doi:10.1111/evo.12282

THE UNIFYING WEDGE

Yoel Stuart,[1] Daniel Bolnick,[1,2] and Robin Hopkins[1]

[1]*Department of Integrative Biology, One University Station C0990, University of Texas at Austin, Austin, Texas 78712*

[2]*E-mail: danbolnick@austin.utexas.edu*

Received September 24, 2013
Accepted September 25, 2013

Review of: Pfennig, D. W., and K. S. Pfennig. 2012. *Evolution's Wedge: Competition and the Origins of Diversity*. University of California Press, Berkeley. 303 pgs.

The idea that ecology and evolution can influence each other simultaneously in a feedback loop has become the lynchpin of the new field of eco-evolutionary dynamics (Pelletier et al. 2009). However, under a different name, eco-evolutionary dynamics is actually a venerable idea. Biologists, starting with Darwin (1859) and later Brown and Wilson (1956), have long recognized that competitive interactions between species lead to evolutionary divergence that facilitates coexistence, an eco-evolutionary process known as character displacement. Despite all the attention lavished on eco-evolutionary feedbacks in recent years, character displacement is often neglected. This neglect likely reflects an uneasy combination of over-familiarity (hasn't it all been done many times over?) and a lingering skepticism after rancorous debates over ecological character displacement and reinforcement.

With renewed interest in eco-evolutionary feedbacks, it is time for a synthetic review to resuscitate the original eco-evolutionary process. Pfennig and Pfennig (2012), who have produced a series of elegant touchstone studies on both ecological and reproductive character displacement in spadefoot toads (*Spea*), are ideally qualified to write such a review. With *Evolution's Wedge: Competition and the Origins of Diversity (2012)*, they have succeeded.

The book posits that competition is a ubiquitous ecological process and that competition's consequence, character displacement, is an evolutionary wedge that generates biodiversity. Pfennig and Pfennig argue that this wedge provides a unifying theory for fundamental questions throughout evolutionary biology and ecology.

In the first chapter, Pfennig and Pfennig cover the basics: definitions, alternative outcomes, and criteria for demonstrating character displacement. The subsequent three chapters provide thorough, and at times speculative, discussions of why, when, and how character displacement occurs. Although each section addresses reproductive and ecological character displacement separately, Pfennig and Pfennig also provide insightful discussions of how the two types of character displacement facilitate and impede evolution of the other. The second half of the book examines how character displacement influences other ecological and evolutionary patterns and processes, like the formation of intraspecies diversity, niche formation, community composition, sexual selection, speciation, and macroevolution.

Pfennig and Pfennig bring valuable perspective to aspects of character displacement that are usually overlooked. For example, they argue that phenotypic plasticity is a key component of character displacement. Plasticity can reveal cryptic genetic variation and consequently may delay competitive exclusion long enough for genetically canalized differences to evolve. Moreover, variation in plasticity itself can be heritable, and thus the strength of plasticity can evolve during character displacement. In addition, the authors attempt to dissolve the dichotomy between reproductive character displacement and reinforcement. Finally, the book includes many examples from the plant literature, something rarely done in the discussion of character displacement.

Evolution's Wedge is not an exhaustive summary of all relevant examples of each phenomenon discussed. Instead, Pfennig and Pfennig focus on historically important and iconic empirical examples with helpful diagrams to cover the essential concepts. The authors seem to have made a conscious decision not to discuss the extensive theoretical research on character displacement in detail. They often refer to general conclusions derived from mathematical models, but never discuss the mathematical details. Some readers may find the lack of equations inviting in a book primarily concerned with general concepts, whereas others may see this as an unfortunate missed opportunity to define and discuss

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

the evidence for character displacement in precise, unambiguous language, and miss the chance to examine details of the models and fuse them with empirical data.

We suspect many readers will pick up this book expecting to find answers and examples but few new questions. Character displacement is, after all, such a classic idea that surely most relevant research questions have been tackled. Instead, those looking for open research directions will be pleasantly surprised by how many gaps remain in our understanding of the causes, frequency, and effects of character displacement. In the final chapter of their book, Pfennig and Pfennig provide a lengthy summary of all that is unknown about the process of character displacement. Clearly, character displacement research is far from closed.

