Repeatability of taxon longevity in successive foraminifera radiations and a theory of random appearance and extinction

(evolution/fossils/speciation/Caribbean)

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ABSTRACT   An analysis of taxonomic longevity for species of the two Cenozoic radiations of Caribbean planktonic foraminifera shows strong similarity in longevity for extinct taxa, though extant species of the latter radiation are biased towards longer-lived forms. In this case, the present is not the key to the past. A simple one-parametric stochastic model predicts generally the shape of the distributions, though there is an excess of species with model longevity and a deficiency of longer-lived forms, relative to the prediction of the model. Although the one parameter may relate to the biology of the group under consideration, the distribution about the mode may reflect random appearance–extinction processes.

Interest among paleontologists in the tempo of speciation and extinction can be traced to Simpson (1) and Newell (2), who both voiced the opinion that much of the evolutionary record reflects deterministic responses of biotas to the physical and biotic environment. Patterns of appearance and extinction were related by these pioneers to intertaxon competition, paleogeographic change, and environmental change. More recently, many have revived the argument; some have introduced more deterministic parameters, such as sea-floor spreading and continental drift (3), and interspecific interactions (4), while others have claimed that the overall pattern of appearance and extinction follows essentially a stochastic process (5). This argument parallels the controversy in island biogeography over interactions among species on islands that might regulate species diversity (6).

Raup and colleagues (7) simulated speciation and extinction and claimed that computer-generated clades could not be distinguished easily from data obtained from the fossil record. In particular, the average time of maximal taxon richness was midway between the first and last appearance of the clade in both simulations and fossil data. Although Flessa and Levinton (8) demonstrated that the timing of appearances and extinctions was decidedly nonrandom, the *shapes* of clades cannot be distinguished from a random model. Van Valen (9) found that the strong right-skewed frequency distribution of taxonomic longevities yields an approximately logarithmic–linear cumulative survivorship plot; he argued from this that the probability of extinction per unit time was constant through the history of the group. This constancy was related to a claimed continual and random appearance of new challenges from competing species and other interspecific interactions.

Iterative Evolution in the Foraminifera

Cifelli (10) described the two remarkable radiations of planktonic foraminifera during the Cenozoic. Globigerinid ancestors in the earliest Paleogene gave rise to a morphologically diverse clade, which decreased strongly in diversity towards

the end of the Oligocene. Subsequently, another radiation in the Neogene reproduced nearly the same spectrum of morphologies. A compilation of Caribbean species longevities (11) permits an evaluation of the quantitative aspects of the two radiations. Can species longevity be related to a change of environment from the period of one radiation to the next, or is it simply a parameter inherent in the biological properties of the species and relatively invariant in different periods of the history of the clade? If the latter is true, then iterative evolution is a substantial part of the history of life and can be quantified via the taxon longevity spectrum. Stanley's (12) argument for a latter-day *scala naturae* among major taxonomic groups would have validity.

To obtain the longevity spectrum, we used a corrective equation (Fig. 1) that related a length of ranges on a stratigraphic range chart to independent radiometric dates presented by Saunders *et al.* (11). We used an exponential fit, but any of a number of other fits do not substantially alter our results. Longevity reckoned by number of foraminiferal zones is not as useful, because zone longevity increases by a factor of 2 in the Oligocene, decreases to approximate Paleocene–Eocene levels [*ca.* 1–1.5 million years (my)] in the Miocene, and then decreases dramatically towards the present. With this data set, we cannot correct for pseudoextinction, the transition of one taxonomic form to another, due to phyletic evolution. This effect tends to decrease taxon longevity by confounding it with morphological evolution. In the case in which pseudoextinction dominates, our estimate of longevity is simply a measure of the lifespan of a given morphotype.

Using the calibration, Fig. 2 shows the distribution of longevities for the Paleogene ($N = 128$) and Neogene ($N = 59$) radiations. They point to a remarkable similarity of modal longevity and distributional shape. Using a logarithmic correction to achieve normality, the mean of the two distributions does not differ significantly (t test, $P > 0.05$). A Kolmogorov–Smirnov test on the cumulative distribution, however, shows a significant difference ($P < 0.01$). The latter test is far more sensitive to differences of small magnitude, with large sample sizes.

