

## BOOK REVIEWS

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### ACCOUNTING FOR BIOLOGICAL DIVERSITY<sup>1</sup>

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The concept of adaptive radiation (or at least the term) was fathered by D. Lack, G. G. Simpson, and other contributors to the Evolutionary Synthesis, and reflected their conviction that most evolution, including differences among species, was caused by environmental agents of natural selection. If that were true, and if cladogenesis often occurs in bursts of almost simultaneous diversification (as inferred by paleontologists and supported by the prolific polytomies in many modern molecular phylogenies), then adaptive radiation, which Dolph Schluter defines as “the evolution of ecological diversity within a rapidly multiplying lineage,” would account for much of the boundless diversity of species and their characteristics. In assessing the prevalence and causes of adaptive radiation for the first time since the Synthesis, Schluter addresses as great, as encompassing, a theme as biology sounds.

The “ecological theory” of adaptive radiation that developed during the Synthesis, Schluter notes, was tripartite: divergence between species is caused by different selection owing to differences in the species’ habitats and resources; evolution of differences in habitat and resource use is driven by competition or permitted by alleviation of competition; speciation (the evolution of reproductive isolation) is a consequence of the divergent natural selection that drives phenotypic and ecological differentiation. At least through the 1950s, the theory was based mostly on patterns described by paleontologists and systematists, and quantitative studies were few. Since then, population genetic models, phylogenetic analyses, experimental studies of form and function, ecological studies, and quantitative genetics have been brought to bear on the elements of the theory, as well as on more recent ideas pertaining to adaptive radiation. Schluter sets out to reevaluate the theory in the light of modern studies, concentrating on diversification at low taxonomic levels (e.g., within genera). He concludes that “[o]n the whole, it should be regarded as one of the most highly successful theories of evolution ever advanced” (p. 242). But as he ably describes, much of the theory’s support is based on only a few well-studied cases and we do not know how far they can be generalized. The role of factors other than divergent ecological selection and competition is poorly understood, and some profoundly important questions are still virtually without answer.

Schluter’s treatment of this grand subject is marked by the same consciousness of hypothesis-testing and experimental

design, statistical rigor, analytical invention, and appreciation of natural history that he has brought to his studies of sticklebacks and geospizine finches (which, appropriately, are among the frequently cited examples). He is often suitably tentative in his conclusions, describes alternative hypotheses, and points out enough unexplored issues to provide inspiration for countless doctoral dissertations (or research careers). Indeed, I can report that his book is an ideal basis for graduate student seminar courses, and can both educate and spark spirited discussion. These strengths abundantly outweigh whatever reservations may attach to some few of Schluter’s arguments.

#### *General Patterns*

An immediate problem is how to distinguish adaptive radiations from other forms of diversification, such as non-adaptive radiation, or diversification in which speciation events are prolonged through time rather than clustered. (Such problems of distinction and measurement plague many aspects of the study of adaptive radiation; for example, making meaningful distinctions among resources to compare diet breadth or “niche breadth” can be very difficult [Colwell and Futuyma 1971].) Schluter describes several ways of detecting “rapid speciation,” but does not use them to determine if any real clades are or are not instances of adaptive radiation. Curiously, he requires that members of an adaptive radiation differ in ecologically important morphological or physiological characters; groups of species such as MacArthur’s famous warblers, that differ in resource use only by virtue of their behavior (surely a phenotypic trait), are excluded.

A more serious issue, I think, is the very important possibility that species in many clades may constitute “non-adaptive radiations,” in part or in whole, in which ecological differences are minimal, or may have evolved well after speciation. Among herbivorous insects, for example, there are many potential examples (cf. Ross 1957). In the skipper genus *Erynnis*, for instance, many sympatric host-specialized species feed on the same species of oaks (Burns 1964). The possibility of undetected ecological differences cannot be ruled out, but the burden would seem to fall as heavily on the advocates of Gause’s axiom as on its skeptics. Schluter recognizes this problem, especially when he discusses “non-ecological speciation” (see below), but he treats ecological differences among related species much more extensively than possible cases of the contrary. We are left without any estimate of what fraction of cladogenetic events are associated with ecological divergence.

