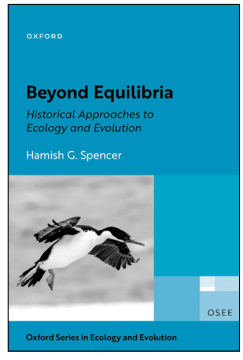
ECOLOGY

Beyond Equilibria: Historical Approaches to Ecology and Evolution. Oxford Series in Ecology and Evolution

By Hamish G. Spencer. 2025. Oxford University Press. 160 pages, 214.99 CAD, Hardcover, 84.99 CAD, Paper. Also available as an E-book.



Across the wide landscape of science publications, there are a few well-known formats. There is the easily digestible, but entertaining, popular science book. There is the dense, heavy, undergraduate introductory textbook. There is also the beautifully illustrated and text-light coffee-table book. Perhaps most rare is the small, technical, advanced research book. Such books are the stated intention of the Oxford Series in Ecology and Evolution. These books are focussed on single topics, most are under 200 pages, and all are definitely targetted at researchers or graduate students already familiar with the field. Each volume takes an idea and looks at it in-depth from many different angles and provides copious up-to-date references looking at a narrow set of questions (e.g., other Oxford University Press titles such as *Metapopulation Ecology* by Ilkka Hanski [1999], *Animal Signals* by John Maynard Smith and David Harper [2003], and *Mitonuclear Ecology* by Geoffrey E. Hill [2019]).

Beyond Equilibria by Hamish Spencer of the University of Otago is the latest entry in this series. The question at hand is that of equilibria as it relates to ecological and evolutionary modelling. For most theoretical approaches that we are taught about evolution and ecology, we are provided with mathematical equations that are used to model certain things. In most cases, Spencer argues, these model equations are based around the idea of some theoretical equilibrium state. Parallel to this process of modelling are the actual states that we observe in nature or in lab-generated situations. What Spencer proposes is that an emphasis on the equilibria described in model equations does not account for history and, therefore, does not effectively describe *in situ* observations.

For example, Lotka-Volterra equations give us a way to predict the population sizes of a predator species and a prey species in a natural environment. The equation uses carrying capacity and the impact that each species has on the other to predict the oscillating population sizes of each one over a long time frame. Regarding this idea, Spencer asks: How do we know at any given time whether those two populations are in equilibrium with each other? Are they truly oscillating between population sizes year-to-year? Furthermore, what would happen if there was a third or fourth species involved and how would they impact each other? Could long-term carrying capacities and population sizes be estimated in this situation? Spencer demonstrates, logically and mathematically, that this is not a simple set of questions to answer.

Spencer also looks at gene frequencies. With an estimated or calculated degree of heterozygote advantage, it is possible to model the equilibrium frequency of alleles in a population, accounting for things like selection and drift. Spencer asks: Does it matter the rate and order in which new alleles are introduced by mutation? Are the gene frequencies observed in a natural population already at equilibrium? If not, can we determine things like selection pressure? It is these sorts of questions that Spencer uses to propose nine different flavours of history that should be considered when looking at biological equilibria. The flavours are contingency, constraint, template, chance, chaos, capriciousness, approach, turnover, and construction, and he devotes a slim chapter to define and provide examples of each one.

Beyond Equilibria is not a book intended to introduce the general reader to ecology and evolution. This is an advanced book aimed at those who already know how to use models in biology. Subheadings like Constant Viability Selection at a Diploid Locus in an Infinite Population with Discrete Populations and the mathematical equations associated are imposing. Despite this, Spencer does an excellent job of presenting his case for including historical considerations in questions of ecology and evolution. Far from an attack on conventional modelling, this book is a brilliant little set of considerations for those that think 'model first' regarding biological questions. Rather like a billiard ball, *Beyond Equilibria* is small, dense, and could be used as an effective weapon (academically).

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