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Genus extinction, origination, and the durations of sedimentary hiatuses

Shanan E. Peters

Abstract.—Short-term variations in rates of taxonomic extinction and origination in the fossil record may be the result of true changes in rates of turnover, variable rates of fossil preservation, or some combination of the two. Here, positive extinction and origination rate excursions among Phanerozoic marine animal genera are reexpressed in terms of the amount of normal, background time they represent. In addition to providing a background-adjusted calibration of rate intensities, this reexpression determines the durations of sampling gaps that would be required to explain entirely all observed rate excursions as sampling artifacts. This possibility is explored by analyzing a new compilation of the timing and duration of sedimentary hiatuses in North America.

Hiatuses spanning more than approximately one million years (Myr) in the marine sedimentary rock record have a mean duration of 73 Myr. There are two major hiatus types—those that form in response to long-duration tectonic cycles and that bound the major Sloss-scale sequences (mean duration 200 Myr), and those that form in response to shorter-duration changes in sediment accommodation space and that occur within major Sloss-scale sequences (mean duration less than 23 Myr). The latter are approximately exponentially distributed and have a mean duration that is comparable to the mean duration of intervening sedimentary rock packages.

Although sedimentary hiatuses are generally long enough in duration to accommodate the hypothesis that short-term variations in rates of genus origination and extinction are artifacts of sampling failures at major unconformities (''Unconformity Bias'' hypothesis), the observed evolutionary rates are not correlated with hiatus durations. Moreover, hiatuses that follow the major mass extinctions are not long in comparison to most other non–mass extinction intervals. These results do not support the hypothesis that hiatuses at major unconformities alone have artificially clustered genus first and last occurrences, thereby causing many of the documented statistical similarities between the temporal structure of the sedimentary rock record and macroevolutionary patterns. Instead, environmental changes related to the expansion and contraction of marine environments may have been the primary forcers of both biological turnover and the spatio-temporal pattern of sediment accumulation. Fully testing this ''Common Cause'' hypothesis requires quantifying and overcoming lingering taxonomic, biostratigraphic, facies, and numerous other biases that are both inherent in geologic data and imposed by imperfect knowledge of the fossil record.

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Introduction

One of the most striking features of the fossil record of marine animals is that rates of taxonomic origination and extinction vary dramatically on both short and long time scales. Over the long term, rates of turnover exhibit a uniform (Raup and Sepkoski 1982; Sepkoski 1993; Foote 2000b, 2003), or perhaps two-step (Van Valen 1984), decline of more than 50% during the Phanerozoic. On shorter time scales, rates of extinction and, to a lesser degree, rates of origination are much more variable, fluctuating by as much as a factor of three on a stage-to-stage basis (Foote 2003). Five such short-term extinction rate increases have been identified as the ''major'' mass extinctions (Raup and Sepkoski 1982), and most of these are thought to reflect a distinct class of macroevolutionary phenomena that can be distinguished from normal, ''background'' rates of turnover (Bambach et al. 2004; Jablonski 2005). Episodes of excess origination generally garner less attention, but several major taxonomic radiations have also been recognized, most notably the Cambrian explosion and Ordovician radiation (e.g., Droser et al. 1996).

Although long-term average rates of taxonomic turnover in the face-value fossil record are, if measured appropriately, unlikely to be strongly biased by incomplete and variable preservation (Foote 2000a), apparent short-term fluctuations in rates of origination and

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extinction are influenced by at least three factors: (1) true changes in rates of biological turnover, (2) incomplete preservation, and (3) temporal variation in rates of preservation. Long-term rate estimates are unbiased by variable preservation because a change in the rate of preservation in one time interval affects apparent rate estimates in adjacent time intervals in such a way as to conserve the long-term mean (Foote 2000a). In this context, ''preservation'' refers to the all-inclusive probability that a lineage extant at time *t* will be recovered from time *t*.

If the fossil record were uniformly incomplete, then short-term variations in true rates of turnover would be smeared forward and backward in time owing to the artificial truncation of taxon ranges (Signor and Lipps 1982; Foote 2000a), but the underlying biological signal would be otherwise undistorted. However, the fossil record is not uniformly incomplete. Rates of preservation are known to vary over time, sometimes dramatically so (Smith et al. 2001; Foote 2003), and this variation can result in the artificial clustering of first and last occurrences in the fossil record (Holland 1995, 1996; Foote 2000a). Thus, any apparent pulse of extinction or origination might be the result of a true biological rate increase, a change in preservation rate, or some combination of the two.

Support for the hypothesis that geologically controlled rates of fossil preservation have significantly distorted paleobiological data (''Geologic Bias'' hypothesis) is found in analyses that document positive correlations between the temporal structure of the sedimentary rock record and several long- and short-term macroevolutionary patterns in the fossil record, including taxonomic richness (Raup 1972, 1976; Peters and Foote 2001; Smith 2001; Smith et al. 2001) and rates of extinction and origination (Smith et al. 2001; Peters and Foote 2002; Peters 2005). Positive correlations between macroevolutionary patterns and the sedimentary record are, however, also consistent with the hypothesis that both sedimentary and macroevolutionary processes are similarly influenced by environmental changes associated with fluctuating sea level and the formation/expansion and destruction/contraction of marine environments (i.e., ''Common Cause'' hypothesis; Newell 1949, 1952; Valentine and Moores 1970; Schopf 1974; Simberloff 1974; Sepkoski 1976; Hallam 1989; Hallam and Wignall 1999; Smith et al. 2001; Peters 2005).

Fortunately, these two end-member hypotheses make some unique predictions regarding the expected relationships between the sedimentary record and macroevolutionary patterns. In its extreme form, the Geologic Bias hypothesis predicts that true rates of biologic turnover have been constant or smoothly declining during the Phanerozoic and that apparent pulses of extinction and origination are artifacts of temporal variability in rates of fossil preservation (Foote 2000a; Peters and Foote 2002) and/or the architecture of the sedimentary record (Holland 1995, 1996; Smith et al. 2001; Holland and Patzkowsky 2002). In the specific case of effective paleontological sampling gaps arising as a result of unconformities, one simple component of the Geologic Bias hypothesis, the ''Unconformity Bias'' hypothesis, predicts that, all else being equal, the average *duration* of a sedimentary hiatus should be correlated with the apparent magnitude of extinction in the previous interval and the apparent magnitude of origination in the following interval because more taxonomic turnover would occur during a gap of longer duration (Fig. 1).

The Common Cause hypothesis, on the other hand, predicts that the durations of sampling gaps are unimportant because it is the *magnitude* of environmental changes associated with the beginning and end of unconformities that is biologically relevant, not the durations of intervening hiatuses (if any). Of course any given rate excursion may be influenced by a unique combination of Unconformity Bias, Common Cause mechanisms, and/or many other potential geologic and taxonomic biases (see ''Discussion'').

Here I specifically address the Unconformity Bias component of the Geologic Bias hypothesis by first calculating the amount of excess turnover represented by all positive extinction and origination rate anomalies observed among marine animal genera in Sepkoski's global compendium (Sepkoski

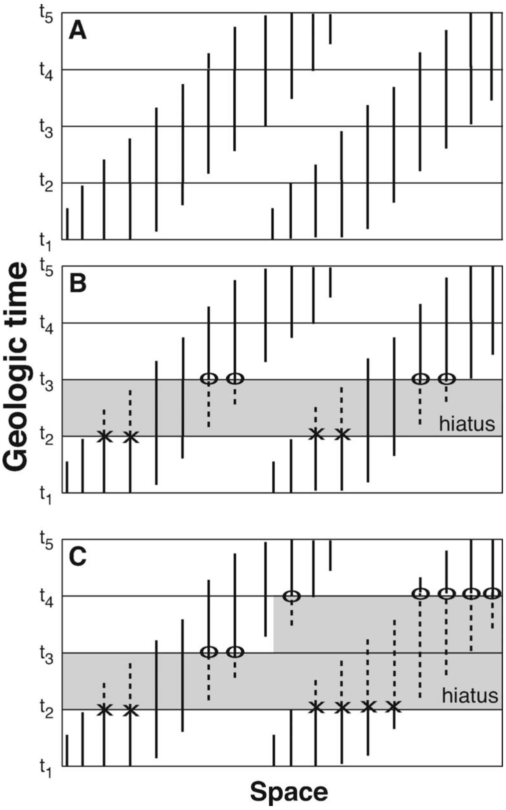

FIGURE 1. Effect of gap durations on apparent rates of taxonomic turnover. Dashed lines show unsampled taxon ranges; circles and crosses represent artificial range truncations that cause turnover rates to be artificial exaggerated (positive rate anomaly). A, Hypothetical true turnover history with no sampling gaps. Rates of turnover are constant in all time intervals (four extinctions and originations in each time interval, *t*). B, Effect of a spatially uniform gap of one time interval on apparent turnover history. Four extinctions and four originations that in reality occurred during the gap appear to occur in other time intervals. Apparent extinction rates are therefore increased in the interval preceding the gap and apparent origination rates are increased in the interval following the gap. Both rates are artificially decreased during the gap. C, Same as B, but with sampling gap lengthened to two time intervals in some regions. Note that in this case, the duration of the effective sampling gap for extinction in t_1 is approximately 1.5 intervals, whereas the duration of the effective sampling gap for origination at t_4 is only approximately one interval, and that the number of offset first and last occurrences reflects this difference. Note also that in all panels the total number of first and last occurrences is the same and that the long-term mean (four events per interval) is conserved. The effect of hiatuses on apparent rates of turnover is herein referred to as ''Unconformity Bias.''

