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A close-up look at adaptive radiation

The Ecology of Adaptive Radiation
by D. Schluter
Oxford University Press, 2000. £19.95 pbk (viii + 288 pages)
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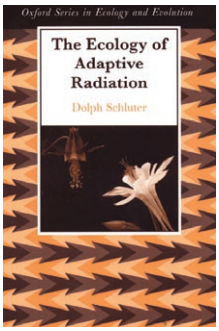

It has been said that, in each decade, one book stands out in terms of its influence on the field of evolutionary biology. The instructor from whom I learned evolution taught that in the 1960s, it was G.C. Williams' *Adaptation and Natural Selection*[1], in the 1970s, Richard Lewontin's *The Genetic Basis of Evolutionary Change*[2], and in the 1980s, John Endler's *Natural Selection in the Wild*[3]. Although one could quibble with the general thesis, no one can deny that each of these played a major role in focusing the mainstream of evolutionary thought. Although only one-year old, this decade might have already produced its member of this pantheon: Dolph Schluter's *The Ecology of Adaptive Radiation*.

Ever since the Modern Synthesis, adaptive radiation has been one of the central concepts of evolutionary biology. Surprisingly, however, the last synthetic treatment of the topic was G.G. Simpson's 1953 classic *The Major Features of Evolution*[4]. Defining adaptive radiation as 'the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage,' Schluter evaluates the progress made over the last half century in understanding the underlying processes of adaptive radiation. Specifically, he investigates what he terms the 'ecological theory' of adaptive radiation, the idea that 'adaptive radiation – phenotypic divergence as well as speciation – is ultimately the outcome of divergent natural selection stemming from environments, resources and resource competition'.

This is not the book that many would write on adaptive radiation. Most of the classic cases of adaptive radiation, for example, the Cambrian explosion, early Tertiary mammals and Australian marsupials, receive little attention. Rather than focusing on broad-scale patterns, Schluter is concerned with mechanisms, and that requires examination of more recent evolutionary events, at lower taxonomic levels, where evidence of evolutionary processes can be detected more clearly. He specifically examines what he identifies as the three main processes of the ecological theory: phenotypic divergence driven by adaptation to different environments and resources; phenotypic divergence driven by interspecific competition; and speciation driven by the same processes that drive ecological and phenotypic divergence ('ecological speciation').

Two features distinguish Schluter's treatment of these hypotheses. First is the depth in which each idea is explored. For example, few would doubt that adaptation to different environments is a means by which lineages diverge, but Schluter's review is exhaustive, not only reporting examples from the literature, but critically evaluating each case study, sometimes even reanalyzing data. His central thesis, that divergent adaptation to different niches implies tradeoffs and the existence of an adaptive valley separating adaptive peaks, is strongly supported, although some examples provide stronger support than do others. Similarly, Schluter's treatment of character displacement is easily the most authoritative yet published; few will come away from this book with doubts about the ability of resource competition to drive divergent evolution. Finally, the review of ecological speciation is thorough, highlighting what we know and what remains to be learned.

Even more significant, however, is the second aspect of Schluter's approach: the development of new ways to look at old ideas, as well as the derivation of entirely new conceptual approaches. The book is chockfull of such nuggets. For example: that adaptive radiations are initiated usually by specialists; that character displacement and, thus, adaptive radiation might involve processes other than interspecific competition (the existence of adaptive radiations encompassing multiple trophic levels is highly suggestive here); that adaptive radiation might be triggered by an increase in the rate of speciation, which provides the fodder for adaptive diversification (thus explaining the role that sexual selection might have in adaptive radiation, as well as indicating that clade-level traits might be associated with adaptive radiation because of their effects on speciation rather than on ecological opportunity); that genetic drift can lead to adaptive radiation if species move randomly along an adaptive ridge; and that the direction of adaptive radiation might be shaped by the genetic architecture of the ancestral species.

What is particularly significant is that these ideas are not only formulated conceptually, but are also tested empirically; Schluter manages to find and analyze whatever data are available to examine his hypotheses. In doing so, he often is obliged to develop new analytical methods or extend previous ones in novel ways. (For example, his treatment of the hypotheses that adaptive radiation is characterized first by divergence in habitat use and, only later by divergence on other resource axes; and that rates of speciation are higher in insular taxa than in related mainland clades).

