

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-

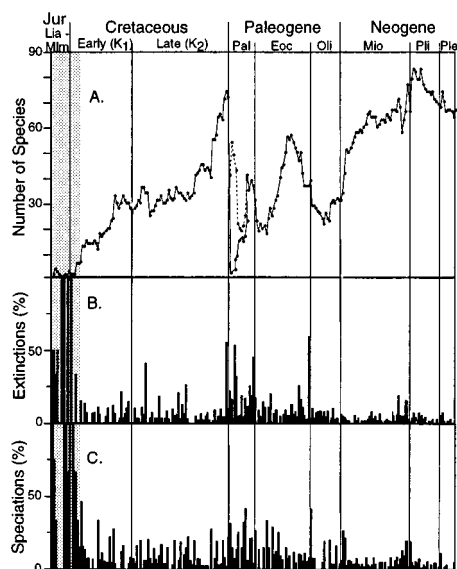


Figure 1. A: Number of planktic foraminiferal species from Jurassic through Holocene as defined by speciation and extinction events. Jurassic and earliest Cretaceous data were excluded (patterned area; see text for details). Integration of Maastrichtian-Paleocene data from MacLeod and Keller (1994; dashed segments) significantly altered species distribution across Cretaceous-Tertiary (K-T) boundary from traditional interpretations. However, analysis of data sets in which planktic foraminiferal species richness collapsed to between two (solid line) and ten species at K-T boundary and results of MacLeod and Keller (see discussion in MacLeod and Keller, 1994) produce nearly identical results. B: Percent planktic foraminiferal extinctions per event. C: Percent planktic foraminiferal speciations per event.

rived reliable planktic foraminiferal data base was reduced to 662 species.

Analysis of paleontological data for recognition of evolutionary processes is usually done at the genus or family level. However, we made our analysis at the species rank, where a much larger number of speciation and extinction events can be detected (Fig. 1). Because the aim of this paper was not biostratigraphic in nature, we used speciation and extinction events, including non-index fossils, allowing us to recognize 212 intervals or "time slices." This method provides a natural means of sorting data for statistical tests. The reported stratigraphic ranges of some taxa vary, depending on the researcher and the part of the global ocean studied. In such cases, we took a conservative approach and assigned taxa-accumulative stratigraphic ranges. Relative speciation and extinction events were also calculated for each interval (Fig. 1, B and C). Because of low species abundances (a single extinction or speciation event commonly represented a significant change in the proportion of taxa) and poorly defined time intervals, Jurassic and earliest Cretaceous data were

excluded from this study. The actual number of intervals employed in our analysis was thus reduced to 196.

One of the major difficulties with the analysis of geological series is time resolution. Most techniques require that equal time increments be sampled. Given the errors in dating, the poorer time resolution of geochronometers deeper in antiquity, and the unequal time intervals of biozones, this is a serious constraint for geologic time series analysis (Conner, 1986). Our approach avoids using time as a variable. Instead, we measure the number of events that occur at distinct speciation and extinction horizons. We view these as being discrete. In mathematics and nonlinear dynamics, a related sampling technique is known as a Poincaré section (e.g., Bergé et al., 1984). Instead of taking a measure of the system at equal time intervals, one can measure where or when the system returns to a particular place in phase space.

We are aware of the danger associated with basing the study on species. One has only to find a single species to document the presence of an entire higher taxon, whereas every species must be found to provide complete documentation of species richness (Signor, 1990). However, we agree with Berggren and Casey (1983) that the exceptional fossil record and high level of research activity carried out on planktic foraminifera provide a relatively accurate assessment of temporal species diversity.

Analytical Technique

In order to test hypotheses that evolution in biological systems is deterministically driven (cross linked), we have analyzed our extinction and speciation data sets using various techniques from nonlinear dynamics and fractal geometry. Following the example of Kauffman (1993), we examined the data set for the signatures of power-law behavior. First, we sorted the time intervals into groups having the same number of "events" for both the extinction and the speciation data. Next, we plotted the log of the number of events vs. the log of the number of groups having a particular number of events. Power-law behavior is confirmed by a straight line of negative slope.

A second method, the return map, distinguishes between randomness and determinism in signals from systems characterized by few independent variables, so-called low dimensional systems. For these, we simply plot values against their predecessors (i.e., x_n vs. x_{n+1}). It is clear that white noise has no correlation between successive values and consequently plots as scatter, whereas deterministic systems have an organized distribution.

