Global occurrence trajectories of microfossils: environmental volatility and the rise and fall of individual species

Lee Hsiang Liow, Hans Julius Skaug, Torbjørn Ergon, and Tore Schweder

Abstract.—Species arise and establish themselves over the geologic time scale. This process is manifested as a change in the relative frequency of occurrences of a given species in the global pool of species. Our main goal here is to model this rise and the eventual decline of microfossil species using a mixed-effects model where groups each have a characteristic occurrence trajectory (main effects) and each species belonging to those groups is allowed to deviate from the given group trajectory (random effects). Our model can be described as a "hat" with logistic forms in the periods of increase and decline. Using the estimated timings of rises and falls, we find that the lengths of the periods of rise are about as long as the lengths of the periods when species are above 50% of their estimated maximal occurrences. These latter periods are here termed periods of dominance, which are in turn about the same length as the species' periods of fall. The peak rates of the rises of microfossils are in general faster than their peak rates of falls. These quantified observations may have broad macroevolutionary and macroecological implications. Further, we hypothesize that species that have experienced and survived high levels of environmental volatility (specifically, periods of greater than average variation in temperature and productivity) during their formative periods should have longer periods of dominance. This is because subsequent environmental variations should not drive them to decline with ease. We find that higher estimated environmental volatility early in the life of a species positively correlates with lengths of periods of dominance, given that a species survives the initial stress of the environmental fluctuations. However, we find no evidence that the steepness of the rise of a species is affected by environmental volatility in the early phases of its life.

Introduction

The study of origination rates, extinction rates, and diversity in the fossil record requires that we be able to estimate when individual lineages originated and became extinct. However, as with most other types of biological sampling (Clark and Bjørnstad 2004; Hortal et al. 2007; Royle et al. 2007), sampling in the fossil record is incomplete for many reasons. This incompleteness affects our estimates of times of originations and extinctions. For a species to be recorded in a database along with information on both geologic time and geographic location, not only must the species have been extant, but also individuals of that species must have been fossilized despite taphonomic and sedimentary vagaries, survived weathering, been sampled by a paleontologist, and been correctly identified and aged (Holland 2000; Kidwell and Holland 2002; Peters 2006). Various methods have been proposed to correct for sampling incompleteness or to fill in temporal gaps in sampling. They are developed variously to reduce biases in specific ways as demanded by the questions being posed. These methods include sampling standardization in diversity studies (Alroy et al. 2001, 2008; Bush et al. 2004; Kiessling and Aberhan 2007), excluding singletons in rate calculations (Foote 2000), setting confidence intervals to stratigraphic ranges (Marshall 1990, 1994, 1997; Solow 2003; Weiss and Marshall 1999), exploiting phylogenetic approaches (Angielczyk and Fox 2006;
Pol and Norell 2006; Wills 2007), embracing sampling or preservation parameters in hypotheses (Foote 2003; Wagner 2000), and including the use of capture-recapture approaches to account for detection probabilities that are less than one (Nichols and Pollock 1983; Nichols et al. 1986; Connolly and Miller 2001; Liow et al. 2008).

A complicating factor that has been emphasized recently is the inevitably lower probability of sampling a lineage at both the beginning and end of its existence: lineages tend to be more frequently sampled in the middle of their life spans, probably owing to true increases in abundance and geographic extent (Foote et al. 2007; Liow and Stenseth 2007). Occurrence probabilities must taper off to zero both at the beginning and at the end of a species’ life. Hence inferences regarding the timing of origination and extinction must necessarily be highly dependent on how this tapering is modeled. This temporally changing probability of sampling a lineage is especially problematic when considering factors that contribute to lineage persistence (Viranta 2003; Liow 2007a,b) because the assumption that rank order durations of lineages are not affected by sampling may not hold despite sampling standardizations and corrections.

In this paper, we develop a model (the “hat”) to estimate the changing probability that individual microfossil species are detected given that they are globally extant, using their observed occurrences in geologic time. Our model is designed to estimate the times of the rises and declines of species instead of the less tractable times of speciation and extinction. As a natural consequence of the model, we can also obtain estimates of the rates of rise and fall of species. We propose “period of dominance” as a new and more robust measure of species persistence. To demonstrate our model, we use data from the public microfossil database, NEPTUNE (Lazarus et al. 2007) to estimate the temporal occurrence trajectories of diatoms, nanoplankton, planktic foraminifers, and radiolarians. We find that peak rise rates are in general quicker than peak fall rates for all the four microfossil groups and that the lengths of periods of rise, dominance, and fall are of the same order of magnitude.

Using estimates from our “hat” model, we also explore a new idea, namely, that the volatility in the environment experienced and survived by a young or establishing species influences the length of its period of dominance. We reasoned that species that are initially conditioned to survive changing conditions have better chances of surviving subsequent environmental changes. Hence we predict that species that had endured volatile beginnings should have a longer period of dominance. This prediction is distinct from how their individual populations respond to shorter-term, more local environmental fluctuations. There is some indication that higher estimated environmental volatility early in the life of a plankton species correlates positively with its lengths of periods of dominance.

Materials and Methods

Species Occurrence Data.—NEPTUNE (Lazarus 1994; Spencer-Cervato 1999; Leckie et al. 2004; Lazarus et al. 2007) is an online species occurrence database based on the Deep Sea Drilling Project and its descendant, the Ocean Drilling Project, maintained and hosted by CHRONOS (http://chronos.org). It comprises data from species of planktic microfossils, diatoms and nannoplankton (phytoplankton) and radiolarians and planktic foraminifers (zooplankton), groups commonly surveyed by biostratigraphers. Our raw data are hence occurrence data of populations with a confirmed identity (“resolved_species_id” in NEPTUNE) identified by a unique sample identification number (“sample_id”) in the database, as we have previously used (Liow and Stenseth 2007). Only valid taxa are used in our study, and specimens identified with “sp.,” “aff.”, and “cf.” are excluded. This filtering gives us occurrence data from a total of 732 nannoplankton species, 688 diatom species, 608 planktic foraminifer species, and 634 radiolarian species. The raw data are each associated with present-day spatial coordinates, based on where the deep-sea core was drilled, and an absolute geological age estimated by age models specific for given
cores (Spencer-Cervato 1999). We limit the data to occurrence data after the Cretaceous (65.5 Ma) because of possible differences in taxonomic practice among workers collecting Mesozoic and Cenozoic data (Smith 2007), because occurrence data are much sparser before the Cenozoic, and because the paleoenvironmental proxy data are better for the Cenozoic. We use only species that are found in at least ten unique samples (i.e., associated with unique “sample-ids”). The subset of the data we ultimately used hence consists of 312 nanoplankton species, 328 diatom species, 271 planktic foraminifer species, and 342 radiolarian species.

