



Review: Population Ecology

Reviewed Work(s):

Population Ecology: A Unified Study of Animals and Plants by Begon, Michael; Martin Mortimer

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REVIEWS

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POPULATION ECOLOGY

Begon, Michael, and Martin Mortimer. 1981. **Population ecology: a unified study of animals and plants**. Blackwell Scientific Publications, Oxford, England. Distributed by Sinauer Associates, Sunderland, Massachusetts. vii + 200 p. \$33.00 (cloth), \$16.95 (paper).

The movement away from community-level ecological research and toward studies of population dynamics is finally being mirrored in undergraduate textbooks. In the past few years, several texts have appeared whose focus has been the ecology and/or evolution of populations. The most exciting of these is Michael Begon and Martin Mortimer's *Population ecology*.

While many population biology texts contain a strong dose of population genetics and evolutionary ecology, Begon and Mortimer choose instead an in-depth approach to the *mechanisms* of population ecology. Little or no notice is given to the evolutionary implications of these mechanisms. The text is organized into three major sections. The first, *Single-Species Populations*, introduces the student to life tables as an accounting device, proceeds through a discussion of intraspecific competition and its consequences, and goes on to models (both discrete and continuous) of population growth. This section closes with a detailed description of transition matrix models of age-structured populations.

The second section, *Interspecific Interactions*, contains two large chapters, one on interspecific competition and one on predation. (Mutualism, regrettably, is only mentioned in passing, relegated to the category of "minor" interactions.) The competition chapter begins with the results of some lab and field experiments, as examples, and then discusses ideas like the niche concept, the competitive exclusion principle, character displacement, and niche shifts. Begon and Mortimer's discussion of these ideas emphasizes the difficulties inherent in the design and interpretation of competition studies. Finally, two models are developed and tested: the Lotka-Volterra model and deWit's model of plant competition. Both this chapter and the preceding one do an excellent job of treating plants as interesting organisms in their own right. The similarities between plants and animals (especially sessile ones) are emphasized; where there are fundamental differences between the two, the text provides independent treatment of theory and experiments for plants.

In the next chapter, the mechanisms of predation are explored in detail: how predators respond to changes in prey densities and to changes in prey distributions, and to interference from other predators. Near the end of the chapter, as with previous ones, the authors develop mathematical models of the interaction. The Rosenzweig-MacArthur predator-prey model one usually encounters in such books is abandoned in favor of the discrete models of host-parasitoid interactions developed by Nicholson and Bailey, Hassell, and May. Though the authors begin this chapter by discussing the many different types of interactions that fall into the category of "predation," the theory and experiments they eventually describe are heavily weighted in favor of host-parasit-

oid systems. Because this emphasis has shaped the chapter's structure so strongly, other kinds of exploitation systems—especially plant-herbivore interactions—don't fit comfortably into the framework. Despite the fact that toward the end of the chapter, predator-prey models are applied explicitly to grazing systems, plant-herbivore interactions receive far too little attention.

The book's last section, *Syntheses*, contains an assortment of topics. The first chapter is on life history strategies, the second on population regulation. The third, the shortest chapter in the book, is entitled *Community Structure*. This final chapter provides, in nine pages, a tantalizing glimpse of such concepts as island biogeography, predator-mediated coexistence, and non-equilibrium community dynamics. Such a brief treatment is inevitably superficial, and this chapter requires considerable supplementing by lectures and outside readings.

This text is praiseworthy in several respects. First, Begon and Mortimer's approach to theory is the best I have seen in any textbook of its kind. Their clear, careful, and critical explanations of how models are developed and why they are important are balanced by well-chosen examples of field and laboratory studies. Some of these studies are included to demonstrate how models can help us disentangle the complexities of the real world; others illustrate the model's limitations. The authors' unusually lucid explanations make difficult concepts accessible. Their presentation is aided by the generous use of tables and figures. They assume no mathematical background past algebra of their readers, yet lead them successfully through a series of complicated ideas.

Secondly, this text provides, for the American reader, a refreshing approach to population ecology. Begon and Mortimer are British, and the bulk of their examples and much of the theory represent work by British ecologists. I found that the text provided harmonious counterpoint to my lectures, which naturally emphasized American work; the difference in styles was thought provoking rather than confusing, thanks to Begon and Mortimer's undogmatic approach. The only disadvantages to using so British a text were that students were sometimes dismayed by being served unfamiliar organisms as examples, and that the authors make extensive use of k -factor analysis. Perhaps because of their lack of experience with this technique, my students invariably found k -values difficult to interpret, and tended to confuse k with K , since these parameters were often discussed simultaneously.

Finally, this book does not pamper students. It is written more in the style of an extended scientific paper than as a textbook: there is no glossary, there are no chapter summaries or "thought questions" or problem sets. The style in which the book is written generates questions from students, and the authors do not pretend that we know all the answers. Students are left with the feeling that there is much still to learn, and are given the tools with which to explore these issues on their own. Examples, theory, figures, and tables are well-referenced, and provide easy entrance into the lit-

erature. There is a very useful author index and an organism index in addition to a good subject index.