Another technique that we employ, the "wimplex" time series predictor algorithm (Sugihara and May, 1990; Fowler and Roach, 1993), is ideally suited to the analysis of both complex (higher dimension) and relatively small data sets (≤ 100 data points). The algorithm selects a datum in the time series and tries to predict its next value (the predictor) by selecting another point in the set that is closest to the original datum. The algorithm constructs and makes predictions in progressively higher vector spaces (embedding dimension) that are constructed from the data set. The result is a plot of the correlation coefficient of the predictee vs. predictor value at each embedding dimension. Analysis of random data does not yield correlations, whereas other data (i.e., chaotic or Markov sets), which appear as noise to more traditional signal analysis techniques (e.g., Fourier), are shown to be deterministic.

RESULTS AND DISCUSSION

Double logarithmic plots (Fig. 2, A and B) of planktic foraminiferal extinction and speciation events have negative slopes (-1.3 and -1.4 , respectively), and significant linear correlation coefficients ($r = 0.86$ and 0.89 , respectively), although they are slightly concave. We interpret this distribution as being indicative of power-law behavior. In contrast, a uniform random data set (Fig. 2C) shows no such behavior.

Interpretation of the return maps (Fig. 3, A and B) is less straightforward. Unlike random data (Fig. 3C), which scatter uniformly across return maps, the foraminifera data (particularly the extinction data) have a tendency to cluster toward low values. This clustering can be indicative of determinism. Deterministic systems tend to evolve to an "attractor" that can be a point, a line, or a highly complicated object, depending upon the complexity of the system's evolution and its "dimensions." One cannot accurately visualize the geometry of a high-dimensional system on two-dimensional plots. Thus, although the return maps indicate that there is a deterministic component to the data, it is difficult to quantify.

Accordingly, we used a predictor technique to search for correlations in higher dimensional space (Fig. 4). We interpret the results of the "wimplex" technique (Fowler and Roach, 1993) for the extinction data to be consistent with a deterministic signal having low dimension. Although the correlations are low in comparison with the deterministic chaotic test signals that we have analyzed elsewhere, the correlations are significant for 196 data points. We consider it meaningful that the correlations are all uniformly positive for extinction data, in con-

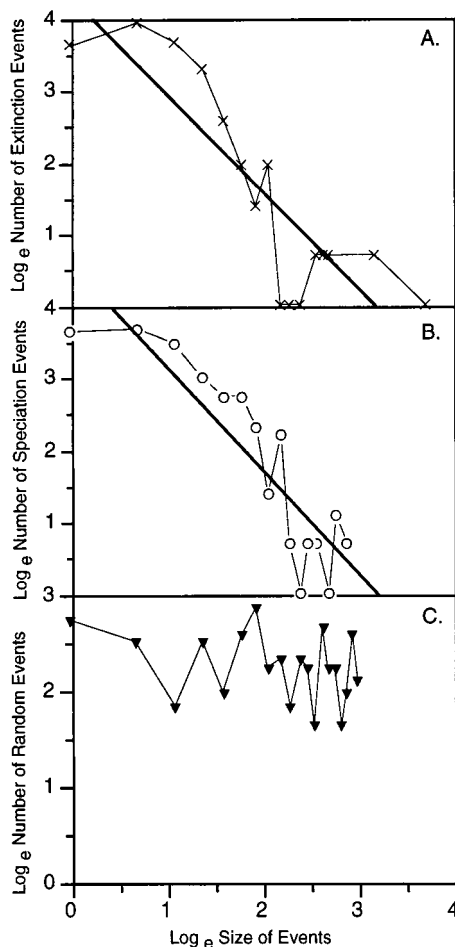


Figure 2. Log_e-log_e plot of event size vs. number of events for (A) planktic foraminiferal extinctions, (B) planktic foraminiferal speciations, and (C) uniform random data. Heavy lines are linear regression best-fit estimates. In A, linear correlation coefficient (r) = 0.86; in B, r = 0.89.

trast to random data (Fig. 4). Thus, the analysis confirms that there is a deterministic component to the signal, but there is certainly also a strong component of noise in the signal. In contrast, the data for speciation show no significant correlations and are seemingly random. Therefore, on the basis of the log-log plots, the return maps, and wimplex analysis, we conclude that the data, at least for the planktic foraminiferal extinction record, have an inherent organization.