Paleoenvironmental Proxies.—The paleoenvironmental proxies used in this study, $\delta^{18}$O and $\delta^{13}$C, are based on an updated version supplied by Mark Pagani (personal communication 2007) of previously published data (Zachos et al. 2001). Briefly, the oxygen isotope fractionation between ambient seawater and foraminiferal calcite during calcification is temperature dependent such that a higher $\delta^{18}$O reflects lower temperature (Fairbanks et al. 1980, 1982). It also reflects the volume of the ice sheets present, because ice sheets sequester $^{18}$O, such that the $\delta^{18}$O values also represent a time-averaged record of high-latitude sea-surface temperature (Zachos et al. 2001). Here we simply interpret $\delta^{18}$O as a proxy for paleotemperature, where a higher $\delta^{18}$O ($\%$) implies a lower temperature. On the other hand, plants and marine algae preferentially assimilate $^{13}$C during photosynthesis. Thus the carbon isotope effect of organic carbon versus inorganic carbon is measurable in the dissolved inorganic carbon (DIC) reservoir, incorporated by marine microorganisms (e.g., benthic foraminifera) such that $\delta^{13}$C can be interpreted as a proxy for paleoproductivity. We recognize that carbon cycle and global climate are closely linked but that cause, effect and feedback loops are complex (Sundquist and Visser 2005).

Modeling.—In order to estimate the times and peak rates of global rise and fall of species, we assume (1) that detection is primarily a function of global abundance, (2) that global occurrence is a reflection of both detection and local site occupancy probabilities, and (3) that local preservation is only influenced by global abundance (see “Discussion”). For clarity, we explicitly avoid using the term “occupancy” as commonly used in paleobiology (Jernvall and Fortelius 2004; Raia et al. 2006; Foote et al. 2007). Instead we follow the usage in ecology (MacKenzie et al. 2006), whereby occupancy is the true presence of a species at a space and time. Occurrence, on the other hand, is detection given occupancy. A null occurrence can be either true absence or presence but with non-detection. We do not deal with partitioning non-detection and absence in this paper, because the estimation of species-specific parameters already contributes to a high computational burden. However, we want to remain explicit about our assumptions, especially regarding detection probabilities. Further, we interpret the changes in occurrence over the life span of each species as causally linked to the ecological processes of establishment, population growth, dispersal, local extinction, and global extinction, as well as the evolutionary process of speciation.

We define the occurrence of a species at a site and in a time bin as its presence in the NEPTUNE database within that site and time bin. An occurrence thus results from either (1) the species being present at the time and space in non-negligible abundance and the subsequent fossilization of the same species and its later detection and correct identification; or (2) fossils of a different species having been misidentified as the focal species and thought to be present at the given time and space. We allow for the second possibility by estimating $p_0$, the probability of a co-occurring species in the same sample being classified as the focal species (see below).

The occurrence trajectory of any given species is assumed to be hat-shaped (Fig. 1), with an initial rise in occurrence following a logistic curve, followed by a period of dominance, and finally tapering off following another (independent) logistic curve. This continuous hat-shaped trajectory is modeled through an occurrence probability function:

$$ h(t) = L \cdot l(\lambda_s(t-S) \cdot l(\lambda_T(t-T))) $$

where $l(z) = 1/(1 + \exp(-z))$ is the logistic function and $t$ is time in millions of years.
The parameters are constrained such that $0 < l \leq 1$, $\lambda_S > 0$, $\lambda_T < 0$, $S > T$. The component $I(\lambda_S(t - S))$ thus increases toward an asymptotic level of 1 while $I(\lambda_T(t - T))$ decreases from 1. The height of the “hat” is controlled by $L$, the estimated theoretical maximum occurrence. A species is characterized by the five parameters $L$, $S$, $T$, $\lambda_S$, and $\lambda_T$. $S$ and $T$ are the absolute time point of inflection of occurrence increase and the absolute time of the inflection of occurrence decline, respectively. $S$ and $T$ are also interpretable as when the species has reached half of its estimated theoretical maximum occurrence during its rise and its decline respectively. The two parameters $\lambda_S$ and $\lambda_T$ determine the maximum rates of increase toward and decrease from $L$, respectively. In summary, the probability of a species occurring at a randomly chosen site in a given time bin in the database is modeled as the “hat” value $h(t)$ for that species.

We grouped the data into 32 time bins of 2 Myr each. These time bins are much coarser than the finest temporal resolution of the database, which is 330 Kyr (Spencer-Cervato 1999). The relatively wide time bins of 2 Myr were used in order to reduce the computational burden involved in optimizing the likelihood function numerically. A species is recorded as present in a sample as long as at least one specimen of that species is found; i.e., we do not use information regarding abundance of specimens within samples, sometimes recorded in NEPTUNE.

Let $y_{ij}$ be the number of records of species $i$ from a total of $k_j$ samples in time bin $j$ (samples within time bins identified by unique “sample_id” values in the database). We assume that $y_{ij}$ follows a binomial distribution with the parameters $(k_j, h_{ij})$, where $h_{ij}$ is the probability that species $i$ is recorded (i.e., extant and detected) in time bin $j$ and where $k_j$ is the number of independent samples (trials) within the time bin. The probability of a species being recorded in time bin $j$ with midpoint $t_j$, i.e., its occurrence probability, is $h_{ij} = h(t_j)$.

Hence, the “hat” model for discrete time bins for a given species $i$ is

$$h_{ij} = \frac{L_i}{1 + L_i} \cdot \frac{(\lambda_S(t_j - S_i)) \cdot I(\lambda_T(t_j - T_i))}{1 + I(\lambda_T(t_j - T_i))}$$

(2)

To allow the basic parameters of the model $L$, $\lambda_S$, $S$, $\lambda_T$, $T$ (Fig. 1) to be species-specific, we use the following mixed-effects model:

$$L_i = I(m_1 + u_{1,i}), \quad u_{1,i} \sim N(0, \sigma_1^2)$$

(3)

$$\lambda_{5,i} = \exp(m_2 + u_{2,i}), \quad u_{2,i} \sim N(0, \sigma_2^2)$$

(4)

$$S_i = q_{25,i} + m_3 + u_{3,i}, \quad u_{3,i} \sim N(0, \sigma_3^2)$$

(5)

$$\lambda_{7,i} = -\exp(m_4 + u_{4,i}), \quad u_{4,i} \sim N(0, \sigma_4^2)$$

(6)

$$T_i = S_i + \exp(m_5 + u_{5,i}), \quad u_{5,i} \sim N(0, \sigma_5^2)$$

(7)

where $N(0, \sigma^2)$ denotes a zero-mean normal distribution with variance $\sigma^2$, and $l(z)$ is the logistic function as before. Here, the $m’s$ are the main effects shared by all species in each of the four groups (diatoms, nannoplankton, radiolarians, and planktic foraminifers). The $u’s$ are “random effects” or individual devia-
tions from the $m$’s. The term $q_{25,i}$ is used for computational convenience, as explained below. In other words, each of the four microfossil groups has a general “hat” trajectory, but each species within those groups is allowed to have its own characteristic variant drawn from the group-specific distribution of “hat” trajectories. We estimated the $m$’s for the four groups separately because of their differences in trophic level and evolutionary history, and because of taxonomic practices, each of which likely contributes to different true values for group-specific main effects. Note that although $S$ occurs in equation (8), $T$-$S$ is independent of $S$.

