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Correlations in fossil extinction and origination rates through geological time

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Recent analyses have suggested that extinction and origination rates exhibit long-range correlations, implying that the fossil record may be controlled by self-organized criticality or other scale-free internal dynamics of the biosphere. Here we directly test for correlations in the fossil record by calculating the autocorrelation of extinction and origination rates through time. Our results show that extinction rates are uncorrelated beyond the average duration of a stratigraphic interval. Thus, they lack the long-range correlations predicted by the self-organized criticality hypothesis. In contrast, origination rates show strong autocorrelations due to long-term trends. After detrending, origination rates generally show weak positive correlations at lags of 5–10 million years (Myr) and weak negative correlations at lags of 10–30 Myr, consistent with aperiodic oscillations around their long-term trends. We hypothesize that origination rates are more correlated than extinction rates because originations of new taxa create new ecological niches and new evolutionary pathways for reaching them, thus creating conditions that favour further diversification.

Keywords: extinction; origination; fossil record; autocorrelation; macroevolution; self-organized criticality

1. INTRODUCTION

Patterns in the fossil record have long been sought as keys to understanding evolutionary mechanisms. It has been proposed that self-organized critical mechanisms control evolution through geological time (Bak & Sneppen 1993; Solé & Manrubia 1996; Solé *et al.* 1999); this hypothesis implies that extinction time-series should be fractal and, thus, that extinction rates should be correlated over all time-scales. Newman & Eble (1999) used Fourier transform power spectra to argue that extinctions are correlated over time-scales of up to 40 million years (Myr) and Solé *et al.* (1997) used power spectra to argue that both originations and extinctions are autocorrelated over hundreds of millions of years—many times the life span of individual species, genera or families. However, the power spectrum is an indirect and imprecise tool for measuring how tightly an extinction or origination time-series is correlated with itself through time. The autocorrelation function is a better tool because it measures the correlation between points on a time-series directly as a function of the lag interval between them. Here, we use autocorrelation functions to test for correlations in 24 fossil extinction and origination time-series.

2. DATA SOURCES

Our source data are Sepkoski's unpublished compilations of fossil marine invertebrate families and genera, as described in Sepkoski (1993, 1996), with updates through 1997, and *The fossil record 2*, a global compendium of plant and animal families (Benton 1993). *The fossil record 2* uses the Harland *et al.* (1990) time-scale, which consists of 76 stratigraphic stages of 1–34 Myr in length, from the Cambrian through the Pleistocene. Sepkoski aggregated some stratigraphic stages and subdivided others, creating a time-scale with 106 intervals of 2.5–12.5 Myr in length covering the same span of time. Since Sepkoski's time-scale contains more stratigraphic intervals and their boundaries are more evenly spaced, his data sets can provide more precise information about correlations through time.

To minimize the influence of Lagerstätten and monographic effects (Sepkoski 1996), we excluded all taxa that occur in only one stratigraphic interval ('singletons'). We assigned all originations within a given interval to the stratigraphic boundary that begins it and all extinctions to the stratigraphic boundary that ends it; other possible assignments (e.g. to the midpoint of each interval) give similar results in the analysis that follows.

Because the suitability of different extinction and origination metrics is controversial (Foote 1994; Gilinsky 1991), we analysed all four that are in common use: (i) counts of first or last occurrences per stratigraphic interval, (ii) counts per million years (counts in each stratigraphic interval, divided by interval length), (iii) percentages per interval (counts divided by total diversity) and (iv) percentages per million years (counts divided by total diversity and interval length). For simplicity, we will refer to all four of these metrics as extinction or origination 'rates' because we will not generally need to distinguish between per-interval metrics and per-million-year metrics. We will refer to metrics which are normalized by total diversity as percentage or per-taxon rates.

3. AUTOCORRELATION METHODS FOR UNEVENLY SPACED DATA

In order to obtain the autocorrelation function of an evenly spaced time-series, the conventional Pearson

