

Title:

Chaos, cyclicity and extinctions in the Phanerozoic record

Authors:

Inti Suárez (1) and Maria-Josefina Hernandez (2)

Addresses:

(1) Zoology Institute, University of Basel, Rheinsprung 9, 4051 Basel, Switzerland E-mail: suarez@ubaclu.unibas.ch

(2) Grupo de Biología Teórica, Instituto de Zoología Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Apartado 47058, Caracas 1041-A, Venezuela.

E-mail: mjhernan@strix.ciens.ucv.ve.

Correspondence should be sent to (1)

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Mass extinctions, fossil record, deterministic chaos, self-organized criticality, local forecasting, response-surface methodology.

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Inti Suárez⁽¹⁾ and **Maria-Josefina Hernandez**⁽²⁾

⁽¹⁾ Zoology Institute, University of Basel, Rheinsprung 9, 4051 Basel, Switzerland
(suarez@ubaclu.unibas.ch)

⁽²⁾ Grupo de Biología Teórica, Instituto de Zoología Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Apartado 47058, Caracas 1041-A, Venezuela
(mjhernand@strix.ciens.ucv.ve).

Abstract

The compilation of data on extinction and origination of taxa covering the whole history of life is the result of extensive work. This has been fundamental for a central issue in contemporaneous biology: the study of global biotic dynamics. Its analysis has proved controversial regarding the identification of the observed pattern. It has been proposed that mass extinction dynamics follow a cyclic behaviour. Alternatively, others suggest predominant linear trends.

In the last decade, deterministic chaos has emerged as an important phenomenon in natural dynamical processes. On the other hand, for some data, self-organized critical phenomena have been proposed, in which case the dynamics resemble chaotic ones, but arise from completely different causal mechanisms. Self-organized criticality arises from large dimensional attractors, while chaotic behaviour is typically produced by low dimensional mechanisms. Recent work has pointed to the existence of critical phenomena in mass extinction time series. The present paper analyses the marine family record of origination and extinction through the Phanerozoic, using methods devised for the study of short, noisy and irregular time series. Our results yield evidence for the existence of low dimensional attractors and also traces of self-correlated dynamics. This brings together both predominant hypotheses in a comprehensive understanding of global biotic dynamics.

1. Introduction

The quest for simple processes that could explain complex patterns is a major task in biology. The fossil record is a complex pattern that has been a continuous source of

controversy. During the last decade, D. Raup , J.J. Sepkoski (1982, 1984, 1986, 1988) have analysed the dynamics of the evolution of Phanerozoic marine families. The diversity curve of these families through geological time was interpreted as the result of diverse dynamical processes, both intrinsic (e.g., background origination and extinction rates) and extrinsic (e.g., meteorite impacts). The latter have been used to explain five massive diversity extinctions during the Phanerozoic: the so-called "big five". Undoubtedly, an interesting result of their analysis is the cyclicity of these mass extinctions, roughly occurring every 26 million years.

The analysis of this diversity curve has been widely debated, especially on statistical (Hoffman 1985; Quinn 1987; Gilinsky 1994) and taxonomic grounds (Patterson , Smith 1987; Foote 1996). An important criticism is the amount of noise present in this kind of time series (Noma , Glass 1987). Recent non-linear techniques of time series analysis, designed for the identification of deterministic chaos, can detect a wider scope of dynamic patterns than those techniques formerly employed (Ellner , Turchin 1995). They differentiate noise from signal by detecting a wider range of dynamic behaviour, equilibrium, cyclicity, autocorrelation and chaos. Chaos seems to occur more frequently in nature than the initial analyses of natural time series suggested (Godfray , Grenfell 1993; Ellner , Turchin 1995). This has deep implications in the way we understand them (Pimm 1991, Hastings et al. 1993). Sensitivity to initial conditions, the signature of chaos, implies that the dynamics of the system cannot be predicted because any disturbance will have macroscopic effects in the long run. Time-regular frequency alterations (quasi-periodic bursts) are expected in chaotic time series (Pei , Moss 1996). Detecting a chaotic regime in Raup , Sepkoski's database allows us to hypothesize that periodic mass extinctions and faunal recoveries might be the result of quasi-periodic events. The plausibility of a chaotic attractor governing the evolutionary record emerges if it is established that predominantly low dimensional processes determine the evolutionary dynamics of the Phanerozoic marine fauna.

