Limits to randomness in paleobiologic models: the case of Phanerozoic species diversity

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The question of how random, or unconstrained, paleobiologic models should be is examined with a case study: Signor's (1982, 1985) inverse calculation of levels of marine species diversity through the Phanerozoic. His calculation involved an ingenious model that estimated species numbers and species abundances in the world oceans of the past by correcting known numbers of fossil species for variations in sedimentary rocks available for sampling and in effort paleontologists might devote to sampling. The model proves robust to changes in possible shapes of species-abundance distributions, but it is sensitive to alterations in the assumption that paleontologists collect fossils at random. If it is assumed that ease of collecting varies with age of sediment (with the Cenozoic offering easy sampling) or that paleontologists tend to seek out rarer fossils, results of the inverse calculation change. In particular, the magnitude of the calculated Cenozoic diversity increase always declines from the factor of about seven as originally reported to something considerably smaller. This leaves open the problem of the magnitude of Cenozoic increase in marine species diversity, awaiting better empirical data and, perhaps, more exacting models, random or otherwise.

Key words: random models, inverse calculation, Phanerozoic species diversity, macroevolution.

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Introduction

Antoni Hoffman was a strong advocate of the use of random null models in evolutionary paleobiology (e.g. Hoffman 1981, 1986, 1988; Hoffman & Ghiold 1985; Hoffman & Fenster 1986; Nitecki & Hoffman 1987). Random, or stochastic, models treat the outcomes of complex phenomena, such as speciation or extinction, as if they were random events that occur with some determinable probability (e.g. Raup 1977). They are much like flips of coins or rolls of dice. However, neither of these two examples is really random but rather determined by a complex nexus of physical causes, boundary constraints, and initial conditions that make any particular outcome unpredictable except as a probability statement. Similarly, the application of random models to problems in paleobiology is not a testament that evolution is random but rather an assumption that the many causes of speciation, extinction, adaptation, etc. are so complex and so contingent upon initial conditions and boundary constraints that the outcome of any particular situation is unpredictable except as a probability statement.

No null model in paleontology is ever completely random. Always, some deterministic boundary constraints or other structures are imposed upon whatever stochastic events are modeled. For example, the seminal investigation of stochastic diversification by Raup et *al.* (1973) imposed a predetermined, constant equilibrium diversity upon the stochastic phylogeny. Similarly, the comparison of phyletic evolution in *Kosmoceras* to random walks by Raup & Crick (1981) assumed a predetermined, constant step size in morphological evolution during any time interval. Finally, the stochastic model of Phanerozoic diversification among marine animals by Hoffman & Fenster (1986) included two predetermined events to emulate the Ordovician radiations and the end-Permian mass extinction.

