Book Reviews

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The Wondering-land of Ecological Modeling

Canham, Charles D., Jonathan J. Cole, and William K. Lauenroth, editors. 2003. **Models in ecosystem science.** Princeton University Press, Princeton, New Jersey. xv + 476 p. $79.50, £52.95 (cloth), ISBN: 0-691-09288-5 (alk. paper); $35.00, £22.95 (paper), ISBN: 0-691-09289-3 (alk. paper).

After about two years into my Ph.D. program at the University of California, Davis, I began wondering what exactly an ecological model does, how useful it is for advancing science, how complex a model should be, and whether it would be possible for me to make a career with the training of simulation modeling. I was assigned to work alone on a highly complex, physiologically based, plant growth model for my Ph.D. degree–a daunting task for a graduate student–for four and an half years. Since then, I have wondered about those questions and had never found satisfactory answers. The book ''Models in ecosystem science'' edited by Charles Canham, Jonathan Cole, and William Lauenroth, adeptly scrutinizes those questions. If you ever wondered about them, too, you need to read this book. In the book, a group of excellent ecologists share with you their experience of working with ecological models, their insights into various modeling issues, and their visions of future directions.

This book evolved from the ''ninth Cary Conference, held in May 2001 at the Institute of Ecosystem Studies, Millbrook, N.Y.'' It is composed of 27 contributed chapters, which are divided into five parts. The first part is six chapters long and addresses general topics of quantitative modeling in regard to its role in: science and policy making; simplicity vs. complexity; and the general attitude of and practice by ecologists. The second part of the book, consisting of eight chapters, focuses on the methods of evaluating and testing models such as traditional validation, Bayesian analysis, model intercomparison, and uncertainty analysis. Six chapters in the third part of the book discuss applications of ecosystem models to research on environmental policy and management. Of the six chapters, one gives overviewed general issues regarding the applications and the other five chapters offer case studies on N deposition, coastal eutrophication, ecological toxicology, plant invasion, and climate change. The fourth part of the book attempts to answer the question: what is the future of modeling in ecosystem science? Two chapters in this part offer practical recommendations on how to incorporate quantitative modeling into undergraduate education and how to advance modeling skills for professional ecologists. One chapter identifies bottlenecks for model development and limitations of model applications. The fifth part of the book consists of three commentaries on the fast-and-frugal ecosystem models to accelerate learning and progress in ecology, the uses of modeling and scenario building to promote communications between scientists and policy-makers, and the community-wide investment in modeling.

Many chapters in the book make a consensual point that a model is an abstraction of reality. How much abstraction should be made during development of a model, however, is a point where viewpoints diverge. Simple models are easy to build and manipulate, in general. ''[T]hrough the process of manipulation, we learn about the abstraction, the model, and relevant aspects of the world.'' Simple models have been widely used in ecosystem science for generating questions, depicting ideas, creating alternate models, evaluating patterns, describing mechanisms, making predictions, and facilitating communications to public and decision-makers (Chapter 4). However, simplicity alone should not guide modeling in ecology as argued by DeAngelis and Mooij in Chapter 5. Models must be question driven. That cannot be overstated (Chapter 6). There are successful examples of mechanistically rich models that address specific questions (Chapters 13–15, 17–21). The challenges inherent in such models are their transparency and their amenability to analysis. No matter how comprehensive a model is, it is not possible for a model to address all questions over all scales. The key step in developing an effective model is the question identification and selection.

Model evaluation and testing is still a topic of perplexity. Traditional approaches to model validation and testing against data are still essential (Chapter 10) and should be well documented in publications (Chapter 11). Other approaches that have emerged or been frequently used in the past decade or so are Bayesian analysis (Chapter 9), intercomparison of models (Chapter 12 and 13), and uncertainty analysis (Chapter 8). Multiple constraints (Chapter 14) and some physical and biological principles, such as the mass balance of nutrients (Chapter 15), are also effective in model evaluation and testing. Nonetheless, it is always a challenge for modelers to enhance our confidence in model output.