The term $q_{25,i}$ (eq. 5) is the 25% empirical quantile among time bins for which the given species has been observed (Fig. 1). We parameterize $S_i$ in terms of $q_{25,i}$ to condition the “hat” to include the time during which there are actually occurrence data for the species $i$. In addition, $q_{25,i}$ eases the computational burden and makes the assumption of a normally distributed random effect ($u_{3,i}$) appropriate.

Errors in assigning taxa are not uncommon, both in neontology and paleontology (Sepkoski 1993; Foissner 2006). To make the model robust against such errors, we introduced a parameter $p_0$, defined as the probability of a co-occurring species in the same sample being classified as the focal species $i$. The probability of an occurrence of species $i$ in time bin $j$ is then

$$p_0 + (1 - p_0)h_{ij}. \quad (8)$$

We assume that $p_0$ is the same in every time bin and for every species in a given group. In practice, it is difficult to distinguish between the true misclassification of specimens (i.e., assignment to the wrong species) and a given species not being preserved at a sampled location (core); thus $p_0$ accounts for the lack of fit of the “hat” trajectory due to both of these circumstances. The “hat” model was fitted using the AD Model Builder (freely available at http://admb-project.org/).

Periods of Dominance, Rises and Falls, and Per-Species Frequencies of Rises and Falls.—The time interval between $S$ and $T$ is termed the period of dominance ($S, T$). Of primary interest is the length of the period of dominance, $T-S$. Note that $h(t)$ is peaked for species having short periods of dominance and flat for those having longer periods of dominance, relative to the steepness of their rise and decline. The length of period of rise (PR) is the time it takes for the occurrence probability of a given group or species to go from 5% to 95% of the estimated theoretical maximum occurrence ($L$) whereas the length of period of decline (PD) is the time it takes for the same to go from 95% to 5% of $L$ during the fall. We tabulated $N_{S_i}$, the number of species that have their $S$ values in a given 2 Myr interval, $j$; $N_{T_i}$, the number of species with $T$ values in $j$; and $N_{(S,T)_i}$, the number of species with periods of dominance ($S, T$) overlapping $j$. Per-species frequency of rise per 2 Myr interval over the time intervals $j$ (where $j = 1...35$) is then observed as $N_{S_i}/N_{(S,T)_i}$ whereas the per-species frequency of fall is $N_{T_i}/N_{(S,T)_i}$. Differenced per species frequency of rises are hence observed as $(N_{S_{i+1}}/N_{(S,T)_{i+1}} - N_{S_i}/N_{(S,T)_i})$, and differenced per species frequency of fall is $(N_{T_{i+1}}/N_{(S,T)_{i+1}} - N_{T_i}/N_{(S,T)_i})$.

Exploration of Preservation Trends.—The quality of preservation for a given species through its lifetime may affect the estimates of its rise and fall. For example, species that become part of the geologic record earlier might be less available for sampling and/or the specimens may be relatively less identifiable. To investigate these potential inherent temporal biases in the data we do two empirical checks and one analytical check. First, we plotted the qualitative preservation codes (Good, Moderate, Poor) assigned to samples in NEPTUNE over time for each species. We also summarized these preservation codes for each microfossil group according to whether they are associated with samples before or after our estimated $S$ and $T$ using box plots. Second, we plotted residuals from the lack of fit of the data to the model for each of the four microfossil groups over time to check if there are unusual trends that may be due to general abnormalities in preservation. These residuals (for each species and each time bin) are calculated as $h - \bar{h}/\sqrt{h(1-h)/n}$ where $h$ is an observed frequency of occurrence, $\bar{h}$ its
value fitted by the “hat” model, and \( n \) the number of sites at a given time bin. Last, we supply a brief theoretical analysis of the types of biases that are generated if global preservation gradually improves over time.

**Environmental Volatility.**—We denote the two paleoenvironmental proxies in general by \( \delta_{\text{env},t} \), that is, either \( \delta^{18}\text{O} \) or \( \delta^{13}\text{C} \) values at time \( t \), and define their lag-1 differenced time series as \( D_t = \delta_{\text{env},t} - \delta_{\text{env},t-1} \). We use a stochastic volatility (SV) model (Harvey et al. 1994) motivated by the fact that the standard deviation of \( D_t \) changes over time (Fig. 2). The time series \( D_t \) is mean-subtracted, and we assume that \( D_t \sim N(0, \tau_t^2) \), where \( \tau_t \) is the environmental volatility process we want to model (Fig. 2). As a model for \( \tau_t \) we use the stochastic process: \( \log(\tau_t) = \mu + X_t \), where \( X_t = \alpha X_{t-1} + \epsilon_t \), is a zero-mean stationary first-order autoregressive process, with independent innovation terms \( \epsilon_t \sim N(0, \omega^2) \) (Brockwell and Davis 1987). This model yields the properties we seek: \( \tau_t = \exp(X_t) > 0 \) and positive serial correlation \( \text{corr}(\tau_{t-1}, \tau_t) > 0 \) when \( \alpha > 0 \). In other words, we use the smoothed estimate of the standard deviation of the differenced series of the paleo-proxies (Fig. 2). In doing so, for time intervals with low values of estimated volatility, \( \tau_t \), the temporal differences in the environmental proxies, \( D_t \), will be small in absolute value, and vice versa. Estimates of the parameters \( \mu, \alpha, \omega \) are obtained using maximum likelihood and empirical Bayes estimates are used for the volatility series \( \tau_t \) (Skaug and Fournier 2006).

Our time bins \( t \) for calculating average \( \delta_{\text{env},t} \) are 0.1 Myr in length. This choice is a compromise between two constraints. We need to make the bins wide enough to have enough observations of the proxy data in each bin. However, making time bins for estimating volatility too large would reduce the relevance of the scale of volatility for the evolutionary and ecological processes we are concerned about. Moreover, 0.1 Myr bins do capture the time scale of some of the longer so-called climate aberrations including the Paleocene-Eocene Thermal Maximum (PETM) at 55 Ma, the early Oligocene glaciation at 34 Ma, and early Miocene glaciation at 23 Ma (Zachos et al. 2001). The age estimates for these paleoenvironmental proxy data are accurate on orbital time scales or at the resolution of 20 Kyr (M. Pagani personal communication 2008).

