Pulsed origination and extinction in the marine realm

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Abstract.—The pattern of variation in taxonomic turnover on short timescales is expected to leave detectable signals even when taxonomic data are compiled at coarser timescales. Global, stage-level data on first and last appearances of marine animal genera are analyzed to determine whether it is more likely that origination and extinction were spread throughout stages or that they were concentrated at a single episode per stage. The analysis takes incomplete and variable sampling of stratigraphic ranges into consideration, and it takes advantage of the fact that empirical sampling rates are within the range of values that allow the within-stage turnover models to be distinguished on the basis of stage-level data. The data strongly support the model of a single extinction pulse per stage over the alternative of continuous extinction within the stage. Pulsed origination is also supported over continuous origination, but the case is not as compelling as for extinction. Differential support for pulsed turnover is not confined to a few stages. Pulsed turnover therefore appears to be a general feature of the evolution of marine animals.

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Pulsed Turnover in Earth History

One of the most striking features of the fossil record is that rates of taxonomic turnover vary greatly over geological time. Within marine animals, average rates of origination and extinction have declined over the Phanerozoic, and this decline has been punctuated by intervals of mass extinction and evolutionary radiation (Raup and Sepkoski 1982; Van Valen 1984; Gilinsky and Bambach 1987; Sepkoski 1998). On the global scale, these patterns of rate variation are documented mainly at the level of stratigraphic stages and series. It is largely unknown, however, to what extent the pattern of punctuated turnover extends to finer temporal scales. Within a given stage of elevated origination, for instance, do new taxa originate fairly continuously throughout the stage, or are the originations clustered at one or more moments in time? The pattern of turnover within a stage is important for understanding the mechanisms of radiation and extinction.

At local and regional scales, many instances of clustered first and last appearances have been documented (e.g., Vrba 1985; Elder 1989; Brett and Baird 1995). Many authors have questioned whether regional turnover pulses reflect true events, however, because they are often accompanied by stratigraphic gaps and facies shifts of just the kind that are predicted to lead to spurious pulses (Holland 1995, 1996, 2000; Behrensmeyer et al. 1997; Smith et al. 2001; Kidwell and Holland 2002). Even if first and last appearances were taken as reasonable approximations of true origination and extinction, it would still be necessary to ask whether the clustering stands out above the expectations of a stochastic process (Baumiller 1996).

At the global scale, the case for pulsed turnover has also been difficult to assess. This is partly because of limits on stratigraphic resolution that result from a variety of factors, including the global aggregation of data that may be highly resolved at the local scale (Bowring et al. 1998). It is therefore necessary to infer patterns of turnover indirectly when analyzing existing global compendia. One way to do this is to specify alternative models of turnover *at a finer temporal scale than has been observed* and to evaluate the predictions they make at the observed scale of temporal resolution. Raup's (1991, 1996) analysis of genus extinction is a case in point. Raup constructed cohort survivorship curves of marine animal genera at the stage level. He then used mathematical modeling of constant versus pulsed species-level extinction *within stages* to show

that the decline of survivorship curves is too erratic to be compatible with stochastically constant species extinction at a uniform rate through the Phanerozoic. Starting with the model of highly pulsed species extinction, Raup then estimated the probability distribution of pulse sizes—the Kill Curve—needed to explain the variation in genus survivorship curves. This approach tacitly assumed that the distribution of species-level extinction pulses, while it is quite variable, is the same for all stages over the course of the Phanerozoic. In principle, however, if extinction rate were constant within a stage but highly variable from one stage to the next, cohort curves would still decline erratically. This alternative possibility was not explicitly evaluated.

In this paper I present an approach to assessing pulsed versus continuous turnover at the global scale; this approach can also be applied to local and regional data. The approach differs from previous considerations of global turnover in two principal ways. First, it does not assume a fixed distribution of turnover rates throughout the Phanerozoic (cf. Raup 1991, 1996). Second, it does not assume that observed first and last appearances necessarily approximate true originations and extinctions; i.e., it takes incomplete and variable sampling into consideration. In fact, the approach uses incompleteness to advantage rather than simply circumventing it.

In brief, the method works as follows: An inverse procedure is used to estimate the true rates of origination and extinction that underlie the observed first and last appearances. The inversion is carried out in turn for evolutionary models of pulsed and continuous turnover, and the goodness-of-fit of the various models is compared in terms of the log-likelihood or support function. The results indicate that, for marine animal genera over the Phanerozoic, there is substantially stronger support for pulsed as opposed to continuous turnover within stratigraphic stages.

Data and Methods

Data

I analyzed stratigraphic ranges of genera of marine animals and animal-like protists from Sepkoski's (2002) compendium, with some minor corrections. I used Sepkoski's basic stratigraphic units, some of which formally are stages and some of which are series (Sepkoski 2002: Table 1). Because nearly all Paleocene and Eocene occurrences are resolved below the series level, I subdivided these two intervals. This yielded 80 operational stratigraphic intervals, which for simplicity I will refer to as *stages.* I used all genera whose first and last appearances both could be resolved to the stage level; all told, there are 30,570 of these.

Evolutionary Models

Here I contrast four alternative evolutionary models of rate variation within a stage; all models allow rates to vary among stages. Origination may occur continuously at a constant per capita rate within a stage, or it may be pulsed, occurring at a moment in time within the stage. The same is true for extinction. The pulses are assumed to occur at stage boundaries. The extinction pulses are arbitrarily assigned to the end of one stage and the origination pulses to the start of the next stage, but this is just a bookkeeping convention. If extinction pulses were assumed to occur at the beginnings of stages, for example, the estimated extinction rates would be the same but they would be shifted forward in time by one stage. To a first approximation, a model with multiple turnover pulses within a stage (Raup 1991, 1996) behaves in effect like the model of continuous turnover. The pulsed model as used here is an extreme one in which there is but a single episode of origination and/or extinction within a stage.

