

How and Why Species Multiply

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How and Why Species Multiply.—Peter R. Grant and B. Rosemary Grant. 2008. Princeton University Press, Princeton, New Jersey. 272 pp., 31 color plates, 46 text figures, 3 tables. ISBN 978-0-691-13360-7. Cloth, \$35.00.—With only 14 species, Darwin's finches seem like unusual candidates for superstar status in the world of evolutionary biology. The diversity of the group pales in comparison with other celebrated evolutionary radiations, such as East African cichlids or Caribbean lizards in the genus *Anolis*. Yet these drab, diminutive birds with curious beaks have contributed immensely to our understanding of evolutionary diversification.

How and Why Species Multiply provides a fascinating window into the radiation of the finches and places results both old and new firmly in the context of modern evolutionary biology. With more than three decades of field research on the birds behind them, the Grants' expertise here is unparalleled. I thoroughly enjoyed reading the book and found it very well written and engaging. The book is both short (167 pages, excluding indices and other back-of-book material) and accessible; the authors have done an excellent job of conveying even complex topics with minimal jargon. The 31 pages of color plates are very effective at communicating both the diversity and ecology of the finches as well as the ecological theater of the Galápagos Islands.

The accessibility of the book makes it highly appropriate for students, and I would recommend it as an accompaniment to any undergraduate evolution course. The book is essentially a romp through the landscape of modern evolutionary biology, and the Grants touch on an impressive number of conceptual themes. Enough detail is provided for the reader to grasp the core ideas, but not so much that there is a risk of becoming bogged in technical nuances. The reader will be struck by the diversity of hypotheses that the Grants have been able to test using data from their longterm studies of the finches of a single tiny island. The finches have been especially useful as a case study of adaptation in the wild and as a model for understanding the initial stages of speciation, and the book treats both of these topics at length.

Much of what we have learned about Darwin's finches falls squarely within the framework of the prevailing evolutionary paradigm, typically referred to as the "Modern Synthesis." This is essentially the world according to evolutionary genetics: genetic variation arises, dispersal redistributes variation among populations, and genetic drift and natural selection mediate changes in gene frequencies within populations. But there is a growing sense among some evolutionary biologists that this body of theory is incomplete or that it fails to address some of the most striking features of the natural world (Pigliucci 2007). I most enjoyed *How and Why Species Multiply* when the authors raised several major questions that typically fall outside the boundaries of the Modern Synthesis. This is where the book is at its best, and where the clarity and conciseness of the writing has the potential to have the greatest impact by making it very clear that we are nowhere near solving some of the most important mysteries of evolutionary biology.

I will give two examples. The first is the idea that a comprehensive theory of evolution must be as much a theory of phenotypes as a theory of genes within populations. The latter is mostly what we have today, yet the origins of strikingly novel traits (e.g., the turtle's carapace, feathers in theropod dinosaurs, echolocation in bats) remain shrouded in mystery. Surely the origin of this variation is itself an important evolutionary question. As the Grants and collaborators have shown (e.g., Abzhanov et al. 2004), and as is discussed in the book, we are coming close to understanding this fascinating piece of the evolutionary puzzle in finches. It is one thing to understand the fitness consequences of variation in beak morphology, and quite another to understand the developmental genetic basis for differences in beaks among finch species. Yet here we may be converging on precisely this level of explanation, and it was exciting to see these results capping the chapter on natural selection.

The second major challenge, elegantly discussed in the final chapters, is to explain why-uniquely among groups of birds that have arrived and persisted in the Galápagos-only the finches have undergone extensive speciation and ecological divergence. I think that this issue has profound consequences for the way we think about evolution, because it forces us to ask whether a "genes in populations" view of evolution really can account for all major features of biological diversity. What is it about being a finch that predisposed this lineage to adaptive radiation? In this respect, the finches are a well-studied but hardly unique example, and even a casual survey of biological diversity reveals that evolutionary radiations differ dramatically in terms of outcomes. Similar patterns are seen in the Hawaiian Islands, where four of five songbird groups failed to radiate (Lovette et al. 2002). Even very closely related organisms show these disparate evolutionary outcomes. For example, most groups of Australian scincid lizards have not radiated, but a single lineage underwent a massive burst of diversification and today comprises nearly 200 species (Rabosky et al. 2007). All else being equal, diverse groups of organisms are more likely to persist over geological time-scales, because less-diverse groups can be wiped out by only a handful of species extinctions. And we are beginning to realize that traits that predispose lineages to radiate can become more frequent over time precisely because high diversity may confer resistance to extinction. These sorts of patterns simply cannot be extrapolated from an understanding of the relative fitness of alleles within populations (Coyne and Orr 2004, Jablonski 2008).

The chapter on the stages of adaptive radiation (chapter 12) may leave some readers a bit puzzled, in part because they may have something rather different in mind when they think of the "stages" of evolutionary radiations (e.g., Streelman and Danley 2003). In the preceding chapters, the Grants have set the stage nicely for a discussion of the macroevolutionary implications of the finch system, particularly with respect to how adaptive radiation occurs and why some groups radiate and others do not. But despite raising these issues, they don't take these ideas as far as they could, and the book concludes with a firm step back into the more familiar territory of the Modern Synthesis. The chapter is largely a review of the genetics of speciation on a level that is so mechanistic that it seemed somewhat disconnected from the previous two chapters. Clearly, the genetics of speciation is an interesting topic, but it answers the question of "how does reproductive isolation evolve?" and only tangentially addresses "how and why do species multiply?" These are not the same: the former emphasizes the genetic consequences of individuals choosing to mate or not to mate with other individuals, and the latter is really a question about why speciation rates are what they are and why they vary between clades.

On the whole, this is an excellent and thought-provoking work. One of the greatest strengths of the book is that the authors never lose focus on either evolution or the finches. This strong organism-centered approach to evolution, combined with a wealth of interesting detail about the history and ecology of the islands, ensures that this book will be of interest to a broad range of readers.—DANIEL L. RABOSKY, *Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853, USA. E-mail: dlr32@cornell.edu*

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