**Early Phases of the “Hat”: Initial Establishment and Expansion Phases.**—We calculated the mean estimated volatility \( \tau \) of each of the two paleoenvironmental proxies for each species over two time periods during the course of individual species “hats” (Fig. 1). The first, “initial establishment,” is the estimated absolute time that elapses between the time a species \( i \) first attains 5% of the estimated theoretical maximum estimated height of the “hat” \( (L_i) \) and when it attains 10% of \( L_i \), i.e., from \( S + (1/\lambda_S) \log_2(\frac{5}{95}) \) to \( S + (1/\lambda_S) \log_2(\frac{9}{95}) \). The second, “expansion phase,” is the estimated absolute time that elapses between when a species first attains 10% of the estimated theoretical maximum estimated height of the “hat” and when it attains 50% of \( L_i \), equivalent to the time point \( S_t \).

A Note on the Explorative Nature of the “Hat” Model.—In the “hat” model, we modeled species as statistically independent random deviations from the main effects (the \( m_i \)’s in equations 3–7). The “hat” model has allowed us to explore the slopes of species rises and falls, as well as the times of rises and falls and the durations of the periods of dominance, among other measures. These are explorations of the data not possible without the “hat” model. However, it is not straightforward to formally test hypotheses regarding species patterns because of the structure of the model. Hence throughout this paper, we refrain from confirmatory analyses but adhere to descriptive statistics, avoiding \( p \)-values and the like. Work is in progress to develop methods to deal with this technical difficulty.

**Computational Details.**—Our mixed-effects “hat” model is fitted by the maximum likelihood method. It contains five random effects (the \( u_i \)’s) per species, yielding about 1500 unknown values for each of the four groups we are considering. For instance, there are 312 species of nannoplankton included in our analyses. There are thus five group param-
eters, $5 \times 312 = 1560$ species parameters, one parameter for the model misfit ($p_0$), and hence 1566 unknown parameters to be estimated. The problem of maximizing the likelihood function is challenging because of the large number of parameters, in combination with the nonlinear structure of the model. The AD Model Builder (http://admb-project.org/) is specially designed for these types of problems: it allows efficient maximization of the likelihood as well as automatic calculation of parameter uncertainties. Originally, we attempted to estimate the variance parameters $\sigma_1^2, \ldots, \sigma_5^2$ by using the Laplace approximation (Skaug and Fournier 2006). It was difficult to estimate the $\sigma$’s from the data, so we manipulated $\sigma_1^2, \sigma_2^2, \sigma_3^2, \sigma_4^2, \sigma_5^2$ to find values that were as large as possible (to

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{Volatility in paleoenvironmental proxies over time. The upper two panels show time-series plots of first differences of the average temperature proxy from time bin to time bin. The differences are calculated from binned data, where each bin spans 0.1 Myr, and are plotted at the second time interval from which the differences are calculated. The dotted lines are two times the standard deviation ($\sigma$) of the differences (see "Methods" for details), representing the estimated volatility we use in subsequent sections of this paper. The bottom panel shows the number of available observations in each time bin contributing to the calculation of the differences for $\delta^18$O. The equivalent plot for $\delta^{13}$C has somewhat fewer observations relative to $\delta^18$O but is essentially the same and hence not presented.}
\end{figure}
Table 1. Parameter estimates (m1 through m5) are shown for the main effects as described in methods and materials. Individual effects are set to zero for \( L, \lambda_S, \lambda_T \), and T-S shown in this table. \( p_0 \) is the probability of model misfit. T-S is the length of the period of dominance, PR the length of period of rise, and PD the length of period of decline; these are all in Myr. The second row in each group shows the standard errors for each of the estimates (those for T-S, PR, and PD are calculated using the delta method).

<table>
<thead>
<tr>
<th></th>
<th>( m_1 )</th>
<th>( m_2 )</th>
<th>( m_3 )</th>
<th>( m_4 )</th>
<th>( m_5 )</th>
<th>( L )</th>
<th>( \lambda_S )</th>
<th>( \lambda_T )</th>
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<th>PR</th>
<th>PD</th>
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<td>1.014</td>
<td>-0.919</td>
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Our “hat” model fits the data well: there are clearly higher occurrences of the given species in the middle portion of its life span. In some situations it appears that a double peaked trajectory could be fitted. For example, in D. deflandrei (Fig. 3), there is a dip around 38 Ma and a second rise around 36-34 Ma, but as specified by our model, only a single rise and fall were fitted. Even for data-poor species, such as D. germanicus (only 12 samples), we are still able to estimate species-specific realized values of \( S \) and \( T \) because of our use of “main effects” or a group trajectory, even though the confidence intervals for \( S \) and \( T \) are much wider for this species. We also point out that the group estimates (main effects) are similar to the averages of species estimates (random effects) although they are not the same (e.g., compare Tables 1 and 2 for slopes and lengths of \( (S,T) \)). This follows because the individual estimates are fitted as normally distributed deviations from the main effects (see eqs. 3–7). We present fits for all the species used in the Supplementary Material (online at http://dx.doi.org/10.1666/08080.s1), not least to show the goodness-of-fit of our model, better assessed on a case-by-case basis.

Results

Group “Hats”: General Observations.—In all the four microfossil groups, species tend to have faster rates of rise than fall (Table 1). Foraminifers and nannoplankton achieve greater proportions of sites occupied (\( L \)) than do diatoms and radiolarians. The latter two groups also rise and fall faster (Table 1). Slower risers have a longer period of dominance while also reaching a greater proportion of sites occupied (Table 1). The standard errors for all the estimates are reasonably small as are the probabilities of model misfit (\( p_0 \)) (Table 1).

Species “Hats”: Model Fit.—As mentioned, each species has its characteristic trajectory of occurrence through time, to which we were able to fit our model. We show examples of the data and the fitted models for selected nannoplankton species to illustrate some characteristic trajectories. In general, for species that are more commonly recorded, such as Coccolithus miopelagicus and Cyclicargolithus florianus (Fig. 3), our “hat” model fits the data well: there are clearly higher occurrences of the given species in the middle portion of its life span. In some situations it appears that a double peaked trajectory could be fitted. For example, in D. deflandrei (Fig. 3), there is a dip in proportion of samples in which it is present around 38 Ma and a second rise around 36-34 Ma, but as specified by our model, only a single rise and fall were fitted. Even for data-poor species, such as D. germanicus (only 12 samples), we are still able to estimate species-specific realized values of \( S \) and \( T \) because of our use of “main effects” or a group trajectory, even though the confidence intervals for \( S \) and \( T \) are much wider for this species. We also point out that the group estimates (main effects) are similar to the averages of species estimates (random effects) although they are not the same (e.g., compare Tables 1 and 2 for slopes and lengths of \( (S,T) \)). This follows because the individual estimates are fitted as normally distributed deviations from the main effects (see eqs. 3–7). We present fits for all the species used in the Supplementary Material (online at http://dx.doi.org/10.1666/08080.s1), not least to show the goodness-of-fit of our model, better assessed on a case-by-case basis.
Figure 3. Plots of each of our model fits to six illustrative nannoplankton species: *Coccolithus miopelagicus*, *Cyclicargolithus floridanus*, *Discoaster brouweri*, *Discoaster deflandrei*, *Discoaster germanicus*, and *Thoracosphaera operculata*. The numbers in parentheses are the number of samples available for the given species. Vertical bars show the observed proportion of sites occupied by each species in 2 Myr bins. Dotted curves are our fitted curves. S and T show the inflection points for the rise and fall of species, respectively. The upper limits of the fitted curves are plotted at the time of first occurrence in NEPTUNE plus 4 Myr and the lower limits at the time of last occurrence in NEPTUNE minus 4 Myr.