The models considered here are end-members: origination and extinction can both be constant, they can both be pulsed, or one can be constant and the other pulsed. Intermediate models could be envisioned in at least two ways: First, some stages could be better characterized by pulsed turnover and others by continuous turnover. This possibility will be explored indirectly below (see ''Stage-by-Stage Support for Alternative Models,'' below). Second, each stage could have some mixture of constant and pulsed turnover. This possibility could be assessed in principle if
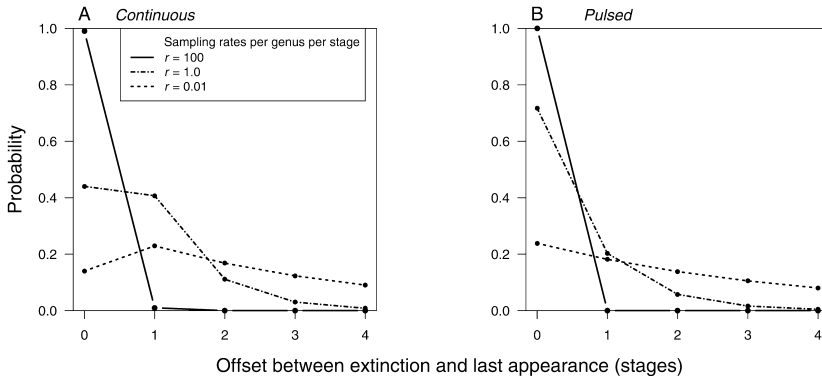
FIGURE 1.   Expected offset between stage of extinction and stage of last appearance. Curves portray the probability, given extinction in a specified stage j, that genus is extant and sampled in stage i ($i < j$) but not sampled after stage i. Probabilities are normalized so that only genera sampled at least once are included. Origination and extinction rates (p and q) are chosen so that there is no net diversity change within a stage and so that the number of new genera originating in a stage is 30% of the starting diversity. Thus, for the continuous model, this means that $p = q = 0.3$, and for the pulsed model, $p = 0.3$ and $q = 0.3/(1 + 0.3) \approx 0.23$. (See Foote 2003a for discussion of rates in the context of the two models.) For a given sampling rate, the continuous model yields a larger offset. Models are difficult to distinguish at very low or very high sampling rates, but they are distinct at intermediate sampling rates, which are empirically realistic. Probabilities are based on equations presented in Foote (2003a,b).

there were some reasonable way to decide a priori which genera are subject to continuous turnover and which to pulsed turnover. When data are pooled, however, genera lose their individuality. The situation is analogous to trying to estimate the bias of two unfair coins from a series of tosses. If one knows which results come from which coin, then the bias of each coin can be estimated. If the results are pooled, one simply ends up with an estimate of the average bias of the two coins.

It may not be intuitively obvious why the models of pulsed and continuous turnover within stages should be expected to leave distinctive signatures when data are resolved only to the stage level. Consider a single stage with an elevated extinction rate relative to previous stages. Under the pulsed model, with extinctions at the end of the stage, all the genera span the entire stage. Under the continuous model, most of the genera that become extinct in this stage will have true durations that span only part of the stage. It is therefore more likely, under the continuous model as opposed to the pulsed model, that a genus will not be sampled in its stage of extinction, in other words that it will have a last recorded appearance in the previous stage or even earlier. Thus a single stage of elevated extinction is more likely to be expressed as two adjacent

stages of elevated last appearance under the continuous model, and as a single stage of elevated last appearance under the pulsed model. Similar reasoning holds for origination, as well as for rates that are not elevated above the background level.

Figure 1 depicts the probability distribution of expected offsets between the stage of true extinction and the stage of last appearance; the probabilities are normalized to include only taxa that are sampled at least once. The curves in this figure show a range of sampling rates. In all cases, net origination and extinction are assumed to be equal to each other and constant from stage to stage. Both models are scaled so that the number of new genera originating in a stage is equal to 30% of the diversity at the start of the stage—a fairly typical value for Phanerozoic marine animals (Foote 2003a) (see Appendix). Average genus duration is thus a little more than three stages. Because data are coarsely binned, the offset in stages between extinction and last appearance of a genus is not generally the same as the gap measured in time or thickness. For example, if the extinction is early in one stage and the last appearance late in the previous stage, a gap of much less than a stage duration implies an offset of one stage. Likewise, if the extinction is late in one stage and the last appearance early

in the previous stage, a gap of nearly two stages counts as an offset of only one stage.

There are three salient features to note about Figure 1. First, as discussed above, the offset between extinction and last appearance is greater under the continuous model. Second, under empirically estimated sampling rates (about one per genus per stage [Foote 2003a]), most genera are expected to make their last appearance either in their stage of true extinction or in the previous stage. Third, and most important for this study, the curves for the pulsed and continuous models are maximally distinct from each other at intermediate sampling rates, and they converge as very low and very high sampling rates are approached. Empirical sampling rates are in the intermediate range that allows a clear separation between the models. It is largely because the record is incomplete, but not too incomplete, that the analysis presented here is possible. If the record were extremely poor or extremely good, the models would make nearly the same predictions about the observed pattern of first and last appearances. Paleontological incompleteness, far from hindering the choice between continuous and pulsed models on the basis of coarsely binned data, is the very factor that enables this choice.

The models are implicitly homogeneous: they assume that all taxa are alike in their evolutionary and preservational properties. Real data must violate this assumption, but simulation studies show that the optimization method is fairly robust if the various taxa follow similar temporal patterns, all tending to show higher- or lower-than-average rates during the same stages (Foote 2001). Because there is evidence that different taxonomic groups tend to follow similar trajectories of extinction (Raup and Boyajian 1988) and sampling (Foote 2001), it is arguably reasonable to use homogeneous models. One consequence of heterogeneity in sampling rates will be touched upon in the Discussion.

Optimization

The method of rate estimation is described in detail elsewhere (Foote 2001, 2003a). It is quite similar to the mark-recapture approach used recently by Connolly and Miller

(2001a,b, 2002), and earlier by others (Nichols and Pollock 1983; Conroy and Nichols 1984). It is also similar in spirit to the Constrained Optimization approach to biostratigraphic correlation (Kemple et al. 1995; Cooper et al. 2001; Sadler and Cooper 2003). Consider a hypothesized time series of true rates of origination, extinction, and sampling. Under an assumed model of evolution, this postulated set of parameters predicts the expected pattern of observed first and last appearances in the fossil record. The parameter space is explored numerically until the set of parameters is identified that yields predicted appearances in maximal agreement with the observed data. This parameter set is the preferred solution. Although this paper focuses on origination and extinction, the solution also includes estimates of sampling probability for each stage (see Foote 2003a).

