

Intergradations

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Hybrid Zones and the Evolutionary Process.
RICHARD G. HARRISON, Ed. Oxford University Press, New York, 1993. x, 364 pp., illus. \$65 or £45. Based on a symposium, College Park, MD, July 1990.

Interest in the causes and consequences of hybridization between genetically differentiated natural populations remains strong in evolutionary biology, both because new molecular and statistical methods make multifaceted studies feasible and because refinements in hybrid-zone theory now provide a richer perspective on thinking about fundamental issues of adaptation and speciation. This compilation provides a timely update on many theoretical issues and includes examples of long-term multidisciplinary studies.

The first four chapters review conceptual issues and practical concerns for field studies. Those unfamiliar with hybrid-zone issues will find chapters 2 through 4 useful. In chapter 2 Barton and Gale describe models used to estimate cline shape and width, linkage disequilibrium between unlinked markers, and the assumptions and limitations of each model and then show how the models are used to estimate the strength of selection maintaining a zone, the number of loci differing between hybridizing populations, dispersal rates, and the facility with which alleles introgress. A fundamental distinction is made between selection maintaining a zone due to extrinsic factors (where fitness varies along an environmen-

tal gradient) and the existence of a "tension" zone in which selection acts against hybrids (intrinsic).

In chapter 3, Howard provides a useful definition of reinforcement (that is, prezygotic barriers to gene exchange improved by natural selection in response to selection against hybridization) and a possible consequence, reproductive character displacement (RCD; a pattern of greater divergence

of an isolating trait in areas of sympatry and hybridization between closely related taxa than in areas of allopatry). Several theoretical objections have been raised regarding the importance of these processes, but most empirical studies cited as failing to support RCD were not originally designed to critically test reinforcement hypotheses.

The last chapter of this section (Rieseberg and Wendel) summarizes much of the literature on plant hybridization and suggests that many plant systems are suitable for studies of the transfer of adaptations once molecular markers have been linked to adaptively significant traits.

The remaining chapters summarize data on a variety of different hybrid zones that display a remarkable diversity of characteristics. Moore and Price describe an extremely broad, ecotonal contact on a continental scale between two subspecies of northern flicker (*Colaptes auratus*), whereas extremely narrow zones are described for two complexes of grasshoppers (*Caledia*, Shaw *et al.*; and *Chorthippus*, Hewitt) from Australia and Europe, respectively, several species of *Iris* from the southeastern United States (Arnold and Bennett), Amazonian butterflies of the genus *Heliconius* (Mallet), European toads of the genus *Bombina* (Szymura), European mice and shrews (*Mus* and

Sorex, Searle), and western North American gophers (*Geomys* and *Thomomys*, Patton). Of these narrow zones, *Bombina*, *Caledia*, *Chorthippus*, *Heliconius*, *Mus*, and *Sorex* form broad contacts several hundred kilometers in length, and many have been studied at multiple transects. Irises and gophers form very limited, patchy hybrid zones, but Arnold and Bennett show the advantages of plant systems for laboratory and transplant experiments. Patton emphasizes that several aspects of gopher demography (exclusive-use territories and polygynous mating systems) make them ideal for studies of how mating systems influence patterns of hybridization and introgression.

Most of these studies concentrate on determining what selective forces are acting to maintain a given zone and, for zones in which there is strong selection against hybrids, whether or not reinforcement might be operating. In many cases, either reinforcement appears not to be operating even with very strong post-mating isolation (*Caledia*) or evidence for it is limited despite seemingly ideal conditions (*Chorthippus*).

Clines for most characters studied are coincident and appear to be maintained by extrinsic factors favoring different genotypes in different habitats (*Colaptes*) or by intrinsic factors coupled with a strong habitat component (most others). The *Heliconius* zones involve a series of Mullerian mimetic morphs of several species, and their structure is unusual in having the dynamics of a tension zone (frequency-dependent selection operates against intermediate phenotypes), but this is due to an ecological agent (avian predators). Some of the *Mus* and *Sorex* chromosomal clines described by Searle are unusual in that they are distinctly noncoincident with each other and form a "staggered" pattern.

The book could have provided a better-integrated exposition of the value of placing process-oriented studies into a phylogenetic context; the matter is mentioned in several chapters, but nowhere is it fully developed. Nevertheless, this book deserves a wide audience; organismal biologists not familiar with hybrid-zone research will be surprised at the number of interrelated topics that require attention. For example, a great deal remains to be learned about the ethological, ecological, and demographic aspects of most hybrid zones, about the genetic basis for ecologically important morphological traits, and about communication signals and mate choice. At the molecular level, the development of new markers will permit more robust estimates of gene flow and facilitate multiple-gene tree comparisons, and causal mechanisms responsible for the generation of new alleles and chromosomal rearrangements in hybrid zones remain only superficially understood. For those with a

mathematical or statistical inclination, the extension of cline theory to describe noncoincident "staggered" clines and two-dimensional and small-sample cases, and a refinement of gene-flow estimators under a variety of different mating systems and selection regimes would repay further effort. This book should also stimulate investigators working on groups underrepresented in the hybrid-zone literature to undertake similar studies; only when enough examples are available will generalities emerge. The diversity of phenomena manifested in the examples in this book suggest that we have a long way to go.

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