Of particular interest is Schluter’s analysis of possible

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trends within adaptive radiations. He concludes, in agreement with long-term patterns in the fossil record, that expansion of a clade's breadth of habitat or resource use is the most general feature of adaptive radiations. He compiles phylogenetic studies to probe the long-standing hypothesis that ecological generalists give rise to specialists more often than the reverse (i.e., specialization is relatively irreversible). Schluter concludes that, at least at low taxonomic levels, there is no evidence of a bias in direction, and specialization is not an impediment to ecological diversification. (As an indication of how rapidly phylogenetic analyses are informing our understanding of such issues, Nosil [2002] has summarized a considerable number of studies of host range evolution in phytophagous insects that have been published even since Schluter's analysis; he largely supports Schluter's conclusion.) It is nevertheless the case that many clades remain limited to a rather narrow adaptive zone for many millions of years (e.g., insect clades restricted to a single host-plant family, swifts restricted to foraging for flying insects), so an ecological version of Dollo's law may sometimes hold at a truly macroevolutionary scale. Schluter also draws attention to "replicate radiations" as evidence of predictability in adaptive radiation. Despite considerable attention to convergent community structure during the optimistic days of "MacArthurian" community ecology (e.g., Orians and Solbrig 1977; Orians and Paine 1983), examples are few, and counterexamples might perhaps have been given more attention. For example, Lack (1969) pointed out that six species of tits (Paridae) coexist in Europe, whereas no more than two species (now assigned to different genera) are typically sympatric in most of North America. The cases of parallel radiation (e.g., Greater Antillean anoles, fishes in postglacial lakes) are as exquisitely appealing as great works of art, but whether or not they are equally exceptional remains to be seen.

#### *Accounting for Phenotypic Disparity*

The chief questions to be asked about phenotypic divergence in evolutionary radiations concern the roles of internal and external factors, the relative roles of selection and non-selective factors such as genetic drift, and the agents of selection.

The hypothesis that genetic or developmental constraints or biases may affect rates and directions of evolution has been rather more popular among macroevolutionists than population biologists, so it is refreshing to read Schluter's serious treatment of the topic. In a genetic exploration of Stebbins's (1974) argument for "adaptive modification along lines of least resistance" (p. 31), my colleagues and I provided evidence that the actual history of host shifts in leaf beetles is partly reflected by different levels of genetic variation for feeding responses to novel potential host plants (Futuyma et al. 1995). In a more sophisticated approach to the question, Schluter reports that morphological divergence among congeneric species in five genera of vertebrates occurs mostly along  $g_{\max}$ , the multivariate axis of greatest additive genetic variance in a "focal" species. Although the direction of evolution increasingly deviates from  $g_{\max}$  over time, Schluter argues that the effect of  $g_{\max}$  can be discerned for as much

as four million years. This is an increasingly active area that yields diverse and sometimes surprising results. For instance, intraspecific phenotypic variance-covariance matrices may predict interspecific divergence patterns better than genetic matrices do (Baker and Wilkinson 2003). Such long-term correspondence between intraspecific and interspecific variation has the important implication that developmental pathways are so structured as to constrain the expression of genetic variation over long time spans, and provides an alluring interface between population genetics and macroevolution.

