

Book Reviews

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STRUCTURE AND DIVERSITY IN FOOD WEB RESEARCH

de Ruiter, Peter C., Volkmar Wolters, and John C. Moore, editors. **Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change.** Elsevier, Burlington, Massachusetts. x + 590 p. \$84.95, ISBN: 978-0-12-088458-2 (alk. paper).

Key words: body size; complexity and stability; food chain length; interaction strength; trophic structure.

Food webs are diagrams of ecological communities that show trophic links among species. They are useful for visualizing communities, as maps for species interactions or energy and nutrient flows, and for predicting impacts of environmental change, extinctions, and invasions. This latest food web book emerged from a 2003 conference of ecologists held in Germany. Every decade, food web ecologists gather to review scientific advances, gain perspective, and brainstorm about future directions. Organizers succeeded in including diverse viewpoints. Authors include prominent modelers, experimentalists, pattern-seekers, and especially those that combine approaches. The 90 authors and coauthors include predominantly North American and European experts. Asia and Australia are represented by just one scientist each. Women scientists comprise ~20% of the authors.

The volume contains 43 chapters grouped into eight sections. Topics include: dynamic food web structure, population dynamics and food webs, body size, resource dynamics, ecosystem function and food web structure, environmental effects on food webs, and a review section. Chapters do not provide abstracts, but sections have introductory chapters. Introductions are generally good, but uneven in providing overviews of their sections. The lack of abstracts may make it difficult for discussion groups to choose chapters for review.

The book seems aimed toward researchers and advanced graduate students, rather than resource managers or new students. A strong background in ecological theory will help readers understand how authors arrive at their conclusions. There is a healthy dose of models throughout the volume. However, even the most mathematical chapters offer accessible interpretations of model results.

Finding the most logical groupings of the chapters in this volume must have been as much fun as trying to define functional groups of species. It cannot be done perfectly because many chapters integrate many concepts. The editors did a creditable job, but readers may occasionally be mystified regarding section assignments. This is not a bad thing if it inspires the reader to consider synergies among the chapters.

The first section of the book gives a tribute to two lost giants of the field, Gary Polis and Peter Yodzis, both of whom brought considerable depth and realism to the study of food webs. The editors then provide some initial perspective on food web research. Winemiller and Layman close by discussing the difficulties of studying real, complex food webs. Their proposed way forward is for researchers to use teamwork, and embed experimental studies of food web modules within surveys and long-term studies of more complete food webs. While this isn't a revolutionary idea, the chapter reassures investigators that it

is feasible and worthwhile to tackle the complexities of food web research.

Food web studies can be grouped into those which seek patterns in static descriptions of food webs, and those that focus on dynamic changes in either species interactions or trophic linkages. Section 2 unifies these themes with chapters that demonstrate feedbacks between species interactions and food web structure. Otherwise the topics aren't very cohesive; they range from single-species dynamics to whole web patterns. Every chapter has thought-provoking take-home points. Leibold et al. reveal that consumer–producer dynamics can be detectable even in complex food webs. Banašek-Richter et al. rehabilitate the old food web pattern that linkage density (LD, or average links/species) is invariant with species number (S). By calculating linkage density as a function of actual energy flow in real webs, they found that the diversity of energy flows remained constant even when interactions were more numerous. McCann et al. cogently discuss how higher-level consumers may stabilize food webs by coupling food web modules in time and space.

Section 3 addresses how changes in species' traits can modify population dynamics and food web structure. An early chapter provides an intriguing model of how trait-based evolution might produce food web structures similar to those found empirically. Later chapters address dynamic and structural consequences of ontogenetic shifts in body size, and prey switching or inducible defenses as stabilizing forces. This section is heavy on models.

Section 4 is fairly cohesive because all of its chapters address the implications of body size for food web structure and dynamics. Warren's introduction is an especially good historical overview of the topic, and Woodward et al. explore future applications of body size research. The section includes an overly long chapter that explores statistical methods for relating body mass to abundance. Subsequent chapters by Persson and de Roos, and Emmerson et al. show how body size influences species interactions, and provide fascinating insights into how knowledge of body size and metabolic rates can be used to predict predator-prey interaction strength.