More specifically, the first and last appearances are cast in the form of a matrix $\mathbf{X}$, in which X_{ij} is the number of genera having observed first appearance in stage i and last appearance in stage j. Each postulated parameter set is used to generate predicted, forward and backward survivorship probabilities: $P_{\rightarrow ij}$ is the probability that a genus with first observed appearance in stage i will make its last appearance in stage j, and $P_{\leftarrow ij}$ is the probability that a genus with last observed appearance in stage j will makes its first appearance in stage i. For any candidate set of rates, the likelihood is calculated as

$$L = \prod_{i=1}^{m} \prod_{j=i}^{m} P_{\rightarrow ij}{}^{X_{ij}} \times \prod_{j=1}^{m} \prod_{i=1}^{j} P_{\leftarrow ij}{}^{X_{ij}},$$

where m is the number of stages. The set of rates that maximizes this quantity is the maximum-likelihood estimate of the rates. In practice, it is convenient to work with the log-likelihood or support, given by

$$S = \ln(L) = \sum_{i=1}^{m} \sum_{j=i}^{m} X_{ij} \ln(P_{\rightarrow ij})$$

$$+ \sum_{j=1}^{m} \sum_{i=1}^{j} X_{ij} \ln(P_{\leftarrow ij}).$$

There are two principal differences between the optimization approach used here and that

which I used earlier (Foote 2003a). First, I previously optimized by minimizing weighted log deviations between expected and observed probabilities:

$$D = \sum_{i=1}^{m} \sum_{j=i}^{m} X_{ij} \left| \ln(P_{\rightarrow ij}/F_{\rightarrow ij}) \right|$$

$$+ \sum_{j=1}^{m} \sum_{i=1}^{j} X_{ij} \left| \ln(P_{\leftarrow ij}/F_{\leftarrow ij}) \right|.$$

where F_{ij} and $F_{\leftarrow ij}$ are the observed forward and backward survivorship proportions. The two methods yield similar rate estimates, but the likelihood approach facilitates formal statistical comparison among alternative models. Second, I previously used the method of simulated annealing (Press et al. 1992) to search the parameter space for optimal solutions. Here I have used the limited-memory Broyden-Fletcher-Goldfarb-Shanno method with bounds (Byrd et al. 1995), as implemented in the R statistical software package (Ihaka and Gentleman 1996: function ''optim''; option ''method=L-BFGS-B''). This is a gradient method that allows specified bounds for the parameter space, for example that all rates be positive and that probabilities be between zero and one. I have found that, compared with my previous approach, this method yields solutions with less computational effort and with a lower chance of settling on local optima. I set all lower bounds to 0.01. I set upper bounds on probabilities to 0.99 and upper bounds on rates to 5.0 per genus per stage. The results are not sensitive to this last upper bound, because all the estimated rates are lower than this.

To compare the evolutionary models, a series of bootstrap samples of size $n = 30,570$ was drawn with replacement from the set of genus stratigraphic ranges. For each sample, the maximum-likelihood solution was obtained for each of the four models, and the difference in support between each pair of models was computed. This procedure was repeated for 100 bootstrap replicates to develop a distribution of differences in support among the models. The purpose of the bootstrap is to assess the variance in the solutions; the mean bootstrap solution is essentially the same as
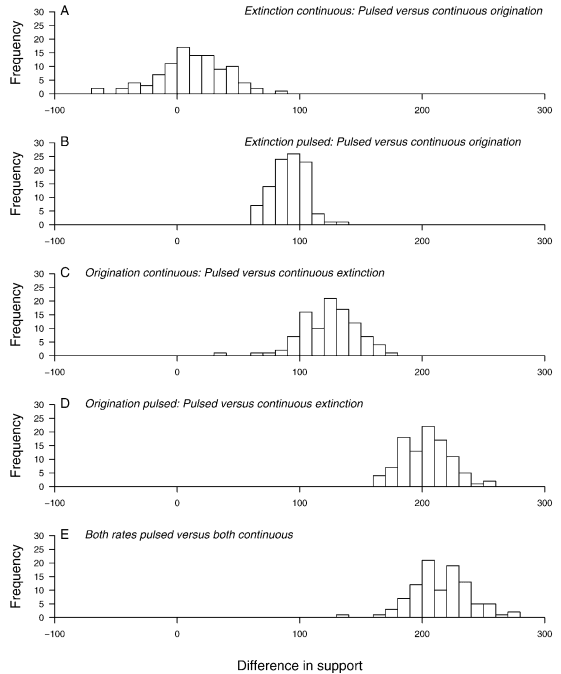

FIGURE 2.   Overall difference in support for alternative evolutionary models. Figure shows frequency distribution for 100 bootstrap replicates. For each contrast, a positive difference indicates stronger support for the model with pulsed turnover. When the extinction model is held fixed, there is slightly stronger support for pulsed versus continuous origination (A and B). When the origination model is held fixed, there is substantially stronger support for pulsed versus continuous extinction (C and D). There is also greater support for a model with both aspects of turnover pulsed rather than continuous (E).

the solution obtained by direct analysis of the data without bootstrapping.

Results

Estimated origination and extinction rates are presented in the Appendix. Here the focus is on comparing support for alternative evolutionary models.

Overall Support for Alternative Models

In comparing the four models, it is most useful to consider pairs of models that differ in only one assumption about evolutionary rates (Fig. 2). For example, Figure 2A contrasts the model in which both origination and extinction are assumed to be constant throughout a stage, against that in which extinction is constant and origination is pulsed. In this and subsequent figures, differences in support are

tabulated so that positive numbers imply stronger support for the pulsed model. The distribution of differences in support is centered just to the right of the zero point. Thus, there is a slight tendency for the model with pulsed origination to have higher support. If extinction is assumed to be pulsed, then pulsed origination is clearly supported over continuous origination (Fig. 2B). Thus, origination is more likely to be pulsed than continuous, but this is unambiguous only if extinction is also pulsed.

The situation is different if we compare alternative extinction models. Regardless of the model assumed for origination, there is stronger support for pulsed over continuous extinction (Fig. 2C,D). This difference is greater if origination is pulsed. The most striking contrast of all is that between the model in which origination and extinction are both pulsed and that in which they are both continuous (Fig. 2E).

Thus, the model of pulsed turnover is better supported than is the alternative of continuous turnover within stages. This difference in support is greater for extinction than for origination, but there is evidence that both processes are pulsed.

Stage-by-Stage Fit to Alternative Models

The models considered here assume that every stage is characterized by the same pattern of turnover: continuous in all stages or pulsed in all stages. With four combinations of rate models and 80 stages, there are 4^{80} or 10^{48} unique models that could in principle be specified. Clearly, not even a tiny fraction of these models can be studied. It is nevertheless desirable to consider the extent to which the data from each stage support pulsed versus continuous turnover. One would like to know, for example, whether the stronger support for the pulsed model reflects first and last appearances for just a small number of stages or whether it is more general.