Table 2. Average lengths of periods of dominance (S,T) and “face-value” stratigraphic durations calculated from first and last occurrence data (Duration) are shown in Myr. Average slopes of the species “hat” are also shown.

<table>
<thead>
<tr>
<th></th>
<th>$T-S$</th>
<th>Duration</th>
<th>$\lambda_S$</th>
<th>$\lambda_T$</th>
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<tr>
<td></td>
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<td>9.1</td>
<td>8.7</td>
<td>13.4</td>
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<tr>
<td>Foraminifers</td>
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<td>7.3</td>
<td>11.9</td>
<td>15.2</td>
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<tr>
<td>Nannoplankton</td>
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<td>7.4</td>
<td>10.9</td>
<td>17.2</td>
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<tr>
<td>Radiolarians</td>
<td>5.2</td>
<td>6.9</td>
<td>10.7</td>
<td>13.6</td>
</tr>
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</table>
similar (Table 2), as opposed to raw stratigraphic durations (see Spencer-Cervato 1999). Both per capita rises and falls are correlated in the pairwise comparisons (Fig. 4), with no time lag except for radiolarian per capita rises. Per capita declines are more strongly correlated than per capita declines. However, in comparisons between foraminifers and the other groups, differenced per capita rises are not significantly correlated whereas falls are marginally positively correlated (Fig. 5). In both nannoplankton and foraminifers, there were slight increases in the frequency of rises and per capita rise rates after the PETM (55 Ma), a global warming event (Gibbs et al. 2006; Zachos et al. 2001) (Fig. 6). The same cannot be said of diatoms or radiolarians, in the latter case because there are no radiolarian species rising before 55 Ma in our data. Looking at the fall frequency, the only generality we observe is that there is a peak of falls in the 4 Ma to 0 Ma bins for all the four groups (Fig. 6). The three highlighted events, namely the PETM and the glaciations of the early Oligocene and early Miocene, do not coincide with fall rate changes (Fig. 6). The changes in per capita rise rates do not appear particularly related to the timing of the early Oligocene and early Miocene glaciations for any of the microfossil groups (Fig. 6).

Preservation Trends.—Inspection of the temporal distribution of preservation codes for each species ("Good," "Moderate," "Poor") gives no indication of a temporal bias (see Supplementary Material). Summaries of these for each microfossil group diagrammed as box plots show that regardless of preservation quality, more samples are found during the period of dominance (Fig. 7). In other words, poorly preserved and well-preserved samples are distributed similarly in time. Residuals from the lack of fit of the data to the model do not show any striking outliers or trends in time (Fig. 8).

Patterns of Environmental Volatility.—Climate has changed through the Cenozoic as reflected through global average values (Zachos et al. 2001). Because we are concerned about how environmental volatility affects species, we have to first ask how paleoenvironmental volatility has varied through the Cenozoic. We find no temporal trend in the differences of the time binned average paleoenvironmental proxies, i.e., the values fluctuate around zero (Fig. 2). This is regardless of the size of the time bins used, even though we only present results using 0.1 Myr bins. Volatility estimates do decrease dramatically after 40 Ma for δ¹³C and after about 60 Ma for δ¹⁸O (Fig. 2; dashed lines bracketing solid line represent differences), but they do not follow the changes in the number of observations available. We note here that the two estimated volatility time series for δ¹³C and δ¹⁸O are correlated (0.57).

Environmental Volatility, Estimated Period of Dominance, and Rates of Rise.—We present scatter plots of estimated volatility experienced at the two phases of establishment (initial establishment and expansion phase), versus the length of the period of dominance (Figs. 9–12). Because these data are non-normal and non-independent, we choose simply to discuss the scatter plots. In these plots, we removed species with estimated T later than 0 Ma because of interpolation problems, i.e., the greater uncertainty of estimating persistence in the future due to the lack of empirical data even though results remain qualitatively the same.

The average volatility experienced during the "initial establishment" phase spans a slightly greater range of values that during the "expansion phase," clearly seen at least for the oxygen isotope proxy (Figs. 9, 10). In all of the plots for volatility in δ¹⁸O over either the initial establishment or the expansion phase, a triangular or fan-shaped distribution can be seen (Figs. 9, 10. Because there is a sharp decrease in global volatility at about 60 Ma, we plotted the species experiencing the beginnings of either their initial establishment (Fig. 9) or expansion phase (Fig. 10) before and after 60 Ma separately. We find that species establishing or expanding before and after 60 Ma show basically the same patterns. Patterns of volatility in δ¹³C, however, show no such trends (Figs. 11, 12). Within each temporal group, there is a randomly distributed scatter of volatilities and periods of dominance.
Figure 4. The temporal correlation of per capita rise and fall rates for pairs of the four microfossil groups. D = Diatoms, F = Foraminifers, N = Nannoplankton, R = Radiolarians. The x-axes show the temporal lag in units of 2 Myr. Axes are not labeled for the economy of space. Dotted lines show the 95% confidence intervals for the correlation.
Figure 5. The differenced per capita rise and fall rates for pairs of the four microfossil groups. D = Diatoms, F = Foraminifers, N = Nannoplankton, R = Radiolarians. Pairs of rates calculated for every 2 Myr are plotted in each panel (see legends). Axes are not labeled for the economy of space. Note that the axes for rise and fall rates are different.
Figure 6. Left, Absolute frequencies of rises and falls for 2 Myr bins plotted in absolute geologic time. Right, Per capita frequencies. The three global climate events—the Paleocene-Eocene Thermal Maximum (PETM, 55 Ma), early Oligocene glaciation (34 Ma), and early Miocene (23 Ma) glaciation—are indicated with arrows.
C. Nannoplankton

D. Radiolarians

Figure 6. Continued.
There is no observed trend in environmental volatility and rate of rise for any of the four groups (Figs. 13–16).

