



## NEW BIOLOGICAL BOOKS

The aim of this section is to give brief indications of the character, content, and cost of new books in the various fields of biology. More books are received by The Quarterly than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.

Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works. Unsigned brief notices, written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them. Regular reviews are more extensive evaluations and are signed by the reviewers. The longer lead reviews consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at Stony Brook University or other appropriate recipients.

The price in each case represents the publisher's suggested list price at the time the book is received for review, and is for purchase directly from the publisher.

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### EVOLUTION AND DOGMA

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A review of  
SPECIATION.

By Jerry A Coyne and H Allen Orr. *Sunderland (Massachusetts): Sinauer Associates*. \$89.95 (hardcover); \$54.95 (paper). xiii + 545 p + 2 pl; ill.; author and subject indexes. ISBN: 0-87893-091-4 (hc); 0-87893-089-2 (pb). 2004.

Speciation is a controversial topic. This controversy results from the inherent complexity that comes from studying a process rather than a single time event, and it permeates all aspects of the field. There is almost a religious fervor associated with opposing camps, and the acrimony of debate is palpable at times. However, it is this same clash of competing

ideas that presents an exceptionally exciting arena for performing research. I say, "*vive la différence!*" and I do not think I am alone in expressing this sentiment. The recognition that there is room for pluralism in speciation studies has been gaining acceptance over the last 15 years. Research has revealed a multitude of evolutionary forces involved in divergence, and no longer does a single mechanism or mode of speciation reign supreme. *Speciation* by Coyne and Orr is not an ecumenical book in this regard. The authors take the stance that to include any notion of pluralism would be to admit defeat. The end result is a volume that is polemical, but not dialogic. In short, *Speciation* is simply dogmatic.

The main take-home message of the book is that speciation is most often driven by natural selection occurring in allopatry to yield species that are reproductively isolated from each other. The tone of the volume is rather disparaging toward ideas that challenge this orthodoxy, and the burden of proof rests disproportionately on the shoulders of those researchers who deviate from this norm. Allopatry and natural selection are deemed the null expectations against which everything else is to be judged. If tests prove to be ambiguous, then allopatry and natural selection are declared the undisputed winners. In the end, Coyne and Orr would have you believe that to think speciation may occur by any other means would be absurd—e.g., “[a]llopatric speciation appears so plausible that it hardly seems worth documenting” (p 123). To perform research outside their paradigm would seem to be downright foolhardy—e.g., “[i]n sum, the evidence for sympatric speciation is still scant . . . it is hard to see how the data at hand can justify the current wave of enthusiasm for sympatric speciation” (p 178). What is particularly disturbing is that proof of strict allopatry, or even the exclusive role of natural selection, is also lacking and is not given the same critical treatment in the book because they are both considered so obvious—e.g., “[w]e have very little mathematical theory describing how indirect selection in allopatry drives speciation. . . . [S]peciation by selection in allopatry is conceptually straightforward and little mathematics is required” (p 387). If the same strict criteria were applied to these ideas, they too would reveal shortcomings of their own. The authors’ support appears to be based more on intuition and familiarity than on empirical rigor.

Coyne and Orr define species by employing a relaxed version of the Biological Species Concept (BSC) that allows for some gene flow. Speciation then simply becomes the evolution of reproductive isolating barriers. The rest of the text that follows requires one to view species and speciation from this single standpoint. Many evolutionary biologists are comfortable with this approach (and I use it in my own research), but there is no getting around the fact that adopting this species concept does lead to some odd predicaments,

and even contradictions, that are readily apparent in this volume. For example, in allopatry, species remain undefined by the BSC because they are not in contact. Yet, Coyne and Orr claim that most speciation occurs in allopatry. Logically, you cannot have it both ways (i.e., you cannot have the most common geographical mode of speciation lead to species groups that remain undefined within that context). Taking their definition of speciation to heart should actually encourage researchers to direct their programs more toward studying cases of sympatry and parapatry, where isolating barriers are more readily detected and the evolutionary forces driving them can be directly tested. In practice, the authors admit to resorting to genotypic, phylogenetic, and morphological criteria to define species boundaries in allopatry because of this difficulty, but, in doing so, they erode the distinctions they have made between their relaxed BSC and competing ideas. Asexual organisms or even organisms that have both sexual and asexual modes of reproduction fall outside the realm of speciation studies altogether within their framework, but can be easily accommodated if other species concepts are applied (e.g., the cohesion species concept or genotypic clustering), making it clear that Coyne and Orr’s treatment of speciation represents only a particular subset of the entire field.