To address this question, I compared the deviations between expected and observed survivorship probabilities for each cell in the matrix of first and last appearances: $D_{\to ij} = |\ln(P_{\to ij}/F_{\to ij})|$ and $D_{\gets ij} = |\ln(P_{\gets ij}/F_{\gets ij})|$, where $P_{\to ij}$ and $P_{\gets ij}$ correspond to the maximum like-

lihood solution, and $F_{\to ij}$ and $F_{\gets ij}$ are the observed values. I computed these deviations separately for the model in which origination and extinction are both continuous and that in which they are both pulsed. I then tabulated the difference in deviation between the two models (continuous minus pulsed). Finally, for each cell I computed the mean and standard deviation of the differences over the 100 bootstrap replicates. A positive difference indicates that the pulsed model fits better for that cell in the survivorship matrix.

Figure 3 depicts differences in fit between the continuous and pulsed models for the entire survivorship matrix. Where the pulsed model fits better, the cells in the matrix are colored black; where the continuous model fits better they are gray. Cells with no data are white. For forward survivorship, of the 1080 non-zero entries in the survivorship matrix, 680 (63%) show better agreement with the pulsed model. The margins of Figure 3 indicate the overall agreement for each stage. If the majority of cells for a stage fit one of the models better, the corresponding color is shown; ties are indicated in white. Of the 75 stages that show a discernible difference overall, 62 (83%) favor the pulsed model. For backward survivorship, 682 (63%) of the cells fit the pulsed model better, and 61 (81%) of 75 stages overall fit the pulsed model better.

Many of the differences between the models shown in Figure 3 are small. If the results are culled so that differences are tallied only if they are at least one standard deviation from zero, then there are many more blank cells in the analogue of Figure 3, but the contrast between the pulsed and continuous models is even more striking. With culling, 207 (69%) of 300 forward survivorship probabilities fit the pulsed model better, and 57 stages show better fit to the pulsed model overall, with 9 stages fitting the continuous model better, and 13 stages showing no difference. For backward survivorship, the pulsed model is preferred for 189 (70%) of 269 cells, and for 51 stages overall, with 9 stages fitting the continuous model better, and 19 showing no overall preference for either model.

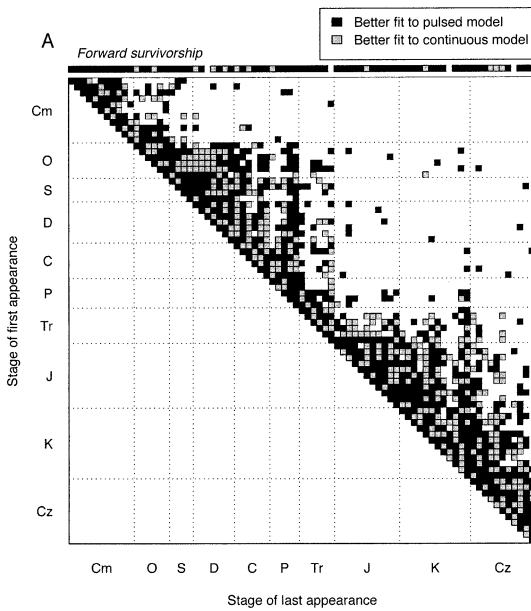On the whole, then, the better fit to the pulsed turnover model is not confined to just

FIGURE 3. Comparison between pulsed and continuous turnover models for the entire survivorship matrix (excluding the Recent). A, Forward survivorship. B, Backward survivorship. Black squares denote cells in the survivorship matrix for which the pulsed model fits better than the continuous model. Gray squares indicate better fit for the continuous model. Blank spaces indicate cells in which there are no data. Marginal boxes indicate which model fits best for the majority of cells within a stage. See text for further explanation.

a few stages. Rather, it is a general feature of the survivorship data.

Analysis of Substages

The contrasting expectations of the continuous and pulsed models can also be explored in a different way, by analyzing first and last appearances resolved to the substage level. In the extreme cases, the continuous model predicts that all substages within a stage should have the same turnover rates, whereas the pulsed model predicts that the rate will be high for one substage and near zero for the others.

For 30 of the 80 stages, greater than 60% of the first and last appearances could be resolved to substage level. I used this percentage as an arbitrary cutoff and subdivided these stages while leaving the others undivided. Of the 30 subdivided stages, 21 are divided into two substages and 9 into three substages. This protocol resulted in 119 stratigraphic intervals and yielded 26,558 genera
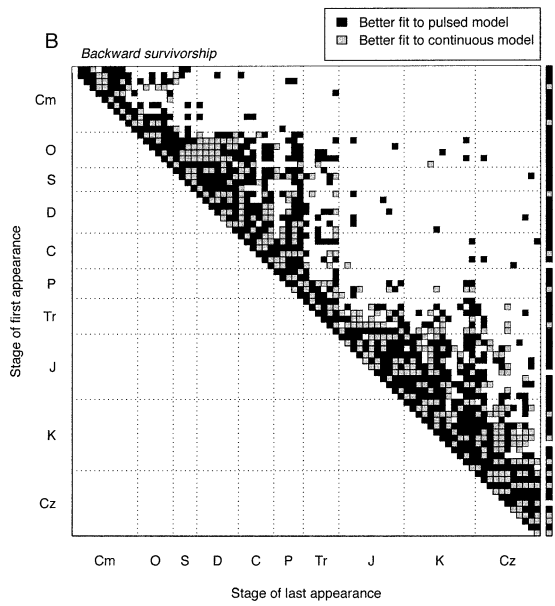
whose first and last appearances could both be resolved to one of these intervals.

Rates at the substage level were estimated in two ways. First, origination and extinction were allowed to vary freely from one substage to the next. This is exactly like the approach taken at the stage level. Second, substages within a stage were constrained to have the same origination and extinction rates. In both cases the sampling probability was allowed to vary among substages. This analysis was performed separately for the models of continuous and pulsed turnover *within substages.* Thus the question is whether there is added support for a solution that includes variation in rate among substages within a stage, assuming a given model of rate variation within a substage.