The data-model fusion has been recently applied to model evaluation and testing in ecology. Unfortunately, this technique is not included in the book. The data-model fusion is an approach that makes use of both process thinking and information contained in data towards a comprehensive synthesis of ecosystem processes. It sometimes is a synonym of inverse analysis, data assimilation, parameter estimation, and multiple constraints for synthetic research. It offers the capability of (1) estimation of model parameters or state variables, (2) uncertainty analysis on parameters and model output, (3) rejection of a model, and (4) quantitative evaluation of sampling strategies. This technique has recently been applied to ecosystem and population ecology. The data-model fusion will be an active, growing point of research in ecology in coming decades.

The book also discusses the role of models in science and decision making. Scientifically, models have been used for synthesis and integration of data (Chapter 6) and predicting the future behavior of ecosystems (Chapter 1). Our confidence in model predictions, however, is a matter of scale and spec-

ificity (Chapter 2). Modeling can productively interact with observation and experimentation. It is highly recommended by several chapters that models be used at the beginning of a research project to infer the logical outcomes that follow from the premises (Chapters 1, 6, 12, and 24). In addition, ecosystem management is a wide spread practice for almost all kinds of ecosystems and models become an effective tool in management. To be effective, the management-oriented models should be built upon the fundamental science bases, make predictions that matter, and quantify uncertainty of the forecasts as recommended by Chapter 16.

Very intriguing is the report in Chapter 3 on the general attitudes of ecologists toward and the extent of application of quantitative models. Ninety-eight percent of ecologists surveyed considered ''simulation modeling an important tool'' whereas only 15% of papers in *Ecology* and 23% in *Ecological Applications* in 1996, 1998, and 2000 ''contained some use of dynamic quantitative modeling.'' This disparity partially results from the lack of training opportunities for quantitative modeling. It is important to incorporate quantitative modeling into undergraduate education in science (Chapter 22) and develop various programs and strategies to advance quantitative modeling skills among professional ecologists (Chapter 23). The key to resolving this disparity probably hinges on changes of the current attitude of reluctance that the research community has toward funding research on the tools and techniques of modeling (Chapter 27).

Overall, this book expertly critiques various aspects of ecological modeling. Experienced modelers or experimentalists with strong interests in modeling can learn a great deal from this book. The book could provide a platform from which to begin a quest for innovation in model development, testing techniques, and applications.

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BAT MAN IN THE TROPICS: STORIES OF ONE MAN'S CAREER IN FIELD STUDIES OF BATS

Fleming, Theodore H. 2003. **A bat man in the tropics: chasing El Duende.** Organisms and Environments, 7. University of California Press, Berkeley, California. xx + 311 p. $50.00, £32.95, ISBN: 0-520-23606-8 (alk. paper).

Those of us who study bats as part of our professional careers in science are truly lucky for two reasons. First, we often travel to unique and remote locations, to spend our time catching, observing, and studying one of the most unique groups of mammals on the planet today. As a result we see and experience things that most people can just read about. Second, we are lucky because it is fun.

In his new book, *A bat man in the tropics: chasing El Duende,* Ted Fleming illustrates these points in a unique and entertaining way. This book is a collection of field experiences and stories, told by the author, over his 30-plus year career as a bat biologist. It begins in 1966 with his first exposure to bat field research on a trip to Panama and takes us through the next 30 years of work in Central America, Australia, and into Mexico, Texas, and Arizona.

In his preface, Fleming identifies the underlying themes that run throughout the book; he calls these themes ''*El Duende.*'' Translated from the Spanish, *el duende* means ''hobgoblin'' or ''ghost,'' in reference to bats, the central theme of this book. Most people know bats only as mysterious creatures of the night. As one of the most misunderstood of all animals, bats are often feared and despised. The stories that the author relates about his research subjects go a long way in dispelling these myths and demonstrate the value and role bats play in ecosystems all around the world.

But *El Duende* also refers to ''will o' the wisp'' things that delude or mislead by luring on—the author's metaphor for scientific discovery. Ted Fleming's contributions to bat biology are well known. He has published numerous papers and books on bats and has emerged as one of the best-known bat biologists in the world. This book is unique in his efforts, an autobiography of sorts. Where it offers little in the way of experiments or data, it instead gives the readers a first hand thrill of scientific discovery, and the wonders of the often hidden lives of bats.

