

On the origin of reproductive isolation

Speciation. (2004). Edited by Jerry A. Coyne and H. Allen Orr. Sinauer Associates Inc. 545 pp. Paperback. £34.99. ISBN 0878930892

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Just as I started writing this review, the news came in that Ernst Mayr had passed away. The grand old man of speciation, who remained active until the very end, must have been pleased with the book by Jerry Coyne and Allen Orr when it appeared around the time of his 100th birthday last year. In many ways, it is a tribute to Mayr, who resuscitated speciation research after it had languished for three-quarters of a century between the publication of Darwin's *Origin* and the forging of the Neodarwinian Synthesis.

Let me say up front: I think *Speciation* is a great book. I can only shudder at the thought of the amount of work Coyne & Orr have done. In almost 500 tightly packed pages, they review, as the more than 1600 (!) references demonstrate, most of the relevant work on speciation since Darwin literally up to the present day. (The references contain many papers only published last year, and even a fair number that were still in press at the time of appearance of the book, a sign that the authors kept revising their work right up to the galley proof stage.)

It is also a unique book. Although the surge in interest in speciation of the past two decades has produced several edited volumes (Otte & Endler's *Speciation and Its Consequences* [1989]; Howard & Berlocher's *Endless Forms* [1998]), journal special issues (e.g. the July 2001 issue of *Trends in Ecology and Evolution*), and popular science books (my own *Frogs, Flies, and Dandelions* [2001]), not since Mayr's *Animal Species and Evolution* (1963) has anyone attempted an exhaustive review. Coyne & Orr's is an extremely valuable book and it will prove its worth in graduate student teaching for many years to come. It is also likely to leave an indelible mark in research, as the authors have gone to great lengths to point out where the gaps in our knowledge lie, and what kinds of studies could fill these gaps.

In addition, it is a tough but stimulating and rewarding read. Coyne & Orr write in a clear and lively style and, in between conceptually complex arguments, allow themselves occasional blips of humour. In spite of the book's 475 pages of text, they keep a close watch on conciseness, and nowhere did I get

the feeling a subject was being dealt with at too great a length. The production of the book is decent, although the complex hierarchy of some chapters would have been easier to follow if the editor had not used a confusing mix of different styles of heading. Also, systematists may cringe at the rather frequent misspelling of common and scientific species names.

Nit-picking aside, I think *Speciation* is a wonderful accomplishment. It could, however, have been even more wonderful. Until the early 1980s, mainstream speciation biology (as put in place by Mayr and Dobzhansky) held that species are reproductively isolated populations, arising by more or less random genetic changes that accumulate after these populations become geographically isolated. Since then, however, data have appeared that show that (1) natural and sexual selection, rather than drift, are the driving forces for the evolutionary change leading to speciation; (2) selection is often strong enough for speciation to happen, even if populations initially remain connected by gene flow.

Some (myself included; *BioEssays*, 22:1134–1141 [2000]) have argued that, rather than being a refinement of the Mayrian programme, these new insights require a conceptual revolution of speciation research. Speciation with gene flow means that species can retain their identity in spite of incomplete reproductive isolation. The Biological Species Concept (BSC) is therefore no longer valid. Also, if selection is the force that results in reproductive isolation, then our understanding of speciation might be better served by focusing more on the selective processes, rather than only on understanding the isolation itself.

Coyne & Orr acknowledge both the importance of selection and its power to overcome gene flow between incipient or established species. They list the many empirical and theoretical reasons why the early enthusiasm for neutral divergence (the peripatric, founder-flush, and transience models) can no longer be justified. They also review the data that reveal the signature of selection in speciation. Yet the book continues to adhere, here and there somewhat fiercely, to the original Mayrian programme, summed up as follows (p. 32): "In our view, then, reproductive isolation is the proper focus for the study of speciation. In fact, we can hardly imagine writing a substantive book on speciation using any concept other than the BSC."

Rather than choosing a different vantage point, Coyne & Orr have decided to shoehorn the recent insights into the "classical" line of speciation research. They adopt a relaxed version of the BSC that requires "substantial but not necessarily complete reproductive isolation" (p. 30). They replace the misnomer "Reproductive Isolating Mechanisms" (RIMs) by the much better term of "isolating barriers", which may include things like disruptive ecological selection in sympatry. In addition, they incorporate parapatric speciation (where selection across an ecotone gradually splits a continuous population in two) into the realm of allopatric speciation, rather

than into that of sympatric speciation, where it was traditionally placed.

I doubt that this has been a wise decision. True, as the authors point out, most work on speciation has focused on reproductive isolation, rather than anything else. For example, all the experimental *Drosophila* studies, seeking to reproduce part of the speciation process in the laboratory, have used reproductive isolation as a criterion to evaluate the outcome of the experiments. An alternative approach would have required the book to be structured along the lines of the various kinds of selection and how these make populations diverge, including the positive feedback loops that result from reduced gene flow. Such an approach would have left several chapters almost empty, since, as Coyne & Orr point out, our knowledge in these areas is still very limited. About investigating how selection pleiotropically produces reproductive isolation, they even write: “Until recently, this important endeavor—the *real study of the origin of species*—has been largely neglected” (my italics).

By focusing on reproductive isolation, which is indeed a field in which great progress has been made, the book sometimes gives the impression that many of the problems of

speciation research have already been solved. Repeatedly, for example, allopatric speciation is considered the “uncontroversial” (p. 7) and “straightforward” (p. 387) “null-hypothesis” (p. 136), “so plausible that it hardly seems worth documenting” (p. 123). Yet just as frequently, the book highlights the many unknowns of this process in terms of the interplay between adaptation, sexual selection and reproductive isolation. My guess would be that future emphasis on these and other problems will have many surprises in store for all of us, including those who find allopatric speciation straightforward.

In spite of being slightly disappointed by the book’s emphasis (or perhaps because of this) I look forward to re-reading and debating it with my students. Coyne & Orr have done the field a great favour by synthesising so much research so comprehensively. I think the book will serve its purpose of teaching upcoming (and existing) generations of evolutionary biologists of what we do and do not know about speciation. It will literally be *the* point of reference for the next ten years.

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