2002). The magnitudes of positive rate anomalies, reexpressed in terms of the amount of excess relative to the amount of expected turnover, correspond to the duration of sampling gaps that would be required to generate the anomalies under a model of constant taxonomic turnover (Raup 1978). I then compare the required gaps with the mean and median hiatus durations observed in the sedimentary rock record. I next compare the time series of apparent genus extinction and origination rates with the time series of gap durations. Finally, I discuss the relative merits of the Unconformity Bias and Common Cause hypotheses in light of these results and then summarize the numerous other biases that must be adequately tested before the relative contributions of Geologic Bias and Common Cause mechanisms can be determined for each interval in the Phanerozoic.

Background Rates, Rate Anomalies, and Required Gaps

All genus rates are based on Sepkoski's global compendium of marine animals and animal-like protists (Sepkoski 2002) and have been calculated for Sepkoski's stages in the Paleozoic and Mesozoic and subepochs in the Cenozoic. Rates are calculated on a per-interval and per-million-year basis (Fig. 2) using Foote's survivorship-based rate metrics (Foote 2000a). These rate metrics are based on the ratio of taxa that span an interval to those that cross the bottom boundary and go extinct (extinction, *q*) or that first occur in the interval and cross the top boundary (origination, *p*). Most interval ages and durations are based on Gradstein et al. (2004), but because some stages in the Cambrian and Ordovician are unresolved in Gradstein et al. (2004), some ages are based on interpolations between known boundaries.

For the purposes of this study, expected turnover rates for each interval were determined by calculating the best-fit exponential functions to the observed rate estimates (Appendix). In all cases, the age at the base of each interval was used for the rate versus time regressions. Observed rates of extinction and origination that are greater than the corresponding best-fit exponential functions con-

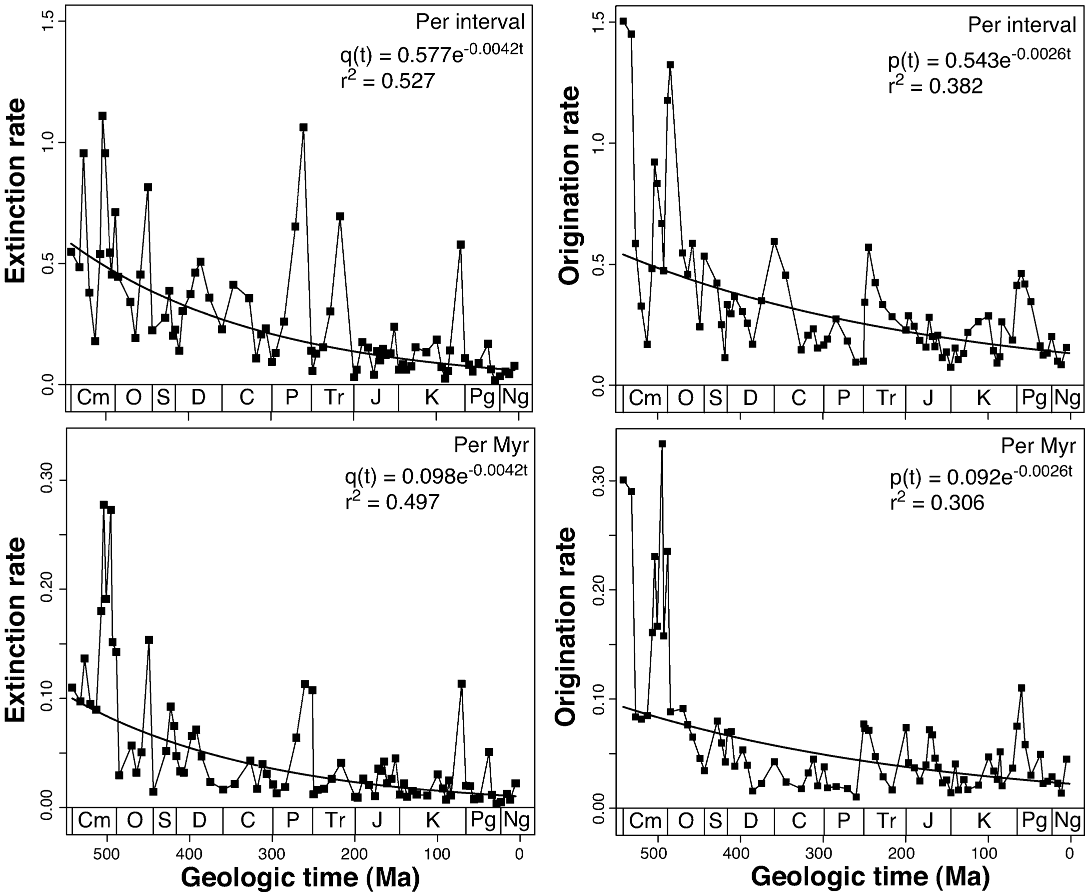

FIGURE 2. Rates of genus extinction and origination in Sepkoski's (2002) global compendium and best-fit exponential functions (for all regressions, $p < 0.001$). The best-fit lines are here hypothesized to represent background rates of turnover. All rates are calculated using Foote's (2000a) survivorship-based rate metrics and are calculated on per-interval (top) and per-million-year (bottom) basis using continuous rates. Data are plotted at the age of the interval base from the base of the Cambrian to Pleistocene.

stitute higher than expected rates and are herein referred to as positive rate anomalies. Other methods of determining the expected rates in each interval, such as locally weighted regressions or moving averages of *n* intervals (Bambach et al. 2004), could be used instead of the exponential fits (Fig. 2), but such approaches require arbitrarily specifying a local weighting scheme and/or window size and explicitly permit shorter-term variations in rates that are here hypothesized to be driven entirely by the Unconformity Bias. Thus, a global fit to the data is most appropriate for this study. Nevertheless, most regression approaches with suitably broad temporal weighting strategies would yield results that are comparable to those reported here.

The notion of ''background rates'' is a hypothetical expectation that serves as a viable hypothesis for the Unconformity Bias scenario, not necessarily a real macroevolutionary phenomenon. However, Jablonski (2005) and others have offered arguments for the validity of treating mass extinction intervals as phenomenologically distinct from other times of normal turnover. The general notion that there is some amount of expected turnover in every time interval is equivalent to ''background rates'' as used herein.

Given expected background rates, one way to express the magnitudes of the observed origination and extinction rate anomalies is simply to examine the positive rate residuals from the best-fit exponential functions (Fig. 2).

Note that although positive anomalies are, for good reason, the focus of this study, there are also negative rate anomalies along the exponential functions shown in Figure 2. These negative anomalies are not being ignored, but are instead expected under the Unconformity Bias hypothesis. As mentioned above, long-term average rates (i.e., background rates) are expected to be conserved despite variable rates of preservation (Foote 2000a). Thus, any positive rate anomalies that are hypothesized to be the result of incomplete preservation must ''borrow'' excess first or last occurrences from other intervals, thereby causing negative rate anomalies (Fig. 1). In other words, negative rate anomalies are required by the Unconformity Bias hypothesis.

Removing the secular decline in turnover rates by de-trending the time series as shown in Figure 2 is a common way to evaluate the distinctiveness of the major mass extinctions relative to other intervals in the Phanerozoic (Raup and Sepkoski 1982; Van Valen 1985; Bambach et al. 2004). However, rather than examining the absolute magnitude of rate anomalies after removing the secular decline by taking residuals about an expected trend, it is perhaps more useful to ask how much normal, background time is represented by each rate anomaly given the expected amount of turnover. Reexpressing rate anomalies proportional to background rates is useful because it removes the long-term rate decline without ignoring the macroevolutionary significance of the average tempo of taxonomic turnover.

The total amount of normal, ''background'' time represented by each positive extinction and origination rate anomaly can be expressed in terms of both millions of years and number of time intervals (Fig. 3). Relative differences between the amount of extra time expressed as millions of years and as number of time intervals reflect the fact that not all intervals have the same duration. To provide some indication of the sensitivity of the calculation to the hypothesized background rates, arbitrary error bars corresponding to ±10% of the estimated background rate (Fig. 2) for each interval are shown. The equations used to generate Figure 3 and their assumptions are explained in the Appendix.

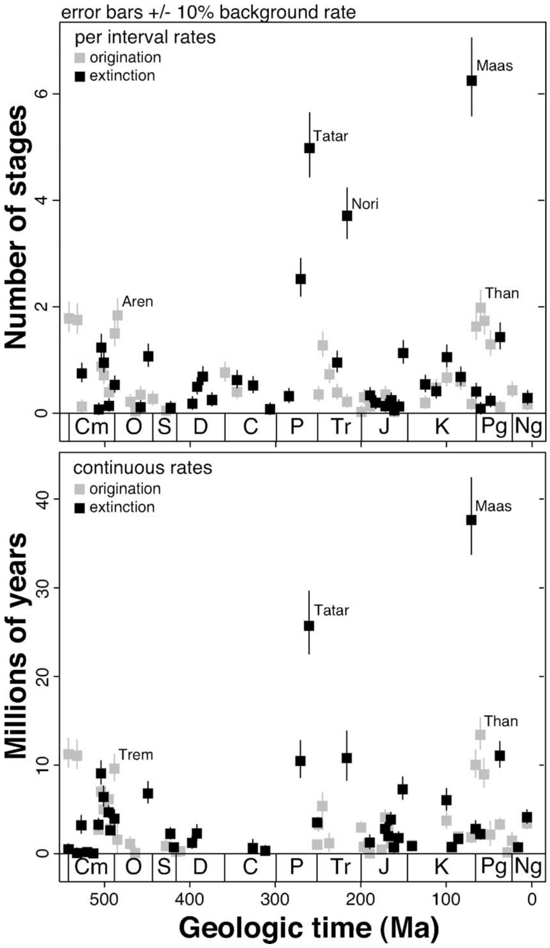

FIGURE 3. Positive extinction and origination rate anomalies (from Fig. 2) reexpressed in terms of the amount of normal, background time they represent. Top panel shows results of calculation based on continuous per capita rates measured per interval. Bottom panel shows results of calculation based on continuous per capita rates measured per million years. Note that only two or three of the major mass extinctions appear distinct relative to other positive rate anomalies when rates are reexpressed relative to background. Data are plotted at the age of the interval base from the Cambrian to Pleistocene. See Appendix for explanation of calculations and assumptions. Aren, Arenigian; Maas, Maastrichtian (K/Pg extinction); Nori, Norian (Tr/J extinction); Tatar, Tatarian (P/T extinction; the Tatarian is a deprecated interval name used in Sepkoski that is approximately equivalent to Changhsingian); Than, Thanetian; Trem, Tremadocian.

