Evidence of self organization in planktic foraminiferal evolution: Implications for interconnectedness of paleoecosystems

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ABSTRACT

We analyzed planktic foraminiferal evolutionary data using techniques of nonlinear dynamics, a methodology new to paleontology. The data set comprises 196 extinction and speciation horizons derived from biostratigraphic ranges of 662 reliably defined species. Both extinction and speciation data sets are well characterized by power-law models. However, return maps and a predictor technique indicate that the extinction data are more highly deterministic than speciation data. We interpret the analysis, particularly extinction data, to be consistent with planktic foraminiferal evolution being organized, and not randomly driven. Our results do not preclude periodic large extinction events driven by external forces as predetermined by another system (e.g., large-body impact), or internally driven extinction processes, where spontaneously derived interdependencies cascade through the ecosystem, or some combination thereof. Our data support a model whereby the internal organization of an ecosystem regulates the response to changes in a deterministic manner, the relative scales of disturbances and extinctions depending on the degree of interdependency within the system. Thus any contention that species interactions are not sufficiently intense to generate mass extinctions can be dismissed. Random walks generated by genetic drift and the transitory nature of *n*-dimensional niche space may explain why speciation is less deterministic than extinction.

INTRODUCTION

Planktic foraminiferal data provide more detailed biostratigraphic resolution than any other group, making them ideal for studies of evolutionary processes (e.g., Berggren and Casey, 1983; Lazarus, 1983; Jablonski et al., 1986). Previous research on extinction and speciation rates of planktic foraminifera has focused on the nature of background extinctions (e.g., Red Queen hypothesis vs. various stationary models; see Benton, 1990; Pearson, 1992, and references therein for discussion). More recently, emphasis has been placed on mass-extinction phenomena (e.g., Hart, 1990; MacLeod and Keller, 1994).

We utilize a different approach to analyze relative extinction and speciation rates among the planktic foraminifera. We apply several analytical techniques of nonlinear dynamics that allow us to determine whether elements of "complexity" are associated with planktic foraminiferal evolution. Recognition of self-organized interdependencies at the species level within this group has important ramifications for our understanding of the dynamics of ecosystems as complex adaptive systems. In addition, because of the high degree of species ecological interconnectedness within the global ocean ecosystem, conclusions drawn from this study may very well apply to additional clades (Plotnick and McKinney, 1993).

METHODS

In contrast to catastrophic theories of extinction and speciation, a central idea of nonlinear evolutionary theories (e.g., Kauffman, 1993; Plotnick and McKinney, 1993) is that ecosystems are highly organized, or deterministic due to feedback that arises from ecological cross linking. Self-organized critical systems owe their "criticality" to complex and generally nonlinear interaction between variables (i.e., feedback or linkages; Bak et al., 1988). A sandpile provides an excellent metaphor to describe self-organized criticality (Bak et al., 1988). The continuous addition of sand eventually results in a pile at its maximum, or "critical," angle of repose. On the basis of the history of the pile (i.e., the linkages of sand grains), input of an additional sand grain may perturb only a few neighboring grains or it may cause a cascade (i.e., a strikingly different behavior from that observed with previous additions of sand grains). Although avalanches may be triggered by random external or internal events (e.g., additional sand, settling of the pile), their distribution is not random; they are organized so that small slides greatly outnumber large ones.

In mathematical terms, self-organized critical systems obey a power law such that the number of events of a given magnitude N_m scales as a power of the magnitude (m):

$$N_m \propto m^{-d},$$

where d is generally a noninteger value. This means that the processes underlying both large and small events must be the same; otherwise the simple observed relation described above would not arise. Continuing with the sandpile metaphor, a plot of avalanche magnitude vs. the number of events of a given magnitude forms a straight line on double logarithmic plots. Physically, this phenomenon exists because (in the absence of slides) there is a buildup of unstable "critical" material until eventually a large event occurs. Thus, numerous small avalanches preclude large ones.

Kauffman (1993) postulated that species interactions form complex webs that he termed a "fitness landscape." If ecosystem dynamics are characterized by a high degree of ecological cross linking (as also suggested by Plotnick and McKinney, 1993), population change may occur as cascades of any magnitude due to the severing of interdependencies within the web. If these hypotheses are extrapolated to real extinction and speciation data sets, certain statistical attributes should be recognizable. Kauffman (1993) provided evidence that extinctions at the family level (using data of Raup, 1986) fit a power-law model. However, Kauffman's data set consisted of only 79 observations (the stages of the Phanerozoic).

Paleontological Data Base

Information on planktic foraminiferal taxa and ranges were extracted from the literature. Ellis and Messina (1940, and yearly supplements) provided descriptions for 1654 species, subspecies, and ecophenotypic variants of planktic foraminifera. Because this catalogue indiscriminately includes all synonyms, homonyms, and intraspecific variants, we had to eliminate all erroneous or superfluous taxa (those that are poorly documented, have indeterminate stratigraphic ranges, or are of such localized fossil occurrence as to make correlation impossible). Fortunately, a large body of work published in recent years provides detailed taxonomic and stratigraphic data on recognized taxa (including numerous references in the following citations; Kennett and Srinivasan, 1983; Bolli et al., 1989; Hart, 1990; MacLeod and Keller, 1994). The subjectively de-