It is inevitable that the unconstrained solution will yield a higher support value for a given data set, i.e., that it will fit the data better, because it includes more parameters. Because the constrained solution is a special case of the unconstrained solution, it is a simple matter to compare the two by using Akaike's Information Criterion (AIC) (Akaike 1973; Burnham and Anderson 1998). Given the support S and the number of parameters k, the AIC is defined as $-2S + 2k$. In effect this
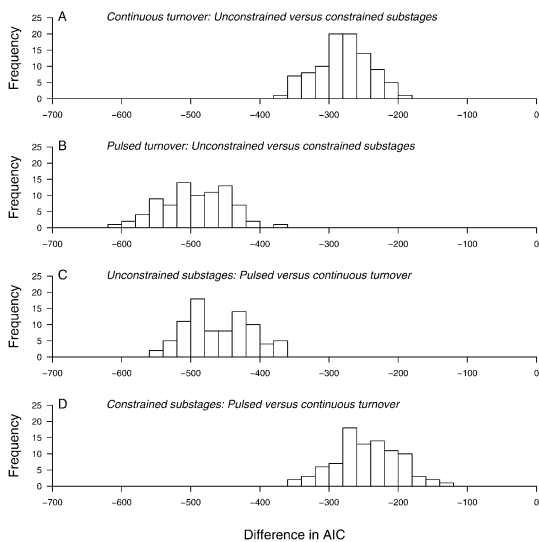
FIGURE 4. Analysis of substage-level data, based on 100 bootstrap replicates. A, B, Difference in Akaike Information Criterion (AIC) between model in which substages within a stage are constrained to have the same taxonomic rates, and that in which these rates are free to vary. Negative values indicate lower AIC for the unconstrained model; this model is therefore preferred. C, D, Difference in AIC for pulsed versus continuous turnover models. Negative values indicate lower AIC for the pulsed model; this model is therefore preferred. Because the comparisons in C and D involve no difference in number of parameters, the difference in support is simply minus one-half the difference in AIC.

weighs the complexity of the model against its explanatory power. On the basis of information theory, the model with the lower AIC is preferred. Thus, to be considered an improvement, a more complex model has to yield an increase in support that is greater than the added number of parameters.

Figure 4 shows the distribution of differences in AIC between constrained and unconstrained, substage-level solutions for 100 bootstrap replicates. The differences are all negative. Thus, there is substantially higher support for the model in which substages within a stage are characterized by different origination and extinction rates (Fig. 4A,B). Although this is true whether turnover is assumed to be continuous or pulsed within substages, the model of pulsed turnover yields a greater difference between constrained and unconstrained solutions. Consistent with the stage-level results, the model of pulsed turnover within substages is better supported, regardless of whether substages within a stage

are constrained to have the same turnover rates (Fig. 4C,D).

Table 1 presents fitted rates for a subset of stages and substages. Included here are stages that show a local peak in origination or extinction, and that are divided into substages for the analysis of Figure 4. For about half the origination peaks at the stage level, the elevated origination rate is concentrated in just a single substage. For nearly all of the extinction peaks, however, there is just a single substage with elevated rates. Moreover, this tends to be the last substage within the stage, especially for the pulsed model. On the whole, these results agree with those of Figure 2 in showing that the case for extinction-rate variation within a stage is stronger than that for origination-rate variation.

Sensitivity Analysis.—Even though the AIC takes the number of parameters into consideration, it is based on approximations that are most accurate when sample size is large relative to the number of parameters (Hurvich and Tsai 1989; Burnham and Anderson 1998). It is therefore possible in principle for a more complex model to overfit relative to a simpler one. To explore this possibility, I simulated data on first and last appearances by using a known model in which substages within a stage are constrained to have the same evolutionary rates. Then, using both the constrained and unconstrained solutions, I fitted the simulated data.

Each simulation took the average best-fit origination, extinction, and sampling rates for the maximum likelihood solution (the substage analogue of Figs. 6 and 7 in the Appendix) and used these to calculate the expected survivorship probabilities $P_\rightarrow$ and $P_\leftarrow$. For each stage or substage i, the observed number of first appearances was taken as given, and the last appearances were distributed at random among the (sub)stages $j \geq i$ with probabilities $P_{\rightarrow ij}$. Similarly, the genera last appearing in (sub)stage j were assigned (sub)stages of first appearance $i \leq j$ with probabilities $P_{\leftarrow ij}$. Thus the number of genera was held fixed at the observed value and the stochastic variation in observed survivorship was simulated. The best-fitting rates were then estimated for this simulated set of first and last appearances,

TABLE 1. Comparison between stage-level rates and substage-level rates for stages that have higher rates than both neighboring stages.

Stage	Stage-level rate	Substage-level rates		
		Lower substage	Middle substage	Upper substage
Continuous-rate solution				
Origination				
Atdabanian	1.5	1.2	—	0.093
Franconian	1.4	0.01	—	1.1
Trempealeauan	1.6	0.23	—	0.69
Llandoverian	1.4	0.73	0.01	0.74
Frasnian	0.79	0.22	0.01	0.01
Bashkirian	0.50	0.49	—	0.01
Induan	1.8	0.87	—	0.79
Callovian	0.19	0.01	0.01	0.061
Albian	0.63	0.069	0.01	0.48
Oligocene	0.48	0.48	—	0.01
Extinction				
Tommotian	0.91	0.01	—	0.01*
Tremadocian	1.2	0.77	—	0.069
Ashgillian	1.3	0.01	0.01	0.82
Famennian	1.3	0.30	0.01	0.73
Serpukhovian	0.72	0.01	—	0.56
Stephanian	0.73	0.038	—	0.60
Induan	1.0	0.76	—	0.01
Norian	1.3	0.01	0.01	1.0
Toarcian	0.44	0.01	—	0.42
Callovian	0.20	0.01	0.01	0.12
Oligocene	0.24	0.31	—	0.01
Pulsed-rate solution				
Origination				
Atdabanian	2.9	0.59	—	2.2
Franconian	2.5	0.89	—	0.71
Arenigian	2.9	2.8	—	0.62
Caradocian	0.95	0.57	0.21	0.01
Llandoverian	1.5	0.27	0.70	0.31
Famennian	0.96	0.89	0.01	0.01
Bashkirian	0.61	0.53	—	0.074
Olenekian	3.5	3.2	—	0.01
Oxfordian	0.29	0.20	0.01	0.01
Tithonian	0.087	0.23	—	0.01
Albian	0.78	0.32	0.01	0.17
Oligocene	0.57	0.23	—	0.33
Extinction				
Tommotian	0.49	0.01	—	0.43
middle Mid Cambrian	0.70	0.01	—	0.67
Ashgillian	0.63	0.01	0.01	0.66
Famennian	0.58	0.01	0.13	0.50
Serpukhovian	0.44	0.41	—	0.078
Stephanian	0.37	0.01	—	0.32
Tatarian	0.73	0.01	—	0.66
Olenekian	0.35	0.01	—	0.39
Norian	0.70	0.01	0.01	0.60
Toarcian	0.30	0.020	—	0.29
Callovian	0.19	0.078	0.01	0.10
Tithonian	0.45	0.01	—	0.40

* Although neither substage of the Tommotian has an elevated extinction rate in the continuous-turnover solution, an elevated rate in the lower Atdabanian may correspond to this stage-level peak.