The fifth section gets down to earth with an emphasis on detrital food webs. Sabo et al. remind us that prey refuges help maintain food web structure. Bengtsson et al. add to our understanding of soil food webs by showing that web structure changes drastically across soil horizons. A complicated chapter by Schröter and Dekker relates patterns of N deposition to food web structure and stability in European sites. Methods for determining stability and some results were too speculative for my taste. Cross et al. provide useful insights into the important of animals in nutrient cycling in streams. The final two chapters by Cousins et al. and Dekker et al. aim to improve food web studies by refining quantifications of energy exchange, and by including indirect effects and spatial heterogeneity in food web models. The last chapter is long on details that should go into models, but short on approaches for making such models tractable.

Beginning with an able introduction by Morin, section 6 addresses how food web research could inform studies of the relationship between biodiversity and ecosystem functioning. Several chapters point out that ecosystem functions vary more when predator diversity is manipulated than when prey richness

is changed (i.e., Downing and Wootton). Chapters by Loreau and Thébault and by Fox present producer–consumer models containing diversity in producer edibility and consumer diet breadth. The emphases of these chapters differ, but some conclusions are reassuringly similar (i.e., productivity of producers can peak at intermediate consumer richness). Setälä gives an insightful review of the dominant properties of soil food webs regarding ecosystem functions. Beisner and Romanuk show empirically that biotic resistance to invasion increases with species richness and decreases with nutrients. In an interesting but inconclusive chapter, Petchey et al. examine whether functional diversity is as useful as species diversity in predicting ecosystem functioning.

Section 7 addresses how perturbations propagate through food webs. This section seemed choppy, with chapters having different goals and methods. Empirical chapters by Culp et al., Layman et al., and Harper-Smith explore how food webs respond to effluents, species removals, and introduced species, respectively. The Layman chapter shows that removing top predators may increase average food chain length, if such predators mainly feed low in the food chain. Harper-Smith et al. demonstrate the usefulness of a niche model to visualize effects of trout on mountain lake food webs. Theoretical chapters by Montoya et al., and Koen-Alonso and Yodzis address the strengths and limitations of predicting community dynamics from models. Both show that models can reveal the importance of indirect effects, with the latter chapter stressing

that small differences in model formulations produce disparate predictions.

The reviews in the final section were useful summaries, but fresh insights were limited. Dell et al. provide an updated perspective on the complexity–stability relationship. Sabo et al. compare and contrast the highly resolved, structural approach to describing food webs with those studies that look in detail at subwebs. Scharler et al. discuss important factors in aquatic food webs. Lastly, there is a good overview of how the spatial scales at which different species operate can affect food web properties. This chapter is already a bit dated, due to the timing of the conference relative to a burst of recent activity on the metacommunity front.

In summary, community, ecosystem, and food web ecologists will find much of interest in this book. The overall quality of the chapters is high, but there is variance. Taken as a whole, it provides valuable perspective on relationships among types of food web studies.

SHARON P. LAWLER

*University of California at Davis
Department of Entomology
One Shields Avenue
Davis, California 95616
E-mail: splawler@ucdavis.edu*

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FINDING A PLACE FOR MICROORGANISMS IN THE FIELD OF ECOLOGY

McArthur, J. Vaun. 2006. **Microbial ecology: an evolutionary approach**. Elsevier, Burlington, Massachusetts. xii + 416 p. \$79.95, ISBN: 978-0-12-369491-1 (alk. paper).

Key words: microbial communities; microbial ecology; microbial evolution; bacteria.

Writing a textbook on microbial ecology is a Sisyphean task. Our knowledge of microorganisms is increasing at an incredibly rapid pace and one could argue that writing a microbial ecology text in 2006 is akin to writing a primer on jazz music in 1935 when Billie Holiday was singing with Benny Goodman's band. While I would agree with this argument, I am also convinced that a textbook on microbial ecology is urgently needed. Ecologists are slowly beginning to accept the richness of microbial life on Earth and are moving beyond the historical focus on plants and animals to integrate microorganisms into the discipline of ecology. At the same time, microbiologists are more frequently leaving the laboratory, where microorganisms primarily exist as isolates on petri plates, to study complex microbial communities found in habitats that are spatially and temporally variable.

