

## EVOLUTION AND ENVIRONMENTAL DETERMINISM

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A favourable comparison is demonstrated between a model for the evolution of marine invertebrates over Phanerozoic time and a deterministic climate model.

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As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of distinct species, or with the physical conditions of life . . .

Darwin (1859): *Origin of Species*.

There it is then. According to the most generally accepted theory of evolution by natural selection, species struggle with and presumably, if unsuccessful in that struggle, respond to their physical environment.

As noted by Dobzhansky *et al.* (1977) evolutionary change through time (anagenesis) and evolutionary diversification (cladogenesis) are not directly promoted by natural selection, but often ensue as by-products of its fostering adaptation. This is significant as we are to talk here of speciation as a measure of evolution. In order to demonstrate a relation between speciation and the physical environment on a long timescale it is not necessary to enter into the interminable debates concerning the relative merits of gradualism, represented by say Darwin (1859) of the last century and Durham (1978) of this, and the punctuational model of evolution sported by such protagonists as Ruzhenstev (1964) and Gould and Eldredge (1977). Nor is it necessary to commit oneself to favouring any of these approaches by comparison with the recent molecular drive model from Dover (1982) or the support that could be claimed for it from the writings of Mason and Tranter (1985) or Denness (1986a). We are not about to comment here on the mechanism of association but merely to illustrate the close correlation of an evolutionary phenomenon with a secular model of environmental change.

Let us take as our evolutionary model the stratigraphical record of the principal groups of marine invertebrates portrayed here as Figure 1, adapted directly from Eicher and McAlester (1980) who consider that the widths of the various columns indicate the approximate abundance of each group; it is admitted that Eicher and McAlester's model is not universally accepted but we have to start somewhere. Unfortunately it is not clear whether that abundance refers to subdivisions such as species, numbers of individuals, or both. Nevertheless by adding the widths of each group an indication of the abundance of the whole sub-kingdom becomes available as a measure of its unclassified numerical success over the full Phanerozoic timescale.

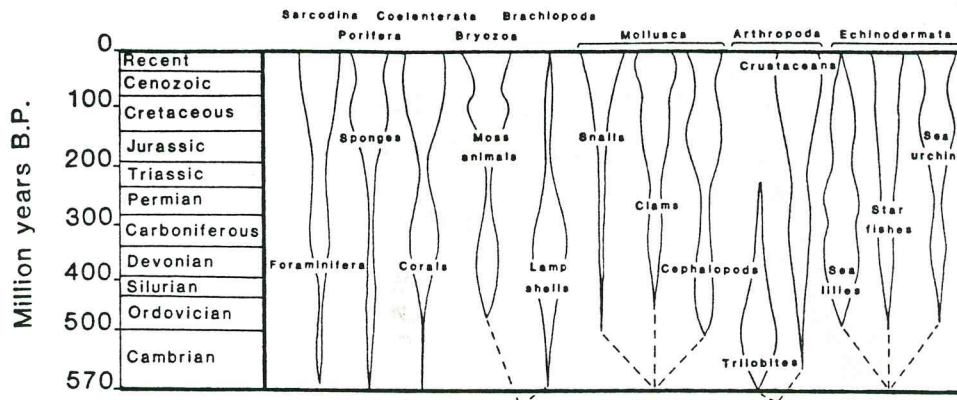


Figure 1.

This reduction is shown by the dotted line in Figure 2 which is somewhat similar in trend to that of the diversification of families of marine invertebrates described by Valentine (1969) and thus favours a species rather than a specimen interpretation of abundance. In any case arguments can be amassed from the literature (e.g. Mayr, 1970; Stanley, 1979) to suggest that the rate of evolution of species is related to their population size so that the abundance of both species and individuals should indeed be related. If that is so the observation by Dobzhansky *et al.* (1977) that

living organisms have a tendency to multiply exponentially ad infinitum without intrinsic constraints. . . (because) . . . each organism is capable of producing, on the average, more than one progeny throughout its lifetime

should also hold true for the diversity of species. Therefore, it seems appropriate to explore the result of subtracting a theoretical exponential expansion from the observed total abundance of marine invertebrates, notwithstanding the alternative support for a cubic-time expansion model suggested by Davidson (1985) and Denness (1986b).

By taking the abundance represented by the exponential expansion portrayed by the dashed line in Figure 2 from the observed abundance described by the dotted line we derive the dot-dash line which can be considered as a measure of the influence of the sum of extrinsic constraints on the abundance of marine invertebrates over the Phanerozoic timescale. Let us now examine these constraints. Among the main factors proposed by Dobzhanski *et al.* (1977) to interfere with the multiplication of organisms is climate variation. This theme is explored at greater length by Pearson (1978) and Ford (1982).