Begon and Mortimer's book challenges the student by encouraging the development of intellectual sophistication. It trains students to think for themselves.

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MODELING OF MEDITERRANEAN TYPE SHRUBLANDS

Miller, P. C. (ed.). 1981. **Resource use by chaparral and matorral: a comparison of vegetation function in two Mediterranean type ecosystems.** Ecological Studies 39. Springer-Verlag, New York. xviii + 455 p. \$39.80.

The accurate computerized simulation of ecosystem growth from physiological starting points is a Platonic ideal to which many ecologist-modelers aspire. In this volume, Philip Miller and collaborators display sufficient confidence in the validity of their physiological models of growth in sclerophyllous shrublands of southern California and Chile that they are willing to use the simulations to test hypotheses about convergence in community function and resource-use optimization on the two continents. The aim is indeed an ambitious one, and if the investigators have fallen somewhat short of their goal, they have nevertheless developed a data base and a set of models which represent a substantial advance on previous knowledge, and an excellent base for further research.

This book reviews and synthesizes the collaborative research of 19 investigators primarily from San Diego State University and Universidad Catolica de Chile, who sought to continue work begun under the International Biological Program as a comparison of similarities along moisture gradients in San Diego County, California, and central Chile. The aim of the present project was to examine whether resource utilization efficiency and patterns of nutrient and carbon allocation were similar in two Mediterranean type shrublands of similar habitat but different phylogenetic history. The cross-continental comparison was limited to the evergreen, sclerophyllous shrubland communities on each continent. Within southern California, there was an additional effort to compare the chaparral with the drier, malacophyllous coastal sage scrub.

Much of the research in this volume has been previously published, and the 12 chapters, written by one to four authors each, vary in the degree to which they mix literature review with new data. The main opportunity in such a book is to provide a synthesis of the body of collaborative research. This goal is best achieved in the chapters in which P.C. Miller is a co-author, probably not coincidentally because he was also the coordinator of the research. In this respect, the book is not as consistently integrated as, say the two volumes by F. H. Bormann, G. E. Likens et al. (1977. *Biogeochemistry of a forested ecosystem*. Springer-Verlag, New York; 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York) which attempted a similar synthesis of the work at Hubbard Brook. Miller's book, however, is more ambitious in scope, seeking to compare field measurements with physiological models of plant growth across species, seasons, sites, and continents, and to incorporate a considerable amount of new data at the same time.

The book begins with a chapter by Miller outlining the major hypotheses to be tested. To a community ecologist, some of the hypotheses will seem simplistic, e.g. that vege-

tations in similar environments converge toward a single pattern of resource utilization, or that community structure can be predicted by use of physiological models of plant growth pieced together and validated from subcomponents of leaf, stem and root growth. Nowhere in the modeling procedure has an explicit attempt been made to incorporate interactive effects of biotic competition or herbivory; the implicit assumption is that vegetative growth is limited by availability of "physical" resources (water, radiation, nutrients). Multi-species communities are compiled simply by adding single plant populations together (Fig. 1. 2). Similarly, in validating the models, the assumption of additivity between subcompartments of the models was made (p. 357), and only subcompartments were checked for performance against field data. The effects of competition for resources between species will, of course, be registered in the field data, so that to the extent that the model fits such field data, it could be argued to incorporate the non-linear, non-additive effects of competition within the observed margin of variation between prediction and field observation. Indeed, in a particularly candid moment, Miller states, "A set of simulation experiments conducted in this study indicate that the range of natural variation in an ecosystem may make it impossible to completely disprove reasonable generalities." Therein lies perhaps both the greatest contribution and the greatest limitation of the modeling work: the fit to field observation is often "reasonable," but rarely sufficiently precise to enable firm distinctions among quantitative hypotheses. Because of this, many researchers will find the tables and figures of raw data the most enduring features of this work.

While the book provides abundant data on certain physiological variables, such as photosynthetic rates and leaf conductances under varying environmental conditions, it gives scantier attention to ecosystem-level attributes. For example, while the Californian and Chilean sites as modeled are taken as comparable, the San Diego site last burned in 1952 whereas the Chilean site was cut for fuel and charcoal until 1959 (p. 393) or 1962 (p. 22). These substantial differences in disturbance history were assumed (Chapter 12) to be negligible since simulated steady-state foliage areas for the two communities were similar to those measured in the field. Studies of succession in coastal sage scrub by community ecologists, however, have shown that while foliar cover may reach a steady state within 2-4 years, quite significant changes in floristic composition, available nutrient pools, etc. continue to occur for decades.

As in any edited book, the chapters vary in quality. I found the description of the computer models and the synthesis chapter particularly well done. The chapter on plant communities, on the other hand, suffered from weaknesses both in methodology and in editing (I counted six figures or tables with unlabeled or unmarked axes or undefined column headings). Because the field of Mediterranean ecosystem ecology is currently quite active, the literature reviews, though mostly completed in late 1980, are already beginning to show signs of age. As a ready reference to the prolific publications on