Although the field of microbial ecology is in its infancy, it is not premature to write a textbook on the topic. Concepts may be revised and better case studies may emerge, but the fundamental principles of microbial ecology are not likely to change in light of future discoveries. This book primarily focuses on the evolutionary ecology of one group of microorganisms, the bacteria. Other microbial taxa (including archaea, viruses, single-celled eukaryotes, and fungi) are mentioned only

in passing, if at all. This taxonomic “bias” is reasonable, considering that it would be nearly impossible to write a microbial ecology text that covers all of the disparate taxa commonly placed in the “microbial” category (an arbitrary grouping if there ever was one). The overarching objective of this book is to compare the evolutionary ecology of microorganisms and “macro”-organisms, with the author emphasizing how concepts largely derived from the study of plants and animals may, or may not, help us understand the ecology of bacteria.

The first three chapters provide a basic overview of key concepts in microbial ecology and evolution. There is an introduction to the biology of bacteria and viruses with a nice discussion of the evolution of microbial life on Earth. Chapter 3 focuses on bacterial speciation and the numerous difficulties associated with applying species concepts to microorganisms.

Chapters 4 through 6 focus on the ecology of microbial individuals, starting with an overview of the difficulties associated with defining an “individual” microorganism and a summary of the various abiotic constraints on microbial growth and survival. There is a comprehensive discussion of light, temperature, and pH effects on microorganisms, but other abiotic variables, namely redox potential and moisture availability, are mentioned only briefly despite their importance. Chapter 5 focuses on microbial nutrition and feeding strategies, followed by an examination of sexual reproduction among bacteria and the ecological implications of horizontal gene transfer.

Microbial population ecology is covered in Chapters 7 through 10, beginning with a review of various conceptual and mathematical models used to predict microbial population growth. There is a nice discussion of *r*- vs. *K*-selection and how

these concepts may apply to microorganisms, followed by an examination of microbial dispersal, the apparent “multi-cellularity” of some microorganisms, and the ecology of individual genes. Chapters 9 and 10 explore the influences of habitat characteristics, genome size, gene exchange, and intercellular communication on bacterial population dynamics, including a thorough overview of bacterial quorum sensing.

The final five chapters examine the community ecology of microorganisms. There is a summary of the various approaches used to survey microbial diversity and an overview of concepts related to the maintenance of community-level diversity. Chapter 12 examines microbial communities in different habitats, with aquatic biofilm communities receiving the bulk of the attention, while Chapter 13 describes the processing of nutrients (namely nitrogen) by microorganisms, linking the evolution of specific microbial processes to the ecology of those processes. The final two chapters examine species interactions, namely predation, phage-host interactions, and mutualistic symbioses. The book finishes with a discussion of what is known (or more importantly, what is not known) about microbial biogeography.

The author does an excellent job of describing fundamental concepts in evolutionary ecology and discussing how these concepts may apply to microorganisms in natural environments. Perhaps more importantly, the author pinpoints how microbial and “macro”-bial ecology are fundamentally different. For example, there is a comprehensive discussion of horizontal gene transfer among bacteria and its importance in microbial ecology and evolution. The author also highlights what “macro”-bial ecologists may be able to learn from the study of microbial ecology. The section on bacterial predation could convince even a diehard animal ecologist that microbial communities could serve as useful model systems for exploring predator–prey interactions.

The book is littered with interesting questions and concepts that will undoubtedly spark reader’s curiosity. Unfortunately, the text is not well organized, so many of these tantalizing tidbits are effectively hidden to all but the most careful and thorough reader. Major concepts are not presented in an orderly manner and there is a significant amount of repetition between chapters. Unfortunately, this disorganization makes

the book less useful for those readers who want to learn about selected topics in microbial ecology and do not have the time or patience to read the entire book.

There are a number of additional concerns that detract from the overall utility of this book. The inclusion of more figures and illustrations would make difficult concepts less confusing and, with a greater number of cited references, it would be far easier for readers to seek additional information on specific topics mentioned in the text. More importantly, the book could be improved with a more judicious selection of case studies to illustrate key concepts in microbial ecology. There is an overwhelming emphasis on studies conducted in streams (and in particular, those studies conducted by the author and his collaborators), when more appropriate case studies could be gleaned from work conducted in other microbial habitats. The author also ignores much of the recent research in the applied microbiology and medical microbiology fields, research that is often directly relevant to the study of microbial ecology. Along these same lines, there is little mention of studies using whole-genome sequencing and metagenomic approaches even though such studies have greatly expanded our understanding of microbial ecology and evolution.