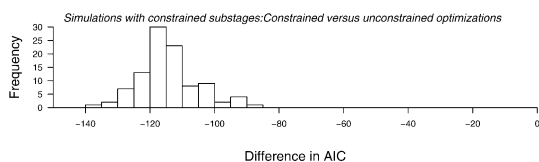Simulations with constrained substages:Constrained versus unconstrained optimizations

FIGURE 5. Sensitivity of estimation procedure to true model. One hundred simulated data sets were generated with the model in which substages within a stage are constrained to have the same taxonomic rates. The best-fitting solutions were obtained with this model and with the unconstrained model. Negative differences in AIC indicate that the true (simple) model is being correctly identified. Results here are for the model of continuous turnover within substages; similar results (not presented) are obtained with the model of pulsed turnover within substages.

and the entire procedure was repeated 100 times to develop a distribution of results. This approach has been used before (Foote 1988; Raup 1991), except that here incomplete and variable sampling is taken into consideration in the calculation of survivorship probabilities.

The unconstrained model must have higher support, because it contains more parameters. If the fitting procedure is accurate however, and not subject to overfitting, the AIC of the constrained solution should be lower, because the data were simulated with constrained substages. Figure 5 shows that this is the case. Thus, there is no reason to think that the support for rate variation among substages within a stage is an artifact of overfitting.

Discussion

For the most part, previous considerations of pulsed turnover have taken first and last appearances as reasonable proxies for origination and extinction events, but there are notable exceptions. Within a section or basin, it may be possible to constrain true times of origination and extinction with confidence limits on range endpoints (Strauss and Sadler 1989). Using different variants on this approach, Raup (1989) and Marshall and Ward (1996) concluded that ammonite disappearances leading up to the end-Cretaceous event at Zumaya, Spain, are consistent with a mixture of pulsed and gradual extinction. The analysis of Jin et al. (2000) yields similar results for marine invertebrates in the Late Permian sections at Meishan, southern China.

The basic method of confidence limits may be of limited use in cases where a facies shift or sequence boundary is responsible for artificial clustering of appearance events (Holland 1995, 2000; Smith et al. 2001). This problem can be circumvented by finding clusters of events that do not occur where they would be expected as artifacts of stratigraphic variation (Holland 1995). Knowledge of sampling intensity can also be used in a variety of ways to estimate true patterns of turnover from stratigraphically well resolved first and last appearances (Marshall 1997; Jackson and Johnson 2000; Hayek and Bura 2001). Such approaches generally assume, like the method used herein, that all taxa are characterized by the same sampling probability. A recent development (Holland 2003) uses the known frequency of occurrence of species along a finely sampled environmental gradient to estimate the sampling probability of each individual species, as a function of facies, within and beyond the observed stratigraphic range. By taking taxonomic variation and facies shifts into account, this approach represents the most realistic application of confidence limits to date.

In light of the various work just mentioned, it is worth restating two points about the analyses presented here. First, the stages of first and last appearance are not read literally as times of origination and extinction. Rather, rates of origination and extinction are estimated by using a model that explicitly incorporates range truncation and temporal variation in the probability of sampling. Second, the analyses draw inferences about rate variation at a temporal scale much finer than the observations. The question is not about rate variation from stage to stage, but rather about the pattern within each stage.

The main inference of this paper is that genus extinctions are distinctly pulsed, being better accounted for by a single episode per stage rather than a constant background rate throughout the stage. This is also true of originations, but the case is not as compelling. It would be reasonable to conclude that the origination of new genera is spread throughout certain stages more so than is the extinction of existing genera.

Preference for the pulsed extinction model

has at least two important methodological consequences. First, it suggests that expressing extinction rates on a per-million-year basis may be not only unnecessary but also misleading, as this practice tacitly assumes that events are spread throughout a stage (Raup and Sepkoski 1984). Second and more important, because optimized and face-value extinction rates are well correlated under the pulsed model but not the continuous model (Foote 2003a: Fig. 9) (Fig. 7D), it suggests that the timing of extinction peaks in global, stage-level data can be largely, albeit not completely, accepted at face value. This has significant implications for many questions, including periodicity (Raup and Sepkoski 1984), and the temporal correlation between observed extinction peaks and environmental changes (Miller 1998; Hallam and Wignall 1999).

Previous comparisons between face-value and optimized rates showed that the record of extinction has higher fidelity than that of origination (Foote 2003a). One aspect of this difference is that larger extinction events tend to occur in stages with relatively good sampling and to be followed by origination episodes in more poorly sampled stages (Foote 2003a). A possible explanation is that both the extinction event and the drop in sampling are linked to a common factor such as marine regression (Newell 1967; Hallam and Wignall 1999; Peters and Foote 2002; Foote 2003a). The results of this study provide an additional explanation. That extinction is more clearly pulsed than origination implies that there is, on average, an offset of fewer stages between extinction and last appearance than between origination and first appearance (Fig. 1).

The analyses presented here support a picture involving short-lived, global extirpations followed by elevated origination that is longer lived than the extinction event. In some cases the results show that elevated origination is largely confined to the stage immediately following the extinction event (e.g., Llandoverian and Hettangian stages after the Ashgillian and Norian extinction events), but in others the interval of higher origination is more protracted (Appendix). The inference of pulsed extinction supports a number of previous analyses of single events (e.g., Jin et al. 2000

on the end-Permian and Raup 1989 on the end-Cretaceous, to cite but two). The pulsed model seems to apply quite broadly, however, and not to be confined to a few extraordinary events.