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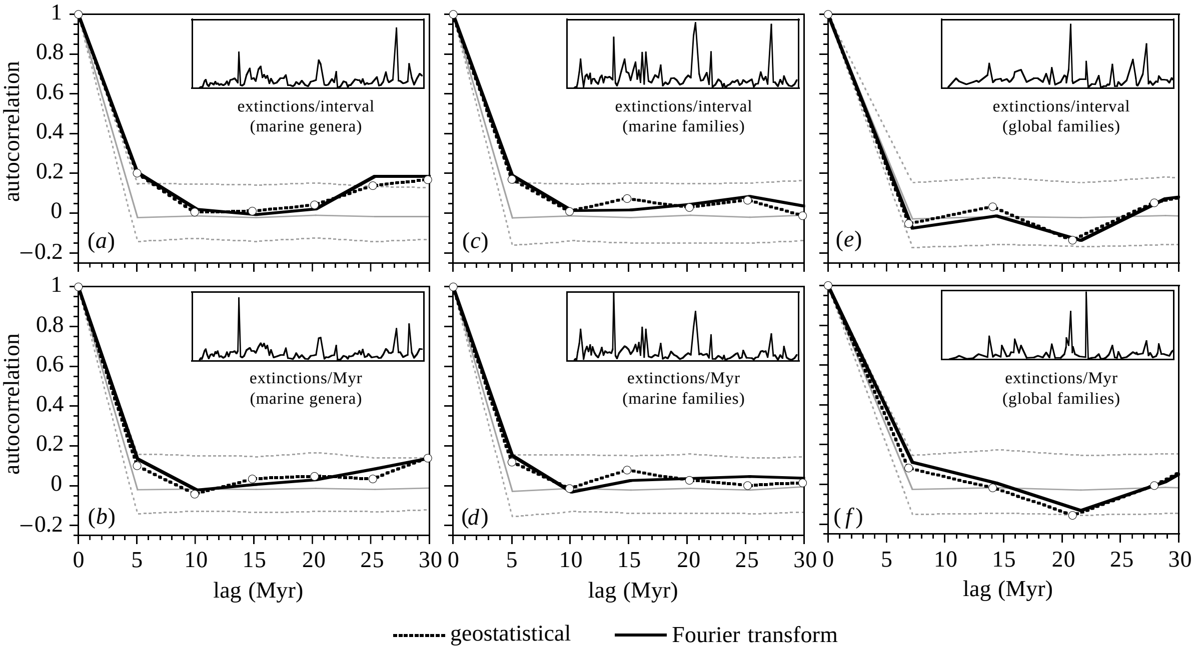

Figure 1. Fossil extinction time-series and their associated autocorrelation functions. The extinction rates are expressed as extinctions per interval (*a*,*c*,*e*) and extinctions per million years (*b*,*d*,*f*) for marine genera (*a*,*b*), marine families (*c*,*d*) and global families (*e*,*f*). The heavy solid line shows the autocorrelation calculated by the Fourier transform method (equation (3)) and the heavy dotted line shows the geostatistical autocorrelation (equation (2)). The thin grey reference line shows the median autocorrelation (calculated by the Fourier transform method) for 1000 uncorrelated data sets, each obtained by randomly reshuffling the original data. The two dotted grey reference lines delimit the upper and lower 5% of the autocorrelations observed in these 1000 randomly reshuffled data sets. The inset figure in each panel shows the raw time-series. The time-axis for each inset figure runs from 550 Myr before the present to the end of the Pleistocene.

product-moment correlation between points separated by a fixed number of steps is calculated, i.e.

$$r(k) = \frac{\mathrm{cov}(X_i,X_{i+k})}{\mathrm{s.d.}(X_i)\mathrm{s.d.}(X_{i+k})},$$
$$= \frac{\left\langle (X_i - \langle X_i\rangle)(X_{i+k} - \langle X_{i+k}\rangle)\right\rangle}{\sqrt{\left\langle (X_i - \langle X_i\rangle)^2\right\rangle}\sqrt{\left\langle (X_{i+k} - \langle X_{i+k}\rangle)^2\right\rangle}}, \qquad (1)$$

where X_i and X_{i+k} are the values of the time-series at pairs of points separated by a lag of k steps and angled brackets indicate averages. This direct approach should not be applied to the fossil record, because stratigraphic boundaries are unevenly spaced in time. Nor should one even out the spacing by interpolating within each stratigraphic interval, because this introduces artefactual correlation among the interpolated points (Schulz & Stattegger 1997; Kirchner & Weil 1998). Instead, we make a geostatistical approximation (Agterberg 1970) to the autocorrelation function by calculating the correlation between all pairs of points X_i and X_j whose separations in time, $t_j - t_i$, fall within a specified range of lag time rather than pairs of points separated by a fixed number of steps, i.e.

$$r(\tau) = \frac{\left\langle (X_i - \langle X_i\rangle)(X_j - \langle X_j\rangle)\right\rangle}{\sqrt{\left\langle (X_i - \langle X_i\rangle)^2\right\rangle}\sqrt{\left\langle (X_j - \langle X_j\rangle)^2\right\rangle}}$$
$$\forall i,j\colon \tau - \frac{\Delta\tau}{2} < t_j - t_i < \tau + \frac{\Delta\tau}{2}. \qquad (2)$$

Equation (2) approximates $r(\tau)$, the autocorrelation at a lag of τ Myr, using the correlation between all pairs of points whose separations in time, $t_j - t_i$, fall within a bin of width $\Delta\tau$ centred around τ. In the analysis which follows, we calculate autocorrelations every $\Delta\tau = 5$ Myr for Sepkoski's data and every $\Delta\tau = 7$ Myr for *The fossil record 2* (approximately the average spacing between points in each data series).

One can also calculate the autocorrelation function of an unevenly spaced time-series from its Fourier transform (Scargle 1989). The power spectrum of a time-series is the Fourier transform of its autocorrelation function (Bracewell 2000) and, therefore, the autocorrelation function is the inverse Fourier transform of the power spectrum, i.e.

$$r(\tau) = FT^{-1}(FT\{X\}FT^{*}\{X\}) = FT^{-1}(|FT\{X\}|^2), \qquad (3)$$

where $r(\tau)$ is the autocorrelation of a time-series X at a lag of τ Myr and FT, FT^{*} and FT^{-1} denote the (complex) Fourier transform, its complex conjugate and its inverse, respectively. This approach is useful because we can calculate the Fourier transform of X from the unevenly spaced fossil data directly, without interpolation, using the Lomb–Scargle Fourier transform (Lomb 1976; Scargle 1982, 1989; Press & Rybicki 1989). When applied to unevenly spaced data, the Lomb–Scargle algorithm has statistical properties similar to those of conventional Fast Fourier Transform algorithms applied to evenly spaced data (Scargle 1982). The geostatistical and Fourier transform approaches (equations (2) and (3), respectively) generally yield similar results, as shown in figures 1–4.