Microbial ecologists need a textbook they can call their own, a textbook that can serve as a reference for students and researchers seeking a broad understanding of this rapidly expanding discipline. While this book does not quite reach this lofty goal, it is unique in that it focuses on general ecological and evolutionary principles instead of rehashing information that could be found in current microbiology textbooks. This book would be most appropriate for readers that already have a solid background in microbiology and are interested in exploring the emerging field of microbial ecology.

NOAH FIERER

University of Colorado
Department of Ecology and Evolutionary Biology and the
Cooperative Institute for Research in Environmental Sciences
Boulder, Colorado 80309
E-mail: noah.fierer@colorado.edu

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CANARIES IN A GLOBAL COAL MINE?

Møller, Anders P., Wolfgang Fiedler, and Peter Berthold. 2006. **Birds and climate change**. Elsevier, Burlington, Massachusetts. xvi + 251 p. \$49.95, ISBN: 978-0-12-373614-7 (alk. paper).

Key words: birds; climate change; migration timing; population dynamics.

The response of species, populations, and ecosystems to environmental change has long been a focus of ecology and conservation biology. No environmental change looms larger in the scientific and, hopefully, public and political consciousness than climate change. The major hurdle facing those with an interest in predicting biotic responses to climate change is the reconciliation of scientific data with social and political mindsets. Although positive strides have been made of late, most notably the assessment and recommendations of the

United Nations Intergovernmental Panel on Climate Change, the design of successful strategies and policies will require both sides of this global predicament (scientists and policy makers) to continue to push their respective envelopes. Climate-change scientists need to be conscious of the context in which their data are collected and presented, while policy makers need to temper the needs of their constituents with the realities of the world in which the constituents live.

Birds have a long history of being used as sentinel species, species whose biology is used as an indicator of environmental conditions, and climate change is no different. Few animal taxa can rival birds for the quality of long-term data sets available to researchers interested in documenting population-level responses to environmental change. Over the past 15 years, ornithologists have noted changes in their individual study species (e.g., changes in migratory arrival dates) that are consistent with long-term climatic warming trends. Importantly, the geographic and taxonomic coverage of avian research is widespread enough

to allow ornithologists to make generalizations about the response of birds as a whole to global climate change patterns. The ability to generalize is the first step in developing the ability to predict responses to future changes and developing policy around those predictions.

Birds and climate change, originally published as part of the Advances in Ecological Research series edited by H. Caswell, is comprised largely of presentations given at a 2003 workshop on climate change and bird migration. Accordingly, the majority of the chapters focus on aspects of migration; however, this edited volume also offers chapters on microevolutionary dynamics, population and community dynamics, and conservation. One similarity among the various chapters is their reliance on and interpretation of the long-term data sets, some dating to the mid-1700s. Another similarity is that the geographic focus of most of the chapters is on Palearctic taxa and study locations. This narrow focus is partially a result of the workshop location at the University of Constance but speaks more to where the majority of long-term climate-related avian research has been undertaken. This focus is somewhat of a double-edged sword. On the one hand, the narrow focus allows for careful reflection and dissection while avoiding tribulations associated with large-scale variation in global climate patterns. On the other hand, limiting geographic scope can limit the ability to generalize and, as a consequence, the ability to make meaningful predictions about the effects of environmental change.

Within the context of focus, the chapters vary considerably. The most narrowly focused chapters were those that addressed specific aspects of migration: fueling and energetics (Bairlein and Hüppop), timing (Lehikoinen et al.), and the utility of bird-banding data and other long-term data sets (Fiedler et al., Møller and Merilä). All four of these chapters present quality data and interpretation, especially with respect to avian biology. However, they do not stand alone with respect to providing much of a climate-change context.

Two chapters in this volume focus on the interactions between reproductive timing (Dunn) and mistiming (Visser et al.) and reproductive performance. These two chapters, to my mind, are the strongest of this volume. They offer comprehensive literature reviews, explicitly document direct links between climate and avian fitness, and provide sufficient context to

facilitate generalization and the generation of meaningful climate-effect predictions.

The remaining data-focused chapters—photoperiod and annual cycle regulation (Coppack and Pulido), microevolutionary effects of climate change (Pulido and Berthold), population dynamics (Sæther et al.), biogeography (Böhning-Gaese and Lemoine)—chart more of a middle course. They provide solid reviews of basic biology and good foundations for prediction development, though they do not stand alone with respect to climate change as well as the chapters on reproductive timing do.