The postulated agent of phenotypic divergence in adaptive radiations is divergent selection, under which, according to Schluter, intermediate phenotypes have lower fitness. He abundantly employs Wright's adaptive landscapes (or, more often, R. Lande's analogue for quantitative traits), so that divergence entails shifts to new adaptive peaks. This is fine if the peaks are dictated by discrete resources to which different phenotypes are best suited, but becomes problematical when competition impels character divergence; if a continuum of character states (e.g., gape size) are best suited to a continuous array of resources (e.g., prey sizes), there need not be fitness valleys, except insofar as these are generated by density-dependent and frequency-dependent selection, in which case the landscape metaphor becomes less useful (as Schluter notes). With or without density-dependent selection, the critical assumption is that each phenotype  $z_i$  has a resource (or habitat) optimum  $r_i$ , that is, that phenotypes display trade-offs in fitness on different resources. Under this assumption, a jack of all trades is master of none, and we should often expect the evolution of ecological specialization, and indeed the indefinite proliferation of increasingly specialized species (Levins 1968; May 1973; Futuyma and Moreno 1988). An abundant literature has been developed on the conditions that favor increased or decreased niche breadth (and its implications for the directionality that now seems less prevalent than expected), but Schluter's treatment of this large topic is rather perfunctory and leaves one of the more conspicuous gaps in his treatment of adaptive divergence.

If trade-offs are supposed to engender divergent selection and hence phenotypic divergence, how shall we document their role? This proves more difficult than we once supposed. Those of us who expected trade-offs in performance in different environments to take the form of negative genetic correlations have often found nonsignificant or even positive correlations instead (e.g., Futuyma and Philippi 1987). Schluter describes this approach as flawed, for an interesting reason that I had not appreciated. (I would nonetheless hope that a Levins' fitness set, a plot of genotypic values of performance in each of two environments, should still enable us to visualize trade-offs.) An alternative is to measure performance in one environment as a correlated response to laboratory selection for performance in another environment, but it is not clear how a true trade-off would be distinguished from diminished fitness caused by hitchhiking of linked deleterious alleles—a well-known phenomenon in artificial selection experiments. Schluter favors reciprocal transplant experiments, whereby performance of two divergent populations is assayed in both populations' environments. He concludes, from the prevalence of crossing reaction norms in such experiments, that trade-offs are ubiquitous and that divergence has been

caused by divergent selection. My reservation about this test is that an alternative hypothesis cannot be ruled out. If population A occupies the ancestral environment, we may expect it to display lower fitness in the environment of the derived population, B. Population B of course has adapted to its environment, but it may have experienced fixation of selectively neutral mutations that diminish fitness in the ancestral environment. If this scenario is at all likely, apparent trade-offs may be the result, rather than the cause, of divergent specialized use of different resources or habitats (e.g., Futuyma 1983; Holt and Gaines 1992). This possibility is exactly why some researchers adopted fitness correlations among genotypes within populations in the hope of testing for trade-offs (e.g., Futuyma and Philippi 1987).

What conditions favor ecological and phenotypic divergence? Surely the simplest hypothesis is that allopatric populations adapt to the different resources or habitats that prevail in different areas, and retain their associations with these resources after they become sympatric. Schluter notes that this is a simple explanation of peak shifts, but (understandably) does not review what must be a huge, relevant literature on adaptive geographic variation. An equally venerable hypothesis (Darwin's, in fact) is that competition between species selects for niche shifts. This had become a highly controversial issue only 20 years ago, but Schluter now can compile abundant evidence for character displacement and trait overdispersion (including instances described by former skeptics) that seems best to fit the competition hypothesis. A third hypothesis is that phenotypic diversification is favored by ecological opportunity—alleviation of competition from taxa other than the focal clade. Under these conditions, the first two hypotheses act to propel species into niches that formerly or elsewhere are preoccupied. The evidence for this, other than mostly long-known cases of island radiations and diversification following mass extinctions, proves to be rather meager. Perhaps most shocking is the virtual lack of any evidence that divergence in adaptive radiations has been fostered by other interspecific interactions, such as predation or alleviation of predation. Although models of divergence due to “apparent competition” into “enemy-free space” have been with us for more than 25 years, the relevant evidence is hardly deserving of the term. If there is one big, vacant adaptive zone in evolutionary-ecological research, this may be it.

