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Evolution's Wedge: Competition and the Origins of Diversity

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degree of control over the structure and stability of a food web" (p. 236; also see Paine 1966), and to the theory of island biogeography championed by MacArthur and Wilson (1967). I also enjoyed the interesting discussion about the different definitions of *stability* from the dynamic perspective in this section.

In reading *Energetic Food Webs*, I found the number of typos a bit annoying. I also found some mistakes in the treatment of consumer functional responses and was surprised that some key references were missing. A concluding chapter boasting a broad perspective, similar to that of the book's opening chapter, would have helped tie the loose ends together. In addition, for some readers, getting lost in technical details is a danger throughout the bulk of the book. Putting some of this detail into an appendix would have improved the book's readability. A final drawback to this volume is that even the paperback version is expensive, despite having no color illustration. However, postgraduate students and researchers interested in food webs should be happy to see the publication of this book, as I am, because there are not many such thorough treatments of this topic available.

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CAUSES AND CONSEQUENCES OF CHARACTER DISPLACEMENT

Evolution's Wedge: Competition and the Origins of Diversity. David W. Pfennig and Karin S. Pfennig. University of California Press, 2012. 320 pp., illus. $75.00 (ISBN 9780520274181 cloth).

The astonishing variety of life on Earth continues to inspire biologists in their search for explanations of the origins and maintenance of diversity. In *Evolution's Wedge: Competition and the Origins of Diversity*, authors David and Karin Pfennig (both at the University of North Carolina, Chapel Hill) synthesize and speculate on one such explanation: Competition among species is the dominant driving force in the divergence of lineages over evolutionary time, and this process of character displacement is ultimately responsible for many of the major features of biodiversity.

Competition was, of course, central to Darwin's (2009 [1859]) theory of evolution by natural selection. His well-known metaphor is an inspiration for this book's title: "The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards with incessant blows, sometimes one wedge being struck, and then another with greater force" (p. 67). Despite this idea's long heritage, our understanding of how competition drives evolutionary diversification remains limited. It is this void that *Evolution's Wedge* aims to fill.

Synthesizing such a diverse theme within a single book is an ambitious task, but the authors are well placed to tackle it. Through a series of careful observations and experiments over the last decade, the Pfennigs have revealed, in unusual detail, the complex unfolding of character displacement between two species of spadefoot toads, *Spea multiplicata* and *Spea bombifrons*, in the southwestern United States (Pfennig and Murphy 2003). This research provides one of the best-documented cases of character displacement in the wild, thus making the authors leading authorities on how biotic interactions shape evolution. Their natural-history perspective is reflected throughout the book through the use of detailed case studies to illustrate key concepts and arguments.

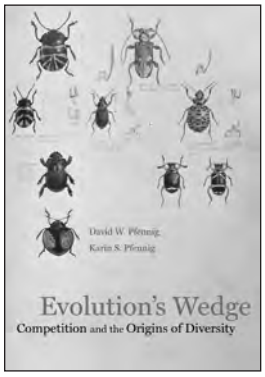
Since Brown and Wilson (1956) coined the term, *character displacement* has often become synonymous with a geographical pattern in which ecological or reproductive traits differ to a greater extent where species co-occur (*sympatry*) than where they do not (*allopatry*). However, the Pfennigs stress that *character displacement* is not simply a pattern but a process, defined as "trait evolution that arises as an adaptive response to resource competition or deleterious reproductive interactions between species" (p. 24). Moreover, they argue for a broader view of the term than is typically appreciated—one that includes not only trait divergence and convergence but also specialization and *escalation* (increased competitive ability). The decision to lump these different evolutionary trajectories under one label could generate some semantic debate. I found this more-inclusive definition to be enlightening, however; it should encourage a more holistic view of the role of competition in evolution.

Evolution's Wedge begins with an outline of the approaches used to study character displacement and the criteria required to demonstrate its occurrence. A more formal review of the evidence might have strengthened the book, although this kind of overview has admittedly been done elsewhere (Schluter 2000, Stuart and Losos 2013). Instead, the authors work from the knowledge that because character displacement has been demonstrated, what is now needed is an in-depth treatment of its causes and possible consequences. The book is divided into two broad sections that reflect these major goals.

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The first section burrows down into the process of character displacement, starting with a clear exposition of both the ecological and the reproductive aspects of the process. Although these have generally been treated in isolation, the authors point out that both are based on competition (for resources and for mates, respectively), and they therefore have similar causes and consequences. Furthermore, these two forms of evolutionary adjustment may often interact, one either facilitating or impeding the action of the other. Indeed, the importance of this close coupling of ecological and reproductive character displacement is a major theme of the book.



The authors also delve into other—perhaps less widely appreciated—facets of character displacement, including the generation of intraspecific variation and the role of phenotypic plasticity. They suggest that, although character displacement is usually reserved for allelic differences among species, environmentally induced shifts (e.g., the avoidance of a flower by a pollinator in the presence of a more aggressive competitor) may also constitute character displacement if variation in plasticity has a genetic basis and has evolved in response to competition. They further argue that, even when those conditions are not met, plasticity may nevertheless be an important step in initiating the process by facilitating coexistence and thus allowing initial facultative differences between species to become genetically assimilated (the *plasticity-first hypothesis*). The Pfennigs have a knack for presenting these somewhat complex ideas in a clear and simple way. I found these chapters to be extremely useful; for me, they were a highlight of the book.

The remainder of *Evolution's Wedge* is devoted to exploring the many possible ramifications of character displacement on biological diversity and on the structure of ecological communities. This section raises a number of thought-provoking ideas. For example, the authors suggest that, whereas the displacement or narrowing of species niches in response to competition can promote coexistence, it may also potentially drive species down an evolutionary blind alley that ultimately ends in their extinction. Both synthesis and speculation characterize these chapters, which focus on the potential role of character displacement in sexual selection, speciation, and macroevolutionary dynamics—how it may explain rapid bursts of speciation, patterns of adaptive radiation, and even the long-term evolutionary trend toward increased body size and complexity.

In addition to being enjoyable to read, *Evolution's Wedge* is an expansive discussion that highlights how little we know about the importance of competition in guiding evolutionary diversification. In the final chapter, the authors expose what they regard as the major unsolved problems with character displacement. As they point out, many of the topics discussed throughout the book concern patterns and processes of evolution that could arise from character displacement. Ascertaining whether character displacement actually is responsible for these patterns and processes remains the key challenge. As a result, the book does not provide a resolution to the debate regarding the importance of interspecific competition as a guiding force in evolution (Stuart and Losos 2013). However, by synthesizing current knowledge from across what have been largely disparate disciplines and by moving beyond old debates, the book will direct and inspire future research toward this goal.

There are few, if any, books that have been written on ecology and evolution that do not mention competition, but the number of volumes devoted solely to this subject is equally rare, and none has attempted such a broad ecological and evolutionary synthesis as has been done here. *Evolution's Wedge* will therefore serve as a valuable resource for any student or established researcher with an interest in Earth's biological diversity.

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