EVOLUTION

The Ecological Theater

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Speciation and Patterns of Diversity

Roger K. Butlin, Jon R. Bridle, and Dolph Schluter, Eds.

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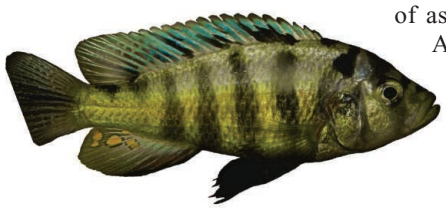
> Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!
>
> –Charles Darwin, *Origin of Species* (*1*)

This bicentenary of Charles Darwin's birth has been marked by such a flood of books, exhibitions, t-shirts, mugs, podcasts, and television programs that few people can be unaware of his ground-breaking ideas about natural selection. His elegant explanation for the evolution of life on Earth has been extensively tested and comprehensively vindicated. However, Darwin's insights into ecology—in particular how the interactions among species mediate speciation and extinction and how evolution shapes the distribution and abundance of species—have received much less attention. These too have the potential to substantially enhance our understanding of the natural world. It is therefore fitting that a new volume explicitly linking ecology and evolution has been published this year. *Speciation and Patterns of Diversity*, edited by Roger Butlin, Jon Bridle, and Dolph Schluter, grew out of a meeting of the British Ecological Society, itself the progeny of an earlier symposium on macroecology. The book poses questions that Darwin, and indeed many early ecologists, mulled over and asks whether recent research on mechanisms of speciation [e.g., (*2*)] has shed light on these long-standing problems. Issues tackled include the uneven distribution of species abundances in ecological communities, the preponderance of rare species, the latitudinal gradient of diversity, and the disproportionate diversity of small-bodied taxa relative to large ones. These are challenging and intractable questions, so it is not surprising that the book fails to deliver comprehensive answers. It does nonetheless make an important contribution by explicitly linking ecology with evolution. It also reminds us that taking a broad view of biology (as Darwin himself did) exposes connections and mechanisms that can be obscured when scientists become highly specialized.

Speciation and Patterns of Diversity covers a lot of ground and, reviewers apart, is not a book to be read cover to cover. It extends from theory (such as genetic models of adaptive radiation) to a speciation transect among Lake Victoria cichlids, covers a diverse range of animal and plant communities (including fossil assemblages), embraces the rapidly emerging field of microbial ecology, draws on powerful phylogenetic analyses, and grapples with difficulties of identifying species (particularly in the context of asexual organisms). As often happens in multi-authored volumes, the focus of different chapters varies considerably, from thoughtful overviews of the field to detailed expositions of a single topic. Not everyone will agree with every idea presented, but I would be surprised if there are any evolutionary ecologists who do not come away better informed or at least able to examine an old problem from a new perspective.



Intermediate cichlid. At Luanso Island, *Pundamilia pundamilia* and *P. nyererei* are merely extremes along a continuum of phenotypic variation.

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Among the conclusions that I found intriguing are Douglas Schemske's suggestion that the existence of greater opportunities for coevolution in the tropics contributes to increased species richness there, Albert Phillimore and Trevor Price's claim of ecological controls on the rate at which new species are formed, and Robert Ricklefs's idea that minimum viable population sizes constrain diversification. A general theme—explicit in some chapters and implicit in others—is that we might use the distinction between "ecological speciation" (due to divergent natural selection across environments) and "nonecological speciation" (attributed to factors such as drift) to tease out the imprint of ecology on evolution and vice versa. These and other overviews will translate into interesting research projects.

However, as Roger Butlin and others make clear, large gaps in knowledge remain, and there are serious methodological hurdles to be cleared. With the exception of polyploidy, the speciation mechanisms that have produced most taxa remain uncertain. It is even difficult to obtain accurate estimates of speciation rates because extant diversity patterns reflect the interplay between speciation and extinction. Indeed, the necessity of working with taxonomic groups that are diverse enough to be useful inevitably biases researchers toward organisms in which speciation outpaces extinction and may give a misleading impression that diversity has increased through time. Likewise, declines in diversity are invisible in phylogenetic trees.

One message that emerges is that although diversity is a potential driver of evolution, the relationship can operate in either direction. Low diversity can mean that there may be empty niches to be filled, whereas high diversity provides opportunities for coevolutionary interactions. In itself, none of this satisfactorily accounts for the universal patterns of commonness and rarity that Frank Preston (*3*) quantified and that Butlin and his colleagues, in their introduction, set out as one of the challenges both evolutionary biologists and ecologists must address. Yet, as is clear from the quote above, Darwin recognized not only that species vary in their abundance but also that this pattern of evenness is a product of the continuing interactions among species through time. At least some of these interactions will occur on tractable time scales. I hope that *Speciation and Patterns of Diversity* will encourage evolutionary biologists to look again at what Darwin had to say about ecology and ecologists to follow his lead in taking the long view and asking how the processes they study translate into rates of speciation and extinction.

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