In a recent paper Sole et al (1997) tested for the existence of self-similarity in patterns of biodiversity fluctuations along the Phanerozoic record. This would be an indication of intrinsic non-linear dynamics in the system, inducing a self-organized criticality behaviour. The authors found that the fluctuations of Phanerozoic extinctions can be characterized by a $1/f$ power spectrum. This result implicitly rejects low

dimensional and deterministic processes (such as cyclic or chaotic dynamics) underlying the marine metazoan evolution during the Phanerozoic. However, Kirchner , Weil (1998) show that Sole et al (1997) results are an artefact of the interpolation used in the data.

In contrast we find evidence of a simple dynamical process, a chaotic attractor, accounting for the record of extinctions during the Phanerozoic. This analysis was performed using no interpolation at all. None of the patterns we found are due to introduced correlation from our techniques of analysis.

In this paper we analyse Sepkoski's diversity database using methods for unravelling chaos in short and noisy time series. These techniques include the surface response methodology (Turchin , Taylor 1992) and a local forecasting method (Garcia et al. 1996) able to detect autocorrelated noise. One of the main findings of this study -evidence for a chaotic attractor- contradicts Sole et al (1997) results on the predominance of long-term correlation. However, we also found evidence for self-correlated phenomena, which suggests that the interaction of both intrinsic and extrinsic dynamical processes is responsible for the macroevolution of marine metazoans during the Phanerozoic.

2. Data and analysis

The Compendium of Fossil Marine Animal Families of the Phanerozoic is the source of data for our analysis (Sepkoski 1992). There are 4045 animal families registered; the first and last dates of occurrence are given in a 160 steps time scale (Harland et al. 1990). Those families for which no precise dates were given were excluded from the analysis to avoid posterior biases. In order to correct for the biodiversity available within each age, we took the ratio of extinct to living families in each time interval. The resultant time series is displayed in figure 1. Total and partial autocorrelation plots, also shown in figure 1, suggest the existence of cyclicity. However this result has to be taken only as a heuristic proposal since for autocorrelation analysis the data were interpolated in order to obtain a regular time series. As was commented above, any interpolation (even assuming the least possible for autocorrelation: a uniform extinction rate inside each time step) can distort the dynamics for further study. The rest of the analyses to follow were carried out using the time series without any interpolation.

For the response-surface analysis the data was log transformed to eliminate the well-known tendency of this ratio to increase as present time is closer - "Pull of the present effect" (Pease 1992; Gilinsky 1994) - and make the series stationary. The surface response technique has been proved and validated in several ecological time series (Turchin , Taylor 1992; Perry at al. 1993; Ellner , Turchin 1995). Its main appeal comes from the integration of model fitting and the Ruelle-Takens theorem, which permits the reconstruction of a multivariable dynamical system with one variable and its delays. The fitted model is an extension of the well-known Hassel model of population growth (Turchin , Taylor 1992). This is:

(1)

The parameters A_i and θ_i were estimated from the data, using nonlinear regression provided by SPSS statistical software. The model is iterated and the resultant dynamics are reconstructed in phase space (Turchin , Taylor 1992). This strategy is more appropriate than the estimation of a Lyapunov exponent from the fitted model (Ellner , Turchin 1995), as we focus in the general pattern of the extinction dynamics.

The forecasting technique used here (Garcia et al. 1996) is a conceptual expansion of previous work (Casdagli 1992, Jimenez et al. 1992). It uses Kronecker's delta metrics, which allows us to distinguish between white and coloured noise.

3. Results

(a) Response-surface methodology

Table 1 shows the coefficients of the fitted model. It is important to note that the R^2 values, which describe the amount of non-explained variation of the data, are quite high: 57 % and 48 %. The row of values corresponding to 92* are the coefficients of the log transformed time series.

Figure 2 displays a simulation of the model reconstructed in phase space. It is observed that most of the points lie on a straight line suggesting a main linear trend, but these clearly embody also pseudoperiodical outbursts.