Closely related to ecological opportunity is the notion of a key innovation, a feature that provides a lineage entry into a new adaptive zone. The replicated sister-group comparisons that Schluter cites provide phylogenetic evidence that diversification rate has been enhanced by postulated key innovations; but how representative these may be, we do not know. The rumen has all the earmarks of a key innovation, and may well have caused the great diversification of the Bovidae, but it has not enhanced the diversity of colobine monkeys and has had minimal effect on the diversity of hoatzins. It is rather distressing that nearly 40 years after Ehrlich and Raven (1964) postulated that a coevolutionary history of key innovations underlies the great diversity of angiosperms (with new defense compounds) and herbivorous insects (with new adaptations to said compounds), there is hardly any evidence bearing on the hypothesis, other than Mitter et al.'s

(1988) demonstration that herbivory as such is associated with increased diversification rate and Farrell's (1998) similar evidence on shifts of beetles from conifers to angiosperms. A huge gap in our understanding is how a key innovation (advantageous to individual organisms) results in increased numbers of species, rather than, say, merely greater ecological dominance of the species in which the innovation evolved. And as Schluter laments, we have no evidence on how key innovations enhance phenotypic diversification.

### *Speciation*

The predominant view of speciation that emerged during the Evolutionary Synthesis was that reproductive isolation (both prezygotic and postzygotic) most often evolves in allopatric populations as a pleiotropic byproduct of the genetic changes that are impelled by divergent ecological selection (Dobzhansky 1951; Mayr 1963). Dobzhansky emphasized, in addition, that selection against hybrids (owing to ecological inferiority or to genetic incompatibility) may reinforce the evolution of prezygotic isolation, and Mayr added a role for genetic drift in his hypothesis of peripatric speciation. Nonetheless, ecological selection was envisioned as the primary, although indirect, agent of speciation. So it is rather shocking to realize that until very recently, there has been almost no evidence that ecological selection plays any role whatsoever in the origin of species. The problem is that both reproductive isolation and ecological and phenotypic differences usually evolve, in parallel, in spatially segregated populations, and it is difficult to show any causal connection between the two. Almost all models of sympatric speciation, on the other hand, rely on some form of disruptive ecological selection (models of sympatric speciation by pure sexual selection are unconvincing; see Turelli et al. 2001), but realistic models, much less evidence, of sympatric speciation are a very recent development.

Tests for what Schluter calls “ecological speciation”—speciation in which ecological selection has played some role—are indirect and have been applied in few cases. Convincing cases of sympatric speciation might be *prima facie* evidence of ecological speciation, but Schluter (p. 241) grants but one good case. (I would go so far as to grant two, if speciation in *medias res* is included.) Schluter's group has developed one of the few examples (in sticklebacks) of “parallel speciation,” in which independently evolved ecotypes mate assortatively by ecotype rather than by ancestry (Rundle et al. 2000). Body size is suspected to be one of the characters contributing to both ecological divergence and reproductive isolation in sticklebacks, and a similar causal association is suspected for beak size and body size in *Geospiza*. Greater sexual isolation between geographic populations of leaf beetles that differ in host plant than between equally old populations with the same host implies a role for selection, over and above genetic drift (Funk 1998). When divergence in floral characters is associated with different pollinators (e.g., Schemske and Bradshaw 1999), ecological selection (for use of pollinators as resources) may be hard to distinguish from direct selection for reproductive isolation—although in his enthusiasm for ecological speciation, Schluter does not raise this issue.