Geostatistical and Fourier transform methods can also be used to calculate the cross-correlation between extinction and origination rates, that is, to measure how closely extinction and origination time-series resemble each other

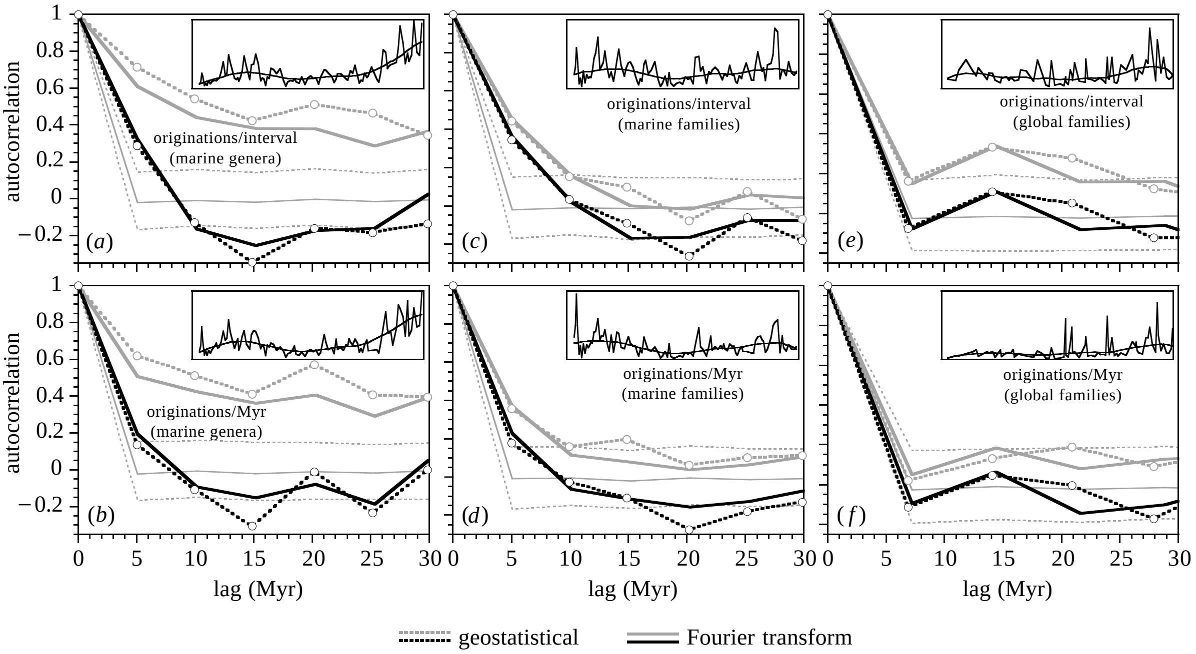

Figure 2. Fossil origination time-series and their associated autocorrelation functions. The inset figure in each panel shows the raw time-series and the long-term trend estimated by LOWESS (see § 5). The autocorrelation functions of the detrended and non-detrended origination rates are shown by heavy black and heavy grey lines, respectively. The Fourier transform autocorrelations are indicated by heavy solid lines and the geostatistical autocorrelations are indicated by heavy dotted lines. The thin, dotted, grey reference lines show the median, fifth percentile and 95th percentile of the autocorrelations in the randomly reshuffled data sets. The origination rates for marine genera (*a*,*b*), marine families (*c*, *d*) and global families (*e*, *f*) are expressed as originations per interval (*a*, *c*, *e*) and originations per million years (*b*, *d*, *f*).

when one is shifted forwards or backwards by a specified lag interval. We have presented results from such a cross-correlation analysis elsewhere (Kirchner & Weil 2000).

4. AUTOCORRELATIONS IN FOSSIL EXTINCTION RATES

Figure 1 shows our calculated autocorrelation functions for the extinction rates (per stratigraphic interval and per million years) in the three fossil databases (marine genera, marine families and global families). Any autocorrelation function converges to a value of one at lags approaching zero because any time-series is perfectly correlated with itself if there is no lag. Therefore, the autocorrelation near-zero lag is not diagnostic. Instead, the correlation structure in the time-series is best reflected in the autocorrelation function at lags equal to or greater than the average data spacing (*ca.* 5 Myr for Sepkoski's marine genera and families and 7 Myr for *The fossil record 2*). At all of these lags, all of the extinction time-series exhibit very weak autocorrelation.

