interest rate; in these circumstances, it makes economic sense to liquidate the capital stock and reinvest elsewhere. Such perceptions help to explain many bioeconomic happenings, including the overexploitation of whales. The work makes it clear that many controversies, as for instance between loggers and conservationists, are essentially differences of opinion about the rate at which the future should be discounted; bioeconomic theory thus can clarify the essential nature of many quarrels about political and social alternatives. Gilpin and Pimm discuss the many different kinds of contributions that ecological theory is making to pressing problems in conservation biology, ranging from the dynamics, genetics, and behavior of small populations of endangered organisms in zoos or in reserves, to insights that may guide difficult choices in acquiring land for preservation. Ehrlich's essay surveys these and other ways in which ecological theory has been useful in resource management and in conservation biology, and suggests lines of further application.

In the eighth section, the paper by Hassell and May reviews the interplay between theoretical and empirical studies pertaining to the population biology of host-parasite and insect prey-predator associations (with "parasite" defined broadly to include viruses, bacteria, protozoans, and helminths). The paper surveys basic ideas about host-microparasite, host-macroprasite, and host-parasitoid systems, along with experimental tests of these ideas. Hassell and May summarize the main conclusions, and give a list of important unresolved questions. This chapter aims to emphasize similarities and differences between the population biology of interactions between hosts and viral, bacterial, protozoan, helminth, parasitoid, and other insect predators, which explains why there is one long chapter rather than separate ones on pathogens and on insect predators. Building on this chapter and on the group discussion, Anderson surveys current accomplishments, and likely future directions, in the use of mathematical models to provide insights about the control of crop pests and insect vectors of disease, or in the design of programs of immunization or chemotherapy against pathogens and parasites.

THE ROLE OF THEORY IN ECOLOGY

As the pages in this volume indicate, theory is the pathway to extrapolation, generalization, and understanding. It provides an antidote to the helpless feeling engendered by the view that nature is so complicated, and evolutionary processes so contingent on accident and history, that all we can ever hope to achieve is detailed understanding of specific situations—Geertz (1973) "thick description" of particular times and places—rather than any general rules or patterns.

Whether we are dealing with the physiology or behavior of individuals, the dynamics or genetics of populations, the structure of communities, or broad paleoecological or biogeographic patterns, theory can suggest possibilities for experiments or observational protocols, can prompt tentative and testable generalizations, can serve as a crude guide to action in circumstances where action cannot wait on the certitude of detailed site-specific studies, as well as provide detailed models that summarize experimental findings in appropriate cases. Knowing which kind of model seems appropriate to which situation is the art of good theory. For example, in some applications, one may prefer a simple model tempered with judgment and experience. Yet a very detailed model seems needed in climate analysis, where a mere degree can trigger an ice age, and where accurate and detailed models are possible. Still, in models with strong nonlinearities, it is increasingly recognized that very detailed models usually provide only an illusion of precision, are not robust in their predictions, and are not reliable tools for management (Ludwig and Walters 1985).

Some contemporary discussion about the role of theory in ecology reflects a more general discussion about how science should be done. In Darwin's day, the prevailing scientific orthodoxy was the Baconian method, and in his books Darwin accordingly portrays himself as first marshalling the facts, and then seeing what conclusions emerge, "patiently accumulat[ing] and reflect[ing] on all sorts of facts which could possibly have any bearing. . . . After five years' work I allowed myself to speculate on the subject, and drew up some short notes . . ." (Darwin 1859). His notebooks, however, tell a very different tale, much more familiar to a practicing scientist. As Gruber and Barrett (1974, p. 122) put it, "The pandemonium of Darwin's notebooks and his actual way of working, in which many different processes tumble over each other in untidy sequences—theorizing, experimenting, casual observing, cagey questioning, reading, etc.—would never have passed muster in a methodological court of inquiry." Today, the early writings of Popper are much in vogue, and some would interpret these as denying legitimacy to any research program not cast in terms of falsifiable hypotheses. It should not be forgotten, however, that philosophies of science are themselves theories rather than revealed truths, and the hypothesis that any one of them provides the only correct way to do science seems to us to be abundantly falsified by the actions of practicing scientists. Lehman (1986) writes: "Those who embrace constraints crafted by others in the form of Popperian or hypothetico-deductive straight jackets may have divined a means to restrict their imagination, but there is no evidence in my view that those constraints encourage break-throughs in biological sciences." The recent book by Gleick (1987) on *Chaos: Making A New Science,* with its account of the contingent, hurley-burley way in which new ideas and new experiments—or, perhaps more important, old ideas and old experiments seen in a new light—were prompted by the vagaries of accidental meetings and conversations, seems to us much closer to how science actually advances than are tidy schemes in which scientific discovery is reduced to a kind of painting-by-numbers. In the words of Feyerabend (1975), "Science is an essentially anarchistic enterprise: theoretical anarchism is more humanitarian and more likely to encourage progress than its law-and-order alternatives."

Just as there is a plurality of ways to do science, there is a plurality of interests and aptitudes among the people doing ecological research today. Somehow theory and empirical activities need to be combined, either by collaborations, or by individuals that take their hand to both. A big need is to develop theories for systems and questions that have been previously neglected. It is especially important not to fill a theoretical vacuum by importing a model developed for one system to a strange and clearly inappropriate context. Instead, new theory will need to be devised and analyzed.

Our aim in this book has been to capture the excitement of theoretical ecology by presenting some of the past and present accomplishments of ecological theory, on a canvas of wider sweep than is seen in volumes focused on just one aspect of the subject. More than this, the book offers speculations and suggestions about possible future directions of research. Sometimes the focus is on fundamental aspects—for example, deriving population parameters from the physiology or behavior of individuals, or understanding the ecological significance of genetic variation, and so forth; at other times the focus is on applications of theory—for example, to resource management, conservation biology, or the control of pests and pathogens.

In all this, our overarching aim is to share a representative collection of empirical and theoretical ecologists' views of where ecological theory is now, and where it may be going next.

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FROM INDIVIDUALS TO POPULATIONS I

Chapter 1

Plant Physiological Ecology: A Theoretician's Perspective

LOUIS J. GROSS

The central issues of plant physiological ecology concern the effects of environment on individual plant growth, survival, and reproduction. In this regard, physiology is viewed as the mechanism through which the joint effects of heredity and environment are coupled to determine the growth form and reproductive success of an individual (Kramer 1948). My goal here is to provide a very brief review of the major questions that the field addresses, with emphasis on the use of theory; give a few examples of how theory has contributed new perspectives; point out some directions I feel are as yet relatively unexplored; and, finally, make some comments about coupling with other levels of organization. This is meant as a theoretical complement to the excellent review and set of recommendations for future research by Ehleringer et al. (1986). What I discuss is limited by my own biases, including a blatantly terrestrial one. A comprehensive review of the area accessible to a general audience is contained in the January 1987 issue of *BioScience*. The most exhaustive compilation of research in the area to date is the series of books edited by Lange et al. (1981, 1982, 1983). Relatively few mathematically oriented books have appeared, but those containing some relevant material include Thornley (1976), DeWit (1978), Rose and Charles-Edwards (1981), Charles-Edwards (1981), Jean (1984), and Gross and Miura (1986). On the biophysical end, the books by Gates (1980) and Nobel (1983) are standards. For a fine collection of papers that take an economic, cost-benefit approach to energy capture and utilization by plants, see Givnish (1986a).