not associated with a known earthquake is in a region north of 35°N, just east of the San Andreas fault. Active folding associated with the Kettleman Hills–Coalinga Anticline may explain the high strain rate here; however, data in this region are relatively less certain.

That past earthquakes would perturb the strain field is not a new idea. That postseismic effects could regionally dominate is, however, stunning. This result shows that although earthquakes probably would not change the overall rate of relative motion across a plate boundary, they could change regional deformation rates over a period of time from years to decades, depending on the magnitudes of the earthquakes. These postseismic effects will complicate efforts to determine long-term slip rates on faults using geodetic data. Relating the strain field to future earthquakes will require an understanding of the effects of past ones. But we can also announce good news: These new data provide tantalizing quantitative information about the crust's time-dependent, inelastic properties. Such properties will, after all, determine how stresses from plate tectonics and past earthquakes provoke future quakes. The observations provide a valuable window into the mechanism of inelastic stress release.

References and Notes

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2. Horizontal Crustal Deformation Velocity Map, Version 1.0, Crustal Deformation Working Group, Southern California Earthquake Center, http://scec.ess.ucla.edu/velmap/welcome.shtml
3. A revised global tectonic deformation model, NUVEL-1A [C. DeMets, *Geophys. Res. Lett.* **22**, 3545 (1995)], predicts a deformation rate of 49 mm/year across plate-boundary dextral motion in California, compared to the value of 50 mm/year estimated by this geodetic study.
4. An earthquake probability report for southern California by SCEC scientists [D. D. Jackson *et al.*, *Bull. Seismol. Soc. Am.* **85**, 379 (1995)] summarizes fault slip rates mainly on the basis of geological estimates.

EVOLUTION

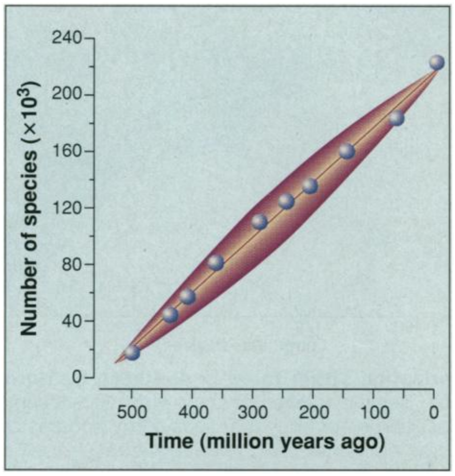
Tempo and Mode of Speciation

Michael L. Rosenzweig

How does one living species become two? And does the evolution of new species proceed fitfully or smoothly? If fitfully, what sort of cataclysms trigger progress? These are the basic questions that Klicka and Zink illuminate on page 1666 of this issue in a fascinating study of the timing of songbird speciation (*1*). From this and other recent work, mixed messages emerge: Speciation serves more than one master. And its regularity depends on the scale at which it is measured.

Birds do not make very good fossils, so they contributed little to our understanding of the principles of evolution until the development of molecular tools such as mitochondrial DNA (mtDNA) sequencing. Because minor variations in mtDNA appear to have no consequences for fitness, mtDNA can be a neutral indicator of time and a valuable evolutionary clock. As more time passes, more random differences will accumulate between species. Now, knowing how to tell molecular evolutionary time, we can ask basic questions about bird evolution whose answers should apply more generally.

Evolutionists believe that speciation usually begins with the subdivision of species into isolated populations by a geographical barrier (allopatry). What better barrier than a continent-sized glacier knifing down through North America and slicing many of its major environments into eastern and western segments? Because many western and eastern species of birds are sisters, evolutionists attributed their speciation to geography and to its ally, the glacial scalpel.



Virtually constant accumulation of species throughout Phanerozoic time. The concave and convex curves show the limits to the curvature of the data given their rate variation (*15*). Maximum rate: 611 species/million years; minimum rate: 292 species/million years.

Klicka and Zink show that we were wrong, at least about the glaciers. It makes one want to reexamine a whole class of geographical case histories—cases that emerged before molecular evidence became available. Were we also wrong to conclude from them that sympatric mechanisms of speciation—mechanisms that do not require geographical subdivision—are unimportant?

Sympatric speciation differs most significantly from geographical speciation in that it is triggered by ecological interactions (*2*). It targets ecological opportunities and produces new species with a high probability of survival. Evidence from fossils now strongly indicates that sympatric speciation was crucial in the radiation of innovative forms of life (*3*). And new mathematical theory (*4*) has removed any remaining genetic qualms about it.

Nevertheless, geographical allopatric speciation usually dominates other mechanisms. To conclude otherwise would require us to explain away too many facts. For example, of the world's 18,818 species of fish, 36% live in fresh water although only 1% of the Earth's surface is fresh water, and fish productivity and population are considerably higher in marine continental shelves and upwelling currents. The myriad opportunities for fishes to form geographical isolates in fresh waters as compared with salt looks like unassailable evidence in favor of the dominance of geographical speciation.

Another fact: The number of species in a biological province such as the Neotropics depends on the area of the province. Larger provinces have more species, and the relation is virtually linear (*2*). Dynamic theory based on geographical allopatric speciation predicts that correlation. Sympatric speciation does not.