(b) Local forecasting

Figure 3a shows the performance of the forecaster with increasing embedding dimension. The maximum of the curve indicates that four is a plausible dimension for

the attractor of the system. A worse performance is expected if either a lower or a higher dimension is used. For comparison, the performance of the forecaster for these data is displayed with forecasters estimated from simulated data (see figure 3b). The extinction series seems to converge to a plateau. This behaviour is qualitatively different from that of white noise, but not from the simulated chaotic or coloured noise. This suggests that a quasiperiodic deterministic process such as a strange attractor can account for part of the dynamics, and that we can definitely discard the predominance of a random walk in the Phanerozoic extinction record. This agrees with earlier work by Raup , Sepkoski (1982, 1984, 1986, 1988), in which a periodic component of the dynamics was identified, but is a conclusion reached from a different dynamic approach. This result points to the existence of an intrinsic cyclicity in the analysed data.

Thus, it is relevant to add to this predominant hypothesis the similarity of the dynamics with autocorrelated simulated data. Which, on the other hand, takes us back to the point of self-correlated phenomena in the extinction dynamics discussed earlier. Note that if this were the underlying predominant mechanism, the data would resemble a stable time series, with outbreaks caused by magnified noise through long term correlations, and in which mass extinctions play no special role in the diversification of life (Benton 1995). Courtillot , Gaudemer (1996) analysed related data and also concluded that there is not a unique mechanism to explain the observed pattern.

Hence, the similarity of this time series with an autocorrelated process agrees with Solé et al's (1997) proposition of self-correlated phenomena in extinction dynamics, but our result was reached without any interpolation. On the other hand, the existence of an optimal embedding dimension contradicts their rejection of low dimensional chaos.

4. Discussion

The fact that most of the points in phase space lie on a line (in both detrended and raw data) supports previous results by M. Benton, who proposed mainly exponential growth in origination and extinction dynamics through time (Benton 1995). The occurrence of significant and pseudoperiodical mass extinctions (bigger loops in phase space reconstruction) confers a more comprehensive view. This result makes clear how

Benton's statement can greatly benefit from that of Sepkoski , Raup's periodicity of mass extinction, in order to explain the whole dynamical pattern.

The non-linear coefficient in the response-surface analysis reinforces earlier claims about the intrinsic non-linearity of this system (Solé et al. 1997; Courtillot , Gaudemer 1996). It was considered before as evidence for the existence of time delayed interactions between the organisms that generate the time series (Turchin 1993). Thus, if the dynamics of families represent the dynamics of species (Raup , Sepkoski 1988), our analysis suggests interactions between species through time. This view is coherent with a global understanding of the complex phenomena under study, in which phylogenetically related species, hence families, are providing the raw data.

It is already known that pseudoperiodical "catastrophes" are observed in autocorrelated time series, not generated by low dimensional attractors. In the analysis devised to distinguish between coloured noise and deterministic dynamics a high similarity was obtained between the extinction and autocorrelated simulated data. This supports the view that the macroscopic phenomena observed are mainly the outcome of complex biological interactions. However, the existence of an optimal embedding dimension is still evidence of a low dimensional attractor. Again, more than one kind of causal process has to be invoked to account for the whole phenomenological pattern. We believe our results show the coexistence of long term correlations, and a lower dimensional mechanism, such as cyclicity in global asteroids shower (Raup 1979).

The iterations of the response-surface model show a different recovery pattern, and a different maximum recovery height follows each 'mass extinction'. These can be interpreted as evolutionary bottlenecks -as proposed for the K-T mass extinction (Raup 1979)- which shift the system to distinct states after each mass extinction. This agrees with the proposal of different 'faunas' after each mass extinction (Sepkoski 1979, Courtillot , Gaudemer 1996), and also with the geographic variation in patterns of biotic recovery (Jablonski 1998), which may reflect sensitivity to initial conditions: a sign for the presence of deterministic chaos. Our analysis supports exponential growth periods punctuated by pseudoperiodical mass extinction, a conclusion reached before with different techniques (Courtillot , Gaudemer 1996), here supported from analyses designed to deal with short and noisy time series (Ellner , Turchin 1995).