Discussion

Pondering the “Hat”.—Occurrences of fossil taxon are commonly denser in the middle of its observed duration. In other words, species and genera are more detectable in the middle of their lifetimes, as seen in mammal genera (Jernvall and Fortelius 2004), marine invertebrate genera (Foote 2007), Cenozoic molluscan genera (Foote et al. 2007) and Cenozoic zooplankton species (Liow and Stenseth 2007). We have already shown that a model of occurrence trajectories should be hump-shaped (Liow and Stenseth 2007), and the “hat” model we develop here satisfies this requirement and also supplies parameters that give biological meaning.

Because occurrence trajectories are often hatlike and even more commonly have shallow slopes, raw global stratigraphic durations are clearly poor estimates for taxon durations. An increase in sampling effort potentially can change the stratigraphic ranges of species drastically. However, changes in sampling effort should have little influence on our estimated lengths of periods of dominance, a measure of a species’ duration of ecological dominance. Although global distributions of duration are quite different for the four microfossil groups (Spencer-Cervato 1999), the average estimated lengths of periods of dominance are similar (Table 2).

Proportionately rare misidentifications of specimens assigned to ages rather far out from the temporal range of the given species also have little influence on our parameter estimates. Taking Coccolithus miopelagicus as an example (Fig. 3), our estimates are $S = 25.5 \pm 0.47$ Ma and $T = 8.68 \pm 0.67$ Ma, whereas the earliest and latest occurrence data in NEPTUNE for this species are 35.32 and 0.13 Ma respectively. Although no expert opinion is available to us on the accepted global first occurrence for C. miopelagicus, its
“highest occurrence” (i.e., most recent occurrence where it is abundant enough to be a useful index species in biostratigraphy) is reported to be 11.020-10.613 Ma (Raffi et al. 2006). The entries for *C. miopelagicus* in NEPTUNE that are dated much younger than 10.6 Ma may involve reworked specimens, erroneous age models, or misidentified specimens. But note that *T* for *C. miopelagicus* is later than when it is considered abundant.

Taking another example, the earliest record for *Discoaster brouweri* in NEPTUNE is 35.47 Ma. However, we estimate that its $S = 9.73 \pm 0.24$ Ma, indicating that the record from 35.47 Ma is an outlier and should be disregarded. Although our plotting convention allows the left tail to be drawn out for *D. brouweri* (Fig. 3), data points far left of the graph have negligible influence on our estimates. We also are aware that the genus *Discoaster* is thought to have gone extinct in the latest Pliocene (Raffi et al. 2006). *T* for *D. brouweri* is $0.5 \pm 1.0$ Ma; thus the estimated time interval of probable decline is later than

**Figure 8.** The lack of fit of the hat model to data over time plotted as standardized residuals (unitless).
the time of its extinction that is commonly accepted in the microfossil literature. We therefore caution that if too many of the identifications or age models are systematically biased, our modeling may still be inadequate for specific cases (such as the decline of *D. brouweri*). To summarize, our model not only gives confidence intervals for the times and rates of rises and falls, it also helps to identify potential spurious records of individual species if these are temporally far removed from the estimated times of rises and falls. Although we are not able to verify records for each species in the database, we encourage taxonomic experts to investigate the fits of species they have studied and to inform those maintaining the database of any inconsistencies and errors.

Our “hat” model is a general and flexible one. Even though good fits of such a general model to every single species cannot be expected, not least because we have not factored in preservation variations and site- and time-specific stochasticities, the species-specific plots show that the general shape of the model is reasonable. Some individual species may have their proportional occurrences far removed from the main “hat”
trajectory as indicated by non-zero $p_0$'s, but these are not an issue for our general conclusions.

In approaches where observations of complete life spans of lineages are required, extant taxa must be excluded, possibly biasing the studies (Liow 2007a,b; Viranta 2003). However, $T_i$ can take values close to the Recent or even into the future and $S_i$ can take values close to 65.5 Ma and older. This allows us to retain both species that are extant and those that were established before 65.5 Ma, avoiding the problem of censoring in survival analysis (Kalbfleisch and Prentice 1980). For example, we used only entries in NEPTUNE that are younger than 65.5 Ma, but we estimated *Thoracosphaera operculata* (Fig. 2) to have $S = 67.1 \pm 2.5$ Ma. However, even though we may not obtain precise predictions on the slope and timing of rise of this species, we may still obtain informative estimates and their uncertainties by extrapolation. In other words, the average length of period of dominance of the group or clade and the distribution of the random effects (around $T-S$ and $\lambda_T$) may inform us on the expected rise of this species.

*Rises and Falls: Asymmetries and Relative Durations.*—Planktic microfossil species tend to rise faster than they fall. An explanation
previously suggested for this quick-rise/slow-fall pattern is the swamping of the data by long-lived, abundant species (Liow and Stenseth 2007). These species may have biological characteristics that allow them to expand in geographic extent quickly, while their abundance and large geographic ranges protect them from a rapid decline. Our estimates (Table 1) show that slower rise rates correspond to a greater estimated theoretical maximal proportion of sites of occurrence ($L$), thus failing to support this hypothesis, given that $L$ is a good proxy for geographic range. We have also suggested previously that a species may rise quickly at the beginning of its observed life span, because its initial problems of establishment had been solved during a period of very low detectability. The fall is even slower because once the species spreads, it needs to experience declines in all the “sites” in which it had been detected such that no one population can “rescue” another, in the sense of metapopulation dynamics, whether the declines in localized sites are due to climate perturbations, predators, parasites, and/or competitors. This asymmetry in rise and fall may also be due to biased sampling, which we discuss below.

**Figure 11.** Length of period of dominance versus volatility in $\delta^{13}C$ over initial establishment phases (see Fig. 9). Species that have risen to 5% of their maximum proportion occupancy after 40 Ma are labeled with crosses and those that have done the same before 40 Ma are labeled with open circles.
Our modeling exercise has shown that species rises and declines are much slower than we previously realized, calling for serious explorations of explanations. Why might species rise and fall so slowly over geologic time? First, the final, total disappearance of a species happens only when the last individual of that lineage dies, but the time from decline until the death of the final individual can be quite long, with population abundance declining along the way. Similarly, it is difficult to infer how long a species has existed before its first observed occurrence because the probability of detecting it during the early phase of its history is likely to be low for several possible reasons: (1) its members are morphologically not well differentiated from members of the ancestral lineage; (2) its population size is smaller compared with its ancestral lineage (even in the case of the equal splitting of one lineage in two, say by a suddenly arising geographical barrier); or (3) local populations have not yet spread out geographically so it is much more difficult to sample them. In other words, the time spent at maximal occurrence is relatively short, compared with the time a species spends rising and then declining to occurrence values presumably low enough for stochastic processes to ultimately drive it to extinction.

**Figure 12.** Length of period of dominance versus volatility in δ¹³C over expansion phases (see Fig. 10). Symbols as in Figure 11.

