Ecology, 91(4), 2010, pp. 1244–1245 © 2010 by the Ecological Society of America

Laws for ecology?

Dodds, Walter K. 2009. Laws, theories, and patterns in ecology. University of California Press, Berkeley, California. xiv +232 p. \$50.00 (cloth), ISBN 978-0-520-26040-5 (alk. paper); \$19.95 (paper), ISBN 978-0-520-26041-2 (alk. paper).

Key words: ecological laws; ecological theory; philosophy of ecology.

Walter Dodds' book aims high. It attempts to identify ecological laws and then use them to build predictive ecological theories. In the first chapter, Dodds outlines his perspective on ecological law, and then proceeds to list 35 laws that rule ecological systems and constitute the blocks ecologists need to build theories. Readers might be struck, as we were, by how different the character of the putative ecological laws listed by Dodds is from that of the laws of classical physics. The laws of physics establish relationships among variables (e.g., $F = Gm_1m_2/r^2$), an important trait that Richard Feynman identified as facilitating the construction of new laws.

Newton derived the inverse square law by melding the observation of the planets' elliptical orbits with his three laws of motion. Rather than establishing functional relationships among variables, however, Dodd's ecological laws comprise an idiosyncratic list ranging from the patent (e.g., "extinction is irreversible") to the questionable (e.g., "organisms are specialized"). Many flirt with truism, and most lack the syntactic fecundity that one associates with a natural law.

Philosophers of science struggle with the definition, and even the existence, of scientific laws. For practicing ecologists, the philosophers' theorizing is interesting, but of limited utility. For us, the relevant question is not whether ecology has laws, but whether these laws will be useful in advancing ecological research. Dodds' introduction suggests they will be, particularly when they are combined to develop predictive theories. Yet Dodds does not in turn use his 35 laws to derive theories, and the connections that he establishes between laws and theories are remarkably thin. In the book's second chapter, Dodds enumerates and describes what he believes are bona-fide ecological theories (but that most ecologists will recognize as research areas). Each theory is accompanied by a list of "Laws and theories most applicable," but in the subsequent discussion those laws and theories are too often forgotten. For example, the two laws applied to the theory of hierarchical structure are "system openness" and "scaling," but there is no subsequent mention of how these laws support a theory of hierarchical structure in ecological systems. Ultimately, it is difficult for the reader to perceive the utility of this exercise in theory development because it remains incomplete.

The logical disconnect between laws and theories is one of this book's most problematic features. Several sub-disciplines of ecology and evolution have logical structures that can be viewed as theories. Here we use the word "theory" to refer to collections of related models that can be combined to derive predictions and to organize observations. Because these theories allow us to establish clear connections among constituent models, they are outstanding tools for application, research, and education. Practitioners of the metabolic theory of ecology have successfully demonstrated the power of developing unified theories by combining models. Many areas of ecology (including population genetics, population biology, and several others mentioned by Dodds) have well-developed theories. Others (including community and ecosystem ecology) have a plethora of models, but so far it has been difficult to organize them into coherent theories. Having relatively coherent and unified theories may or may not be possible in these areas, and may or may not be useful. A variety of successful and fertile disciplines (e.g., physiology) lack unified theories, suggesting theories are not sine qua non for scientific progress. But if many areas of ecology have developed strong theories, why is it that Dodds did not deduce ecological theories from his lengthy list of laws? We believe that this is partly because in ecology, as in many other disciplines, we do not build theories with laws, but with families of models.

Consciously or not, Dodds adopted the philosophical perspective of logical empiricism (or the "syntactic" view), which turned classical physics, the dominant scientific discipline until the mid 20th Century, into an exemplar of how scientific disciplines are structured. The syntactic view regards science from the outside, as a body of knowledge that must be logically organized, and holds that proper scientific theories must be built deductively from natural laws. We suspect that the law- and theory-based view of science has been largely supplanted among philosophers of science by the model-based (or "semantic") view. The semantic view is a perspective that regards science from the inside, from a scientist's point of view. It regards it as both a body of knowledge and as a way of asking questions. Because it stresses what scientists do, and how they do it, the semantic view emphasizes models over theories and laws.

Successful scientific programs in ecology may or may not have laws and unified theories, but they always have models. Very few ecologists are in the business of discovering ecological laws and combining them into synthetic theories. However, all ecologists use, build, and/or test models, whether they are mathematical, statistical, verbal, or graphical. We derive them from a priori assumptions, construct them as summaries of statistical regularities, or build them as combinations of the two. We can often link them to construct ecological theories. Dodds' book devotes only 7 of 192 pages to models. Because this book is intended as a guide to ecological theory for graduate students, the light treatment of models is unfortunate.

