ters, and the king) involved in the practice of natural history.

This well-documented and well-edited book demonstrates Spary's great knowledge of French Revolutionary sources (both manuscript and published) and the French language. The fresh and lively account in *Utopia's Garden* offers valuable perspectives on the shaping of natural history in late 18th-century France.

BOOKS: EVOLUTION

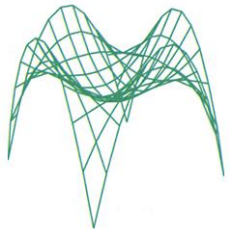
Holy Landscapes!

James Mallet

A number of intractable controversies in evolutionary biology date from the 1930s, and the topic of this book is one of them. Epistasis exists when the effects of substitution at one locus depend on alleles at other loci, so that genes interact in their effects on fitness. At first glance, it is hard to know what the fuss is about, because epistasis must be virtually universal. Every complex adaptation, such as the vertebrate eye or flight, always requires synergy among genes. Unfit hybrids between any pair of species also demonstrate epistasis because the genes causing sterility and inviability work just fine on their normal parental background.

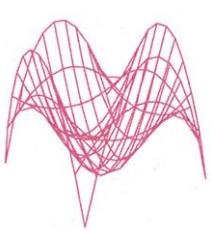
Epistasis and the Evolutionary Process
Jason B. Wolf, Edmund D. Brodie III, and Michael J. Wade, Eds.
Oxford University Press, New York, 2000. 344 pp. $85, £62.50. ISBN 0-19-512806-0.

The controversy is therefore not whether epistasis exists or is important, but about how it arises in evolution and whether it can throw additional light on other topics, such as molecular evolution or the evolution of sex. Classically, epistasis and other nonadditive effects are unimportant in the construction of adaptations: epistasis is noise, a mere "interaction term"; only the additive or "main effects" contribute to evolution by natural selection. Darwin used essentially this argument when he proposed advantages for each small step in the evolutionary construction of the vertebrate eye, and in 1930 Ronald A. Fisher formulated a quantitative genetic model of the same idea. Fisher's great rival, Sewall Wright, almost immediately proposed an alternative argument in which epistasis was crucial. Wright imagined a rugged "adaptive landscape," with multiple peaks representing high-fitness gene combinations. Classical additive evolution would get stuck on local adaptive hillocks and be unable to explore peaks of greater fitness. Wright's solution was his "shifting balance" theory, in which genetic drift, idiosyncratic selection, and spatial population structure allowed different adaptive combinations to be explored in different parts of a species' range. (Stated like this, who can deny that the shifting balance, in some form, is likely?)



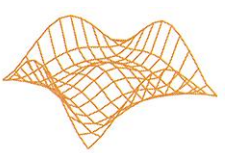
Curiously, *Epistasis and the Evolutionary Process* hardly covers the recent flurry of papers on the shifting balance, but instead explores newer topics. An excellent introductory chapter by P. Phillips, S. Otto, and M. Whitlock defines epistasis as a deviation from multiplicative (rather than additive) fitness as being the most natural measure and summarizes several of the book's main themes. In contrast, E. Brodie's introductory overview was spoiled for me perhaps because I am not a "Deadhead"; actual examples of epistasis such as in mimicry would have been more edifying than the analogy of Jerry Garcia's guitar music in different rock bands.

Among the theoretical chapters, I thought the discussion by J. Kelly about the buildup of linked epistatic modifiers particularly fascinating. Where a polymorphism is maintained by balancing selection, linked epistatic modifiers are expected to evolve; these can eventually produce a multiple-component, epistatic "supergene." The idea that the sex chromosomes characteristic of the heterogametic sex (such as the mammalian Y chromosome) degenerate over evolutionary time is an extreme example of this general argument. In contrast to classical and still unproved ideas about mimicry supergenes, Kelly's ideas do not require evolution of linkage, but merely the co-opting of variation in already linked elements. These ideas can explain some hitherto puzzling linkage disequilibria in molecular data such as the alcohol dehydrogenase (*Adh*) region of *Drosophila*.



Although a large part of the book is theoretical, I particularly enjoyed some of the empirical surveys. A. Templeton demonstrates epistasis in a variety of human genetic diseases, including some (such as sickle-cell anemia) classically termed "single-locus" polymorphisms. I also liked the evidence presented by S. Rice for interactions in morphology between vertebrate skull elements. A number of useful chapters demonstrate divergent exploration of adaptive peaks in spatially separated populations or species. The existence of epistatic peaks in the adaptive landscape is, however, unsurprising and neither confirms nor disproves the idea that epistasis contributed to their evolution, which could have proceeded via additive selection, ever upwards in a monotonic but "holey" adaptive landscape (to use Sergey Gavrilet's metaphor). The adaptive "holes" are revealed when populations are crossed to produce unfit hybrids, but they are not necessarily waystations in the divergence process.

In a chapter relevant to this question, L. Meffert reviews the well-known experiments on houseflies in which population bottlenecks caused increased additive genetic variance. She demonstrates that this is probably due to conversion of epistatic variance. Nonetheless, although the increase in additive variance may not be due to an increase in the frequency of simple recessive deleterious alleles as suggested by some critics of these experiments, epistatic and dominant effects are nonadditive interactions of a fundamentally similar kind. An increase in additive variance could simply reflect an increase in frequency of deleterious epistatic alleles, and would then be as irrelevant for adaptative progress as simple deleterious recessives.



One of the most interesting empirical chapters was M. Palopoli's review of the molecular interactions within meiotic driver systems, particularly the segregation distortion system in *Drosophila*. Segregation distortion is usually harmful and seems always to require tightly linked epistatic elements. As shown by A. Peters and C. Lively, recombination can be advantageous by breaking down genetic combinations deleterious to the organism as a whole. Thus, it is even possible that sex evolved primarily to police Mendelian segregation.

I learned a great deal from *Epistasis and the Evolutionary Process*, and I congratulate the editors on an excellent choice of authors. Graduate students and other scientists will find the book a very useful smorgasbord of recent research into theory and facts of epistasis. The volume does not attempt to resolve the 70-year-old controversy about the importance of epistasis and shifting balance. Instead, it shows that epistasis plays a central role in a much wider and more interesting variety of evolutionary problems than seemed possible even ten years ago.

SOURCE: J. CHEVERUD/WASHINGTON UNIVERSITY, ST. LOUIS

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