It is useful to compare the observed autocorrelations in the extinction rates against the range of autocorrelations which might arise by chance in random uncorrelated time-series. We evaluated this null hypothesis for each of the panels in figure 1 by randomly reshuffling the original data sets 1000 times and calculating the autocorrelation functions of each of these random uncorrelated time-series. We kept the same stratigraphic boundaries as in the fossil data sets, but randomly reassigned the extinction data among those boundaries. Reshuffling the data preserves the original values while destroying any serial correlation between them. The median autocorrelation in these reshuffled data sets is shown by the thin grey solid line in each panel, while the thin grey dotted lines delimit the upper and lower 5% of the autocorrelations observed at each lag in these null hypothesis data sets.

The autocorrelation functions of the extinction rates generally lie well within the range of autocorrelations expected for randomly reshuffled and, therefore, uncorrelated data (figure 1). There is a slight tendency for the extinction rates of marine families and genera to be positively correlated at lags near 5 Myr. This might be expected even without any serial correlation in the actual extinction rates, because the Signor–Lipps effect (Signor & Lipps 1982) may smear apparent extinctions backwards in time and, thus, create some degree of positive correlation at short lags. Alternatively, this weak autocorrelation may indicate that the extinction rates are correlated, but over time-scales which are too short to be reliably reflected in Sepkoski's data sets, given their average interval length of 5 Myr.

The visual impression given by figure 1 is that, in general, the extinction rates are not significantly more autocorrelated than random data. We quantified the statistical significance of the observed autocorrelations using Monte Carlo methods. First, we measured how much the real fossil data's autocorrelation deviated from the median of the 1000 null hypothesis data sets' autocorrelations at each lag from 5 to 30 Myr. Next, we scored the deviation from the null hypothesis in two ways: (i) by taking the largest deviation from the null hypothesis at any lag, and (ii) by taking the root mean square (RMS) of all of the deviations, i.e.

$$\text{RMS deviation} = \langle [r_{\text{data}}(\tau_k) - \text{median}(r_{\text{null}}(\tau_k))]^2 \rangle^{1/2}. \quad (4)$$

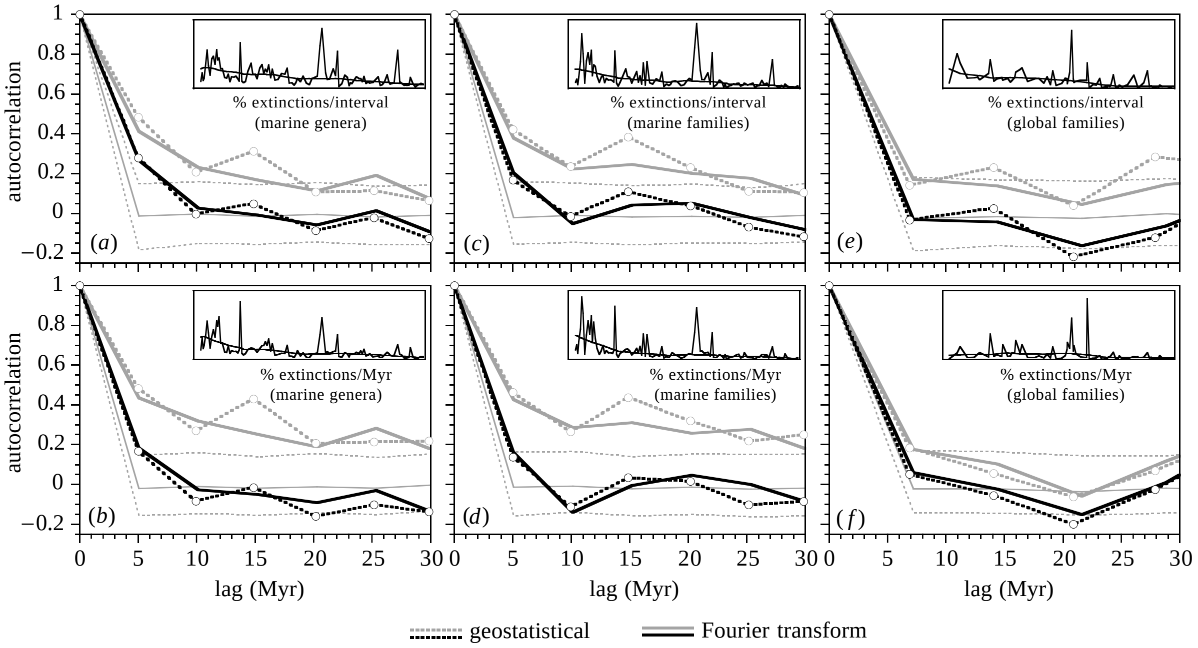

Figure 3. Per-taxon extinction time-series and their associated autocorrelation functions with lines and symbols as in figure 2. The percentage extinction rates for marine genera (a, b), marine families (c, d) and global families (e, f) are expressed as extinctions per taxon per interval (a, c, e) and extinctions per taxon per million years (b, d, f).

We repeated these calculations for each of the 1000 randomly shuffled data sets and tallied the fraction of cases in which the peak or RMS deviation in the randomized data exceeded the peak or RMS deviation for the real fossil data. This procedure answers the question 'What are the chances that random, uncorrelated time-series could yield autocorrelations as large—positive or negative—as those observed in the real fossil extinction rates?' The results from this Monte Carlo analysis (table 1) show that the autocorrelations in the fossil extinction rates are usually small enough that they could readily arise by chance in random uncorrelated time-series.