The magnitude of difference between the two radiations is quite small. The second radiation does show a slight excess of a few longer-ranging species. We note, as a result, a slight difference in median and modal longevity between the two radiations: Paleogene median longevity = 3.40 my, modal longevity = 1.5 my; Neogene median longevity = 3.62 my, modal longevity = 2 my (extinct taxa). A backwards-looking Lyellian analysis of longevity (one estimates longevity by the rate of disappearance of extant forms, going backwards in time), based upon Holocene forms, yields an anomalous mean longevity estimate of 12.02 my. This estimate is consistent with other such Lyellian studies (12) but stands in strong contrast with mean longevities of 4.94 my and 6.52 my, respectively, for the Paleogene and Neogene groups,

Abbreviation: my, million years.

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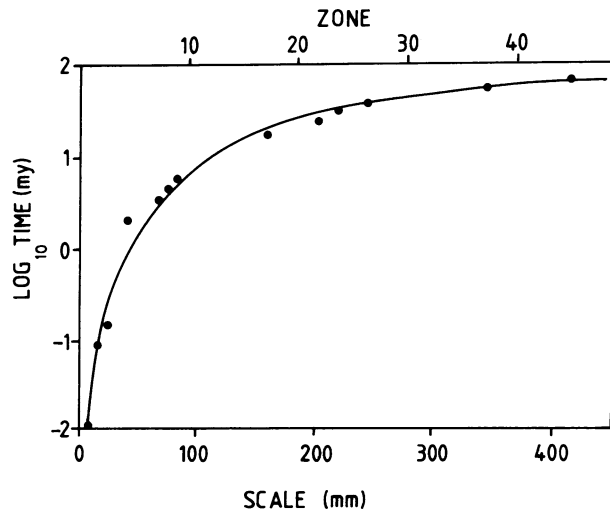*Proc. Natl. Acad. Sci. USA 81 (1984)* 5479

FIG. 1. Calibration curve used to calculate the actual time ranges of fossil species. An exponential curve was used to relate a stratigraphic (millimeter) scale to a set of radiometric dates. The equation is $\log_{10}$ time $= 2 - 4 \exp[(k - 8)^{0.6}(-0.084)]$, in which k is the number of millimeters measured directly from the stratigraphic range chart (insert in ref. 11).

obtained by a direct measure of extinct forms from the stratigraphic range charts. Extant forms, apparently, represent a sample of planktonic foraminiferal evolution biased in favor of more longevous forms. The present-day fauna are not necessarily an accurate key to the average characteristics of the group in the past.

Can Longevity Be Explained by a Random Model?

Levinton (13) suggested that a stochastic model might be sufficient to account for temporal patterns of species richness. As a clade diversifies in an overall environment of resource limitation, the median species population size will tend to decrease. This process will continue until population size decreases to the extent that stochastic variation in the environment causes extinction sufficient to balance speciation. Populations plunging below a threshold size might tend to go extinct in a milieu of change that is random with respect to the population in question. Here we present a stochastic model that predicts the distribution of taxonomic longevities with no assumption of resource limitation. It estimates the time over which a population with a zero average growth trend fluctuates before extinction.

Consider a population growing exponentially with a stochastically varying growth rate:

$$\frac{dN}{dt} = [r + \sigma\varepsilon(t)]N, \qquad [1]$$

in which N is the population size, t is time, r is the mean growth rate, σ is the standard deviation of the growth rate, and $\varepsilon(t)$ is the standard normal white noise process [mean (ε) = 0, variance $(\varepsilon) = 1$].

For the initial population size N_0 and the critical level $N_c < N_0$ the probability density of the first passage of the process $N(t)$ through the critical level N_c is given by the well-known result (14):

$$F(t, N_0/N_c) = \frac{\ln(N_0/N_c)}{\sigma\sqrt{2\pi}t^{3/2}} \exp\left\{-\frac{[\ln(N_0/N_c) + rt]^2}{2\sigma^2 t}\right\}. \quad [2]$$