Pfennig and Pfennig nicely summarize the tumultuous history of character displacement, an idea that was wholly accepted at its inception, then vehemently rejected, but which has become widely accepted again today. Such oscillation in opinion can be partly blamed on character displacement sometimes being described as a pattern and sometimes as a process. Given the numerous examples of the pattern, conflation of pattern and process has led to the misconception that there is adequate understanding of the process. Therefore, we applaud the authors for providing, at the outset, a clear process-oriented working definition of character displacement: "*trait evolution* [a process] *that arises as an adaptive response to resource competition or deleterious reproductive interactions between species*" (p. 24). We lament, however, that Pfennig and Pfennig did not include other types of interactions that can also drive divergence (e.g., deleterious effects of shared predators or pathogens, interference competition, intraguild predation). Although these interactions sometimes carry the word "competition" (e.g., apparent competition via predators), lumping them all as competition stretches the use of that term beyond recognition.

In the spirit of the authors' explicit goal of unifying disparate fields in ecology and evolution, we suggest a more general definition: character displacement is the evolution of increased phenotypic distance between entities (species, populations, morphs or individuals), when three conditions are met: (1) the entities engage in mutually deleterious interactions; (2) this mutually deleterious interaction is mitigated by greater phenotypic distance between the entities; (3) as a result of (2) the entities are subject to divergent selection favoring increased phenotypic distance. Although resource competition and reproductive interference are common forms of deleterious interaction, our proposed definition need not specify an underlying ecological cause at the outset (e.g., resource competition), thus challenging researchers to test mechanism directly rather than assume one a priori, potentially revealing new insights into the process. This definition specifically highlights testable criteria that could guide research programs seeking to identify cases of character displacement, encompasses character displacement within and among populations and species, and accommodates asymmetry in the mutually deleterious interaction. Finally, our definition explicitly (and more traditionally) requires trait divergence rather than just trait evolution, meaning that character convergence and red-queen escalation are excluded (whereas in this book these processes are somewhat oddly lumped together under character displacement).

With their definition, Pfennig and Pfennig make the a priori assumption that competition for resources and reproduction is *the* source of biological diversity but spend surprisingly little time justifying the primacy of competition above all other biotic (e.g., mutualism, predation, and parasitism) and abiotic (e.g., temperature, aridity, altitude) factors. Pfennig and Pfennig gloss over extensive theoretical and empirical literature debating how and under what conditions competition is thought to deplete resources, change population carrying capacities, alter the relative fitness of individuals within populations, and drive competitive exclusion. The authors, it seems, just take competition as a given.

Yet, we suspect that making this a priori assumption was a carefully calculated measure. Given the turbulent history of competition in ecology, it does seem wise to decouple discussion of character displacement from this specific, controversial mechanism; Pfennig and Pfennig wield their assumption as a double-edged wedge and cut through the historical, theoretical, and empirical thicket presented by competition. This enables Pfennig and Pfennig to be intentionally provocative; in their own words, they try "throughout this book ... to emphasize open questions ... [ask] what *might* or *could* occur, because so little is known in some areas" (emphasis by the authors). They take a speculative approach to character displacement's role in evolutionary processes as broad as niche evolution, sexual selection, speciation, and macroevolution. This approach may be the strongest aspect of this book, turning Evolution's Wedge into a fount of testable predictions, intriguing hypotheses, and promising suggestions for future research. For one example that brings us full circle, Pfennig and Pfennig point out that few studies of character displacement subsequently examine the ecological consequences of character displacement, which in principle should alter population growth, dynamics, and persistence (i.e., the feedback to ecology in eco-evolutionary dynamics). In the end, some of the hypotheses put forward by Pfennig and Pfennig will likely be proved wrong, but we suspect that many more will be proved right. The lasting impact of the book will be the diversity and ambition of the hypotheses they suggest and the spurring of new research on character displacement. For that reason alone, Evolution's Wedge deserves its place on any evolutionary biologist's bookshelf. The book will make provocative reading for graduate seminars, in particular.

LITERATURE CITED

Brown, W. L., and E. O. Wilson. 1956. Character displacement. Syst. Zool. 5:49–64.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, Lond.

Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. Philos. Trans. R. Soc. B: Biol. Sci. 364:1483–1489.

Pfennig, D. W., and K. S. Pfennig. 2012. Evolution's Wedge: competition and the origins of diversity. University of California Press, Berkeley.

Associate Editor: M. Wade