Origin of Species in Stressed Environments

Data from marine and terrestrial communities unexpectedly reveal the preferential origin of evolutionary novelties in species-poor environments

There is always something intensely satisfying in the convincing demonstration of a state of affairs that is distinctly counterintuitive. This is precisely what David Jablonski, John Sepkoski, David Bottjer, and Peter Sheehan have done on page 1123 of this issue. They have shown that throughout much of the history of life in continental shelf environments, the principal source of major evolutionary innovations has been in nearshore communities, which, compared with offshore communities, have low species diversity and a low rate of origin of new species.

The traditional assumption has been that environments that support rich and complex assemblies of species, which includes the tropics as against higher latitudes in general and offshore as against nearshore communities in the marine realm in particular, would also be the font of major evolutionary novelties. Such innovations constitute new species that are more than just variations upon a theme: they are the foundations of distinctly different adaptations or architectural forms, the beginnings of new genera, families, or even higher taxonomic groups. Seeing rich evolutionary potential in rich species diversity appears to be a very reasonable assumption. But, apparently, it is likely to be wrong, perhaps for the most interesting of reasons.

Not only are there fewer species in nearshore environments but each species has a lower speciation rate; that is, is less likely to split to produce new species. This low speciation rate in nearshore species just happens to be matched by a lower extinction rate too. Species in the offshore communities are characterized by high speciation and high extinction rates. One consequence of this slow species turnover nearshore and fast turnover offshore is that, geologically speaking, individual nearshore species are older than those further out on the continental shelf.

What Jablonski and his colleagues found, however, is that, judged by biological criteria, the nearshore/offshore age distribution is reversed. Nearshore species, which individually may have substantial geological longevity, represent the most recently evolved forms of life. Likewise, offshore species, which individually may be geological youngsters, represent the longest established life-forms. A trip across the seabed from the edge of the continental shelf to the water's edge is like a trip through time, traversing the oldest through the newest evolutionary inventions.

The authors of the accompanying paper see this general pattern in the fossil record at two geological points: the Cambrian-Ordovician interval, 500 million years ago; and the late Cretaceous, 60 million years ago. The pattern implies a continuous process of territorial expansion of the newest evolved forms from the nearshore communities down and across the continental shelf.

The obvious question is, why are evolutionary novelties preferentially generated nearshore? Until this pattern was discerned one line of argument would have been that all speciation events are equally likely to give rise to a true novelty, rather than simply a variation upon a theme, and that, therefore, the environment in which speciation rates are highest would accumulate most novelties. This is clearly not the case in these marine communities, as the reverse seems to be true.

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Perhaps, suggest Jablonski and his colleagues, novelties are indeed equally likely in all speciation events, but the greater extinction resistance of nearshore species permits novelties to persist long enough to diversify. A second possibility, which has the more intriguing evolutionary implications, is that the ecological constraints of certain types of environments enhance the likelihood of large evolutionary jumps during speciation events.

Traditionally, evolution of new species is viewed as completely opportunistic, with variations going where they may, a process that is undifferentiated with respect to where true novelties are likely to arise. The idea that species in certain environments are more likely to yield major innovations when they speciate adds an unpredicted hierarchical level to the macroevolutionary process, for it is the appearance of major innovations that sets the pace and pattern of community evolution.

Is there any reason why nearshore environments might promote evolutionary innovation? Compared with offshore habitats, which are relatively stable, the nearshore is a hazardous place to live. One consequence is that offshore species are able to thrive as small, geographically restricted populations, whereas nearshore species typically are composed of large, geographically distributed populations. A corollary is the existence of wide dispersal capability of larval forms in nearshore species, which contrasts with nondispersing larval forms typical offshore.

The population structure of the nearshore species conforms with what geneticist Alan Templeton of Washington University has suggested is conducive to the appearance of major evolutionary innovations. Peripherally isolated groups, drawn from a large, widespread population, may undergo minigenetic revolutions, which may shift developmental patterns sufficiently to produce truly novel forms. Genetic transilience, he calls it. The idea, honed against fruit fly genetics, has yet to be demonstrated elsewhere.

Jablonski and his colleagues cannot yet decide between the differential extinction and differential origination possibilities, both of which seem equally likely at present. But they are not alone in seeing patterns with distinct macroevolutionary implications. First of all, others have recognized patterns in marine communities like those described in the *Science* paper, but no one has run with the observation before. More recently, Leo Hickey and co-workers described the apparent preferential origination of plant and animal species in the cold, species-poor Arctic latitudes, which then expand south.* And William Zinsmeister of Purdue University has recorded, but not yet published, a similar phenomenon in the Southern Hemisphere. Processes may be different in these different circumstances. But the unexpected, disproportionate production of evolutionary novelties in stressed, species-poor environments does seem to be real and widespread.—**Roger Lewin**

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