Our conclusion is that a definitive discrimination between autocorrelated and chaotic processes cannot be established for this time series. The use of modern non-linear techniques for short and noisy data overcomes weak points in previous works. The existence of quasiperiodic mass extinction (Raup , Sepkoski 1988) is still maintained, and so is the growth of the origination-extinction dynamics of the Phanerozoic biota (Benton 1995). Both views are complementary results from the analysis.

Acknowledgments

This work would have not been possible without the help of M. Sanchez and R. Cipriani in obtaining the data. We are indebted to J. Jimenez for kindly assisting us with the forecasting technique. Relevant discussions during the analysis were carried out with D. Rodriguez, E. Klein, G. Gutierrez, O. Arenas, O. Linares, M. Benado and D. Vizoso. Finally, the comments of R. Cipriani, M. Doebeli, S. Stearns and R. May greatly improved the written version.

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Figure Captions

Figure 1. Analysed time series (heavy line). Ratio of alive/extinct families through geological intervals in millions of years. Total (ACP) and partial (PACP) autocorrelation plots, on an interpolated time series generated from the one shown here, assuming uniform rate of extinction in each time interval.

Figure 2. Phase space reconstruction of data generated by the response surface estimated model. The total number of iterations (data points) is the same as in the original time series. Two views from the same iteration are shown: (a) highlights that the majority of data points lie on a straight line. (b) A “frontal view” shows clearly the “loops” interpreted as mass extinctions.

Figure 3. Local Forecasting results. (a) Slope of the ratio = probability of the best predictor being the closest neighbour / the number of neighbours used to construct the forecast. A slope of -1 corresponds to a completely stochastic process. The embedding dimension used is in the x axis. (b) Centred correlation between predicted and real data vs the steps in the future in which the prediction is done. The analysis is essayed on the time series of ratio extinct/alive families and compared with similar simulated long time series (see text).

Short title

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Key words

Deterministic chaos, mass extinctions, fossil record, self-organized criticality, local forecasting, response-surface methodology.

Figure 1
Suárez & Hernandez

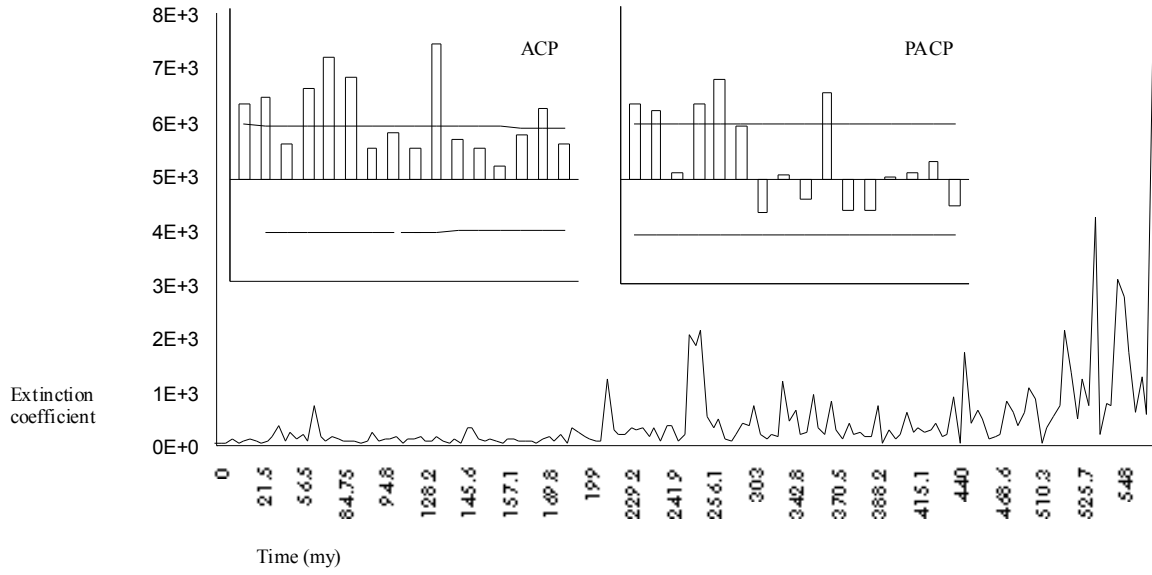


Figure 2
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