Analysing diversification through time: reply to Sepkoski and Miller

Two major classes of explanatory models for the diversification of life have arisen – equilibrium and non-equilibrium – as I outlined in my Perspectives essay[1]. Equilibrium models assume that there have been, and presumably still are, limits to global diversity of all life, or of major segments of life, and that these equilibrial carrying capacities have remained constant for tens or hundreds of millions of years. Non-equilibrium models make no such assumption.

Sepkoski and Miller[2] are quite right to emphasize the nature of rebounds and other phases of seemingly rapid radiation as possible evidence for equilibrium models. I noted this phenomenon in my essay. After mass extinctions, diversity is reduced rapidly, but it commonly recovers rapidly to pre-extinction levels, and then diversification reverts to a more sedate rate. One interpretation of such rebounds is that they point to the existence of an equilibrium: as global diversity approaches the equilibrial level, diversification rates slow[3]. When many species are removed by a mass extinction, the standing crop of species falls far short of the equilibrium and diversification can occur rapidly until the equilibrium level is approached again. Other interpretations are possible, however, including a variety of below-equilibrium[4], and non-equilibrium models[5–10], and the quality of fit of some of these is claimed to be as good as for logistic models[4].

The non-equilibrium models include some that are broadly diversity-dependent[4], others in which speciation is diversity-dependent but extinction is diversity-independent[6–8], and others in which rates of speciation and extinction are both diversity-independent[9,10]. Miller and Sepkoski's[3] analysis was indeed quantitative and their coupled logistic model was consistent with the data. However, such models can only be descriptions[11]. Other descriptive models are possible[4–10] that involve fundamentally different assumptions. Sepkoski and Miller[2] refer to tests that might distinguish between equilibrium and non-equilibrium models. These tests are predicted outcomes of both models that are to be considered in various real cases. However, none of the tests is simple and decisive, and they generally involve a decision by the investigator about whether an empirical pattern is best explained by one or another model.

As Sepkoski and Miller[2] note, my conclusions should be considered only as opinions. However, in my essay, I noted observational evidence in favour of both equilibrium and non-equilibrium models and I suggested that the only direct evidence for a global equilibrium, the so-called 'Palaeozoic plateau' in marine animal diversity, might be an artefact of taxonomic level. My opinions, and the opinions of Sepkoski and Miller, require much further investigation.

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Natural microcosms

The term 'microcosm'[1] should not be restricted to 'ecosystems in containers'. Historically, 'microcosm' has been used to describe the microscopically small world of plants, animals and microbes. The scientific journal *Mikrokosmos* was founded more than 70 years ago! And there are 'natural' microcosms, not in artificial containers or subject to experimental manipulation.

The water and gas-filled, fist-sized bubbles in Antarctic lake-ice, discovered by Wilson[2] in 1965, are a unique habitat. Encapsulated and sealed from the world outside, the bubbles and their mixtures of microscopic plants and animals (diatoms, ciliates, nematodes, rotifers, etc.[3]) may remain trapped inside the ice for several years. In 'Deep Lake' (Cape Barne: 77°35′S; 166°15′E), clumps of algae are detached through their own buoyancy from the lake-bed more than 30 m below the permanent ice cover (which is up to 7 m thick); on the underside of the ice they become encapsulated, and during the weeks of summer slowly work themselves upwards through the ice as they melt their immediate surroundings. In the long and dark winter months all activity in the ice-bubble 'prison' ceases, and it may take several years before one ice-bubble finally reaches the surface of the ice and breaks open. Thereupon, the contents dry out and die or are dispersed by the wind.

The facts that the ice-bubble communities exist in total isolation from neighbouring bubbles, that the icy 'trap' and the physical conditions provide an extremely constant environment and that only a very small number of species are interacting with each other, show that the Antarctic ice-bubble communities are, indeed, microcosms on a par with the Ecotron[4] or Biosphere 2 (Ref. 5), only much, much smaller – 'micro'-microcosms perhaps.

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