Several interesting patterns emerge when the intensities of genus extinction and origination are reexpressed in terms of the amount of background time they represent (Fig. 3). Perhaps most notably, when time is expressed in millions of years, only two pulses of extinc-

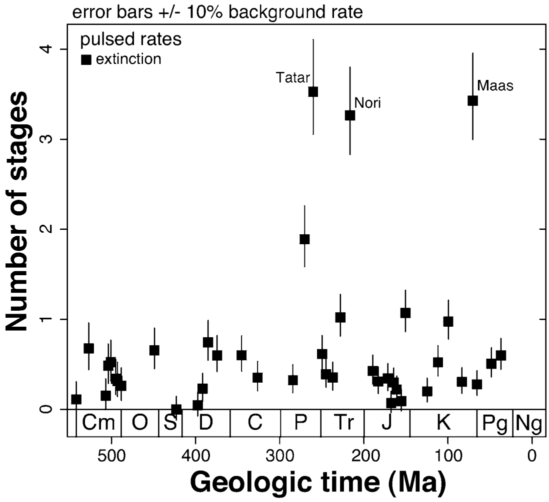

FIGURE 4. Positive extinction rate anomalies reexpressed in terms of the amount of normal, background time they represent, as in Figure 3, but based on a pulsed rather than continuous extinction model. Stage abbreviations as in Figure 3. Data are plotted at the age of the interval base from Lower Cambrian to Pleistocene.

tion, the end-Permian (P/T) and end-Cretaceous (K/Pg), appear to stand out above other positive extinction rate anomalies (Fig. 3). When rates are expressed per interval rather than per million years, the end-Triassic (T/J) extinction anomaly increases significantly because the Norian (which in Sepkoski's data includes the Rhaetian) is long in duration relative to most other Phanerozoic intervals.

Reexpressed rates of extinction highlight the distinctiveness of the end-Permian, end-Cretaceous, and perhaps end-Triassic extinction intervals relative to other positive rate anomalies in the Phanerozoic. The remaining two of the ''big five'' major mass extinctions (Raup and Sepkoski 1982) are lost in the scatter of other positive rate anomalies, which may not be surprising given that the severity of the end-Ordovician extinction has been questioned on ecological grounds (Droser et al. 1997) and the magnitude of Late Devonian extinction downplayed (Raup and Sepkoski 1982; Bambach et al. 2004).

Although the end-Permian is widely recognized as the most severe mass extinction of all time (Raup 1979; Raup and Sepkoski 1982; Sepkoski 1984; Erwin et al. 2002), relative to the tempo of expected background extinction, the K/Pg mass extinction is the largest acceleration of extinction in the Phanerozoic. All told, the K/Pg extinction peak represents an amount of extinction that would have normally occurred over approximately 38 Myr, or just over six stages, if extinction had proceeded at the expected background rate (Fig. 3). The K/Pg extinction appears larger than the P/T extinction because the estimated rates of background extinction in the Late Cretaceous and Cenozoic are low in comparison to those at the end-Permian (Fig. 2). Thus, all else being equal, the end-Permian interval is expected to have a greater amount of background extinction than the late Mesozoic, and this expectation is reflected in the recalibrated extinction rate intensities (Fig. 3).

It should be noted that the results of these calculations (Fig. 3) are based on rates derived from Sepkoski's (2002) global compendium. Because the end-Permian extinction is manifested as several adjacent positive rate anomalies in the genus data (extinction rate increases through all of the Permian; Fig. 2), it is conceivable that incomplete preservation of taxon ranges (i.e., the Signor-Lipps effect) has weakened a single biological P/T extinction peak by distributing it over two intervals. Indeed, there is evidence to suggest that just such distortion has occurred in virtually all time intervals in the Phanerozoic (Foote 2003). However, it is not clear why the end-Permian would be the only mass extinction subject to this type of distortion unless preservation rates were unusually low throughout the entire Permian, which does not appear to be the case (Foote 2003).

If extinctions are in reality concentrated near the end of intervals, rather than distributed continuously throughout each interval, as assumed by the calculations shown in Figure 3, it is necessary to use a pulsed extinction model that presupposes extinctions to be concentrated at the end of each stage (Foote 2005). The pulsed model generally reduces the amount of background time represented by extinction anomalies, but it also restores the end-Permian to its place of prominence, if only by a very small margin (Fig. 4).

Origination rates, which are less variable than extinction rates for most of the Phanerozoic, also exhibit interesting temporal structure when reexpressed relative to the amount of expected background origination. Perhaps most notably, high origination rates in the Cambrian and Ordovician (Fig. 2) are, when reexpressed relative to background, comparable to the high rates of origination that follow the K/Pg and the P/T (Fig. 3). In fact, positive origination rate anomalies tend to be of similar magnitude relative to background throughout the Phanerozoic. Positive origination rate anomalies also tend to be distributed over several intervals that follow single positive extinction rate anomalies (Fig. 3). Although low volatility and clustered positive rate anomalies of low magnitude could be the result of lower fidelity in face-value origination rates relative to extinction rates (Foote 2003), it is also possible that recoveries from extinctions tend to be of comparable magnitude relative to the tempo of background origination and that they tend to be drawn out over several time intervals following extinction pulses (Sepkoski 1984; Kirchner and Weil 2000; Kirchner 2002).

Raup (1978) performed a very similar calculation to those shown in Figure 3 for the P/T extinction based on a cohort analysis of genus survivorship. Using genus data and age estimates for period boundaries as of 1978, Raup determined that the excess extinction observed near the end-Permian represented approximately 85 Myr of normal, background extinction. This estimate is more than three times the magnitude of the end-Permian extinction excess calculated here (Fig. 3). The reason for the discrepancy between Raup's (1978) calculation and those shown in Figure 3 cannot be identified precisely, but it is probably due to several factors, including the use here of much finer temporal resolution that partitions genus last occurrences within the Permian, updated genus data and additional field studies that have resulted in overall lower turnover rates in the Permian, as well as updated absolute age estimates for interval boundaries, revised stratigraphic correlations, and log-linear survivorship curves (although the latter is unlikely to be significant over the rather short time intervals required here; Fig. 3).

In contrast to Raup's (1978) dramatic estimate of 85 Myr for the end-Permian extinction peak, these results (Figs. 3, 4) indicate that most positive origination and extinction rate anomalies do not require excessively long gaps in order to be explained as sampling artifacts. The largest extinction pulse relative to background is the K/Pg, and this rate increase requires an effective sampling gap of only approximately 38 Myr. The vast majority of positive rate anomalies require gaps of less than 10 Myr. In fact, the mean gap required is just 4.7 Myr, or approximately one stage.

The macroevolutionary implications of the reexpressed extinction and origination histories could be discussed at length, but for the purposes of this study, positive rate anomalies (Figs. 3, 4) should be interpreted as the durations of sampling gaps that would be required in order to artificially generate the observed rate anomalies under a scenario of constant taxonomic turnover (Figs. 1, 2). Under the most simplistic of Unconformity Bias scenarios, both extinction and origination are expected to be identically distorted around an unconformity (Fig. 1B). Because the positive rate anomalies for origination and extinction are quite different in magnitude and not at all symmetric (Fig. 3), this simplistic notion of unconformity bias can be discounted. Nevertheless, asymmetry in extinction and origination rate anomalies (Fig. 3) cannot rule out more complicated temporal patterns in mean hiatus durations that may differentially affect extinction and origination (e.g., Fig. 1C). The extent to which actual sedimentary hiatus durations predict apparent rates of extinction and origination is the focus of this study.

Hiatus Data

The American Association of Petroleum Geologists Correlation of Stratigraphic Units of North America (COSUNA) charts (Childs 1985) were used to derive the temporal ranges of rock packages and intervening hiatuses in the continental United States and southern Alaska. These charts provide a rather complete description of the known geologic record that is resolved at a minimum temporal resolution of Phanerozoic stages (Salvador 1985). Peters (2006) presents a detailed discussion of the COSUNA data and the more general use of gap-bound rock packages as measures of the temporal structure of the geologic record.

The minimum duration required for the identification of a hiatus on the COSUNA charts (i.e., the duration threshold) is not explicitly stated, but the inferred temporal resolution based on the chart data is approximately 1–3 Myr, although the actual temporal resolution undoubtedly varies regionally and with the state of knowledge at the time of chart publication (generally the early to mid 1980s).

Data for all gap-bound rock packages were manually read from the printed charts and entered into a database for analysis. Human-induced data entry errors potentially occurred at two critical steps (reading the charts and entering the data), but cross-checking suggests that these errors are relatively uncommon (less than one error per COSUNA column) and not concentrated in particular time intervals (i.e., errors are likely to be randomly distributed).

All hiatuses were assigned times of first and last occurrences and then binned according to the timescale used by Sepkoski (2002), which mostly includes Paleozoic and Mesozoic stages and Cenozoic subepochs (median duration is 5.4 Myr). Because of limitations in the temporal resolution afforded by the COSUNA charts, the Lower and Middle Cambrian are not included in any fossil-hiatus comparisons, although hiatuses with first occurrences in these intervals may contribute to gap estimates at later time intervals. All analyses are limited to the Phanerozoic, and hiatuses that begin sometime in the Proterozoic and that persist into the Phanerozoic are here assumed to start only at the base of the Cambrian.

