The Stamp of History and Ecology in Amazonia

Although Charles Darwin published his most famous book more than a century and a quarter ago, the origin of species remains one of the most hotly debated issues in evolutionary biology. Questions about the size and ecological context of a population that is most conducive to speciation and the rate of the process once it is initiated are certain to draw many answers—not least because speciation more than likely occurs along several different routes, depending on prevailing circumstances. It is probable, however, that one or other is more common than the rest: the question biologists face is, Which one?

Most evolutionary biologists now agree that new species most often arise in spatially isolated (allopatric) populations, but, again, how that isolation might arise is cause for differences of opinion. For instance, one major school of thought argues that a fragment of the major population may split off and subsequently become separated by some kind of ecological barrier: this is known as the founder effect, or peripatric speciation. Another school sees changes in the physical environment as being instrumental in fragmenting populations: this is known as vicariance.

C. H. Greenewalt/VIREO

Selenidera maculirostris. *This species of toucan, which lives in southeastern coastal Brazil, is one of seven whose distribution may point to vicariance as being instrumental in their history.*

In principle, these two modes of speciation will produce different patterns in the biota, which is what Joel Cracraft of the University of Illinois and Richard Prum of the University of Michigan went in search of among the birds of Amazonia. They argue that what they found—specifically among species of parrots and toucans—indicates that vicariance has been important. Moreover, they suggest that the physical events that fragmented ancestral populations may well have occurred much earlier than is allowed for by the currently most popular interpretation of Amazonian biota.

The notion of vicariance places a heavy emphasis on history, such that if a once-continuous population is divided in two by, for instance, the rise of a mountain range, the geographical distribution and evolutionary history of the modern descendant species is the outcome of that ancient geological event. The key point about vicariance, however, is that each physical event is likely to affect a wide range of taxa, not just one, in the same way thus producing a congruent set of patterns of geographic distributions and evolutionary histories among many groups of modern endemic species. By contrast, peripatric speciation seems much less likely to generate such recurrent patterns.

Finding the congruence predicted by the vicariance hypothesis has proved tricky, however, partly because geological and biological perturbations since the vicariance event tend to blur the patterns, but also because researchers typically work on one group of species rather than several, thus making comparisons difficult. Cracraft and Prum believe that their elucidation of congruence of geographic distribution and evolutionary history among four (monophyletic) groups of parrots and toucans is one of the few empirical demonstrations of vicariance.

The notion that large-scale physical events drive evolution, through vicariance, is intuitively attractive. And, as Cracraft told *Science*: "Speciation rates increase in areas with high topographic complexity, suggesting that vicariance is higher in those areas. This is an approach for testing the concept." In this respect, evolutionary history is a direct consequence of Earth history.

One aspect of Earth history that has for some time been invoked as an explanation for the biogeography of Amazonia is fluctuating glacial periods of the Pleistocene (from 2 million to 10,000 years ago). As the intensity of the ice ages oscillated, so too did the coverage of tropical forest, forcing species occasionally to be restricted to isolated refugia, which became the foci of high speciation rates. If this Pleistocene refugia hypothesis is correct, then most of the species whose biogeographic pattern it is meant to explain should be less than 2 million years old. Not only is there little evidence to support this, say Cracraft and Prum, but newly emerging data indicate that it is unlikely to be true. Furthermore, they say that there is a series of major pre-Pleistocene physical events that could very well have generated the pattern of vicariance they claim is present among the species of toucans and parrots they studied.

Militating against the pure vicariance interpretation, admit Cracraft and Prum, are biogeographic patterns from other taxa that are not congruent with those of the toucans and parrots. Moreover, as John Endler of UC Santa Barbara argues, other interpretations of the modern patterns are possible, including their being the result of current ecological barriers to gene flow. "The problem is that it is often impossible to distinguish between possibilities," says Endler. "But I suspect that history and current ecology are equally important." ■ **ROGER LEWIN**

ADDITIONAL READING

J. Cracraft and R. O. Prum, *Evolution* **42**, 603 (1988).