Although it has traditionally been done this way, defining speciation solely in terms of geographical parameters is not as straightforward or as useful as the authors would lead one to believe. Because most speciation requires time, geographical designations can, and often do, shift during the course of divergence. They recognize this fact and devise new geographical designations that only exacerbate the problem, such as para-allopatry and allo-sympatry. In reality, strict allopatry (where gene exchange between two diverging populations is equal to zero) during the entire course of speciation may be less common than Coyne and Orr indicate, especially if identifying “which reproductive barriers were involved in the *initial* reduction of gene flow between populations” (p 57) is the main goal of speciation studies. Because the Isthmus of Panama—their prime example of allopatric

speciation (pp 92–93)—took a long time to form while being subjected to numerous sea level fluctuations, it is likely that some *initial* divergence between populations on either side of the Isthmus occurred while gene flow was low, but not necessarily zero. This situation would then be considered a case of parapatric speciation by their strict definition. Obviously, it is much too difficult to determine the initial cause of reduced gene flow so precisely in most circumstances to make a definitive judgment about the geographical context in which the critical phase of divergence may have actually occurred. To that end, declaring initial divergence to be most critical in all of speciation is also too restrictive. It could be just as easily argued that later phases (e.g., those that operate during reinforcement) are more important because they involve evolution reaching a point of no return, which may be more relevant to understanding the process of generating new species than innumerable false starts. At the opposite end of the spectrum, Coyne and Orr define sympatric speciation as occurring only when diverging populations freely exchange genes. Strict sympatry in this sense is also uncommon, leaving parapatry (which includes everything else) by default as the most common mode of speciation. Therefore, geography as defined by allopatry, parapatry, and sympatry becomes relatively meaningless to the study of speciation. A more innovative approach would be to measure the relative contributions of different evolutionary forces to the process of speciation to explore the scope of their applicability under different geographical scenarios (which is what most researchers are actually doing in the field). In almost all cases, the process of speciation cannot be reduced to a single, all-important element, nor should it be.

The discussion of selection versus drift (Chapter 11) is the worst in all respects, and the best example of what is wrong with this book. The debate is presented as drift *or* natural selection acting in isolation. Yet, the two need not be mutually exclusive. It is clearly not an either/or situation. This topic is made needlessly polemical when presented in this polarized manner, and merely echoes the cross-purpose arguments that have plagued

the ongoing Fisher-Wright controversy (see Skipper 2002). In conclusion, Coyne and Orr regard drift as being completely irrelevant to all speciation. Nevertheless, I say there is plenty of room to investigate how drift working in conjunction with natural or sexual selection may be qualitatively different than natural selection operating alone during speciation. The authors admit that models of speciation that incorporate the action of drift work when translated into mathematics, yet still dismiss the role drift may play in the process because these mathematical models seem unnecessary when compared to adaptive ones: “Thus, although one of the standard objections to founder effect models—that they do not work when translated into mathematics—now appears incorrect, the *other* standard objection—that the models seem unnecessary when compared to adaptive ones—still carries some weight” (p 398). Detailed models of selection-based speciation are never presented because they are deemed too obvious (p 387). Once again, natural selection is presented as the null expectation with the burden of proof resting squarely on drift.

Although the treatment of some material in the book (namely, sympatric speciation, reinforcement, and the role of drift in speciation) is disappointing, the majority of the volume does deserve high praise. One highlight is the treatment of the genetics of reproductive isolation. Coyne and Orr are truly in their element and have produced a summary that exhibits the wisdom of researchers who have been in the field for a long time. It is also the one place they allow a little bit of pluralism (albeit begrudgingly) by concluding that multiple genetic mechanisms are responsible for Haldane’s rule: “After two decades of intensive study, a consensus has emerged that two forces, dominance and faster-male evolution, cause Haldane’s rule” (p 298). A real effort was made to admit that a single explanation for Haldane’s rule is not appropriate, although Coyne and Orr still feel compelled to give dominance the upper hand: “One of these forces—dominance—differs from the others in several ways. First, only dominance can explain Haldane’s rule

for hybrid sterility *and* inviability and in taxa with heterogametic males or females. Second, several of the other theories rely, in one way or another, on dominance. . . . One could argue, therefore, that dominance plays a more fundamental role in Haldane's rule than the other theories" (p 298). This last point illustrates the general style of argument used throughout the text that makes the book read more dogmatic than need be, missing the opportunity to be truly synthetic.

Regardless of the criticisms above, *Speciation* is most certainly an important and timely publication. Coyne and Orr present an encyclopedic compendium of knowledge about species and speciation that surpasses many current textbooks. Recent revitalization of the field has been spurred by our ability to gain greater genetic detail for more organisms than ever before. This book is a very im-

pressive summary of this vast and complicated literature. *Speciation* is thought provoking to say the least. One may not always agree with the interpretations the authors present, but this book is definitely required reading for anyone serious about the study of speciation, and will inspire new research in the area, if only (as Coyne and Orr presciently point out on page 6) to prove them wrong. I have no doubt this book will be cited widely and often. It is the first book I have seen on the topic of speciation in recent years that will rightfully join the ranks of Mayr's *Animal Species and Evolution* (1963) and Dobzhansky's *Genetics and the Origin of Species* (1951). The fact that *Speciation* is so clearly conceived from a single point of view leaves the door open for alternative perspective pieces to be written. Let us just hope this book does not become the final word on the subject.

#### REFERENCES

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