The brief section on models exemplifies one of this book's weaknesses. Dodds uses the same terms for a wide variety of different philosophical categories. For example, he uses the term "principle" indiscriminately as (1) a weak law, (2) as a law from chemistry or physics, and (3) as a theory. He uses the word "theory" as a synonym for "area of research with high predictive power," model, and "scientifically accepted principle." Quibbling about the right definition of words is seldom useful, as different people can reasonably and usefully employ the same word to mean different things. However, to avoid semantic morasses, especially when referring to complex philosophical categories, it is helpful to define words carefully and use terms consistently. Readers are likely to become confused when the neutral theory of ecology is referred to as a model, a theory, and a pattern of nature within the span of four pages.

Dodds' goals for this book are both urgent and worthy. Our discipline benefits when ecologists position their research in the broad conceptual contexts of their research area. And Dodds has adopted a commendably broad perspective by considering all of ecology. Importantly, he has also conveyed to us that ecology, though a young science, has created a bountiful body of knowledge—an "entangled bank" of ideas, if you will. Unfortunately, though, his expansive perspective is narrowed by his adherence to a single philosophical lens, and his attempt ultimately fails. The view from laws and theories does not begin to capture the conceptual and theoretical richness of ecology. To make sense of the complex patterns in ecology's entangled bank, we must labor under a variety of perspectives. There is a grandeur in ecology's view of life. The scope of our philosophy must be ample and diverse enough to encompass it.

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Ecology, 91(4), 2010, pp. 1245–1246 © 2010 by the Ecological Society of America

Bioeconomics of invasive species

Keller, Reuben P., David M. Lodge, Mark A. Lewis, and Jason F. Shogren, editors. 2009. **Bioeconomics of invasive species: integrating ecology, economics, policy, and management.** Oxford University Press, New York. xiv + 298 p. \$99.00 (cloth), ISBN: 978-0-19-536798-0 (acid-free paper); \$49.00 (paper), ISBN: 987-0-19-536797-3 (acid-free paper).

Key words: economics; exotic species; risk; spread; valuation.

I found it refreshing to review a book that has an intended audience of ecologists and economists, groups that often sit alone in different buildings at every university. The primary strength of the book is in setting two modest goals: to reinforce the role of bioeconomic research in invasive species management and policy making; and to show how bioeconomic research can generate realistic policy recommendations for invasive species. To their credit, the editors and authors do more to identify the twelve tasks of Hercules, rather than try to complete them. They suggest a logical framework to explain the impacts of harmful exotic species to the public and policy makers in a currency they understand—dollars and common sense.

The book is well organized, with two chapters outlining the rationale for the book, four chapters devoted to risks associated with species invasions and common methods to quantify those risks, one very important chapter on uncertainty, and finally, with four case studies that bring home many of the main points. Keller et al. (as editors) enlist the aid of 20 well-known scientists, who contributed the 13 chapters of this excellent reference text.

The book's opening chapter by Lodge et al. provides positive examples of invasive species eradication (*Caulerpa*), control (sea lamprey), and slowing the spread (gypsy moth) before presenting us with the bad news. Most other invasive species continue to spread, costing us many billions of dollars in damage each year. Lessons from epidemiology (e.g., SARS, West Nile virus) further show our unpreparedness as a society. The challenge, and this book's framework, is ours to accept or face heavy costs and consequences. As the second chapter makes perfectly clear, integrating economics and biology is long overdue.

In a book under 300 pages long, it is unreasonable to expect that all of the important subtopics in each chapter could be covered equally well. Quantifying risks of invasion, limitations of risk assessment, identifying suitable habitat for invasive species, predicting spread rates and ecological impacts, and quantifying those impacts in space and time are each worthy of complete volumes. Still the editors and authors provide valuable introductions to each of those topics, drawing on their favorite examples to set the stage for future works.

Additional strengths of the book include an underlying subliminal message that a sea change is needed to move from *multi-disciplinary research*, where economists and ecologists conduct studies in tandem, to truly *interdisciplinary research*, where economists and ecologists develop hypotheses together and work closely together on all aspects of studies from the proposal stage through the publication stage. The simple differential equations scattered throughout the book provide the essential first steps to assign costs to species impacts. We need to walk before we run. Economists take risks with every estimate. I appreciated the need to include economists in invasion research with each passing chapter. We all will!

