PALAEOBIOLOGICAL TESTING OF MODELS OF EVOLUTION IN MULTISPECIES SYSTEMS[1]

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ABSTRACT. Two rival models of evolution in multispecies systems were tested against the empirical patterns of taxonomic survivorship and accretion in the Oligocene through Holocene pelagic plankton of the Pacific Ocean. The modified Red Queen model of Van Valen predicts that rates of speciation and extinction are constant and non-zero at equilibrium. Evolution is continuous even in the absence of abiotic environmental change and is driven by diffuse biotic interactions. The Stationary model of Stenseth and Maynard Smith, by contrast, predicts that rates of speciation and extinction decline to zero at equilibrium. Evolution responds principally to changes in the abiotic environment.

Both these models are plausible theoretically but the variables causing the system to conform to one or the other model are not measurable in practice. Consequently, the only available method to test which model more appropriately describes evolution in multispecies systems is empirical. It becomes necessary to analyse the actual patterns of evolution in order to determine which model's predictions provide the better fit. The differential predictions of the rival models are such that, under a constant effective environment, the Red Queen model requires constant positive rates of speciation and extinction, whereas the Stationary model requires zero rates. Hence, the relevant evolutionary patterns to be analysed include taxonomic survivorship and taxonomic accretion.

Survivorship curves describe the cumulative frequency distribution of species durations and graphically portray the probability of extinction as a function of species age. Accretion curves describe the cumulative origination of species in the system as a function of its age. Both patterns obviously involve the evolutionary time-scale.

The empirical patterns of cohort and polycohort species survivorship provide evidence that the assumption of constancy in the effective environment of the investigated pelagic plankton has to be rejected. The actual relationship of speciation and extinction rates to species diversity renders disputable, but not necessarily untenable the assumption of the system's position close to an evolutionary equilibrium. Because neither of these two critical assumptions was demonstrably met in the analysed system, adequate palaeobiological testing requires that the predictions of the two models be adjusted.

Under qualitative adjustments, the results of the analysis are inconclusive. The best-fit model of extinction probability is not independent of species duration, as predicted by the Red Queen model. The best-fit model of accretion rate, however, suggests that accretion is diversity-dependent, a finding consistent with the Red Queen model.

Both the Red Queen and the Stationary models offer some explanation for the observed empirical patterns of species-level survivorship and accretion. This finding suggests that neither model can yet be accepted without qualifications and that neither model should be unequivocally rejected. The patterns expressed in the data imply that extinction and speciation are dynamic responses to a changing effective environment, the product of both abiotic changes and biotic evolution. Two sets of variables are important. What we now need is independent evidence of the effect of one, so that we may deduce the importance of the other.

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