For this analysis, times of first and last occurrences of marine sedimentary rock packages were used to determine the timing and durations of intervening gaps in marine sedimentation for each of the 541 columns compiled from the COSUNA charts (Peters 2005: supplementary Fig. 1). Time intervals that preserve no rock, or rock that is not marine and sedimentary in origin, are here included within hiatuses. Thus, it is possible (but relatively rare) for a COSUNA column to have a single hiatus that spans the entire duration of the Phanerozoic if that column preserves no marine sediments of Phanerozoic age.

Because sedimentary hiatuses were tabulated separately for each of 541 columns, the number of hiatuses in each interval is a measure of the areal extent of coeval unconformities. Similarly, the duration of an individual hiatus represents the duration of a hiatus at a particular location in North America. Thus, some geographically widespread unconformities in the sedimentary record might represent long hiatuses in some regions, but brief hiatuses in others (e.g., Fig. 1C).

All sedimentary rock units that were not explicitly identified as non-marine in origin were assumed to be marine. However, because marine and terrestrial sediments are inconsistently distinguished from one another on the COSUNA charts, some hiatuses in marine sediment accumulation may be longer in duration than those reported here. Because all hiatal ranges are based on the binning strategy of Sepkoski (2002), the minimum duration of a hiatus (and genus) is constrained by the length of each stratigraphic interval. Many hiatuses may therefore be shorter in duration than reported here if they do not span the entire interval of their first and/or last occurrence. Hiatuses may also be longer than reported here if the sedimentary rock packages that bound them do not entirely span their interval of first and/or last appearance. Because binning can give rise to both positive and negative errors in hiatus durations, the binning protocol used here is unlikely to have systematically distorted the hiatus time series or concentrated errors in particular time intervals. It should also be noted that binning the hiatus data in exactly the same manner as Sepkoski's fossil compendium permits direct quantitative comparisons between these two disparate data sets (see also Peters 2005).

The COSUNA charts include both surface and subsurface rock, and this has a substantial effect on the temporal structure of the data. For example, much of North America is blanketed by Cambrian sediments deposited during the Sauk transgression (Sloss 1963), and therefore the sedimentary record of the

Cambrian is extensive and continuous in comparison to many other Phanerozoic time intervals. This characteristic of the Cambrian sedimentary record is accurately reflected on the COSUNA charts, but because the vast majority of preserved Cambrian rock remains sequestered in the subsurface, it is not particularly well sampled by paleontologists and should perhaps be considered a gap for the purposes of testing the Unconformity Bias hypothesis. Unfortunately, it is not yet possible to separate precisely the subsurface component of the COSUNA data to test this effect, but the data to do so are currently being compiled.

It should also be noted that all Phanerozoic stages are represented by at least some marine sedimentary rock and that there are therefore no complete stage-duration gaps in the global sedimentary record. However, it has already been shown that truncations in the sedimentary rock record of North America, as recorded on the COSUNA charts, tend to correspond to global genus extinction (Peters 2005). Similarly, the onset of sedimentation in North America tends to correspond to global genus origination (Peters 2005). The results of Peters (2005) are therefore critical to this study because they demonstrate that the temporal structure of the sedimentary record, as recorded on the COSUNA charts, is intimately related to the temporal structure of the global marine animal fossil record. This result is consistent with the hypothesis that large truncations in the sedimentary rock record are followed by long hiatuses and that the rock-fossil agreement reflects an Unconformity Bias of the type outlined in Figure 1. The present study seeks to test this possibility by comparing empirical hiatus durations with observed rates of taxonomic extinction and origination.

Results

Temporal Distribution of Hiatuses.—To understand how the quantitative temporal structure of hiatuses is related to apparent rates of taxonomic turnover in the fossil record, the first thing that must be documented is the overall frequency of sedimentary hiatuses. On average, the total number of hiatuses in 74 time intervals from the Lower Cambrian to the Pleistocene outnumbers by approximately a factor of four the total number of marine sedimentary rock packages (Fig. 5A). Thus, with respect to marine sediments, most of the Phanerozoic record of North America consists of hiatuses. The rock and hiatus time series are nearly antithetical, but because it is possible for a single COSUNA column to have multiple rock packages in a given time interval, they are not perfectly so (Fig. 5A).

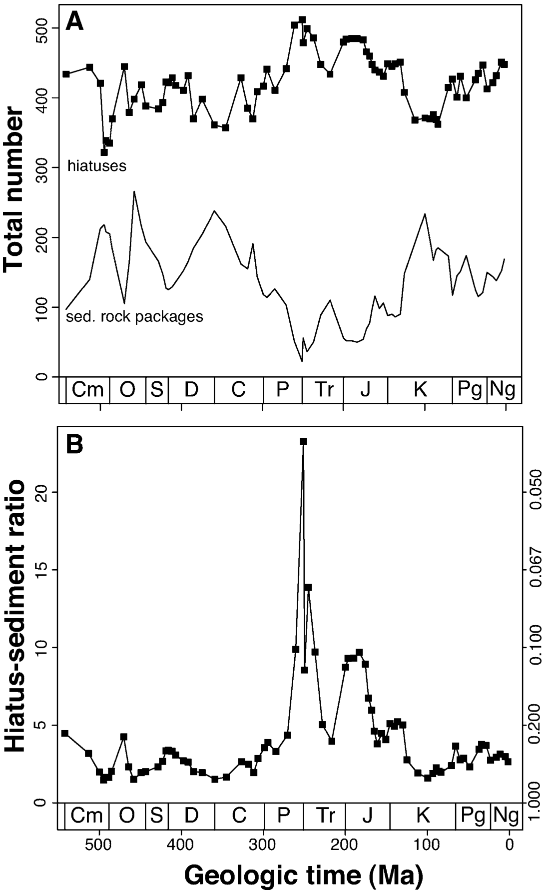

FIGURE 5. Number of hiatuses and marine sedimentary rocks. A, Time series of the total number of hiatuses in the marine sedimentary rock record (dark line, points) and total number of marine sedimentary rock packages (gray line, points not shown but based on same binning strategy). Time series are not perfectly antithetical because it is possible for a single COSUNA column to have more than one rock package in a given time interval. B, Time series of hiatus-to-rock ratio from A, with right axis showing approximate proportion of continent covered by marine sediment. The hiatus-to-sediment ratio is particularly large in the Permian–Jurassic interval, which is an interval in North America that is poorly represented by rock. Data are plotted at age of the interval base from the Lower Cambrian to Pleistocene.

The total number of sedimentary rock packages and the total number of gaps are area-weighted measures of rock quantity and gap extent (see ''Hiatus Data''). Thus, a Phanerozoic average gap-to-rock ratio of approximately four means that, on average, one-fourth of continental area is covered by marine sediment of a given age and the other three-fourths preserves no sediment. However, this ratio varies considerably over time (Fig. 5B), reaching a maximum of 23 at the P/T boundary (~4% sediment coverage) and a minimum of 1.5 in the Franconian (~67% sediment coverage).

To better quantify the temporal distribution of hiatuses in the sedimentary record, it is useful to partition the total number of hiatuses in each time interval into four characteristic types, X_{FL}, X_{bL}, X_{Ft}, and X_{bt}, where X refers to the number of entities in a time interval, F and L refer to first and last occurrences, and b and t refer to bottom and top interval boundaries (Foote 2000a). The total number of gap first occurrences in a given time interval is $X_{FL} + X_{Ft}$, the total number of last occurrences is $X_{FL} + X_{bL}$, and the total number of gaps that span an entire interval is X_{bt}. The purpose of adopting this classification system is to convey the temporal persistence of hiatuses in a way that emphasizes times of initiation and termination, as is done for fossil taxa (Foote 2000a), and in a way that is relevant to the Unconformity Bias hypothesis (Fig. 1).

Overall patterns of gap first and last occurrences (Fig. 6) resemble the time series of rock package first and last occurrences (Peters 2005: Fig. 2) because a truncation in the sedimentary record must be associated with the initiation of a hiatus and vice versa. However, because most of geologic time at most locations is represented by hiatuses rather than by marine sedimentary rock (Fig. 5), there are many more through-ranging hiatuses in each interval (Fig. 6).

Rates of hiatus turnover (i.e., the ratio of hiatuses that span an interval to those that first or last occur in an interval and pass out of that interval) are rather low because most hiatuses in any given interval range through that interval. Another way of expressing the turnover of sedimentary hiatuses is to calculate

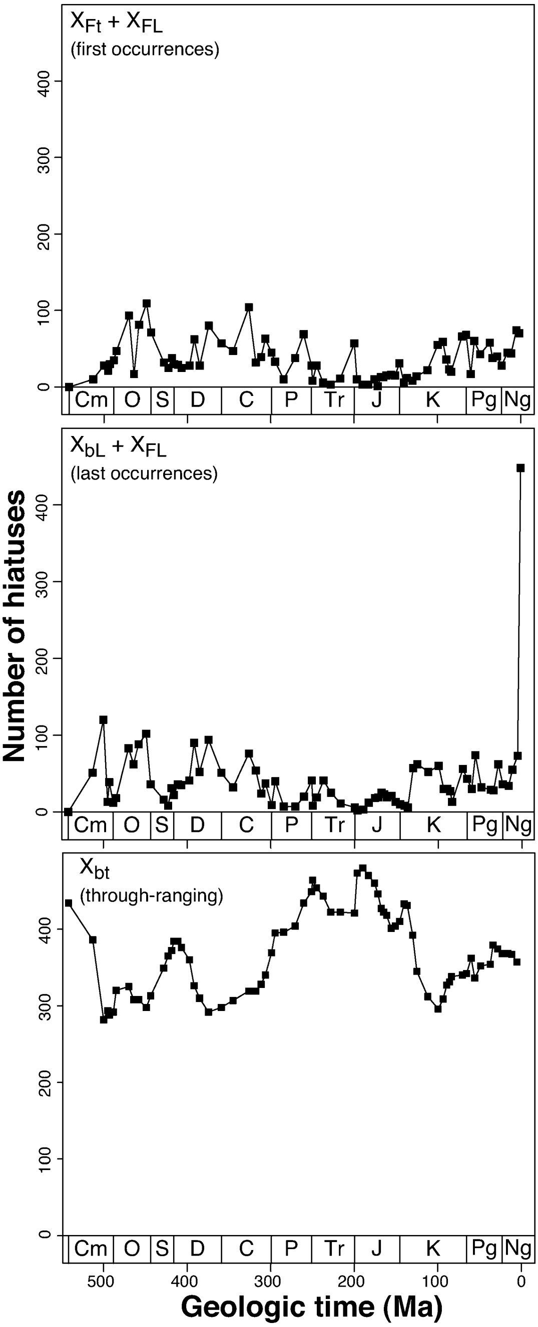

FIGURE 6. Time series of the total number of gaps that start in each interval ($X_{FL} + X_{Ft}$), end in each interval ($X_{FL} + X_{bL}$), and span each interval (X_{bt}). Note that most gaps in an interval range through that interval. Data are plotted on identical scales and at age of the interval base from the Lower Cambrian to Pleistocene.