5. AUTOCORRELATIONS IN FOSSIL ORIGINATION RATES

Unlike the extinction time-series shown in figure 1, the origination time-series shown in the insets in figure 2 exhibit significant long-term trends through time. These trends could reflect biological mechanisms (Van Valen & Maiorana 1985; Sepkoski 1998) or biases in the fossil record, such as the 'pull of the Recent'. Whatever their cause, long-term trends can create artefactual correlations between nearby points and, thus, could potentially confound our analysis of the short-term autocorrelations. Consider, for example, a time-series consisting of white noise fluctuations superimposed on a long-term rising trend. All of the data points that are early (or late) in the series will be correlated with each other; their values will be low (or high) on average compared to the rest of the data set. Thus, the autocorrelation function for such a data set could show significant short-range correlation (because points close together in time will be more similar than points far apart) even if the only source of correlation is the long-term trend. The strength of this misleading autocorrelation will depend on the length of the record and the steepness of the trend compared to the amount of short-term variation in the data.

When analysing short-term correlations in data sets with long-term trends, those trends should first be subtracted. A common procedure is to choose a functional form (such as a polynomial or exponential) and then fit this function using least-squares regression. However, with highly skewed data, such as many fossil time-series, least-squares fitting can produce significant artefactual correlation: a single high data point can deflect the fitted function upwards in the region nearby, thus deflecting all the adjacent residuals downwards and creating artefactual correlation among them. To minimize this problem, we estimated long-term trends in the fossil time-series using LOWESS, a robust, flexible curve-fitting technique which ignores extreme data points (Cleveland & McGill 1984). We set the LOWESS smoothing window width at 200 Myr; this makes the LOWESS fits flexible enough to follow the long-term pattern in the data, but stiff enough to preserve the short-term fluctuations. The LOWESS curves are shown superimposed on the fossil data in the inset panels in figure 2.

The autocorrelation functions of the origination time-series are shown by heavy grey lines (undetrended data) and heavy black lines (detrended data) in figure 2. For the marine genera in particular, long-term trends create significant correlations in the origination rates. The long-term trends produce similar, though much smaller, autocorrelations in the marine and global family data sets. Comparing the six panels in figure 2, one sees that the short-term correlations in the undetrended origination rates (heavy grey lines) are approximately proportional to the amplitudes of the long-term trends. This suggests that the long-term trends are largely responsible for the short-term autocorrelations in the undetrended origination data.

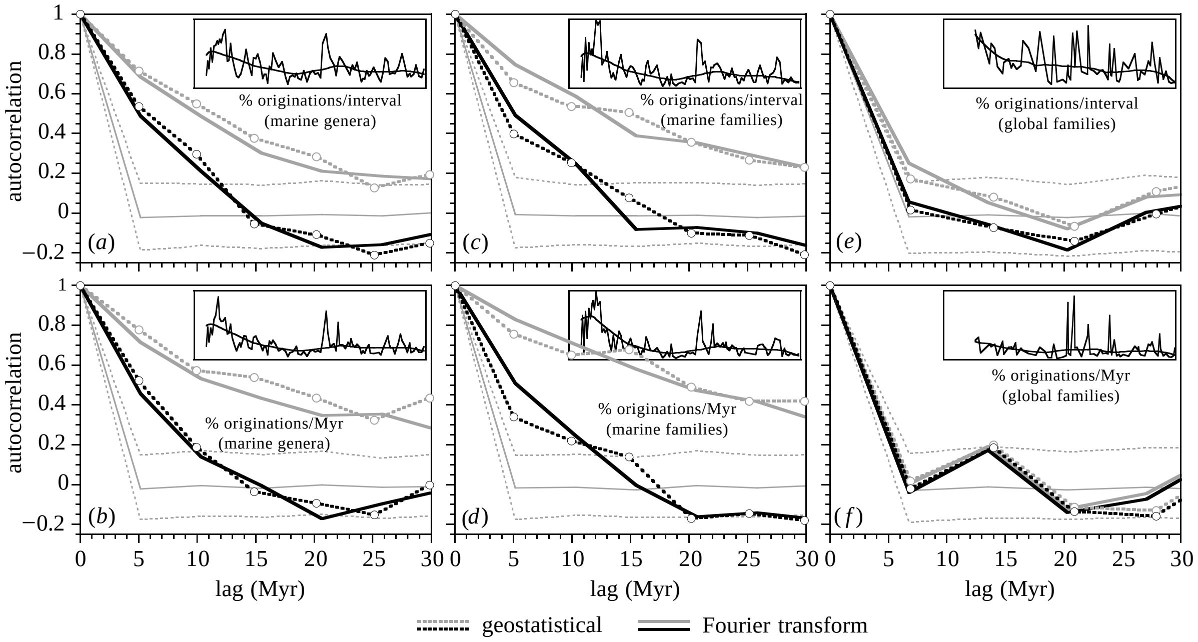

Figure 4. Per-taxon origination time-series and their associated autocorrelation functions with lines and symbols as in figure 2. The first four data points in the record were omitted from the inset graphs and autocorrelation calculations because their low levels of standing diversity lead to anomalously high per-taxon origination rates. The percentage origination rates for marine genera (*a*, *b*), marine families (*c*, *d*) and global families (*e*, *f*) are expressed as originations per taxon per interval (*a*, *c*, *e*) and originations per taxon per million years (*b*, *d*, *f*).