By focusing on whether or not a given chapter provides everything necessary to make generalizations and predictions of climate change effects, I do not intend to demean the efforts involved in concise presentation and analysis of rigorously collected data. All of the chapters in *Birds and climate change* achieve these goals, despite some troubling translation and editing in certain chapters. However, ornithologists need to be aware of the unique position they are in, given the quality of many long-term avian data sets, to contribute to ongoing management and policy discussions involving climate change. As a case in point, the concluding chapter authored by the volume's editors provides a list of provocative research goals and needs; however, the authors do not explicitly relate the intent of the identified research gaps to their value for those charged with developing or changing policy.

This volume is not a stand-alone reference for those looking for an introduction into climate change or for those interested in a detailed treatment of biotic responses to published future climate-change scenarios, nor do I think it was intended to act as such. *Birds and climate change* will be a valuable reference for ornithologists, for those interested in specific biotic effects of climate change, and for those looking for a portal to data sets amenable to building predictive climate-effect models.

JASON JONES

Vassar College
Department of Biology
124 Raymond Ave.
Poughkeepsie, New York 12604
E-mail: jajones@vassar.edu

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OUT OF EQUILIBRIUM?

Rohde, Klaus. 2005. **Nonequilibrium ecology**. *Ecology, Biodiversity and Conservation*. Cambridge University Press, New York. ix + 223 p. \$120.00 (cloth), ISBN: 0-521-85434-2; \$60.00 (paper), ISBN: 0-521-67455-7.

Key words: community assembly; density dependence; equilibrium; resource competition; vacant niches.

When trying to explain the baffling complexity of the living world, ecologists and evolutionary biologists tend to use two contrasting frames of reference. One view is that biodiversity has mainly been shaped by directional processes like natural selection and competition. This view tries to explain individual traits as adaptations to the local environment, population

densities as the result of intraspecific competition, and communities as the outcome of a coevolutionary process leading to specialisation and niche differentiation. The contrary perspective is that many if not most patterns are better explained by a combination of stochasticity and historical accidents. This viewpoint stresses mutation and random dispersal rather than selection and competition, saltational change rather than gradual transformation, and historical contingency rather than determinism and predictability.

Many historical debates in our field reflect these contrasting perspectives. Examples include the selectionist–neutralist debate in population genetics, the debate on (adaptive) sympatric versus (non-adaptive) allopatric speciation, or the debate on the relative importance of niche-assembly versus dispersal-assembly in community ecology. There have always been attempts to reconcile and integrate both perspectives, but some ecologists

(most notably Rob Hengeveld and Gimme Walter) consider that such attempts are futile, arguing that the two perspectives represent inherently incompatible scientific paradigms.

Undoubtedly, ecology and evolutionary biology have, to a large extent, been dominated by the selection-competition approach. In a sense, this approach is more rewarding since it is much easier to build theories, to form hypotheses, and to design experiments if one can assume that the world is governed by directional and deterministic processes with largely predictable outcomes. The intellectual appeal of the theories built on the selection-competition approach does, however, not imply that the world around us is indeed structured along these lines. Evolutionary biologists like Stephen Jay Gould and ecologists like Joseph Connell have stressed that selection and competition are more often assumed than proven, and that the relatively simple theories based on selection and competition may have misguided whole generations of scientists into thinking that the world around us is also simple and predictable.

Reviewing both theoretical arguments and empirical evidence against the allegedly overruling importance of competition is the main goal of Rohde's *Nonequilibrium ecology*. Before discussing the book in more detail, I have to remark that the title of the book is very misleading. Based on the title, I expected this book to be mainly a critique of "equilibrium thinking" in ecology. This is a topic close to the heart of my own work. Together with my colleagues I have shown that classical models of ecology and evolution do not necessarily lead to equilibrium, even in a constant and homogeneous environment. Moreover, we could demonstrate that much of the textbook knowledge on resource competition and sexual selection hinges on equilibrium considerations, being actually wrong and misleading in nonequilibrium situations. Topics like these do not feature prominently in Rohde's book.