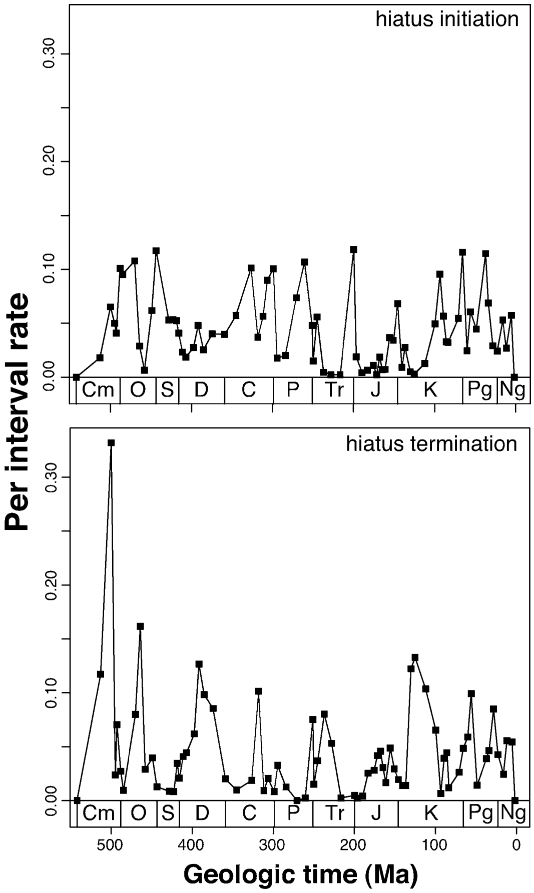

FIGURE 7. Rates of gap initiation (analogous to taxonomic origination), and gap termination (analogous to taxonomic extinction) measured using Foote's (2000a) survivorship-based rate metrics. Compare gap turnover rates with those in Figure 2, top panels. Note that hiatuses have much lower long-term rates of initiation and truncation than do marine animal genera, indicating that duration tends to be longer for hiatuses than for marine animal genera. Data are plotted at age of the interval base from the Lower Cambrian to Pleistocene.

their rates of initiation (i.e., origination) and termination (i.e., extinction; Fig. 7) using the persistence-based rate metrics of Foote (2000a). These rate metrics correspond to the area-weighted rates of expansion and contraction of hiatuses over the continental surface (Peters 2006), and therefore pulses in hiatus origination correspond to the truncation of sediment and the areal expansion of hiatuses, and pulses in hiatus extinction correspond to the expansion of sediment and the widespread truncation of hiatuses.

Hiatus initiation and termination rates (Fig. 7) are low relative to genus turnover rates (per-interval rates in Fig. 2) and there are few prominent pulses. According to hiatus termination rates (Fig. 7), the expected duration of a sedimentary hiatus (which is equal to the inverse of the termination rate) is approximately 20 time intervals, or 100 Myr. By contrast, the average duration of a sedimentary rock package is approximately 25 Myr (Peters 2006).

If hiatus durations were exponentially distributed, then the inverse of the hiatus termination rate (Fig. 7) would equal the mean gap duration. However, hiatus durations are not exponentially distributed (Fig. 8) because there is a small and diffuse mode at very long durations (300–500 Myr). This mode increases the mean duration of hiatuses and likely results from mixing two rather distinct hiatus types—those that completely bound the major Sloss-scale sequences (Sloss 1963) and those that occur within and between the major Sloss-scale sequences.

To preliminarily identify hiatuses as belonging to one or the other major type without imposing an arbitrary duration threshold, all hiatuses that start at the base of the Phanerozoic or that occur in the Pleistocene (i.e., hiatuses bracketing the beginning and end of the Phanerozoic) were identified as ''inter-sequence'' gaps, and all others were identified as ''intra-sequence'' gaps. The inter-sequence gap durations are bimodal (Fig. 8). The lower mode reflects the base of the Cambrian Sauk sequence, which generally interrupts a sedimentary hiatus persisting from the base of the Phanerozoic. It also includes young Cenozoic marine sediments that are truncated by the current low-stand in sea level. The long-duration mode reflects hiatuses that bound major sequences. Many of these gaps span much of the Phanerozoic and are therefore several hundred million years in duration. Intra-sequence hiatuses, on the other hand, lack a long-duration mode and are approximately exponentially distributed and have a mean duration that is comparable to the average duration of intervening sediment packages (Peters 2006). Note that there are many fewer inter-sequence gaps than intra-sequence gaps (Fig. 8).

Because this study seeks to compare the

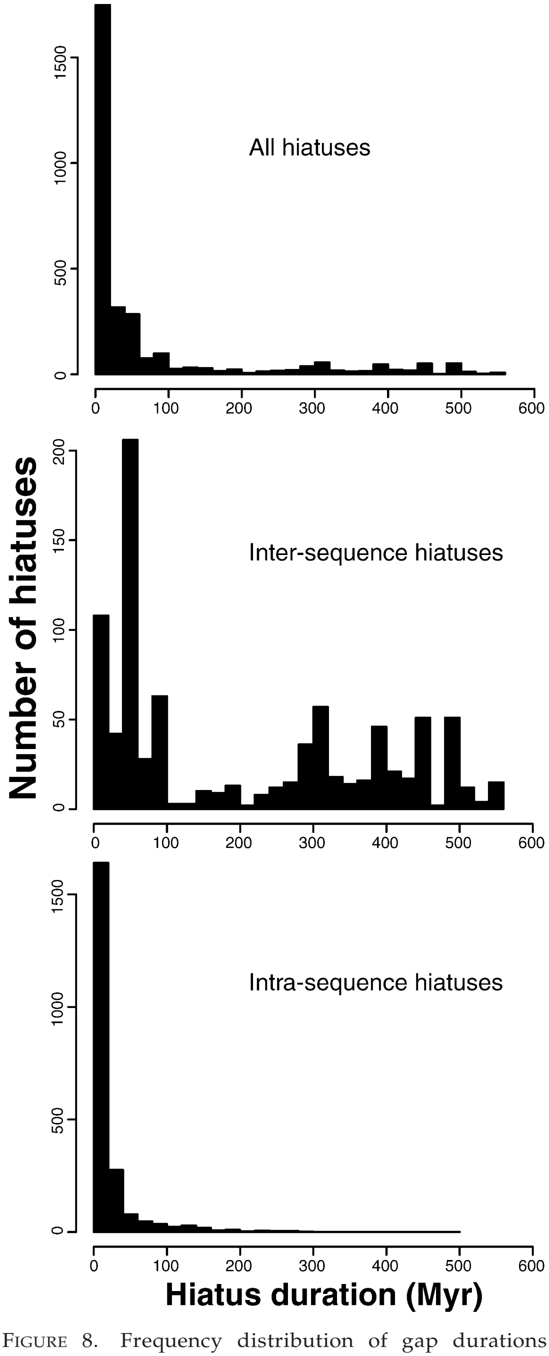

FIGURE 8. Frequency distribution of gap durations measured in millions of years (Myr). Combined distribution is positively skewed and shows evidence of a small, broad mode at long durations (300–500 Myr). Hiatuses are subdivided into two groups, those that start at the base of the Phanerozoic or that range into the Pleistocene (''inter-sequence'' gaps), and those that have first and last occurrences sometime between these time intervals (''intra-sequence'' gaps). See text for discussion.

temporal structure of hiatuses and their durations with observed rates of turnover in the fossil record, a central question is, how do the average durations of sedimentary hiatuses change over time? To generate mean and median hiatus durations for each time interval, all hiatuses with a first and/or last occurrence in a given time interval were grouped together. The resultant mean and median hiatus durations provide an estimate of the duration of sedimentary hiatuses that start and end in each time interval (Fig. 9) and that are therefore most relevant to the simple Unconformity Bias hypothesis (Fig. 1). Through-ranging (X_{bt}) hiatuses are not included in the tabulation of mean and median hiatus duration because these hiatuses also contribute to hiatus durations in adjacent time intervals and therefore do not contribute to the Unconformity Bias for turnover rates in adjacent time intervals.

Differences between mean and median hiatus durations for each time interval (Fig. 9) reflect the skewness of the underlying frequency distribution of durations for that interval (mean higher, positively skewed; mean lower, negatively skewed; mean and median equal, symmetric). Because hiatuses are constrained to range within the Phanerozoic (i.e., hiatuses are truncated at the Precambrian/Cambrian boundary and cannot range into the future), there are edge effects that limit mean and median gap durations (Fig. 9). However, for most intervals, edge effects do not appear to be strongly influencing the estimated mean/median hiatus durations. This is particularly true with respect to short-term changes in hiatus durations (i.e., interval-to-interval changes, or first differences), which are the most salient patterns for the present analyses.