The book has a few weaknesses, primarily in aspects of modeling invasive species distributions, the effects of scale on the ecological and economic models, and the daunting task of fully quantifying and appreciating the uncertainties of invasions. Many new approaches for modeling species-environment relationships in invasions are not even mentioned. The GARP models presented have performed poorly in model comparison studies for many other invasive species.

Too little attention is given to the effects of scale on ecological and economic models. The extent or "area of interest" affects species-environment relationships as different forcing mechanisms operate over different scales. Estimating species abundance and thus, species impacts, is difficult for all but a handful of species in relatively closed systems (e.g., the Yellowstone Lake example). Many invasive species have human-assisted migrations that are extremely difficult to quantify or predict spatially. Likewise, predictions in time are influenced by trade and transportation, population and land use change, and climate change, and provide significant challenges to the next generation of ecologists and economists. The BOOK REVIEWS

important lessons in my favorite chapter (Chapter 7, "Uncertain invasions," by Jerde and Bossenbroek) seemed to be glossed over too quickly in the case studies. The book is unbalanced, with many aquatic examples and fewer examples of terrestrial species and pathogens and diseases. However, I consider these shortcomings to be very minor relative to the take home messages in the book.

The final chapter by Keller et al., "Putting bioeconomic research into practice," sounds the call to action. In the end, readers will agree that these editors easily accomplish their two goals by informing us that (1) bioeconomics can inform policy, and (2) bioeconomics is the way of the future. I hope that policy makers read this book and see the urgency in establishing coordinated prevention and early detection programs for harmful invasive species. I would recommend this book to economists, ecology students, and graduate students in related fields. The book is worthy of investment, and the avenue of bioeconomic research remains our only hope to reduce the costs of present and inevitable, future invasions.

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Ecology, 91(4), 2010, pp. 1246–1247 © 2010 by the Ecological Society of America

Understanding systems on the cusp

Scheffer, Marten. 2009. **Critical transitions in nature and society.** Princeton University Press, Princeton, New Jersey. xi + 384 p. \$99.50 (cloth), ISBN: 978-0-691-12203-8 (alk. paper); \$45.00 (paper), ISBN: 978-0-691-12204-5 (alk. paper).

Key words: attractors; dynamical system theory; regime change; resilience; resource management.

Abrupt change pervades our contemporary life. Globalization and global change have altered our geopolitical and economic circumstances in ways we have not yet absorbed. In just the present decade, life in the U.S. has been profoundly affected by acts of terrorism, realigned political coalitions, economic recession, health care debate, and a sense of the looming consequences of climate change. All of this seems relatively abrupt in the human perspective. We have uneasily come to realize that systems assumed to be stable can not only change, but may change rapidly.

A continuity exists between a psychological-sociological realization of abrupt change and how ecologists are coming to conceptualize system behavior. The traditional view of disturbance followed by succession leading toward a steady-state is becoming modified by recognition of much more complicated dynamics under the rubrics of *catastrophe theory*, *complex adaptive systems*, *regime shifts*, *resilience*, and *panarchy*. These representations expose the possibilities of multiple stable states and adaptive behavior, especially—surprise—in complex systems. Judging by the program for the 2009 Annual ESA meeting, abrupt systemic change is arguably one of the hottest topics in the discipline today. In fact, investigators of such phenomena seem so well organized as to suggest that ecology is experiencing an intellectual "movement" of unusual depth and breadth for such a polyglot discipline.

Marten Scheffer, Professor of Aquatic Ecology and Water Management at Wageningen University and recent recipient of the Spinoza Prize from the Netherlands Organization for Scientific Research for his "pioneering contributions to our understanding of critical transitions in complex systems," is a central figure within this movement. He is intellectually well positioned to synthesize this subject for us—which he does with sure-footed lucidity. We interpret the purpose of his book to be to describe and explain how some natural and social systems undergo critical transitions. But Scheffer is no single-minded evangelist. He recognizes that sudden change is the exception and not the rule. Nevertheless, it is these abrupt changes that get our attention. They are the ecological surprises, the resource management disasters, and the turning points of human history. We can thank Marten Scheffer for an intelligent, solidly documented, broadly scoped, and easy read into this intriguing and important subject.

Following the introduction, the book is divided into three parts and, as Scheffer says, one can read any of the three parts independently and in different orders depending on one's interests. Part 1 is on the theory of critical transitions, a sufficiently comprehensive explanation of the limit cycle, complex dynamics, and basin-boundary collisions. Diagrams, some rather complex, are liberally sprinkled throughout the text and the mathematics underlying this theory is provided separately in an appendix. Part 1 together with the appendix would, by itself, provide a fine core text for a course on system dynamics.