The book is well written and entertaining. It is designed to be of interest to the student, field biologist, and lay person alike. In it Fleming does a superb job of communicating the excitement for field work and love for the creatures he studies, something all of us in the field have experienced during the course of our own careers. Most of us have experienced the euphoria of field work but we seldom get the opportunity to express it in our scientific writing. While reading the stories in this book, I often found myself reflecting back on my own field experiences, with some relish and satisfaction. Over the years many of us have heard Fleming tell one or two of these stories at conferences, often to the delight of graduate and undergraduate students. It is all the more satisfying to see them laid down in print to be shared by all.

Each of the 11 chapters introduces readers to a new location where they become acquainted with tropical nature and scientific field work. We explore the excitement and trials of living and conducting research in the field and learn a great deal about the biology of bats as keystone species. Fleming's work over the years revealed much about the role that bats play in an ecosystem and demonstrated their critical contri-

bution to ecosystem stability. Perhaps one of this book's best contributions is that Fleming's portrayal of the ecological importance of bats can be equally well understood by the biologist and lay person.

There are 28 black and white photographs in the book, about half of which are of bats, photographed by Merlin Tuttle. Tuttle is widely known for his outstanding bat photography but the black and white images just don't do justice to the subjects. Most of the remaining photos are of Fleming, or those he has worked and lived with in the field. Field biologists and graduate students will recognize many of the names and photos of Fleming's collaborators in each chapter, many of which are well-known biologists in his or her own right. Each chapter also begins with an illustration by the author of bats or other mammals encountered in the field.

The book contains two appendices which are useful to the non-scientist. The first provides a brief overview of the diversity of bats, with a short description of the Order Chiroptera, and each of the 18 bat families. Appendix two is a cross reference of scientific and common names for each of the species, including plants that are mentioned in the text. In addition, there is a nice section that provides a list of general references on bats, as well as specific sources for each chapter.

Lastly, Fleming makes a point in his epilogue, which all students of biology need to be reminded of from time to time. While technology has progressed, and biologists have many new tools and computers for examining and analyzing data, we must be sure we don't lose sight of the real world and the organisms that inhabit it. It is, after all, curiosity about and love of those organisms that first attracted us to this profession.

A bat man in the tropics: chasing El Duende is a truly unique contribution to the bat literature, and one that can be enjoyed by field biologists, past, present, future, and even the arm-chair variety who prefer to dream about the excitement of field work. All will enjoy the opportunity to share Fleming's experiences.

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EVER SINCE HUTCHINSON: THE BOTTOM-UP VS. TOP-DOWN DISCUSSION CONTINUES

Gliwicz, Z. Maciej. 2003. **Between hazards of starvation and risk of predation: the ecology of offshore animals.** Excellence in Ecology, 12. International Ecology Institute, Oldendorf/Luhe, Germany. xxvii +379 p. €54.00, ISSN: 0932–2205 (acid-free paper).

Modern ecology owes much to Hutchinson, whose original insights into the paradox of plankton diversity in lakes have stimulated much ground-breaking theoretical and experimental work. When faced with a perplexingly high diversity of zooplankton in the seemingly homogenous pelagic environment, Hutchinson proposed that different morphologies among the zooplankton allow them to feed on different resources in the water column, thus preventing competitive exclusion among species. His idea has since triggered many studies on resource partitioning among sympatric species in different habitats, and this ''bottom-up'' view continues to influence the mainstream of ecological thoughts to date. Like Hutchinson before him, Gliwicz is interested by the paradox of plankton diversity, but he tackles the issue from a different angle. He correctly points out that freshwater zooplankton, mostly filter-feeding cladocerans, show no or little selective feeding; thus, resource partitioning is not a satisfactory explanation for the observed high species diversity. Instead, he asks how predation from the top down may play a role in maintaining plankton diversity.