Mean and median gap durations, grouped by their times of first and last occurrence, vary considerably during the Phanerozoic (Fig. 9). Some intervals have mean and median gap durations that span more than 100 Myr. Other intervals have mean and median gaps that are little more than 10 Myr in duration. Below, the time series of gap duration (Fig. 9) and gap areal extent (Fig. 5) are compared with the time

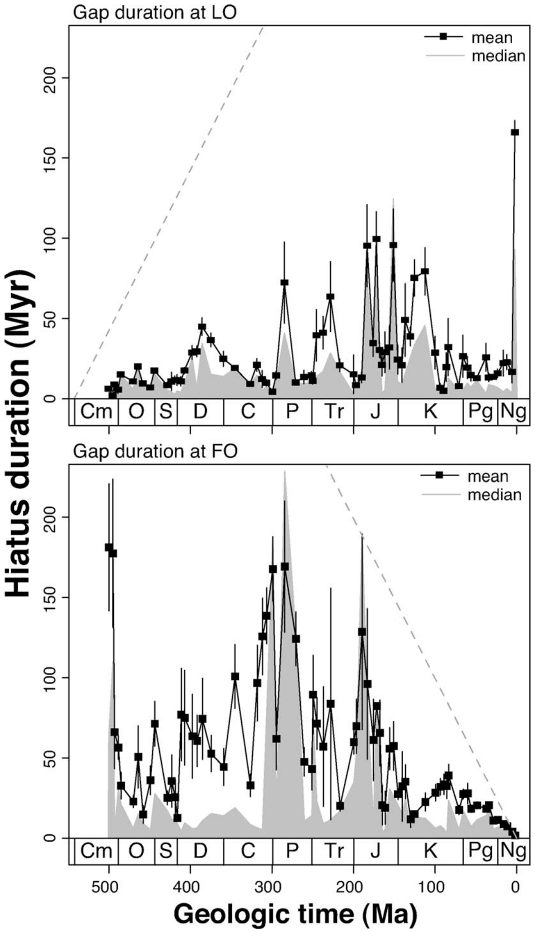

FIGURE 9. Time series of mean (dark lines and points) and median (shaded area) gap durations plotted at the time of their last (top) and first (bottom) occurrence, as in Figure 6. Dashed lines show expected limits of edge effects on hiatus durations. Note that the mean and median gap durations in most time intervals are 10 or more million years. Compare observed mean gap durations with those required under the Unconformity Bias scenario (Fig. 3). Data are plotted at age of the interval base from the Dresbachian to Pleistocene. Error bars show ±1 standard error of the mean duration estimate in each interval.

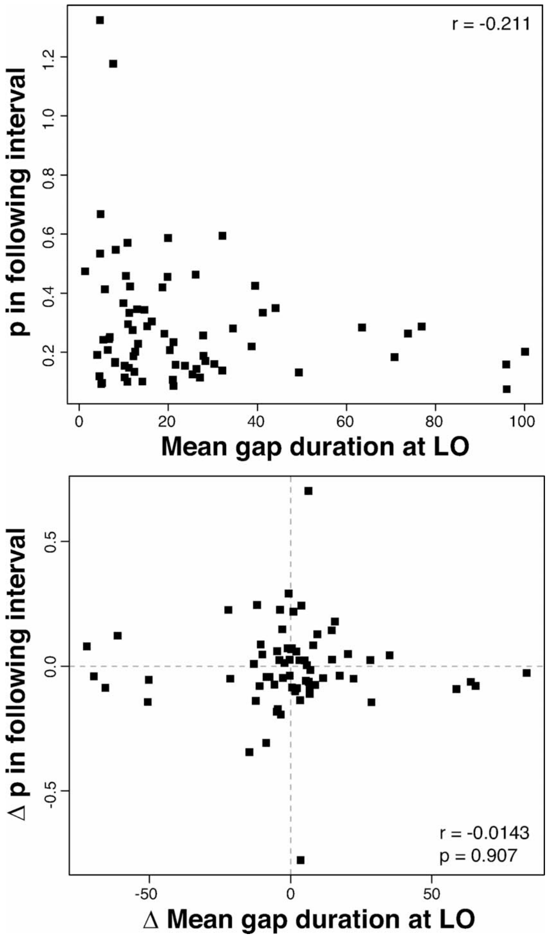

FIGURE 10. Relationship between mean duration of a gap at its time of last occurrence and apparent genus origination rate in the following time interval (see Fig. 1). Both the untransformed time series (top) and the detrended time series (first differences) are shown. There is no correlation between gap duration and apparent rate of genus origination in the following interval. Linear product-moment correlation coefficients and *p*-value for first differences are shown. See Table 1 for similar comparisons using different measures of the durations of sedimentary hiatuses.

series of evolutionary rates observed in the fossil record.

Hiatuses and Taxonomic Rates.—If variations in apparent rates of genus origination and extinction are primarily artifacts of gaps in the fossil record, as expected under the Unconformity Bias hypothesis, then mean gap duration should be positively correlated with the apparent magnitude of extinction in the previous interval and the apparent magnitude of origination in the following interval (Fig. 1). However, there is no significant correlation between mean hiatus duration and genus origination rate in the following interval. This is true for both the raw time series and the detrended data (i.e., first differences; Fig. 10). Similarly, there is no significant correlation between mean hiatus duration and genus extinction rate in the previous interval (Fig. 11). Results are comparable if median durations are used and if durations are (inappropriately) based on all hiatuses, including those that span intervals (Table 1).

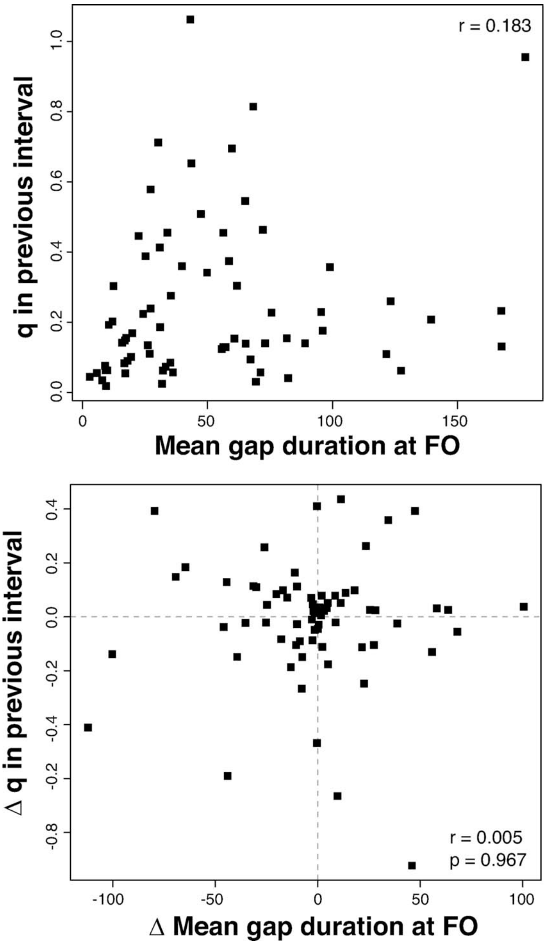

FIGURE 11. Same as Figure 10 but for rates of genus extinction plotted against mean duration of gap at its time of first occurrence. There is no significant correlation between gap duration and rate of genus extinction in the previous interval (see Fig. 1).

If, instead, mean and median hiatus durations for each interval are weighted by the number of hiatuses (i.e., the area of a hiatuses that start or end in each interval), then the hiatus-rate correlations improve, but they remain rather weak (Table 1). Including through-ranging hiatuses in the hiatus duration estimates for each interval also yields one significant correlation for origination, but this analysis is less appropriate because it introduces much stronger edge effects and does not target the gaps in the record that are relevant to the apparent rates of taxonomic turnover in adjacent time intervals (as in Fig. 1). Thus, the importance of the weak, negative correlation between the mean duration for all gaps in an interval and genus origination (Table 1) in the following interval is questionable and, moreover, goes in a direction contrary to the Unconformity Bias hypothesis (i.e., correlation is negative, not positive).

Although the durations of sedimentary hiatuses do not consistently predict apparent rates of genus turnover in a manner that conforms to the Unconformity Bias hypothesis, there are significant positive correlations between several measures of the areal extent of sedimentary hiatuses and the corresponding evolutionary rates. The detrended (i.e., first differences) time series of the total number of hiatus first occurrences is significantly and positively correlated with first differences in the number of genus last occurrences in the previous interval (Fig. 12). There is also a positive correlation between the detrended time series of hiatus last occurrences and the number of genus first occurrences in the subsequent interval, but the correlation is weak and nonsignificant (Table 1, Fig. 12). Similarly, if hiatus turnover rates are used instead of first and last occurrences (Figs. 2, 7), then the detrended time series for hiatuses (i.e., the area-weighted rates of areal expansion and contraction of hiatuses) are significantly and positively correlated with the corresponding, lagged evolutionary rates (Table 1). In all cases, the correlation between hiatal areal extent and extinction is stronger than the correlation between hiatal extent and origination.