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**Diatoms**

**Foraminifiers**

**Nannoplankton**

**Radiolarians**
Environmental Events and Temporal Patterns of Rise and Fall.—Per capita rise and fall rates appear to be correlated for pairs of groups of microfossils. Each group tends to decline when other groups are declining, and this is especially prominent for foraminifers. This may indicate that the microfossil groups are responding to the same environmental changes. Although some studies have singled out the effects of prominent environmental events on some microfossil groups (Gibbs et al. 2006; Kamikuri et al. 2005), we do not observe such events to affect the frequency of either rises or falls. Why may that be? First, our estimates are global and even though some populations may be affected adversely by environmental change, other populations of the same species may mitigate the effects of that change. Second, our bins are rather wide (2 Myr); hence, unlike studies restricted to single deep-sea cores with very high temporal resolution, we cannot detect events that occur on a finer time scale, even if they are large in magnitude, if the effects are not long-lasting. We have no reason to believe that time bin size will affect our general conclusions in this paper. The “hat” trajectory fits most species quite well and dividing the data temporally at

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**Figure 13.** Estimated rates of rise ($\lambda_S$) versus estimated $\delta^{18}$O volatility averaged over the initial establishment phase of each species (time elapsed between achieving 5% and 10% of the height of the “hat”) for each of the four groups. Species that have risen to 5% of their maximum proportion occupancy after 60 Ma are labeled with crosses and those that have done the same before 60 Ma are labeled with open circles.
a finer scale is not justified. A third explanation for our findings is that we did not include rarer and perhaps more environmentally sensitive species. Fourth, our approach estimates the times of a species’ rise and fall, rather than studying the times of its origination and extinction. The time points of rise and fall are not expected to translate in a straightforward manner to origination and extinction time points, not least because the slopes of rises and falls for species and groups are different. Fifth, environmental disturbances over the long term may be more consequential to occurrence dynamics than previously suspected (De Blasio and De Blasio 2009); hence, large, abrupt events may have affect the rise and fall of species less than does the accumulation of lesser environmental changes. Last but not least, biotic interactions may modulate the effects of environmental disturbance.

Pondering Preservation.—As is common for paleontological data, our data contain fewer sampled cores from earlier in geologic time (Spencer-Cervato 1999). A clear benefit of our modeling approach is that a reduced frequency of samples earlier in geologic time will not bias the shape of the “hat,” but only makes the estimates less precise. Foraminifers and nannoplankton are better-studied groups

**Figure 14.** Estimated rates of rise versus volatility in $\delta^{18}$O over expansion phases (time between achieving 10% and 50% of the height of the “hat”). Symbols as in Figure 13.
in NEPTUNE, where species are more frequently identified and entered in the database. Our approach does not lead to biased estimates for different groups, but only leads to a lower precision of the estimates for diatoms and radiolarians.

If preservation probability for each species through time were known, it would be simple to estimate the true occupancy trajectory of a species. However, a species’ preservation probability is unknown and most likely not a smooth function of time and would have to be estimated (MacKenzie et al. 2006). Trying to estimate the preservation explicitly through our already complex model would make computations more burdensome. In setting up our model, we made several broad but explicit assumptions about preservation and detection. We acknowledge that geological changes such as rise and fall of sea level and sequence stratigraphic effects can contribute to site- or time-specific variations in preservation (Holland 2000) and detection, whereas biological traits such as size, test robustness, and mineralogy may contribute to species-specific variations. We have, however, no reason to believe that these species-specific and site- and time-specific factors

![Figure 15. Estimated rates of rise versus in δ13C volatility over initial establishment phases. See Figure 13 for details. Species that have risen to 5% of their maximum proportion occupancy after 40 Ma are labeled with crosses and those that have done the same before 40 Ma are labeled with open circles.](image)
contribute to the general patterns we have found here.

On the other hand, it is useful to discuss the fact that the focal parameters of our analysis ($T-S$, $\lambda_S$ and $\lambda_T$) are little affected when the preservation is slowly increasing with time, whereas $T$ and $S$ are somewhat positively biased.

Defining occupancy probability, $o$, as mean local abundance over a time bin, and assuming that each individual is preserved with probability $\pi$, then occurrence probability is simply $o \cdot \pi$. If preservation probability is constant, the occupancy trajectory $o(t)$ is proportional to $h(t)$.

If we consider the global trend of increasing preservation probability with geologic time (Spencer-Cervato 1999; Kidwell and Holland 2002; Smith 2007), then preservation probability $\pi(t)$ gradually increases as a function of time, $t$. In this case, the true occupancy trajectory $o(t)$ is filtered, such that $h(t) = o(t) \cdot \pi(t)$. Both occurrence and occupancy trajectories are regarded as hat-shaped, but the issue remains as to how the initial and the terminal inflection points of the occupancy trajectory are mapped into the corresponding points of the occurrence trajectory.

Let $S_{occ}$ be the initial half-points of the first logistic part of the occupancy trajectory,
corresponding to \( S \). An increasing preservation probability makes \( h(S_{\text{occ}}) < h(S) \) and consequently \( S > S_{\text{occ}} \). There is also a positive bias in \( T \). The derivative of the hat-function at \( S \) is \( (L \cdot \lambda_S)/4 \) and the derivative at \( T \) is \( (L \cdot \lambda_T)/4 \). By a first-order Taylor expansion of the occurrence trajectory about its inflection points, we find the bias to be approximately \( S - \sigma \approx 2/\lambda_S \left( 1 - \left| \pi(S) / |\pi(Y)| \right| \right) \), where \( Y \) is a time at which the rising logistic curve of the ‘hat’ is nearly 1 (say 0.99 making \( Y = S + 4.6/\lambda_S \)), and \( T - T_{\text{occ}} \approx (2/\lambda_T) \left( 1 - \left| \pi(Y) / |\pi(T)| \right| \right) \) with \( Y \) similarly defined. For a species with nearly equal rates of rise and fall, a slowly increasing preservation probability will map the occupancy trajectory to an occurrence trajectory closer to the present, but the length of the period of dominance, \( T - S \), changes minimally. Likewise, the slopes of rise and fall (\( \lambda_S \) and \( \lambda_T \)) are nearly unaffected. Because most of our discussions center on \( T - S, \lambda_S, \) and \( \lambda_T \), we temporarily shelve the issues of how global secular trends and local idiosyncrasies in preservation may affect our general results.

On the other hand, the quality of preservation for a given species through its lifetime may affect the estimates of its rise and fall. For example, species potentially entering samples earlier in geologic time are preserved less frequently and/or the specimens may be relatively less identifiable. Depending on exactly how these more poorly preserved samples are distributed temporally, this preservation bias could produce asymmetric rates either where rises are quicker than falls or vice versa. However, we see no bias in the temporal distribution of preservation quality for any of the four microfossil groups.