We can soon expect more direct tests for ecological speciation, by identifying genes that contribute to postmating isolation (e.g., Ting et al. 2000) and determining their physiological and perhaps ecological functions. Distinguishing ecological from nonecological speciation will be more difficult, however, for premating or prezygotic isolation. As Schluter notes, the possibility that speciation is often caused by sexual selection would be a major challenge to the ecological theory of adaptive radiation if sexual selection is causally, entirely independent of ecological divergence. The possible proliferation of ecologically “redundant” species by sexual selection would constitute nonadaptive evolutionary radiation. This is a very viable hypothesis for many of the Hawaiian *Drosophila*, for instance (not all of which clearly differ in larval food), for many insect groups that differ in genitalia and sex pheromones but not necessarily much else, and perhaps many other organisms. Whether or not sexual selection enhances rates of speciation requires more documentation than has been provided thus far by sister-group comparisons of species numbers. I am convinced by comparisons of clades of birds that differ in mating system, but I am unsure that sexual dichromatism indicates stronger sexual selection than monochromatism, because sexually monomorphic birds might well experience strong sexual selection on voice or behavior (e.g., wrens, cranes), and many sexually monomorphic groups are highly colored (e.g., *Tangara* tanagers, many parrots) or ornamented (e.g., auks; cf. Jones and Hunter 1993). The claimed effect of mating system on speciation rates in insects is unconvincing because most comparisons have been based on distantly related (rather than sister) clades that may differ in age.

Schluter accepts divergent sexual selection as a strong engine of speciation, and is inclined to consider “chase-away” sexual selection (Rice 1998) the most plausible nonecological model. He notes that sexual selection can contribute to ecological speciation if ecological factors influence signal transmission or biases in female preference. He does not treat “good genes” or handicap models of sexual selection in any depth, although it is here that the most critical issues may lie. If it is often true that male signals are honest indicators of genetic quality, and if speciation by sexual selection is to qualify as ecological speciation, then the male characters that honestly indicate quality must differ, depending on ecological factors that differ, for example, between allopatric populations. I know of no research on this point, and I must say that it stretches my credulity to suppose that this scenario explains the proliferation of different color patterns, pheromones, vocalizations, and displays found in any clade of animals.

As Schluter says, the implications of prolific nonecological speciation by sexual selection are profound, for the causal chain in the ecological theory (in which divergent ecological selection causes both speciation and ecological divergence) would be reversed (with speciation preceding ecological divergence). At one point, Schluter seems to wish away the significance of this scenario (in which nonecological speciation “may merely produce many largely allopatric, ecological equivalents that remain as such and contribute little to ecological and morphological diversification” p. 214). But reproductive isolation is a precondition for the long-term per-

sistence of genetically different populations and for whatever ecological differences may eventually evolve between them (Futuyma 1987, 1989), so that the potential contribution of nonecological speciation by sexual selection might be profound.

#### CONCLUSION

*The Ecology of Adaptive Radiation* is a finely crafted, deeply thoughtful, if not entirely complete, summary of the impressive progress that has been made in the many parts of evolutionary biology. The extensive development of population and quantitative genetic theory on topics such as character displacement, phenotypic evolution, and speciation is on full display. Although the ecological theory of adaptive radiation is often tested by ecological (i.e., field) experiments and observations, ecological theory as such is strangely absent, other than in logistic-based models of character displacement and in glancing references to predator-prey and apparent competition theories, neither of which have been brought to bear on empirical examples. There may be an opportunity for developing more explicitly ecological, and testable, theories of adaptive radiation. Likewise, as Schluter emphasizes, the virtual lack of evidence on the role of interspecific interactions other than competition is scandalous and calls for imaginative research. Schluter is quite right to call speciation the “least understood part of adaptive radiation” (p. 212), and to call attention, in his final pages, to the opportunities we now have to analyze the genetic architecture of species differences, the role of new mutations versus standing genetic variation in adaptation and divergence, and the causes of the genetic covariances that may guide the pathways of adaptive radiation. But it is equally necessary to determine if our few well-studied examples can be generalized, and to understand more fully the form and agents of selection that generate diversity. This cannot be done without knowledge of functional biology (e.g., physiology, functional morphology), field ecology, and, above all, the natural history and systematics of organisms.

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