This conjecture is confirmed by the autocorrelation functions of the detrended origination time-series (heavy black lines in figure 2). When the long-term trends are removed, the marine genera and marine families show weak positive correlations at lags of 5 Myr, followed by weak negative correlations at lags of 10–30 Myr. These correlation functions suggest that the origination rates oscillate erratically around a long-term trend. Even after detrending, the origination rates in marine genera and marine families exhibit stronger autocorrelation than would be expected by chance (table 1).

In contrast, the origination rates in the global family data do not show significant autocorrelation at any lag after detrending (table 1 and figure 2*e*,*f*). There are at least three reasons why origination rates might be less autocorrelated in *The fossil record 2*'s global family data than in Sepkoski's marine genera and family data. First, the time-scale on which *The fossil record 2* is compiled contains fewer stratigraphic intervals and its intervals are more uneven in length. As a result, fossil data compiled on *The fossil record 2*'s time-scale (Harland *et al.* 1990) will not reflect any underlying correlations as accurately as will compilations on Sepkoski's (1996) time-scale. Second, whereas Sepkoski's database contains only marine animals, *The fossil record 2* includes both plants and animals in both terrestrial and marine habitats. Origination rates could be autocorrelated within individual taxonomic groups or habitats, but these correlations could be obscured when groups or habitats with out-of-phase fluctuations are combined. Third, because *The fossil record 2* and Sepkoski's database were compiled by different investigators using somewhat different approaches, the underlying data in the two databases may be different in ways which affect the autocorrelation of their origination rates. Because both of these databases are in wide use, they merit a systematic comparison; to our knowledge no such comparison has yet been published.

6. AUTOCORRELATIONS IN PER-TAXON EXTINCTION AND ORIGINATION RATES

The per-taxon extinction and origination rates, that is the extinction and origination rates corrected for total diversity, generally trend downwards through time (figure 3). Because these downward trends could generate spurious autocorrelation, we removed them by LOWESS detrending. In addition, because the very low levels of standing diversity early in the record lead to anomalously high per-taxon originations, we excluded the first four per-taxon origination data points from our autocorrelation calculations.

Before detrending, the per-taxon extinction rates exhibit significant correlation through time (figure 3). Similar autocorrelations were previously found for marine per-taxon extinction rates by Quinn (1987) who used equation (1) rather than the more rigorous approaches used here. However, after detrending, the per-taxon extinction rates exhibit no statistically significant short-term autocorrelation for lags longer than 5 Myr (figure 3 and table 1). This indicates that almost all of the apparent autocorrelation in the per-taxon extinction rates is due to their long-term declining trends. When these trends are removed, the per-taxon extinction rates exhibit the same lack of short-term autocorrelation observed in extinction rates that have not been corrected for standing diversity (figure 1).

Before detrending, the per-taxon origination rates in the marine record show significant correlation through time (figure 4*a*–*d*); after detrending, they show significant

Table 1. *Statistical significance of autocorrelations in fossil extinction and origination rates*

(p(peak) and p(RMS) are the fractions of randomly shuffled data sets with peak or RMS autocorrelations equalling or exceeding those observed in the fossil time-series, respectively. Low values of p(peak) and p(RMS) (shown in bold) indicate levels of autocorrelation which are unlikely to occur by chance in random data. An asterisk indicates LOWESS-detrended data (see § 5).)

		geostatistical method		Fourier transform method	
metric and database	figure	p(peak)	p(RMS)	p(peak)	p(RMS)
extinctions per interval					
marine genera	1*a*	0.16	0.07	0.08	**0.04**
marine families	1*c*	0.28	0.38	0.12	0.20
global families	1*e*	0.71	0.69	0.63	0.63
extinctions per Myr					
marine genera	1*b*	0.40	0.36	0.31	0.35
marine families	1*d*	0.49	0.59	0.22	0.34
global families	1*f*	0.55	0.50	0.39	0.39
originations per interval					
marine genera*	2*a*	< **0.01**	< **0.01**	< **0.01**	< **0.01**
marine families*	2*c*	< **0.01**	< **0.01**	< **0.01**	< **0.01**
global families*	2*e*	0.76	0.71	0.76	0.76
originations per Myr					
marine genera*	2*b*	**0.02**	**0.01**	0.11	**0.04**
marine families*	2*d*	**0.05**	**0.03**	**0.04**	**0.04**
global families*	2*f*	0.58	0.55	0.71	0.57
extinctions per taxon per interval					
marine genera*	3*a*	**0.04**	0.12	**0.01**	0.07
marine families*	3*c*	0.35	0.36	0.10	0.24
global families*	3*e*	0.31	0.36	0.51	0.64
extinctions per taxon per Myr					
marine genera*	3*b*	0.34	0.23	0.14	0.29
marine families*	3*d*	0.55	0.57	0.25	0.30
global families*	3*f*	0.30	0.36	0.43	0.45
originations per taxon per interval					
marine genera*	4*a*	< **0.01**	< **0.01**	< **0.01**	< **0.01**
marine families*	4*c*	< **0.01**	< **0.01**	< **0.01**	< **0.01**
global families*	4*e*	0.80	0.89	0.51	0.65
originations per taxon per Myr					
marine genera*	4*b*	< **0.01**	< **0.01**	< **0.01**	< **0.01**
marine families*	4*d*	**0.01**	< **0.01**	< **0.01**	< **0.01**
global families*	4*f*	0.20	0.20	0.27	0.34