Although Gliwicz's inclination toward a ''top-down'' view is quite obvious throughout the book, he does not force his opinion upon the readers. Instead, through systematic and logical arguments, backed by abundant empirical data from the literature, Gliwicz step-by-step unfolds his view while maintaining a balanced discussion of both top-down and bottom-up factors. The book is organized into ten chapters, each beginning with a synopsis. Chapters 1 and 2 outline the basic characteristics of an offshore habitat: the presence of environmental gradients primarily in the vertical dimension, the dominance of microscopic life forms at the base of the food web, the lack of physical shelters from predators, and the intense competition for food among the organisms. In such an environment, life is a constant struggle between finding food and avoiding predators, which is the subject of discussion in Chapter 3. This discussion continues in Chapters 4 and 5, but is focused more specifically on crustacean zooplankton in freshwater systems. Here the author revisits Hutchinson's famous paradox and looks at both bottom-up (resource limitation) and top-down (predation) factors in controlling zooplankton diversity. Given the characteristics of an offshore habitat as outlined in the first two chapters, Gliwicz argues that predation is a more important mechanism to prevent the dominance by a single zooplankton species and allow co-existence of multiple species. Because in many natural habitats both bottom-up and top-down factors are at work simultaneously, the role of predation is better understood by studying habitats where planktivorous predators are absent, examples of which are thoroughly discussed in Chapter 6. In lakes where planktivorous fish are either absent or suppressed, monopolization of resources by a single zooplankton species

becomes more common, which often leads to low algal biomass in the water column. The idea of regulating water quality in lakes and reservoirs via a trophic cascade has wide appeal to engineers and resource managers, but successful stories are rare because, as Gliwicz explains in Chapter 7, the behavioral and physiological plasticity at each trophic level tends to dampen the overall top-down effects. In the last three chapters, Gliwicz admits that although one can in theory distinguish between bottom-up and top-down factors, in reality they work simultaneously to shape the plankton community. The effects of the two factors sometimes counter each other, sometimes reinforce each other. These effects may be further mitigated by various environmental factors, and the outcome is rarely as clear-cut as what theories predict.

Overall, Gliwicz has given us a comprehensive treatment of one of the core issues in ecology. The book is written with clarity, objectivity, and a personal tone. A broad range of ecological concepts are explained in simple terms, making the book accessible to even readers with little ecological training. Nevertheless, some improvements could be made. For example, the author seems to repeat some of the same issues in several places, such as the effects of predation on the body size of cladocerans, and cyclop-cladoceran interactions. In Chapter 4 the author mentions only briefly the requirements of essential nutrients, such as polyunsaturated fatty acids (PUFAs) and phosphorus, among zooplankton; yet the state of the art is more advanced than what is acknowledged in the book. If one takes food quality into consideration, the bottom-up effect would appear more complex than what is addressed in this book. Also, marine offshore habitats are not discussed at all in the book. The marine zooplankton community is significantly different than the freshwater one. For example, the major zooplankters in the marine pelagic zone are copepods, many of which are omnivorous, feed selectively, or can switch between prey types. This feeding mode is fundamentally different from that of freshwater cladocerans, and more likely to allow resource partitioning among different species. While examples of fishless lakes exist, and fish predation can be easily manipulated in lakes and reservoirs, the lack of physical boundaries and the dynamic water movement in marine offshore habitats make large-scale experimental manipulation difficult, if not impossible. This perhaps explains why major advances in zooplankton ecology are spearheaded by limnetic scientists more often than their marine colleagues.

In brief, this book summarizes decades of brilliant work by Gliwicz on zooplankton ecology, and his unique insights into predator-prey interactions in offshore habitats. For ecology students, it is an excellent introduction to the subject of top-down vs. bottom-up control with extensive literature data and references. For zooplankton ecologists, this book will be a fine addition to their collection, along with Hutchinson's classic work.

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CONSUMING INTERESTS

Murdoch, William W., Cheryl J. Briggs, and Roger M. Nisbet. 2003. **Consumer-resource dynamics.** Monographs in Population Biolgy, 36. Princeton University Press, Princeton, New Jersey. xiii + 462 p. $79.50, £55.00 (cloth), ISBN: 0-691-00658-X (alk. paper); $35.00, £24.95 (paper), ISBN: 0-691-00657-1 (alk paper).

