

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*