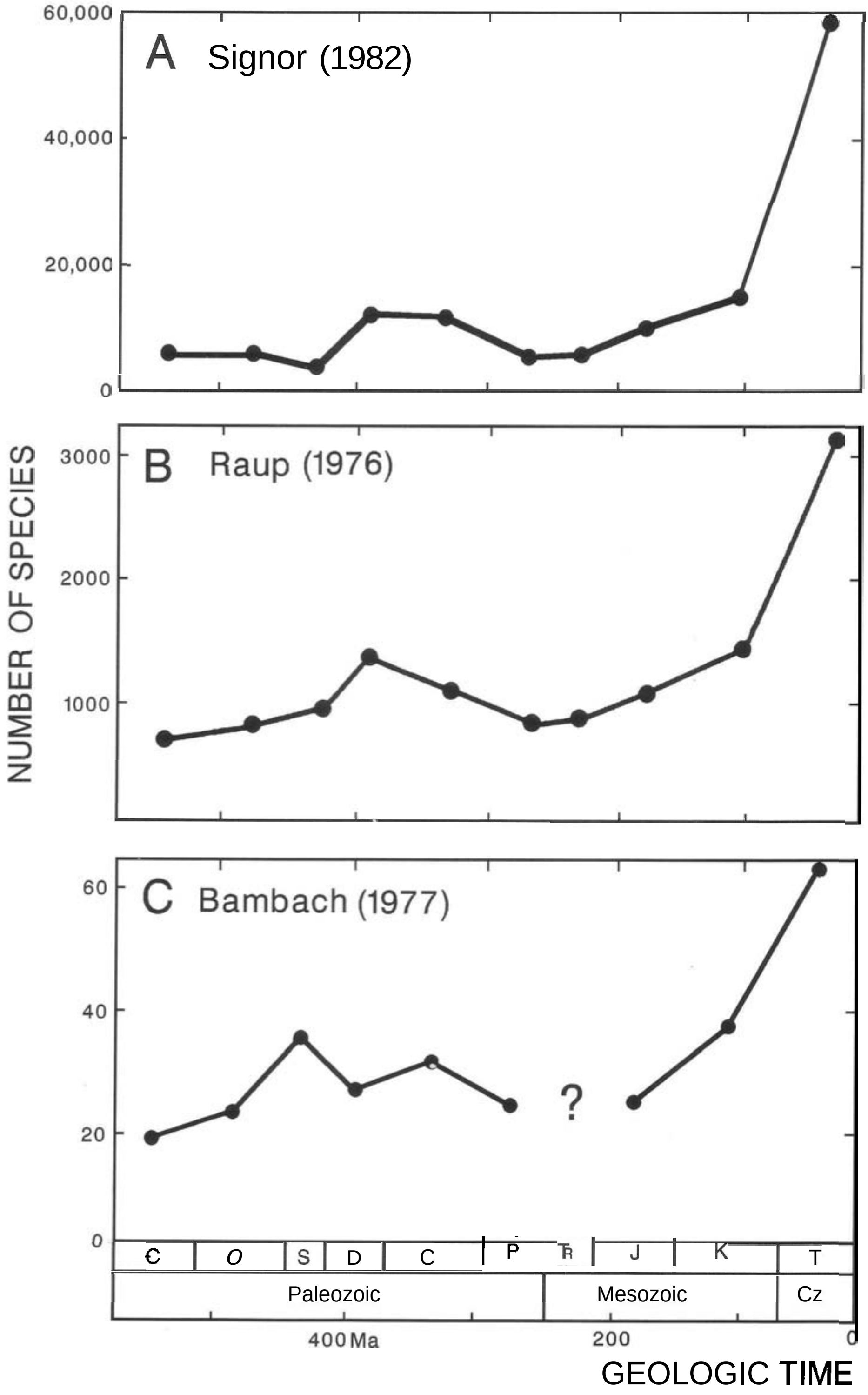
An extremely interesting use of random models with minimal deterministic structure is Signor's (1982, 1985) inverse calculation of standing levels of species diversity during geologic periods of the Phanerozoic. This calculation incorporated two assumptions of randomness:

(1) Abundances of species are determined by a complex nexus of additive causes that interact with multiplicative population growth to produce a lognormal distribution (Preston 1948, 1962; see also May 1975; Pielou 1975; Whittaker 1975; Magurran 1988).

(2) Paleontologists collect fossils and identify (or describe) them randomly in proportion to preserved species' abundances.

Using a range of parameter values for how long species persist and how much opportunity paleontologists have to sample fossils, Signor reached a seemingly robust conclusion that species diversity in the oceans has increased by a factor of 7 or more since the Paleozoic, with most of the increase occurring during the Cenozoic Era (Fig. 1A).

Fig. 1. Estimates of the average standing diversity of marine animal species through the ten geologic periods of the Phanerozoic. □A. Signor's (1982, 1985) calculated global diversity, recomputed using the time scale of Harland *et al.* (1990). □B. Raup's (1976a) empirical curve for global diversity of invertebrates and animal-like protists. Average numbers of species per period have been rescaled by dividing total numbers by period durations in Harland *et al.* (1990) and multiplying by 5 Ma (1 Ma = 10^6 years), the approximate average duration of marine species. □C. Bambach's (1977) empirical curve for average numbers of fossil species within local communities in open-marine environments; no data were available for the Triassic, and the point for the Permian was scaled from data in Sepkoski (1988). All three estimates of marine species diversity indicate a substantial increase during the Cenozoic (abbreviated Cz) Era, but Signor's inverse calculation indicates a much greater increase than the empirical measurements.