Over the long run, it is reasonable to assume that $r = 0$. In this we assume that a species has no long-term positive or negative growth trend due to deterministic forces. We then
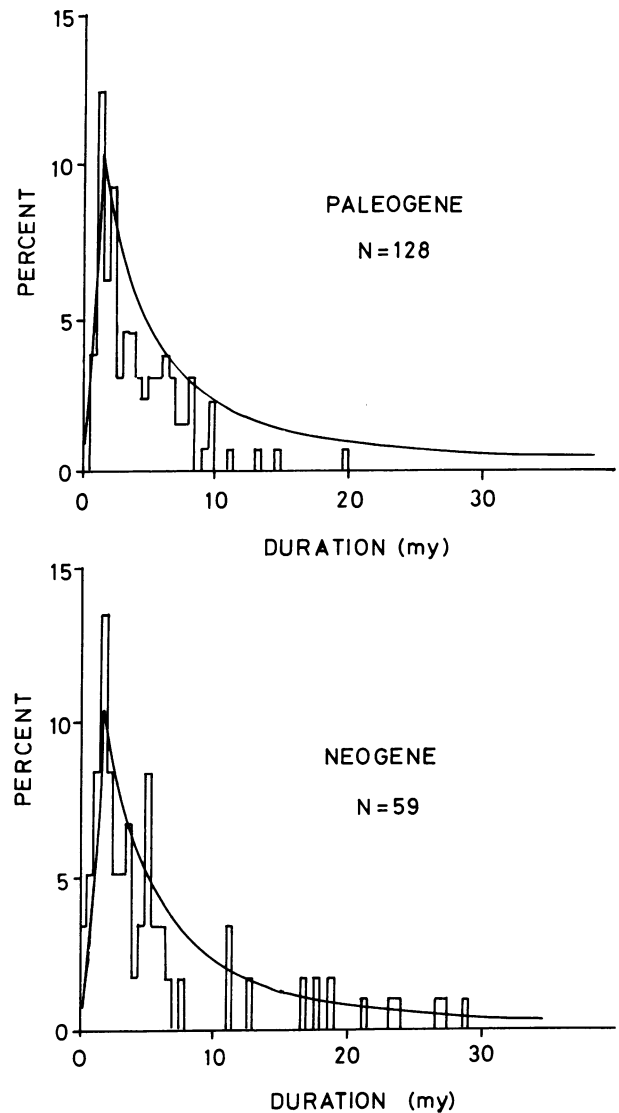

FIG. 2. Histogram of species longevities for the Paleogene (*Upper*) and Neogene (*Lower*) radiations of planktonic foraminifera. Curve shows fit of distribution generated by stochastic model described in text.

compute the first-passage time distribution as:

$$f(t, \alpha) = \frac{\alpha}{\sqrt{2\pi}t^{3/2}} \exp\left[-\frac{\alpha^2}{2t}\right], \qquad [3]$$

in which

$$\alpha = \frac{\ln(N_0/N_c)}{\sigma}. \qquad [4]$$

The mean first-passage time does not exist with this distribution (it exists only with $r \neq 0$). The modal time to extinction, t_m, can be found by considering $f(t) = 0$, giving the predicted longevity of maximal frequency. Omitting the algebra, we obtain:

$$t_m = \frac{1}{3}\frac{(\ln N_0/N_c)^2}{\sigma^2}. \qquad [5]$$

The typical appearance–extinction process with $r = 0$ should look like the diagram illustrated in Fig. 3. Here N_R is the threshold of abundance above which one recognizes the taxon in the fossil record, t_A is the time of first appearance,
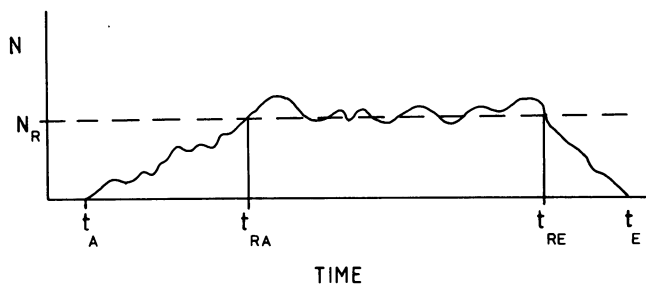
FIG. 3. General picture of stochastic model of a species history showing first and last passage through a recognition threshold of fossil abundance. See text for explanation of symbols.

t_{RA} is the time of recognized appearance, t_{RE} is the time of recognized extinction, and t_E is the actual time of extinction. The observed longevity, which is the total time range over which it is possible to collect the taxon as fossils, $(t_{RE} - t_{RA})$, is the time between the first and last passage of the stochastic trajectory through the recognition level. Period $(t_E - t_{RE})$ is much shorter than period $(t_{RE} - t_{RA})$. Recognizing the small error of omitting the time between recognition and actual extinction, let us consider the time of first passage through $N_c = 1$, starting with $N = N_R$, as a sufficient estimate for the longevity of the species.