A major problem in comparing evolutionary progress with climate variation has always been the paucity and unreliability of data on both counts. However, recently a synthesis of a large number of time series relating to proxy and real climate data has resulted in the compilation of the time-based deterministic climate model introduced by Denness (1981), substantiated by Denness (1984a and b) and addressed to relatively short-term applications by Denness (1983a and b; 1984c and d, 1987 and in press) and Burns and Denness (1985). Briefly that model represents global temperature variation, with its various implications for related climatic phenomena, by the sum of a sine series in which each successive component is of half the period and 0.84



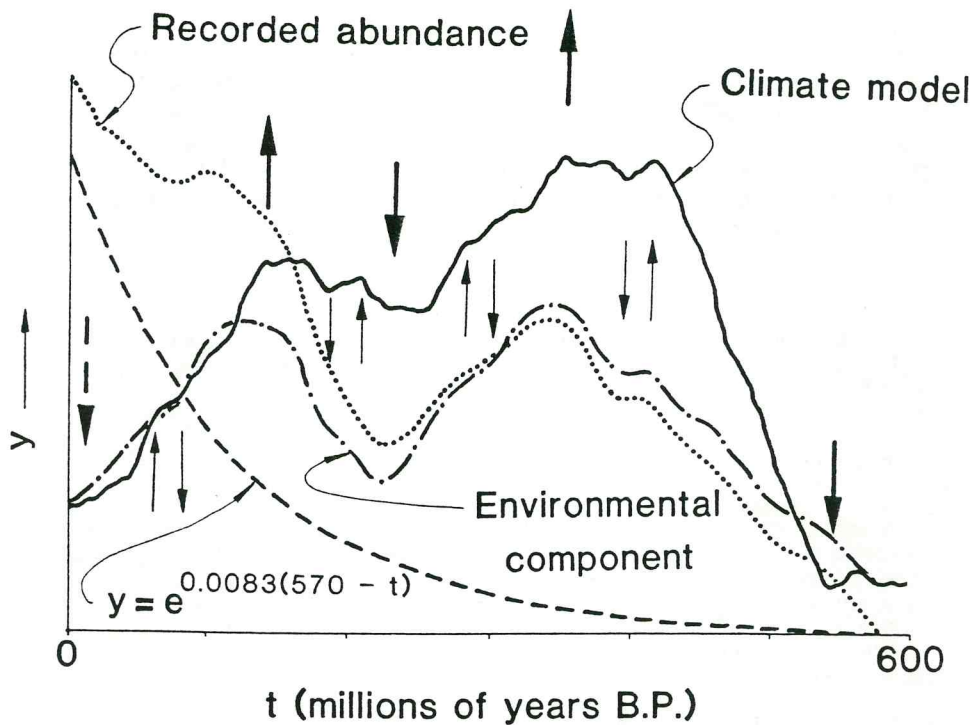


Figure 2.

times the amplitude of its more fundamental neighbour. Its portrayal over the Phanerozoic timescale, after smoothing by the moving average technique, described fully by Denness (1984a and b) is seen in the continuous line in Figure 2.

A comparison is thus available between the environmentally constrained component of evolution and the climate model. Both a general and detailed coincidence are apparent. The large arrows draw attention to the maxima and minima of the climate model which are similar to those of the constrained evolutionary tract. The smaller coupled arrows emphasize the temporally near-coincident, more subtle inflections of the progress of both the climatic and evolutionary models.

A simple yes-no test (Does each maximum and minimum of the climate model coincide with that of the evolutionary model?) leads to five favourable responses to a 50:50 option on the grand timescale, i.e. odds of 32:1 against the derivation of such a coincidence by chance. If sufficient confidence can be generated for the coincidence of the more subtle inflections these odds can be greatly expanded, perhaps even to 8192:1. Therefore, it is suggested that this may represent a real demonstration of the association of evolutionary progress with climatic change and no other extrinsic factor, especially as the climate model and evolutionary model were derived independently from the works of different researchers and did not use similar data sources.

A final word of caution is in order, however. Though this note illustrates the close association of evolutionary progress with a climatic model it does not necessarily imply a cause-and-effect connection as most theories would have it. Instead it is

preferred to leave the stage open for the possible later introduction of a more universal model which allows both environmental and evolutionary change to be influenced simultaneously by a higher order driving force as postulated by Denness (1986a).

A prominent model of evolutionary success compares favourably with a recent model of climatic variation over the Phanerozoic timescale. There may be grounds other than environmental determinism to explain this association.

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