positive correlations at lags of 5–10 Myr and negative correlations at lags of 20–30 Myr. These patterns are qualitatively similar to but quantitatively stronger than the patterns observed in figure 2. The per-taxon origination rates in the global family database do not show significant autocorrelation, with or without detrending, presumably for the reasons outlined at the end of § 5 (figure 4*e*–*f*).

7. DISCUSSION

Our calculations show that fossil extinction rates exhibit almost no correlation through time, except for that which arises artefactually from long-term trends in per-taxon extinction statistics. This result is robust across both of our analysis techniques (the geostatistical method and the Fourier transform method), all three of our data sets (marine genera, marine families and global families) and all four of our metrics (extinctions per stratigraphic interval, extinctions per unit time, extinctions per taxon per interval and extinctions per taxon per unit time). The three statistically significant extinction correlations in table 1 (6% of the 48 statistical tests performed) are almost exactly the 5% that one would statistically expect to arise by chance in the absence of any underlying correlation in the extinction data.

Therefore, although the long-term trends in the fossil record produce apparent correlation, our analysis does not support recent suggestions that self-organized criticality produces long-range correlations in extinction rates (Solé *et al.* 1997, 1999; Hewzulla *et al.* 1999). The hypothesis that macroevolution is controlled by self-organized critical mechanisms (Bak & Sneppen 1993; Sneppen *et al.* 1995; Solé & Manrubia 1996) implies that extinction time-series should exhibit fractal $1/f$ scaling (Bak *et al.* 1987; Solé *et al.* 1997; Pelletier 1999). Such fractal time-series would be autocorrelated over all time-scales, exhibiting long-range correlations and even stronger short-range correlations. Since fossil extinction rates do not exhibit significant short-term correlations (figures 1 and 3), it is unlikely that their longer-term correlations are internally generated. It is more plausible that the long-term trends in fossil extinction and origination rates result from gradual shifts in overall diversity and evolutionary processes through time, from long-term changes in fossil preservation and geological exposure, and from variations in palaeontological sampling and taxonomic practices.

Our findings contradict recent studies that used spectral analyses to infer long-range correlations in extinction rates. Solé *et al.* (1997) calculated power spectra for many extinction and origination metrics, finding in every case that they obeyed fractal $1/f$ scaling, consistent with self-organized critical models (Bak & Sneppen 1993; Solé & Manrubia 1996). However, to obtain evenly spaced data, Solé *et al.* (1997) interpolated every million years between the uneven boundaries of the fossil record, thereby introducing significant artefactual correlation. Solé *et al.*'s (1997) interpolation scheme, in conjunction with their analysis methods, artefactually generated the $1/f$ scaling they observed (Kirchner & Weil 1998). Recently, Newman & Eble (1999) reanalysed marine family extinctions using slightly different spectral methods and a square-wave interpolation scheme rather than the linear interpolation scheme used by Solé *et al.* (1997). They detected a distinct interpolation artefact at high frequencies, but found that, at low frequencies, the power spectrum exhibited exponential (rather than power-law) scaling, with a characteristic correlation time of *ca.* 40 Myr. However, our analysis shows that extinction rates exhibit little or no correlation, even over lags as short as 5 Myr, the shortest resolvable time-scale. This illustrates the difficulty of inferring correlations from power spectra rather than directly from autocorrelation functions.

Recently, Hewzulla *et al.* (1999) analysed two time-series of fossil diversity (rather than extinction or origination rates) from *The fossil record 2* by subtracting the long-term exponential trends from the two diversity curves and then calculating the power spectra of the residuals. The resulting power spectra exhibited scaling between $1/f$ and $1/f^2$, which was interpreted as support for the self-organized criticality hypothesis. However, since diversity integrates extinction and origination rates through time, taxon counts must be strongly autocorrelated, whether or not extinction or origination rates are autocorrelated (Kirchner & Weil 1998); the power spectrum of taxon counts must be steeper than that of the origination and extinction rates by a factor of $1/f^2$ (Cartwright 1990). If origination and extinction rates were pure white noise (scaling as $1/f^0$), diversity time-series would be random walks (scaling as $1/f^2$). The diversity patterns analysed by Hewzulla *et al.* (1999) were not more correlated than a random walk (their power spectra were not steeper than $1/f^2$), which implies that the extinction and origination rates in *The fossil record 2* database cannot be much more correlated than white noise, consistent with our analysis.