Fig. 2 shows that fit of Eq. 3 to the actual frequency distributions. The calculation is performed by taking the modal longevity, t_m, from the data and calculating, with the aid of Eqs. 4 and 5. The overall fit is good in both Paleogene and Neogene radiations, though there is clearly a significant excess predicted for the right tail of the distribution and a predicted deficiency at the modal longevity, relative to the actual data. By using a one-sample G test, the difference with the model is significant (first radiation: $G = 102.4$, 39 df, $P < 0.001$; second radiation: $G = 56.7$, 39 df, $P < 0.001$).

The reason for a significant difference between the model's prediction and the actual data may be due to at least three possible sources of empirical and theoretical error. First, some long-lived taxa may be artificially absent. If taxa are defined by pseudoextinction—that is, morphological change—then a long-lived single taxon might appear in the data as a chain of morphologically transitional shorter-lived taxa. Phyletic evolution from one morphologically defined species to another is common in planktonic foraminifera (15). This would tend to underestimate longevity by a large amount for some taxa. This is an inevitable shortcoming of the taxic approach to evolution, which tends to ignore phyletic evolution and cladal structure in general. Second, we have assumed that r, the intrinsic rate of population increase, equals zero. If $r \neq 0$, then the variance of r would be an important component of stochastic extinction, and, hence, taxonomic longevity. If $r \neq 0$, we can improve our fit of the model to the data substantially. As we have no basis to select the value of parameters, such an attempt at this stage would constitute mere curve fitting. Finally, of course, the model may be incorrect. The relatively kurtotic aspect of the real data, combined with a deficiency of long-lived forms, may suggest that some nonrandom process narrows the longevity spectrum.

If $N_c = 1$ and $N_0 = N_R$ is between 10 and 10^5 we have $\ln(N_c/N_c)$ between 2.5 and 11.5. With time measured in million years and $1 < \alpha < 10$ ($\alpha = \sqrt{3t_m}$), we have σ of the order of 10^0 to 10^1. As σ has a dimension of population size/time, we obtain on a per year basis that $10^{-3} < \sigma < 10^{-2}$. In other words, fluctuations in the growth rate, r, around zero of the order of a fraction of 1% a year are sufficient to generate the picture that we see in Fig. 2, with a few million years for the typical lifetime of a species.

The observed histograms of taxonomic longevity can, of course, be approximated by a variety of distributions. What is surprising about the one we suggest here is that it is based on a model of population growth and extinction, has only one parameter, and produces a fairly good distributional fit for a one-parametric class. This may suggest that the underlying model may be a reasonable approximation of the actual process generating distributions of taxonomic longevity in the fossil record.

Different major taxonomic groups may have different modal extinction times; this would be reflected in our model in the level of stochastic variability, σ, in the growth rate. The value of σ could be taxon-specific if a given ecological life-style placed a taxon in an environment with a predictable amount of population variability. Variation in social structure (12), trophic level (16), competitive interaction (4, 9), and habitat might all contribute to among-taxon variance in population growth rate.

Our results demonstrate that the two Cenozoic episodes of foraminiferal evolution in the Caribbean are indeed iterative, at least with respect to longevity. Emiliani (17) has argued recently that extinction in planktonic foraminifera is probably random. He suggests that species originate in oceanic margins and that oceanic taxa disappear upsection with no obvious descendants. Although a linear taxonomic survivorship curve for foraminifera has been reported, it does not necessarily support the hypothesis of random extinction (18). A recently published extensive summary of Neogene foraminiferal evolution (15) suggests that ancestor–descendant links can be found commonly in the oceanic fossil record.

The model we propose would be valid if there were an overall property "being a foram," which supercedes all other variation. Our model is not in conflict with the "Red Queen" hypothesis (9), which invokes random biological interactions as the source of extinction. Van Valen's hypothesis would be consistent with ours if the biological challenges caused random fluctuations in population size of the species under consideration. We simply suggest that an inherent set of biological properties of a taxonomic group, placed in a defined environmental setting with random population fluctuations, sets both the modal species longevity and the distribution of longevities about the mode.

It is of interest that estimates of longevity, based upon a Lyellian analysis of Holocene forms, are much larger than the directly measured ranges of extinct species. Our direct estimates of mean species longevity fall closer to Emiliani's (17) estimate for Cenozoic species than to the Lyellian estimates. The explanation for the discrepancy is not clear. There may be a methodological problem. It is also possible that the post-Miocene cooling event has inhibited morphological evolution, thus extending the temporal range of species recognized by morphotype. It is also possible that higher-latitude and long-ranging forms have become more common within the Caribbean faunas since the Miocene. No matter what the cause, a backwards look from the present is clearly not the key to the past.

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