Planktic Foraminiferal Extinction

Extinction events have received considerable attention in the past few years, particularly since Alvarez et al. (1980) proposed that the Cretaceous-Tertiary (K-T) boundary mass extinction could have been triggered by an extraterrestrial large-body impact. Since then, researchers have presented data suggesting that mass extinctions at other times through the Phanerozoic could also have been caused by similar impacts (Alvarez, 1987; Raup, 1992). This drift

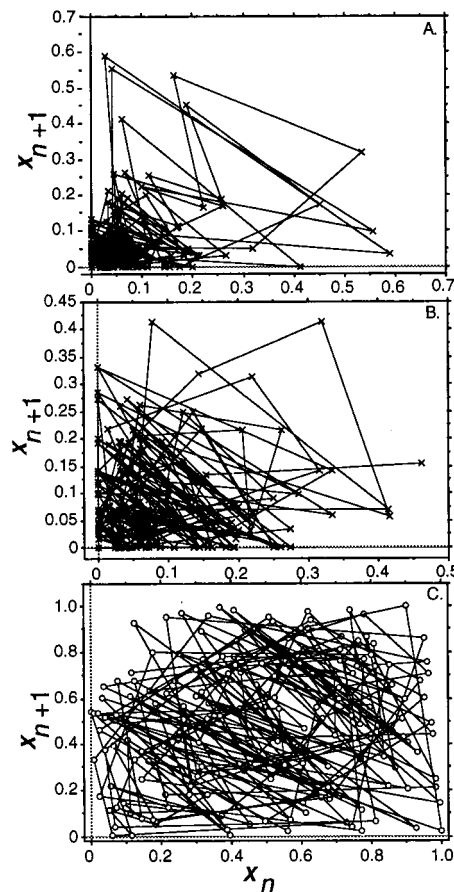


Figure 3. Return maps (plots of value at one event [x_n] vs. [x_{n+1}]) for (A) planktic foraminiferal extinctions, (B) planktic foraminiferal speciations, and (C) uniform random data.

within the paleontological community to a neocatastrophist outlook has culminated in the suggestion that perhaps as much as 60% of all extinctions have been caused by extraterrestrial agents (Raup, 1992). Under this scenario, a large-body impact would appear as a random event with respect to ecosystem dynamics.

Against this background, the results of our wimplex time series, return map analysis, and power-law tests indicate that planktic foraminiferal extinction processes are deterministic. In a reanalysis of Phanerozoic extinction data (as presented by Raup, 1986), Kauffman (1993) produced plots consistent with power-law behavior. Kauffman (1993) interpreted his plot (less linear than ours), based on limited Phanerozoic extinction data, as indicative of a deterministic system "on the frozen edge of chaos." Realizing the limitations of the data set—extinctions at the family level for the 79 stages of the Phanerozoic—Kauffman (1993) concluded that his results show that coevolutionary avalanches propagate through ecosystems, although frequency vs. size distribution are dependent on the parameters controlling the system. He suggested that with higher res-

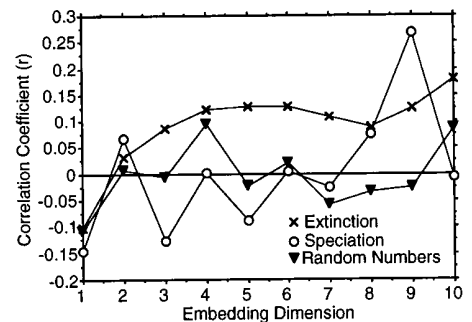


Figure 4. Wimplex time-series predictor analysis for planktic foraminiferal extinctions, planktic foraminiferal speciations, and uniform random data. Ordinate is linear correlation coefficient for predicted vs. actual values of time series as function of embedding dimension (abscissa).

olution data, this approach might be used to link both the impact of internally generated avalanches within the ecosystem and the extent of external perturbations (large-body impacts) to the distribution of extinction events. Our much higher resolution planktic foraminiferal data set more closely approximates a power law. Our results provide better evidence that every scale of recorded extinction events (including mass extinctions) can be explained as the natural interaction of perturbations to, and ecological cross linkages within, the system. Moreover, the data may best be interpreted as discrete, short-lived cascades rather than continuous processes, which are slow on the geologic time scale.