What are the implications of this work for biostratigraphy? Many stage boundaries are recognized on the basis of apparent faunal change, so it would seem obvious that pulsed turnover has facilitated the erection of such boundaries. The offset between extinction and last appearance implies, however, that even discrete pulses of extinction could be hard to recognize. A substage-level analogue of Figure 1, scaled to represent average sampling rates, would show last appearances spread rather evenly throughout the stage. One solution to this apparent contradiction is to make the reasonable suggestion that average sampling rates for marine animals as a whole greatly underestimate the sampling rates for the biostratigraphically useful groups. For example, if sampling rate were on the order of ten per genus per stage, rather than one, then some 85% of genera that became extinct at the end of the stage would have a preserved last appearance in the final 20% of the stage. Such a concentration of last appearances should be sufficient to recognize the faunal change.

First appearances are sometimes deemed more reliable than last appearances in biostratigraphic correlation and zonation, on the assumption that the first appearances of individual species are less diachronous (G. Klapper personal communication 1988; P. M. Sadler personal communication 2004). This assumption has been questioned, however, because graphic correlation, integrated with physical time markers, has shown that first appearances may be as diachronous as last appearances (Mann and Lane 1995) or even more so (Dowsett 1989: Table VII). The present study has nothing to say about diachroneity at the level of single species, but the greater tendency toward pulsed extinction versus origination does imply that biotic events consisting of many first appearances are likely to be spread through more time, and therefore to be less useful as time markers, than are corresponding last appearance events. There is no reason to think, however, that the originations

or first appearances are sufficiently evenly dispersed in time so as to serve as a biotic clock.

A long-standing question in paleobiology is whether the largest biotic turnover events are distinct from background events, for example in having different causes, exhibiting different patterns of selectivity, or representing a distinct mode in a frequency distribution (see recent overview in Wang 2003). One viewpoint that has emerged is that biotic transitions throughout the Phanerozoic, not just at major events, are largely caused by physical perturbations of varying magnitudes (Raup 1991, 1996; Miller 1998). The better fit of the pulsed model to events of all sizes, as documented here, agrees with this view. It does not provide unequivocal support, however. For example, many theoretical models based upon biotic interactions also predict short-lived turnover events following longer periods of quiescence (Newman and Palmer 2003).

Summary

1. Models of pulsed versus continuous turnover within stratigraphic stages make different predictions regarding first and last appearances resolved only to the stage level. These models can therefore be discriminated by using stage-level data.
2. For Phanerozoic marine animal genera, there is stronger support for pulsed versus continuous origination, but this difference is unequivocal only if extinction is also pulsed.
3. For extinction, the pulsed model is much more strongly supported regardless of the origination model.
4. That extinction is more clearly pulsed than origination contributes to the higher fidelity of the extinction record compared with that of origination.
5. The better fit of the pulsed model is a rather general feature of the Phanerozoic record. It is not confined to just a few stages of extraordinary turnover.

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Appendix

Origination and Extinction Rates

The maximum likelihood rate estimates for the four models are presented in Figures 6 and 7. Superimposed on these figures as a dashed curve is the sequence of apparent rates based on the raw data, i.e., uncorrected for incompleteness. In large part, the major features of origination and extinction are similar regardless of which model is assumed. Like the raw data, each solution shows a decline in background rates punctuated by intervals of elevated turnover. There are some discrepancies between the timing and magnitude of peaks in the raw data versus the optimized solution, and these discrepancies tend to be greater for origination than for extinction. It is also evident that the discrepancies vary among models. These issues are discussed at greater length elsewhere (Foote 2003a).

Included in the analysis are 4232 genera that are still extant. Complete sampling of the Recent fauna is not assumed, but, as it turns out, the optimization consistently estimates sampling probability of the Recent to be equal to the imposed upper bound of 0.99. Because the survivorship probabilities reflect secular changes in sampling, including the high probability of sampling of the Recent, those aspects of the Pull of the Recent (Raup 1979) that concern sampling are implicitly circumvented.
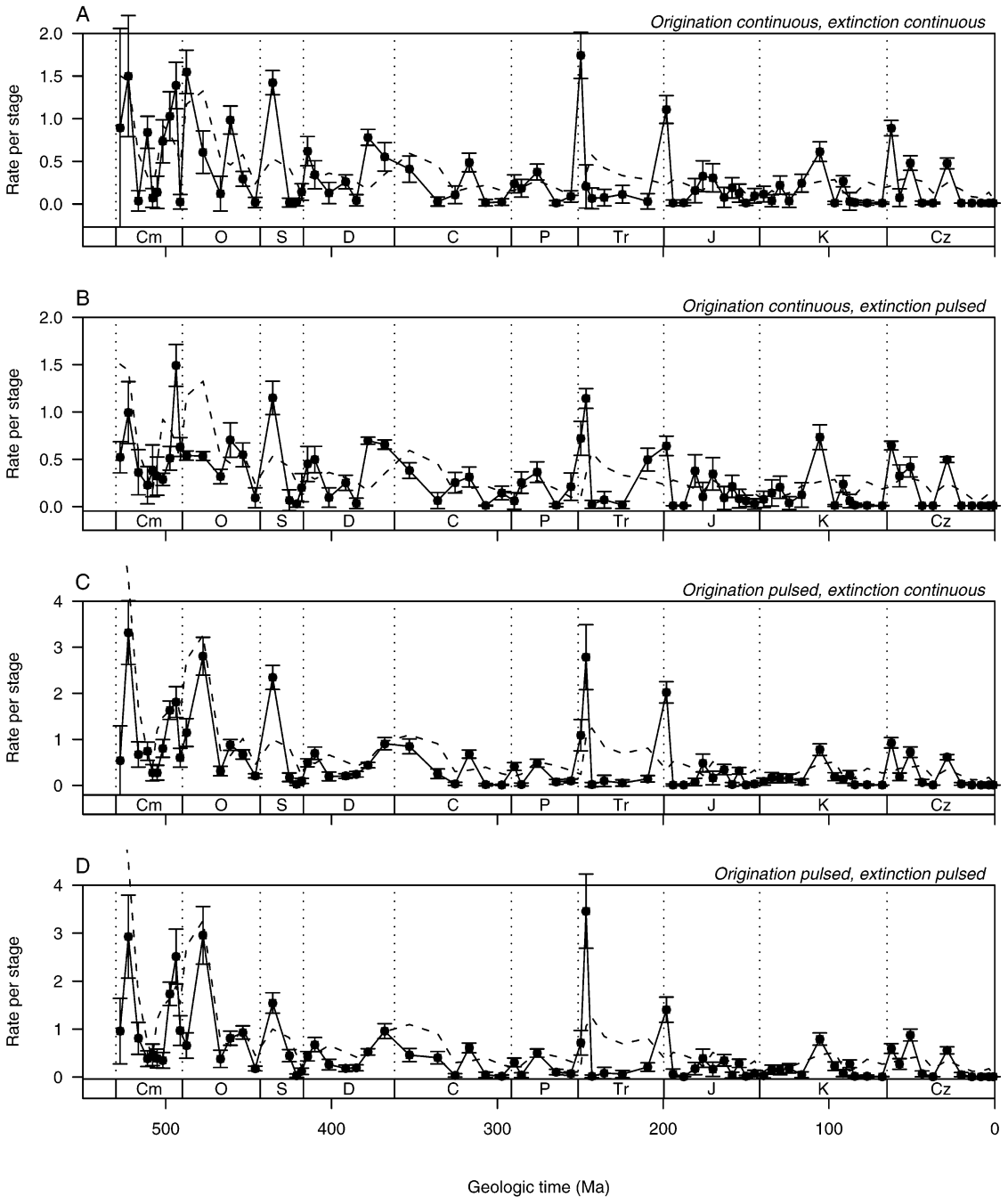
Origination