The terms "equilibrium" and "nonequilibrium" occur repeatedly on almost every page of the book, but they are used in an extremely restricted sense. The advertising text on the back cover sets the scene by stating that "the assumption that competition is of overriding importance is central to equilibrium ecology." It turns out that Rohde views the terms "equilibrium thinking" and "competition thinking" almost as synonymous. In fact, these concepts are quite unrelated. "Equilibrium" refers to a system in steady state. Such a state can be brought about by competition, but also by many other factors. "Competition" refers to an interaction structure governing the dynamics of a system. A competitive system may or may not approach equilibrium. Mixing up the two concepts is unfortunate and highly confusing. Viewed this way, empirical studies showing that populations are kept at equilibrium by predation pressure are viewed as evidence *against* equilibrium ecology. Conversely, limit-cycle oscillations and other complex behavior are subsumed under the heading "equilibrium dynamics."

It took me some time to overcome my confusion and to realize that Rohde's evaluation of "equilibrium ecology" is in fact an evaluation of "competition ecology." The book discusses in considerable detail a large body of work relevant to its topic. Throughout, a diversity of opinions is presented in a fair and objective way. This has the advantage that the reader gets a good idea about the field, without having to consult the original literature. On the other hand, presenting the results, arguments, and opinions of a variety of ecologists side by side gives the book a mosaic-like and somewhat unorganized appearance. Moreover, the reader is often left in confusion, since the author does not act a guide helping the reader to separate the wheat from the chaff.

The book starts with two chapters giving an overview of the central ideas and concepts, followed by two chapters discussing the alleged role of interspecific competition for structuring

communities (character displacement, niche separation). Chapter 5 on "Noncompetitive mechanisms responsible for niche restriction and segregation" might play a central role, but it is surprisingly short and mainly focused on behavioral mechanisms related to mate finding and prezygotic isolation. A brief chapter on whether the fossil record provides evidence for or against stasis (equilibrium) on an evolutionary time scale is followed by four chapters focusing on "detailed examples" at the population, community, and macroecological level. The book is concluded by a (rather brief) chapter on "prospects for an ecology of the future."

Nonequilibrium ecology is a useful compilation of facts, theories, and opinions related to the competition debate, but it has to be consumed with care. As to the facts, it is clear from all parts of the book that the author has a strong bias in favor of marine parasites. Rohde justifies this bias by his own expertise and by the fact that parasites represent "probably the largest component of the Earth's fauna and should therefore not be ignored when determining the 'mainstream' of ecological thought." Although he may have a point here, the focus on parasites weakens the take-home message of the book considerably. In fact, even hard-core "competition ecologists" will readily agree that parasites are often more strongly limited by their hosts than by their conspecifics, and that host-parasite interactions have an inherent tendency for exhibiting nonequilibrium behavior. Although they are of obvious ecological relevance, host-parasite systems just do not form the arena for the discussion on the relative importance of competition.

The book is certainly useful because of the rather unique compilation of a broad diversity of theoretical ideas on the importance of competition. However, a number of assertions on theoretical models, some even at the core of the matter, are plainly wrong. For example, the statement that population densities in the discrete-time logistic growth model never reach carrying capacity (in the legend of Fig. 1.2) is not correct. In fact, overshooting the carrying capacity is a crucial aspect of this model. Other statements related to theory are misleading. The finding that fish parasites do not conform to the packing rules predicted by a model developed by Ritchie and Olff is, for example, interpreted as evidence "that competition for limiting resources has not been important in evolution." This conclusion is not convincing, since there is no reason to assume that the parasite fauna satisfies the assumptions of the model (which was built for competing herbivores in a fractal landscape). Accordingly, even "competition ecologists" would not expect a fit to the packing rules. Rohde expects much from modern theories like the metabolic theory of ecology or Stephen Wolfram's "new kind of science." However, it did not become clear to me what these theories have to offer with respect to the competition debate. Rohde may be misguided by his belief that the metabolic theory "does not rely on equilibrium assumption." In contrast to this statement, adaptation, resource competition, and equilibrium considerations all play an important role in this theory.

Despite of its many deficiencies, *Nonequilibrium ecology* is a useful book providing much food for thought—even for ecologists considering selection and competition as factors of prime importance (like myself), it is healthy to be confronted with arguments and evidence to the contrary.

FRANZ J. WEISSING

*University of Groningen
Centre for Ecological and Evolutionary Studies
9751 NN Haren
The Netherlands
E-mail: f.j.weissing@rug.nl*