Part 2 presents a series of case studies organized by chapter on lakes, climate, evolution, oceans, terrestrial ecosystems, and humans. Clearly, the best empirical examples and experimentally based understanding of critical transitions are derived from fast-operating systems such as lakes and ponds, but the historical literature and data on climate and evolution is rich with evidence of critical transitions as well. The application of critical transitions in terrestrial systems is either not as well developed, or less relevant because of the high resilience (inertia) of such systems to change within the time perspective of humans, or less prominent due to the buffering effects of spatial heterogeneity. The last chapter, on human behavior at the individual and societal level, incorporates contemporary psychological, sociological, and political interpretation on heuristic thinking and how that leads to societal inertia and denial of all-too-obvious needs. A valuable aspect of this section (along with sections 1 and 3) is Scheffer's brief synthesis of each chapter following his exposition of the system. These syntheses are useful benchmarks that facilitate comparison of the reader's interpretation of the chapter with Scheffer's perspective on the important highlights.

Part 3 is an optimistic treatment of how we can recognize whether systems are vulnerable to alternative states, whether the system is close to a threshold, and how we can better manage social-natural resource systems with this knowledge. Scheffer is quite familiar with the relationships among scientific understanding, uncertainty, and policy, and he has no Pollyanna illusions about the difficulties in effecting changes against entrenched interests. While optimistic, Sheffer's suggestions regarding the application of principles of critical transitions to real-world problems are essentially practical; he well recognizes that understanding and managing change is just as much a human problem as it is a scientific or mathematical problem.

Aside from the extraordinarily well-written and well-organized qualities of this book, it is a handsome production. The text is copiously documented with endnotes collected by chapter at the end. American readers may discover important European references to leaven their possibly provincial knowledge of the literature on this topic. Nostra culpa! Besides the appendix illustrating mathematical treatments of some aspects of system dynamics, there is a glossary of terms specific to dynamical system theory, and a word index, not including authors of references. We noted only four trivial, and perhaps arguable, editorial errors.

We recommend this book as the best integration of the multiple rubrics (resilience, regime change, panarchy, complex-

ity, dynamical systems theory) found on the subject of critical transitions or abrupt change, and as an enjoyable as well as enlightening synthesis of a timely and important topic bearing on many of the crucial dilemmas of our time.

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Ecology, 91(4), 2010, pp. 1247–1248 © 2010 by the Ecological Society of America

Using R to explore ecological principles

Stevens, M. Henry H. 2009. A primer of ecology with R. Use R! Springer, New York. xvi + 401 p. \$64.95, ISBN: 978-0-387-89881-0 (acid-free paper).

Key words: ecological statistics; models; population ecology; R; textbook.

R is a powerful, open source, and free programming and statistical software environment for Windows, Mac, and Linux operating systems. It was first developed in 1996 and is enjoying a meteoric rise in popularity. It is likely that most ecologists have at least heard of R, perhaps even downloaded and installed it, and are contemplating "moving to it" for their research (to find R search the letter "r" on the internet). With the arrival of M. Henry H. Stevens' book *A primer of ecology with R*, ecologists have an excellent guide to using R for exploring population and community models.

As the author states, this book is "geared toward graduate students" above the level of Nicholas Gotelli's well known *A primer of ecology* (2008. Sinauer Associates, Sunderland, Massachusetts) and with similar coverage of topics, although in more depth and with explicit code to implement the models. Stevens also notes similarities to Joan Roughgarden's *Primer of ecological theory* (1997. Benjamin Cummings, San Francisco, California), which is based on MATLAB. Another important and noteworthy text is Ben Bolker's *Ecological models and data in R* (2008. Princeton University Press, Princeton, New Jersey), which introduces more modern approaches to statistical data analysis and model fitting.

The text is divided into three main sections covering, in order, single species models, two-species interactions, and finishes with four chapters on "special topics." The book closes with two appendices that introduce R and then take readers into the details of getting up and running with programming in R. Each chapter ends with a brief summary and a set of problems based on the models presented. Problems are helpful and lead the reader to a deeper understanding of the models.

Chapter 1 begins with density-independent growth. Interestingly, the chapter starts with a two-panel graph of data, followed by the text that begins "Between 1966 and 1971, Song Sparrow ... abundance ... increased" This seems to define the book's approach of jumping right into the material. However, we soon pick up a few typos (e.g., Fig. 1b shows "Growth Rate" vs. "Count" and the legend states "Relative Annual Change vs. N" and Fig. 1.2 is referred to as Fig. 1.3 in the text). Although these are minor problems, they can cause concern to readers.