Discussion

Numerous analyses have linked paleobiological patterns to the architecture of the sedimentary rock record at different temporal and spatial scales, ranging from local sections and individual depositional basins (Holland 1995, 1996, 2000; Smith et al. 2001; Holland and Patzkowsky 2002) to entire continents/sub-continents and the global fossil record (Raup 1972, 1976; Peters and Foote 2001, 2002; Smith et al. 2001; Crampton et al. 2003; Peters 2005). Given nothing more than significant positive correlations between the temporal structure of the rock record and macroevolutionary patterns, it is tempting either to assume that geologically mediated sampling biases distort fossil data so as to be completely

TABLE 1. Correlation coefficients for various measures of gap duration and gap extent versus apparent per capita rates of genus origination (p) and extinction (q) measured on a per-interval basis using Foote's (2000a) continuous, survivorship-based rate metrics. Comparisons are grouped according to those that are expected to be positive and significant under the Unconformity Bias and Common Cause hypotheses. ''Area-weighted'' refers to hiatus durations weighted by the number of hiatuses. Linear product-moment correlation coefficients (r) and Spearman rank-order correlation coefficients (ρ) and corresponding p-values are shown. All correlations are based on lagged time series (Fig. 1) that have been detrended by taking first differences. Time series consist of 70 intervals, from the Dresbachian to Pliocene. Coefficients with p-values less than 0.05 for both Pearson product-moment and Spearman coefficients are shown in bold. FO, first occurrence; LO, last occurrence. See text for discussion.

Unconformity Bias Hypothesis

Comparison	r	p	ρ	p
Extinction				
Mean hiatus duration at FO vs. q	0.005	0.967	−0.050	0.685
Mean hiatus duration at FO (area weighted) vs. q	**0.363**	**0.002**	**0.319**	**0.008**
Median hiatus duration at FO vs. q	−0.024	0.846	0.077	0.530
Median hiatus duration at FO (area weighted) vs. q	0.225	0.062	0.354	0.003
Mean duration of all hiatuses vs. q	−0.159	0.191	−0.276	0.022
Origination				
Mean hiatus duration at LO vs. p	−0.014	0.907	0.020	0.871
Mean hiatus duration at LO (area weighted) vs. p	0.180	0.139	0.229	0.059
Median hiatus duration at LO vs. p	−0.045	0.713	0.016	0.892
Median hiatus duration at LO (area weighted) vs. p	0.128	0.294	0.209	0.084
Mean duration of all hiatuses vs. p	−0.145	0.233	−0.192	0.114

Common Cause Hypothesis

Comparison	r	p	ρ	p
Extinction				
Hiatus FO vs. genus LO	**0.572**	**<0.0001**	**0.632**	**<0.0001**
Hiatus FO vs. genus q	**0.304**	**0.011**	**0.342**	**0.004**
Hiatus p vs. genus q	**0.528**	**<0.0001**	**0.479**	**<0.0001**
Origination				
Hiatus LO vs. genus FO	0.135	0.268	0.168	0.169
Hiatus LO vs. genus p	0.230	0.057	0.273	0.023
Hiatus q vs. genus p	**0.335**	**0.005**	**0.402**	**<0.001**

biologically meaningless or, worse still, to dismiss the correlations out of hand and forge ahead in interpreting fossil patterns biologically (e.g., Sepkoski et al. 1981; Benton 2003). However, the Unconformity Bias hypothesis, an important component of Geologic Bias, is inherently linked to the temporal distribution of gaps in the sedimentary record, not the temporal distribution of sedimentary rock, and therefore this analysis brings a new perspective on the interpretation of rock-fossil correlations.

The results of this study do not support a simple Unconformity Bias model (Fig. 1) as a viable explanation for the strong statistical correlation between rates of genus extinction and origination and the temporal continuity of sedimentary rock (Peters 2005). Although it is true that substantial, widespread unconformities do tend to correspond in time to large increases in apparent rates of genus turnover, such unconformities are not associated with gaps that are particularly long in comparison to many other gaps in the sedimentary record, and there is no positive correlation between the temporal duration of hiatuses and rates of genus turnover (Table 1). Thus, the rock-fossil similarity (e.g., Peters 2005) does not appear to be imposed exclusively by the temporal structure of hiatuses.

When hiatus durations are weighted by the number of hiatuses to account for their geographic extent, several significant positive correlations with evolutionary rates emerge, but these correlations are generally no stronger than when hiatal durations are ignored altogether and only the areal extents of hiatuses are considered (Table 1). Thus, there is little evidence to suggest that the mean durations of hiatuses explain any significant component of

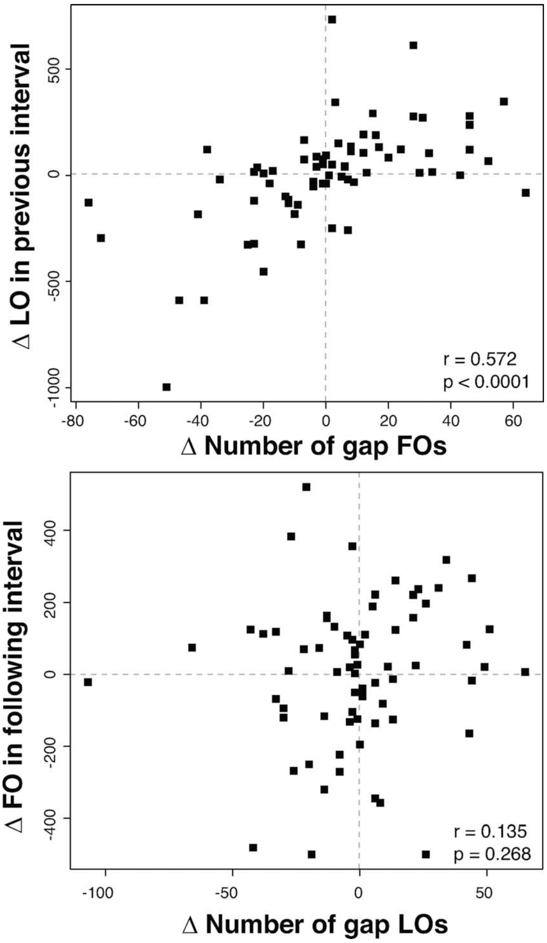

FIGURE 12. Relationship between detrended time series (first differences) of number of gaps (i.e., areal extent of hiatus) versus corresponding number of genus first and last occurrences, as in Figures 10 and 11. There is a significant positive correlation between the number of gaps in an interval and the number of genus last occurrences in the previous interval. There is a positive correlation between the number of gaps and origination rate in the following interval but the correlation is not significant. See Table 1 for similar comparisons using different measures of the areal extent of sedimentary hiatuses.

the apparent variation in rates of genus origination and extinction. The areal extents of hiatuses are, on the other hand, significantly and positive correlated with evolutionary rates. These results are consistent with the hypothesis that both the sedimentary record and macroevolutionary patterns are similarly structured by a shared set of forcing mechanisms (i.e., Common Cause hypothesis).

The most likely Common Cause mechanisms involve fluctuating sea level and concomitant changes in the area of shallow marine seas and the expansion/contraction and formation/destruction of unique epicontinental marine environments (Newell 1949, 1952; Valentine and Moores 1970; Schopf 1974; Simberloff 1974; Sepkoski 1976; Hallam 1989; Hallam and Wignall 1999). Because high-stands in sea level are associated with widespread epicontinental seaways that frequently have environmental conditions differing substantially from those found in more openly circulating, passive margin settings, not only are oscillations in sea level likely to cause changes in the absolute area of shallow marine settings, lateral shifts of facies tracts, and geographic expansions and contractions of unconformities, but they also will be associated with the wholesale formation and destruction of distinctive epicontinental marine environments. Fluctuations in sea level may also be an important symptom of many other environmental factors, such as global climate (Miller et al. 2005), that may enhance the biological effects of sea level change.

Given the forcing mechanisms that are relevant to the Common Cause hypothesis, this scenario is also supported by the fact that rates of genus extinction more closely match the areal extent of sedimentary hiatuses than do rates of genus origination (Table 1). In fact, the geologic record consistently reproduces patterns of extinction better than it reproduces patterns of origination (Peters and Foote 2002; Peters 2005). This extinction-origination rate discrepancy is not expected under the simple Unconformity Bias scenario (Fig. 1), but if the evolutionary opportunities afforded by sea level rise and the corresponding expansion of epicontinental seaways do not immediately result in the origination of novel genera, and if genus extinction can match the timing of sea level fall and environment shifts that result in the loss of marine environments, then, all else being equal, there should be an empirical disconnect between origination rates and the rock record relative to extinction rates and the rock record. Of course it is also possible that other biases (see below) may differentially affect taxonomic origination and extinction rates, but these remain to be quantitatively evaluated.

The Common Cause hypothesis finds some additional measure of support in an independent approach to addressing the problem of variable preservation in the fossil record. Using an optimization algorithm that simultaneously finds the most likely time series of true origination, true extinction, and rates of preservation given only observed forward and backward taxon survivorship matrices, Foote (2003, 2005) has shown that apparent rates of genus extinction and origination in the fossil record can neither be taken at face value nor ascribed entirely to variation in preservation rates. If the Unconformity Bias were entirely responsible for the rock-fossil correlations that have been documented elsewhere (Peters 2005), then Foote's rate-fitting algorithms would have correctly identified the variable sampling component in Sepkoski's data and fit constant or smoothly declining true rates of evolution (as in Fig. 2). However, the survivorship structure of Sepkoski's data is not consistent with a simplistic Unconformity Bias model (Foote 2003). This result provides support for the Common Cause hypothesis, but it does not unequivocally rule out alternative biases, because the ''preservation'' term in Foote's rate fitting algorithms includes all aspects of preservation, not just preservation related to unconformities and their hiatuses, as studied here.

Additional Biases in Fossil Data.—Although the results of this study support the Common Cause hypothesis and refute a simplistic Unconformity Bias scenario (Fig. 1), fully testing the Common Cause hypothesis requires evaluating the effects of numerous other biases in fossil data.

Two primary biases afflict macroevolutionary patterns in the fossil record: ''extrinsic biases'' and ''intrinsic biases'' (Table 2). Extrinsic biases do not involve fossil data and would therefore persist even if every fossil specimen preserved in every cubic meter of sediment all over the globe were perfectly described, classified, measured, placed into a phylogenetic framework, precisely and accurately dated, and indexed. Extrinsic biases cannot usually be addressed by sampling standardization, additional field collecting, taxonomic/phylogenetic revision, or modeling. Instead, extrinsic biases must be measured directly, as independently of fossil data as possible, and then evaluated in their own right. Intrinsic biases, on the other hand, are related to the scientific and social processes of accumulating knowledge and are therefore mutable and can be overcome by some of the above-mentioned devices. Both extrinsic and intrinsic biases must be simultaneously addressed in order to achieve a complete and accurate understanding of the true evolutionary history of life.