**Patterns of Environmental Volatility during Formative Periods.**—We predicted that species that had endured volatile beginnings should have a longer period of dominance, all other things being equal. If species are able to survive environmental fluctuations during the earlier phases of their lives, they may be adept at handling unpredictability and fluctuations later on. A prominent feature of the physical environment is temperature, which in turn may affect another important factor, the productivity of the local environment, both of which can be estimated in the fossil record by using proxies such as \( \delta^{18}O \) and \( \delta^{13}C \). Temperature changes have been seen as an important driver of biological change (Thunell 1981; Janis 1993; Bown et al. 1994; Schmidt et al. 2003; Gillooly et al. 2005; Hunt and Roy 2006; Wright et al. 2006; Currano et al. 2008; Kürschner et al. 2008) and likewise, productivity or energy availability is also thought to influence diversity (Bonn et al. 2004; Gross and Cardinale 2007).

Currently there is no inherently intuitive way to determine the length of period during which we should consider the environmental volatility at the beginning of a species’ life. This problem is not unique to this study or this dataset. The period during which speciation occurs can be understood in many ways both theoretically and empirically (Coyne and Orr 2004). For example, speciation may be considered the period from when two populations begin to diverge until they attain reproductive isolation. Or, it may also be more loosely considered the time when gene flow ceases, regardless of reproductive isolation. In practice, however, speciation rates are often calculated from diversification rates minus extinction rates (Coyne and Orr 2004). Similarly, in the theory of island biogeography and its offspring, invasion biology, the beginning of establishment is a difficult concept, because a species must first disperse, establish, and then build up populations large enough to make an ecological impact and/or for biologists to sample (MacArthur and Wilson 1967).

We emphasize that the exact point of a species’ beginning is impossible to establish, either biologically or statistically. Therefore, instead of trying to determine when the species began its life, for which the uncertainty is very large, we use the period of time from when 5% of the maximum height of the “hat” is achieved to when 10% of the same is attained as an approximation for the “initial establishment” phase in a species’ life. As can be seen from the individual species “hats” (Fig. 3 and Supplementary Material), this period, the length of which varies according to both the slope of increase and the maximum height of the “hat,” may or may not encompass observed samples. Similarly, the “expansion
phase” of a species is arbitrarily taken as the period of time from when 10% of the maximum height of the “hat” is achieved to the inflection point, S. This may be interpreted as the period when the species is initially dispersing, increasing the number and spread of its populations. Again, we expect that if the species manages to disperse despite environmental volatility, this early “training” should prepare it for later environmental perturbations, and hence contribute to a long period of dominance.

We found that the average volatility experienced during the “initial establishment” phase spans a slightly greater range of values than during the “expansion phase.” This is reasonable because values averaged over a longer period of time are less likely to be swamped by large extremes. In general, there are few species in any of the four groups that are likely to persist if they experience an average estimated δ¹⁸O volatility value of more than about 0.3. Note that none of the radiolarian species in our data experienced very high volatilities—this is in part due to their arising later. Given that a species persists after an initial period of higher environmental volatility, the length of its period of dominance (T-S) may be greater than expected if there is no relationship between T-S and initial environmental volatility (Figs. 9, 10). Species that experienced lower volatilities at the beginning of their lives do not exhibit long periods of dominance. However, those that experience higher volatilities at the beginning of their lives either do not persist much longer than those that did not experience higher volatilities, or they persist longer than expected. Although volatility in global temperature volatility decreases sharply ca. 60 Ma, we find that species establishing or expanding before and after 60 Ma show basically the same patterns. Patterns of volatility in δ¹³C, a proxy for productivity, show random scatters with respect to length of period of dominance. We interpret these as indicating that the volatility in paleotemperature has an effect on species persistence but not the volatility in paleo-productivity.

We also expected high environmental volatility to dampen rise rates, because attempts to build populations or disperse may be thwarted by frequent reversals of environmental conditions. However, our results show no such relationship between environmental volatility and rate of rise for any of the four groups.

There are, of course, many potential biases in volatility estimates: for example, the isotope readings serving as our paleoenvironmental proxies may reflect local events even though we assume that the values, averaged over time and space, at least in part reflect global tendencies. We emphasize, however, that the mismatch between the size of the environmental proxy bins (0.1 Myr) and that of the raw occurrence data (2 Myr) is not problematic because we use the estimates from a smooth “hat” to estimate the volatilities experienced during the initial and expansion phases of species. Moreover, the isotope readings come from several different micro-organisms, each with their species-specific and habitat-specific effects influencing the readings (Katz et al. 2003). Additionally, older species might persist longer simply by having more time to persist, although according to our data (Figs. 9–12), the period of dominance is not strikingly different for older species (specifically those having S larger than 60 or 40 Ma). The estimated periods of initial establishment and the expansion phase depend on the form of species “hats,” which in part depend on the length of the period of dominance. We also note that perhaps surviving great environmental volatilities even earlier in the lives of species than what we can estimate (i.e., “initial establishment”) contributes more strongly to periods of dominance, but because of the uncertainty of estimating the durations of these very early phases, we are unable for now to progress further than this attempt.

Conclusions

1. We have shown that it is possible to fit a changing temporal trajectory of occurrence for individual species, using a model including both main and random effects. Despite needing to estimate large numbers of parameters, our estimation procedure converged on reasonable solu-
tions. The parameters estimated, as well as the trajectory estimated from the parameter values, can be interpreted ecologically. A new species has a period of low detectability, possibly due to low morphological divergence, low population abundance, and/or low global occupancy. If this species survives, it can be modeled as having a sigmoid rise in the proportion of sites occupied, until it reaches a characteristic "carrying capacity" estimated in terms of maximum proportion of sites occupied. As the species approaches its final demise, it declines as an inverted sigmoid curve in the proportion of sites occupied, after which it never recovers, although it may linger on for variable periods of time.

2. In light of this model, it is clear that estimating the points of the "true" times of speciation and extinction is close to impossible. Hence we propose that at least for certain types of macroevolutionary and macroecological questions, it may be more meaningful to use the times of peak rise and fall as the primary data.

3. Our model indicates that it takes a very long time for a species to rise to and fall from its maximum frequency of occurrence: the periods of rise and fall are about as long as the period of dominance. This observation begs for a biological explanation.

4. The peak rate of rise is generally greater than the peak rate of fall.

5. Species with long periods of dominance tend to have been established during environmentally more volatile times. We postulate that species that were established during less volatile times are less likely to persist for long periods because environmental conditions are likely to change on longer time scales. However, species that were established during more volatile times do not all have long periods of dominance; rather, they can be divided into those that have a relatively short period of dominance and others with a long period of dominance, as compared to species established during less volatile times.

6. We see little correlation between environmental volatility and the frequency of rise of species. Nor do the three well-known global environmental events at 55, 34, and 23 Ma affect the frequency of rises in all four microfossil groups.

7. We close by stressing the explorative nature of this study. The "hat" model is a parametric one that filters raw data in order to highlight species patterns, allowing the exploration of processes of species' rises and falls central to evolutionary biology.

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