In this way, *The Ecology of Adaptive Radiation* is reminiscent of another book that made an indelible mark, not only by advancing an important main thesis, but also by developing related ideas that, in their own right, formed the basis of decades of research and theoretical development: MacArthur and Wilson's *The Theory of Island Biogeography*[5]. High praise, indeed, and a high standard by which to judge any book, but Schluter's work might be up to it. Needless to say, this book will make an excellent anchor for graduate seminars. More importantly, it will lead to new avenues of research and new ways of thinking about adaptive radiation.

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The 'how-to' book of ecosystem study

Methods in Ecosystem Science
edited by O.E. Sala, R.B. Jackson, H.A. Mooney and R.W. Howarth
Springer-Verlag, 2000. £41.00 pbk (xxii + 421 pages)
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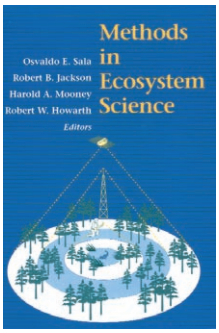

Although ecosystem-level approaches to studying ecology date back to the 19th century at least, and there was already a large body of established literature in this area 30 years ago[1], the study of ecosystems has gained new momentum over the past decade. There are two reasons for this. First, there has been an increasing recognition that some of the most interesting ecological questions occur at the intersection of population- and ecosystem-level ecology[2,3], for example, in relation to what species do in ecosystems[4], and how biodiversity might influence ecosystem functioning[5]. Second, it is increasingly appreciated that an improved understanding of the consequences for the ecology of the earth of human-induced global change phenomena (e.g. CO_2 enrichment, nitrogen deposition, climate change, land use change and globalization of the biota of the earth) is achieved best through an ecosystem-level approach. As a result, large international networks have been formed, such as 'Global Change and Terrestrial Ecosystems' (GCTE) and a new journal (*Ecosystems*), devoted entirely to ecosystem-level research, was launched in 1998.

Any approach to ecosystem-level ecology is inherently multidisciplinary, and requires practitioners with a broad range of knowledge and skills. It can incorporate elements of climatology, hydrology, atmospheric science, physiology and community ecology. Despite the increasing popularity of ecosystem-level research, however, the methodologies needed to study ecosystems are spread very diffusely throughout the published literature. This creates obvious difficulties for any ecologist attempting to initiate new work on ecosystem-related topics, because this first requires searching this literature for guidance as to what methods are available for addressing the particular question, as well as their relative merits. For this reason, this book is extremely timely and is, indeed, one of the most useful books on ecosystems to appear in the past decade, because it brings this literature together in a remarkably succinct manner.

This book is wide ranging and contains chapters written by established authorities in a diverse range of topics, from climate manipulation to acidification of lakes, fertilization experiments to gas exchange, and stable isotopes to productivity and decomposition. Each chapter reviews the methodology of a given topic, the pros and cons of different approaches, useful tips on applying the methods and a list of appropriate literature. The odd chapter is a bit superficial but, on balance, the chapters are of consistently high quality, clearly presented, easy to follow, thorough and comprehensive. Given the very broad range of approaches that are relevant for studying ecosystems, it would not be possible to cover all of them in a book of this length. For example, the editors freely admit that 'description of the manipulations of nutrients in terrestrial ecosystems does not have an aquatic counterpart in this book, and the analysis of animal manipulations belowground lacks a counterpart of aboveground manipulations'. A book such as this will, however, probably become an evolving document, and subsequent editions would no doubt include new chapters based on reader feedback about the current edition. One aspect that could feature more prominently involves mini-ecosystem approaches to ecosystem-level ecology; the book as it stands is geared mostly towards field ecologists, whereas some of the most interesting recent insights into understanding how ecosystems function have emerged from microcosm and mesocosm studies[6,7].

Probably the only criticism I have of this book is its heavy North American slant in some places. Eighteen of the 22 chapters are written by authors in the USA and, although several of these authors provide excellent global syntheses of the literature, others do not. There are instances in which only American literature is cited, even on topics in which European ecologists have arguably made the greatest contribution and, indeed, in one chapter, 92% of the cited references that I recognized were sourced from the USA (with half the remainder being Canadian). This is unfortunate, because, in these instances, the reader is not always being directed to the most useful literature on the topic.

This issue notwithstanding, this is a remarkably useful book, and those contemplating new ecosystem-level research projects will now have a compendium of relevant methods and literature to consult. Because the text is generally clearly written, it is accessible to research students as well as those with little background in the specific topics covered. I have little doubt that, in due course, any major laboratory involved in carrying out research at the ecosystem level will include a well-thumbed copy. Such a book has become increasingly timely and necessary as an increasing number of ecologists converge on the ecosystem as the unit of study.

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