Hypotheses to explain foraminiferal extinction events include: (1) periodically recurring logistic-style events wherein the interdependencies caused by competition necessitate large drop-offs at population maxima; these population avalanches are followed by sharp rises of new successors (Eldridge, 1991); (2) periodic large extinction events driven by external events as predetermined by another system (e.g., large-body impact; Raup, 1992); (3) completely random extinctions driven by either internal or external stochastic events; (4) internally driven extinction processes where spontaneously derived interdependencies cascade through the ecosystem (McKinney, 1989; Plotnick and McKinney, 1993); and (5) some combination of hypotheses 2 and 4. We reject hypothesis 1 on the basis that speciation as well as extinction events in such a well-regulated system would have to be deterministic, or at least behave similarly. We reject hypothesis 2 because the data are not harmonic. However, it is conceivable that our results may be explained by extraterrestrial forcing at all scales, from microtectonics to large-body impacts. We reject hypothesis 3 because our extinction data do show organization.

Our results preclude neither hypothesis 4 nor hypothesis 5. On the basis of modeling of extinction processes using percolation theory, Plotnick and McKinney (1993) demonstrated that small disturbances can produce large extinctions, and large disturbances can produce small extinctions, depending on the degree of interdependency within the system. Thus, Raup's (1992) contention that species interactions are not sufficiently intense to generate mass extinctions can be dismissed. However, the idea that extinction may be triggered by random processes is not ruled out. Our results show the data to be partly deterministic, consistent with randomly generated events that either cause cascades or are damped by the ecosystem cross linking. Because of the interconnectedness of ecosystems (Plotnick and McKinney, 1993), the tempo and mode of planktic foraminiferal extinction dynamics can probably be extrapolated to other clades. Because of the general long-term stability of open-ocean ecosystems (Lazarus, 1983; Lazarus et al., 1995), the coevolutionary response (cascades) to similar stimuli in more ephemeral neritic and terrestrial environments (Tokioa, 1979) will probably be found to produce even more pronounced results than observed for the planktic foraminifera. However, our results do not preclude large-body impacts as an extinction mechanism. Certain mass-extinction events, such as the K-T boundary event, are demonstrably associated with a large-body impact. Other mass-extinction events for which such evidence is lacking could have been internally driven.

Planktic Foraminiferal Speciation

Our analyses provide contradictory results when applied to planktic foraminiferal speciation data. As observed in the extinction data, the slightly convex speciation plot (Fig. 2B) approaches a power law, suggesting that planktic foraminiferal speciation is deterministic. However, the return map of the speciation data is more scattered than that of extinction data, and the wimplex time series analysis provides no evidence of determinism. We must therefore conclude that evidence of determinism for planktic foraminiferal speciation is at best weak.

Eldridge (1991) argued that little intra-species or interspecies evolutionary change occurs until an external perturbation, such as a large-body impact, disrupts the ecosystem and causes species to become extinct. In this hypothesis, mass extinction is an important causal cornerstone of macroevolution, because it opens otherwise unavailable eco-space for new species. As discussed above, we would expect levels of determinism to be roughly equivalent for rates of both specia-

tion and extinction. However, because the speciation data are not nearly as deterministic as the extinction data, we presume that other factors impacting speciation must also be considered.

Random walks generated by genetic drift (Sheldon, 1990) may partially explain the less deterministic nature of planktic foraminiferal speciation. Genetic drift and clinal sympatric and parapatric speciation have been suggested as major modes of speciation in planktic foraminifera, because species are very broadly distributed in long-lived stable water masses, where peripheral isolates do not generally persist long enough to have evolutionary consequences (Lazarus, 1983; Bookstein, 1987; Lazarus et al., 1995).

The nature of n -dimensional niche space may also provide an explanation for our observations (Lewontin, 1983). Niche space in large homogeneous ocean masses is relatively stable. Following mass extinctions of planktic foraminiferal taxa in the open ocean, survivor generalist species become more widely distributed and inhabit broad swaths of the water column. Speciation events among planktic foraminifera result in the water column becoming more and more finely divided (Hart, 1980). As new species are inserted and old species are deleted, the nature of species interactions changes, because niches inhabited by any set of species at any particular time are the result of a complex set of biotic and abiotic interactions (Futuyma, 1986). New species, the product of selection pressures and preadaptations derived from genetic drift of selectively neutral characters, thus create their own new niches, never precisely identical to those inhabited by previous species, and are thus difficult to predict and seemingly random (Lewontin, 1983).

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