It is time to begin the consolidation of ecological theory into a form that we can both teach and use. Undergraduate ecology texts treat logistic and Lotka-Volterra models as more-or-less useless hoop-jumping exercises for students. Most ecology texts don't even offer quantitative problems. Why should they? The theory is so unrealistic that any fairly alert ecologist recognizes the implausibility of a direct application to real ecological problems. But there are real ecological problems that cry out for quantitative approaches.

Consumer-resource dynamics (CRD) is a valuable addition to the recent wave of books that investigate population ecology theoretically with an eye towards real data. (I would include Peter Turchin's two books [1998. *Quantitative analysis of movement.* Sinauer, Sunderland, Massachusetts. 2003. *Complex population dynamics: a theoretical/empirical synthesis.* Princeton University Press, Princeton, New Jersey], Ilkka Hanski's *Metapopulation ecology* [1999. Oxford University Press, New York] and William Morris and Daniel Doak's *Quantitative conservation biology: theory and practice of population viability analysis* [2002. Sinauer, Sunderland, Massachusetts]. *The ecological detective: confronting models with data* by Ray Hilborn and Marc Mangel [1997. Princeton University Press, Princeton, New Jersey] goes deeper statistically than ecologically, but is an indispensible component of the wave). Murdoch, Briggs, and Nisbet investigate the eater-eaten ecological relationship, and they search out explanations to reconcile the oscillatory and often unstable nature of predator-prey dynamics with the persistence of so many species.

All organisms consume resources, and most resources are organisms, so the subject is enormous and important . . . and surprisingly neglected. When did we last get a book on predator-prey relationships from a coherent point of view? Robert Taylor's 1984 *Predation* (Chapman and Hall, New York)? CRD covers predator-prey relationships, host-parasitoid relations, and even a little epidemiology. The approach is the-

oretical, using variants of the Lotka-Volterra system of differential equations, Ricker models, and Nicholson-Bailey difference equations. The models are carefully derived and well explained, consuming the first four chapters of the book.

Chapter 5 introduces stage structure, a Briggs and Nisbet specialty. Detailed discussion of host-parasitoid interactions extends across Chapters 6 and 7. Michael Hassell's 2000 (*The spatial and temporal dynamics of host-parasitoid interactions*, Oxford University Press, New York) book on host-parasitoid ecology is not superceded, but CRD provides more derivations and stage structure. Competition among consumers is treated at length in Chapter 8. The attention to resource dynamics allows a more realistic examination of the classic coexistence problem for competitors, but CRD does not produce any surprises. Gause's competitive exclusion principle still holds. The addition of resource age structure creates little new opportunity for consumer coexistence.

The chapter on biological control, a Murdoch specialty, is slightly misplaced. It should occur after the spatial process chapter (10). It is also short, regrettably so, because of the practical implications and the fascinating available data set. DeBach's classic *Aphytis*-red scale system is examined in some depth. Other systems are skimmed. The spatial process chapter deals with local aggregation à la Hassell, not with reaction-diffusion equations or metapopulations.

Consumer-resource dynamics does not solve all our problems. 1) It lacks an historical review of the subject, either in theory or experiment. Huffaker appears but not Gause or Elton. Volterra appears but not Kolmogorov. Ratio-dependent interactions and Robert Taylor's modest overview are neglected. Spatial diffusion models à la Murray get a bare mention. The authors decide that an historical review is beyond the scope of their book, but it is not beyond the scope of the reader's wishes. 2) There are no workable problems, making this a less useful graduate text. 3) Notational peculiarities are not as awkward as they usually are in the primary literature, but the student and the teacher long for a consistent notation from the researchers. Why not use S, I, and R for SIR models instead of the authors' H, J, and P?

Consumer-resource dynamics needs to be on any ecological theorist's bookshelf. Predator-prey ecologists cannot ignore the book. Parasitoid researchers will set it firmly next to Hassell 2000. Wildlife biologists and fisheries biologists will have to puzzle out the book, since the examples do not lean their way. Where is our new Graeme Caughley to put this valuable theory into a wildlife context? Life history researchers and others with an interest in stage-structured models will need the book. It will be a difficult sell for graduate students unless they have an inordinate fondness for parasitoids or stage structure. Those of us who are fond of parasitoids or stage structure owe the authors considerable gratitude for a careful, detailed analysis, and a well-written book.

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