FIGURE 6. Per capita origination rates estimated with four different evolutionary models. Points are means ±1 standard error based on 100 bootstrap replicates. Dashed line shows the origination rate that would be obtained by taking the data at face value, i.e., not correcting for incomplete and variable sampling. For the top two panels, the face-value origination rate is calculated as $-\ln(X_{bt}/X_t)$, where X_{bt} is the number of genera that range through the entire interval and X_t is the number observed to cross the top interval boundary. For the bottom two panels, the face-value origination rate is calculated as X_F/X_b, where X_F is the number of first appearances and X_b is the number of genera observed to cross the bottom interval boundary. Because interval length is not relevant for the pulsed turnover model, all rates are portrayed on a per-stage basis to allow comparisons among the models. The Recent is excluded. (See Foote 2003a for further discussion of rate measures.)
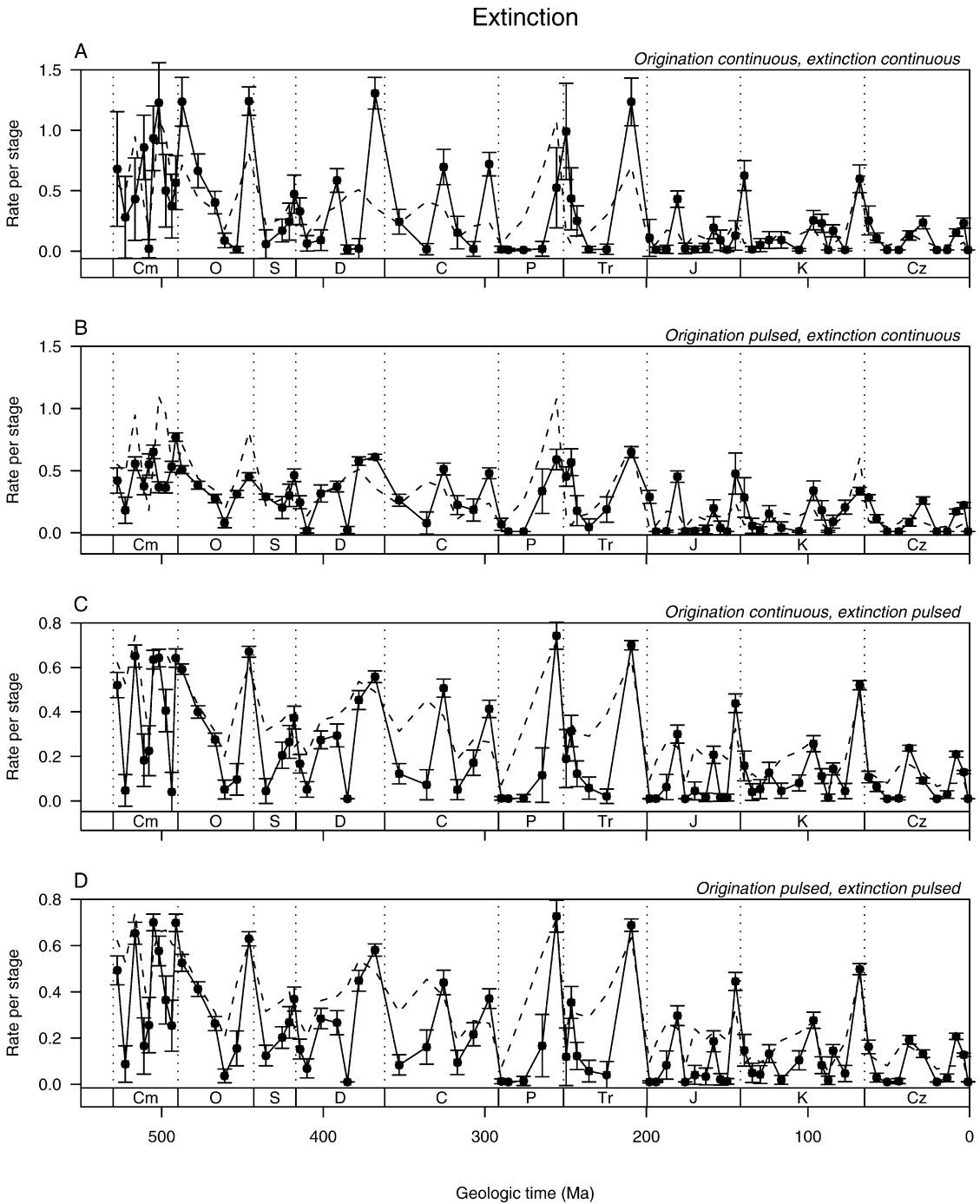
Extinction

FIGURE 7. Per capita extinction rates estimated with four different evolutionary models. See Figure 6 for explanation. For the top two panels, the face-value extinction rate is calculated as $-\ln(X_{bt}/X_b)$, where X_{bt} is the number of genera that range through the entire interval and X_b is the number observed to cross the bottom interval boundary. For the bottom two panels, the face-value extinction rate is calculated as X_L/X_{tot}, where X_L is the number of last appearances and X_{tot} is the total observed diversity in the stage.