The chapter then moves to elementary geometric growth using R. We are provided code to produce a figure for N vs. time for geometric growth with $\lambda < 1.0$, $\lambda = 1.0$, and $\lambda > 1.0$, add text to the graph, and add a reference line for $\lambda = 1$. I mention these details because I don't know of another way to so easily produce such informative graphics. The chapter then introduces exponential growth (continuous time), shows the reader how to write a function, and then provides the tools to write a stochastic simulation and view multiple iterations on a single graph.

Chapter 2 introduces demography and matrix algebra, including eigenanalysis with sensitivity and elasticity analyses. The latter part of the chapter confronts these models with data by estimating parameters and introduces bootstrapping. The chapter includes several boxes on working with matrices in R.

Chapter 3 tackles density-dependent growth using discrete and continuous models. Stevens introduces the reader to the discrete logistic equation, chaotic dynamics, a bifurcation plot, and sensitivity to initial conditions before covering the continuous-time model. This chapter also includes a section on fitting models to data and takes the reader through a mixedmodel analysis. In this exploration we are well introduced to the statistical tools and logic required to understand how increasing resources affects the growth rate of an alga within a food web. Chapter 4 deals with spatial population dynamics (source-sink dynamics, metapopulations, and applied problems) and introduces the use of stochastic simulations to evaluate extinction probabilities.

Part two has just two chapters, on competition and enemyvictim models. The latter includes coverage of the standard Lotka-Volterra model with stability analysis, Rosenzweig-MacArthur model, host-parasitoid dynamics, and the SIR model. For the predator-prey model, for instance, Stevens discusses the framework for the system of equations, helps the reader with the unit analysis of the coefficients, and then provides the model in a box (seven lines of code and a reference for help with the code solver). We learn about functional responses and how to graph them using R. The Jacobian stability analysis is shown using two lines of R code.

The final section on "special topics" includes four chapters, first covering food webs, the second covering multiple basins of attraction, the third covering competition, colonization, and niche partitioning, and the last chapter dealing with community composition and diversity, including a discussion of Hubbell's neutral theory of biodiversity.

In addition to the book, the author has provided an R "package" called "primer" that should be downloaded from the R site. This package, as with all R packages, provides tools that offer greater functionality and convenience for users. It also is necessary to run some of the available code. The primer package also includes data sets that readers can use along with the text. The code I tried worked after some work, including changing my working directory and installing other required packages. The success of the code can be attributed to the author's use of Sweave, which allows one to imbed code into the LaTeX files and use R on-the-fly to generate figures. Therefore, the code must be correct when it goes to print.

The book is not without some editorial challenges, from a variety of typos to more subtle issues. One example involves the definition of zero net growth isoclines in the Lotka-Volterra predator-prey model that "tell us when populations tend to decrease or increase." Instead, more technically, these indicate when populations do not change. In this example we are saved by the math which shows us that the isoclines emerge when the growth rates are set equal to zero. In another example, the text introduces projection matrix multiplication and the worked

example has a non-zero element in the main diagonal that is ignored. Nonetheless, we see the error is later corrected. This reviewer, however, is not greatly troubled by these oversights and, instead, sees these issues as learning opportunities for my students. Such challenges, however, may interfere with learning by those new to both the models and R. The author's website includes a list of known problems in the book ((http://www.cas. muohio.edu/~stevenmh/primer/)).

I find the writing to be casual and fresh. My students will get the sense that the author is a real person and that ecological models can be fun, interesting, and understood by readers. We see descriptions of model output as "cool" and that we can use projection matrices to "calculate all kinds of fun and useful stuff..." which makes the reading pleasurable.

The text is built upon the premise of learning by example and, as a result, is replete with worked examples. Readers should read the book with R running on a nearby computer. I must stress that this book is different from many others where the models are passively explained. This is a book to really work with. And the software that it is based on is freely available. To help facilitate code entry, the author provides all of the code on the accompanying website. The vast majority of the code I tried worked and provided output exactly as it appeared in the text. The examples in the book, however, can be completed without use of the website.

In conclusion, I found the text to be an excellent foray into ecological models using R. I plan to use this book in my upcoming modeling course for upper-level undergraduates, a course cross-listed in the math and biology departments. The models will present some challenges for my students but I think the pace of the text will work for them. In addition, many of my students will be new to R, and to programming, but the text does a great job of integrating an introduction to R with the models. I can see this book being valuable to graduate students and research ecologists wishing to work with these foundational models in R. It is now time to jump into R!

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