TABLE 2. Major types of biases that afflict the study of evolutionary patterns in the fossil record. ''Extrinsic'' (not specific to fossil data) and ''intrinsic'' (specific to fossil data) biases can each be subdivided into two major types of biases that operate largely, though not necessarily entirely, independently of one another. Biostratigraphic biases and other correlation errors are intrinsic biases that are related both to sampling and taxonomy and are therefore shown to bridge these two realms.

Extrinsic Biases	
Geologic Bias	*Taphonomic Bias*
Rock quantity	Preservation potential
Unconformity	Quality of preservation
Facies/environment	
Geographic	
Diagenetic	
Intrinsic Biases	
Sampling Bias	*Taxonomic Bias*
Sample size	Pseudoextinction
Publication	Pseudo-origination
Geographic	Nomenclatural
Signor-Lipps	Equivalence taxa
Biostratigraphic/correlation	

Here, I have been careful to specify that only one type of extrinsic bias, Unconformity Bias (sensu Holland 1995), is being tested. However, there are many other types of extrinsic biases (Table 2) that have not yet been quantified and that may still influence the results of this and other studies. For example, it is here assumed that all sedimentary rock packages are homogeneous, and that there are no systematic environmental trends within gap-bound rock packages. However, sedimentary rock packages might, on average, preserve environmental trends (e.g., shallowing upward) that result in effective sampling gaps that are much longer in duration than the hiatuses measured here. It is also possible that the areal extents of unconformities are correlated with temporal patterns of facies preservation and environmental representation. In fact, lithofacies are known to shift on both long and short time scales during the Phanerozoic (Ronov 1978; Ronov et al. 1980; Walker et al. 2002; Peters 2006), so it is eminently possible that large unconformities tend to be followed by substantial facies changes that greatly lengthen the effective paleontological sampling gaps with which they are associated. Because several studies have suggested that facies biases can be more important than unconformity biases in driving taxon range offsets in local depositional basins (e.g., Holland and Patzkowsky 2002), it is likely that larger-scale facies biases have strongly affected turnover rate estimates. Other geologic biases may also be important (Table 2) and may similarly covary with the temporal architecture of sedimentary rock, thereby confounding the interpretation of these and other results.

Although several extrinsic biases are likely to be influencing the correlations between geologic data and paleobiological patterns, the possibility that intrinsic biases might covary with extrinsic biases poses significant challenges to the interpretation of these and many other results. In particular, if taxonomic errors and/or biostratigraphic correlation errors tend to be preferentially concentrated at widespread unconformities in the sedimentary record, then it is possible that geologic and macroevolutionary patterns are structured less by a shared set of forcing mechanisms than by a shared set of correlated errors.

Previous work has suggested that many taxonomic and stratigraphic errors might be randomly distributed in large taxonomic databases, which would not significantly distort apparent macroevolutionary patterns (Adrain and Westrop 2000). Several other studies, however, suggest that some aspects of the macroevolutionary patterns derived from global compilations may be significantly biased by taxonomic errors and/or ambiguously defined higher taxa (Culver et al. 1987; Patterson and Smith 1989; Smith and Jeffery 1998; Jeffery 2001; Ausich and Peters 2005). Testing and overcoming any taxonomic biases and associated biostratigraphic errors, and documenting the quantitative relationships between such errors and the temporal structure of the sedimentary rock record, remain exciting and critical next steps in understanding the pervasive positive correlations between the sedimentary rock record and macroevolutionary patterns and in testing fully the Common Cause hypothesis.

Conclusions

1. Background-adjusted rates of genus extinction in the face-value fossil record suggest that only two or three major mass extinctions stand out above other positive rate anomalies in the Phanerozoic. The most severe of these appears to be the K/Pg, which is shown to have an extinction excess equivalent to approximately 38 Myr (about six stages) of expected background extinction. The P/T has an extinction excess equivalent to approximately 26 Myr (about five stages), and the Tr/J has an extinction excess equivalent to approximately 11 Myr (about four stages). All other positive extinction rate anomalies are of comparable magnitude and generally represent extinction excesses of less than 10 Myr.
2. Background-adjusted rates of genus origination show no prominent pulses (all represent less than 14 Myr of normal, background origination) and are distributed among several stages that often follow positive extinction rate anomalies. Positive origination rate excursions in the Cambrian, which are large relative to those in all other time intervals, are comparable to rates of origination that follow the P/T and K/T when reexpressed relative to background.
3. Hiatuses spanning more than approximately 1 Myr in the marine sedimentary rock record of North America have a mean duration of approximately 73 Myr.
4. On average, approximately one-fourth of North America is covered by marine sediment of a given age. The other three-fourths of the continent is covered by hiatus. The end-Permian through Jurassic departs markedly from the Phanerozoic average by having particularly widespread

hiatuses and relatively little marine sedimentary cover.

5. Mean and median hiatus durations, grouped by their times of initiation and termination, vary considerably on a stage-to-stage basis, ranging from approximately 150 Myr to less than 10 Myr.
6. The three largest positive genus extinction rate anomalies in the Phanerozoic are not associated with hiatuses of unusually long duration.
7. Rates of genus extinction and origination are not correlated with hiatus durations, as expected under the Unconformity Bias hypothesis.
8. Rates of genus extinction and origination are positively correlated with the areal extents of hiatuses. This result is consistent with the notion that the sedimentary record and macroevolutionary processes are similarly influenced by a shared set of forcing mechanisms (Common Cause hypothesis). The most probable mechanism is sea level change and correlated environmental factors, but numerous other biases that are both inherent in the geologic record and unique to fossil data must be tested before alternative hypotheses can be ruled out.

Acknowledgments

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Appendix

Background Rates

Face-value rates of genus extinction and origination were calculated using Sepkoski's (2002) global compendium and Foote's (2000a) per capita rate metrics. Only genera with first and last occurrences fully resolved to stages in the Paleozoic and Mesozoic and subepochs in the Cenozoic were used to calculate all rates.

To calculate the best-fit exponential function for the face-value rate data, Sepkoski's evolutionary rates were transformed using natural logarithms and then regressed against time using least-squares linear regression. Ages for each rate estimate were based on the age at the base of their respective time interval using Gradstein et al. (2004). All analyses were conducted in R 2.2.0 for Mac OS X (http://www.r-project.org/).

Positive Rate Anomalies

Positive rate anomalies were identified as all positive rate residuals on the rate-time regressions described above and shown in Figure 2. Given these positive rate anomalies and the expected background rates, the amount of normal, background time represented by each anomaly was calculated as follows:

For per capita, continuous rates measured per million years, the excess number of X_{bL} in time interval Δt is given by the number of observed X_{bL} minus the number expected if extinction rate were equal to the expected background rate, $\bar{q}$. The latter is given by the number of taxa that cross the bottom boundary times the probability of going extinct in time interval Δt:

$$X_{bL}(excess) = X_{bL} - (X_{bL} + X_{bt})(1 - e^{-\bar{q}\Delta t}), \tag{1}$$

where $\bar{q}$ is derived from the best-fit exponential function to the observed rate data in time interval Δt. The expected number of X_{bt} is given by the number of taxa observed to cross the bottom boundary times the probability of survival to the end of the interval based on the expected background rate, $\bar{q}$:

$$\bar{X}_{bt} = (X_{bt} + X_{bL})e^{-\bar{q}\Delta t}. \tag{2}$$

Setting equation (1) equal to equation (2) times the probability of going extinct in time interval Δt and then solving for Δt yields the amount of normal, background time, under the hypothesized $\bar{q}$, that is represented by each positive rate anomaly:

$$\Delta t(need) = \frac{-\ln\left[1 - \dfrac{N_{bL}(excess)}{N_{bt}}\right]}{\bar{q}}. \tag{3}$$

The same calculations apply to origination, but in the opposite temporal direction:

$$\Delta t(need) = \frac{-\ln\left[1 - \dfrac{N_{Ft}(excess)}{N_{bt}}\right]}{\bar{p}}. \tag{4}$$

For per capita, continuous rates measured on a per-interval basis, the calculation is simpler because per-interval rates scale linearly with interval duration (Foote 2000a). The excess amount of extinction relative to background in the per-interval case is given by

$$\Delta t(need) = \frac{q - \bar{q}}{\bar{q}}, \tag{5}$$

where rates are measured on a per-interval basis and excess time is expressed in number of intervals. Similarly, the excess amount of origination relative to background measured on a per-interval basis is given by

$$\Delta t(need) = \frac{p - \bar{p}}{\bar{p}}. \tag{6}$$

All of the above calculations assume that each cohort has a constant $\bar{q}$ and $\bar{p}$ (a reasonable assumption for the generally short durations required) and that extinctions and originations are exponentially and continuously distributed through time intervals.

A recent analysis by Foote (2005) found that evolutionary rates, and in particular rates of extinction, are best modeled as concentrated at interval boundaries (i.e., extinction is ''pulsed'' rather than continuous and exponentially distributed throughout an interval). When rates of extinction are measured using the pulsed model (Foote 2005), the amount of normal, background time represented by positive extinction rate anomalies is given by

$$\Delta t(need) = \frac{\ln(1 - q)}{\ln(1 - \bar{q})} - 1, \tag{7}$$

where $\bar{q}$ is the expected extinction rate calculated as described above but based on pulsed extinction rate estimates (which are calculated as percent extinction, or $\{X_{bL} + X_{FL}\}/\{\mathrm{X}_{\mathrm{FL}} + X_{bL} + X_{Ft} + X_{bt}\}$).