The tempo of speciation also speaks in favor of a geographical mechanism. Sympatric speciation predicts that new species will emerge at an ever decreasing rate. But species form rather steadily during most periods. We see this in the fossil record (*5*), as well as in North American songbird DNA. And geographical speciation predicts it.

Yet, like a digital clock, genetic change is discrete at the finest scale. A digital clock seems to operate spasmodically at the scale of a second, but quite smoothly at that of an hour. Surely, at the scale of an individual base substitution, mtDNA change must resemble a "second hand." But the glacial hypothesis sought to extend fitfulness to a larger scale: 10^5 to 10^7 years.

The new DNA data from songbirds demonstrates that speciation events did not clus-

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ter as a result of the glaciation of North America. To a certain extent these events are distributed randomly throughout the time interval during which these pairs of species diverged. That is not unique. For instance, mammal fossils from the Meade Basin of Kansas show a similar scatter of speciation over a similar period (*6*).

But the bird DNA may also signal a real pulse of new species about 2.5 million years ago. One would ordinarily attribute the high value of the mode at 6% divergence to the workings of probability (*7*). But a second set of 17 independent bird species shared this value almost exactly. Moreover, this pulse echoes a similar pulse in speciation events among antelopes, rodents, and hominids at about the same time in Africa (*8*). Something suspicious is going on. This period coincides with the onset of a major global cooling off, a change that led eventually to the ice ages (*9*). As a matter of fact, that very climate change may well have triggered our own speciation (*10*). It certainly comes close to the time that hominids first began to show increased relative brain sizes (*11*). Curious indeed. The geographical barrier of the glacier itself does not create a ripple in speciation rate, but the climate change that preceded it does.

Undoubtedly, the fossil record at scales of tens of millions of years shows a mixture of regularity and pulses. The pulses come in the form of mass extinction events that—perhaps periodically—sweep away 30% to 97% of the world's species and trigger prolonged episodes of replacement speciation (*12*). During such times, I am not so sure that geographical speciation predominates.

Once we step back to the scale of hundreds of millions of years, however, the signal of pulses vanishes. The ups and downs of diversification disappear into a smoothness that almost defies belief. In the figure, I plotted the adjusted numbers of marine invertebrate fossil species that first made their appearance during one of the 10 major time periods of the Phanerozoic (*13*) (adjustments correct for the sampling bias generated because we have less old rock than young rock). The ordinate is cumulative so that the slope of the curve gives the estimated rate of speciation. The data cluster closely about a straight line. That line—fit by regression—shows where the data would be if the rate of speciation had been absolutely constant.

So, like the proverbial fractal coastline, the rhythm of speciation looks jagged at very fine scales, takes on a smoother but still complex appearance at intermediate ones, and loses virtually all traces of irregularity when we look at the history of life at its grandest scale. This signifies the presence of worldwide steady states in diversity (*2*, *14*). Negative feedback loops hold its component process rates within bounds by acting through a single parameter—the extent of the area that the average species occupies. Because of competition and predation, high diversity leads to reduced average area. In turn, reduced area lowers speciation rates and elevates extinction rates. Variations in these rates may be extremely difficult to distinguish from noise.

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15. First, arrange the data in order of declining accumulation rates, so that the "first" period has the highest rate and the "last" has the lowest. This imposes the largest possible negative second derivative on the data. Second, reverse the order (so that the one with the lowest rate is first). This imposes the largest possible positive second derivative on the data. The results are, in the first case, an exponent of 0.866 in a power fit, and in the second, an exponent of 1.204. The figure shows the polynomial approximations of these curves.
16. Title respectfully purloined from my late colleague, G. G. Simpson. I thank W. DiMichele, D. Jablonski, K. Flessa, M. McKinney, A. Miller, K. Niklas, S. Pimm, J. Sepkoski, and D. A. Thomson for stimulating ideas, advice, and feedback.

WEB FEATURE

The Forest and the Trees

What happens to a forest after it is clear-cut for logging or agriculture? A complete answer can require centuries of waiting. Now a special peer-reviewed feature in this week's issue of *Science Online* (*1*) answers the question in a matter of minutes. Deutschman *et al.* describe computational simulations of forest dynamics using the model SORTIE. Their simulated "forest" contains nine species of trees scattered throughout a 9-hectare square. The species (among them red oak, beech, and hemlock) come from an actual forest in the northeastern United States, and each is characterized by 10 parameters, including the size of a tree's crown and how much light passes through that crown to nourish seedlings below.

The model simulates clear-cuts of various dimensions and then calculates the forest composition for the next 1000 years. Three-hectare clear-cuts that remove all trees yield remarkably different succession patterns than those that leave as few as 10% of the seedlings. A comparison of growth with the computationally intensive method of calculating light for each of several thousand trees and with the approximation of average light level over the entire forest reveals the forest-wide importance and effect of local conditions. Although the model is simple conceptually, the interaction over time of each particular combination of parameter values is hard to predict—but easy to appreciate graphically.

Gilbert J. Chin

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These simulations of forest growth are offered to the readers of *Science* Online as a new feature for your evaluation. Click on the Web Feature on the *Science* Online home page (www.sciencemag.org). The visualizations are embedded in a two-tier arbor: The button labeled Quick View takes you to a conspectus, and the button labeled Paper is the entire project. Is this a useful mode for communicating scientific research? Let us know. Direct your comments by e-mail to editors@aaas.org.