Our results do not rule out the possibility that biological mechanisms may underlie many of the observed fluctuations in extinction rates. However, our results show that, whatever these mechanisms might be, they do not produce significant correlations in extinction rates over the time-scales observable in these data sets. Our results support the reasonable null hypotheses that fluctuations in extinction rates are largely random or that extinction rates fluctuate too abruptly to be correlated across multiple stratigraphic intervals.

In Sepkoski's data sets, the origination rates show somewhat stronger autocorrelation than the extinction rates both before and after detrending (figures 1–4, *a–d*). This is apparent in the short-term behaviour of the time-series themselves: the origination time-series tend to 'wobble' around their long-term trends, while the extinction time-series 'flicker', with visibly less short-term correlation. The stronger autocorrelation in origination rates compared to extinction rates, before detrending, results from the stronger long-term trends in the origination time-series.

We have recently used geostatistical and Fourier transform methods to calculate the cross-correlation between the extinction and origination rates in Sepkoski's data sets (Kirchner & Weil 2000). That analysis showed that per-taxon origination rates lag per-taxon extinction rates by an average of 10 Myr throughout the fossil record, even after mass extinction events and their recoveries were removed. That result led us to hypothesize that origination rates respond to extinction, but do so at a pace regulated by the dynamics of the diversification process itself, rather than by the characteristics or magnitudes of individual extinction events. The results presented here show that, in the same data, per-taxon origination rates exhibit significant autocorrelations out to lags of *ca.* 10 Myr (figure 4), corroborating this part of our hypothesis. The autocorrelation in per-taxon origination rates indicates that they cannot shift abruptly and, therefore, implies that they should exhibit delayed response to extinction events. The origination rates lag the extinction rates by approximately the same time-span as that over which the origination rates exhibit significant autocorrelation, further suggesting that the delayed response of originations to extinctions results from intrinsic limits on the speed with which origination rates can change.

We expect origination rates to be more strongly autocorrelated than extinction rates for at least two biological reasons. First, each new species represents a potential evolutionary starting point for new originations. In the extreme case, key innovations may result in adaptive shifts which allow radiation; one should expect the appearance of new organisms with key innovations to be serially correlated with subsequent diversification of descendent taxa. Second, each new species represents a potential evolutionary starting point for new originations, and new taxa themselves constitute new niches (for their predators, parasites and symbionts). Thus, each origination event should create new opportunities for further radiation (Kirchner & Weil 2000). In this view, the primary mechanism driving diversification events is the creation of new ecological niches (and new evolutionary pathways for reaching them) by diversification events themselves rather than the emptying of static niches by extinction events.

The stronger short-term correlations in origination rates than in extinction rates suggest that, as one would expect, the biological processes associated with diversification are necessarily more gradual than those associated with extinction (Sepkoski 1993). Because episodes of rapid origination should create conditions under which further originations are more likely and vice versa, one would expect that periods of high or low origination rates should tend to persist for extended periods of time. (The extinction of taxa can likewise eliminate the niches which they create, leading to knock-on extinctions of other taxa, but such extinction cascades are presumably too rapid to create serial correlations at a time-scale which would be observable in the data sets we have analysed.) Limited persistence in origination rates, as they are perturbed by abiotic processes and by the consequences of extinction events (Kirchner & Weil 2000), should result in origination time-series which cycle aperiodically, with weak positive correlations at short lags and weak negative correlations at somewhat longer lags. The autocorrelation functions of the fossil origination rates (figures 2 and 4) are generally consistent with this hypothesis.

8. CONCLUSIONS

We quantified the autocorrelation in fossil extinction and origination rates using two different methods, three different fossil databases and four different metrics. Our results, which are shown in figures 1–4 and summarized in table 1, support the following general observations.

(i) For lags longer than 5 Myr, extinction rates exhibit no statistically significant autocorrelation, that is, no autocorrelation stronger than that which could readily arise by chance in a random, uncorrelated time-series (figure 1).

(ii) Per-taxon extinction rates, when detrended to remove long-term drift, likewise exhibit no statistically significant autocorrelation over lags longer than 5 Myr (figure 3).

(iii) The lack of correlations in extinction rates, even at the shortest resolvable time-lags, does not support the hypothesis that self-organized criticality generates long-range correlations in extinction statistics.

(iv) The origination rates in Sepkoski's data sets exhibit significant autocorrelation, largely resulting from long-term trends. After detrending, these origination rates show weak positive correlations at lags of 5 Myr and weak negative correlations at lags of 10–30 Myr (figure 2).

(v) Before detrending, the per-taxon origination rates in Sepkoski's data sets exhibit significant autocorrelation; after detrending, they show positive correlations at lags of 5–10 Myr and weak negative correlations at lags of 20–30 Myr (figure 4).

(vi) The stronger correlation of origination rates suggests that origination is not the obverse of extinction, nor is it controlled by the emptying of ecological niches through extinctions. Instead, the autocorrelations in the origination rates from Sepkoski's data are consistent with the hypothesis that opportunities for diversification are primarily controlled by the creation of new ecological niches, and new evolutionary pathways for reaching them, by diversification events themselves.

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