A Signor (1982)
60,000
40,000
20,000
0
B Raup (1976)
3000
2000
1000
NUMBER OF SPECIES
C Bambach (1977)
60
40
20
0
?
Є
O
S
D
C
P
Tr
J
K
T
Paleozoic
Mesozoic
Cz
400 Ma
200
0
GEOLOGIC TIME

This conclusion is at variance with the only two empirical measures of Phanerozoic species diversity that are available. Raup (1976a) estimated numbers of newly described species of fossil invertebrates and animal-like protists listed in 70 years of the *Zoological Record* (Tab. 1); from these data he constructed a curve for average number of species in each geologic period, which showed Cenozoic diversity exceeding earlier levels by a factor of about three (Fig. 1B). Barnbach (1977) compiled published numbers of species occurring together in benthic paleocommunities through the Phanerozoic (Appendix). His data indicate that Cenozoic marine communities were only about twice as diverse as Paleozoic and Mesozoic communities (Fig. 1C). However, global species diversity is not entirely dependent upon local community diversity because provinciality, resulting from geographic and climatic barriers, affects global diversity independent of local communities. This argument was made strongly by Valentine (1969, 1970, 1973) who favored an order of magnitude increase in Cenozoic species diversity on the basis of empirical family-level diversity patterns and genus-to-family and genus-to-species ratios (see also Valentine et *al.* 1978). Thus, the results of Signor's (1982, 1985) inverse calculation for Phanerozoic species diversity seem more commensurate with Valentine's estimate than with Raup's and Bambach's measurements (see also Signor 1990a, b).

Below, I examine Signor's inverse calculation in detail, paying special attention to its components incorporating randomness. First, I outline the ingenious structure of the calculation. Then I examine some modifications based upon recent ecological conclusions and plausible evolutionary considerations. Finally, I incorporate nonrandom models of paleontologic sampling. My principal conclusion from these exercises is that the huge Cenozoic increase in global species diversity may not be as robust as originally argued on the basis of random models.

Structure of Signor's model

The structure of Signor's (1982, 1985; see also 1978) inverse model needs to be explained in some detail in order to clarify what he actually did and to show where different assumptions can be incorporated. The model begins with the ecologic observation that large ensembles of species often have abundances that approximate a lognormal density distribution (Fig. 2). Using Preston's (1948, 1962) formalization based on a doubling, or 'octave', scale of abundances, the number of species, y_R, with 2^R individuals is

$$y_R = y_O \exp[-(aR)^2] \qquad (1)$$

where a is a constant and y_O is the number of species in the modal octave at $R = 0$.

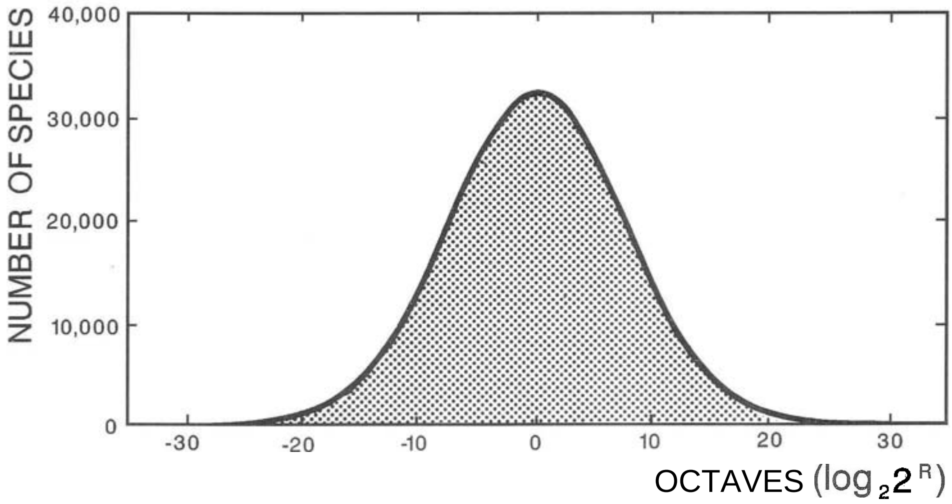


Fig. 2. A lognormal distribution of species abundances. Abundance intervals on the x-axis are termed 'octaves' *(R)* and are plotted on a base 2 logarithmic scale. The mode of the distribution is placed for mathematical convenience at octave 0. This distribution was computed for the Cenozoic Era, using the parameter values in Eq. (9).

May (1975) demonstrated that the parameter, a, can be approximated when species numbers are large as

$$a \approx \frac{\ln 2}{2\sqrt{\ln y_T}} \tag{2}$$

where y_T is the total number of species in the ecosystem. (Signor treated y_T as the total number of animal species in the world ocean.) Given an estimate of y_T, the number of species, y_O, in the modal octave is

$$y_O = \frac{a\, y_T}{\sqrt{\pi}} \tag{3}$$

where $\pi = 3.14159...$ (see Signor 1978, 1985).

At this juncture, the relative abundance of a species in any octave can be calculated, assuming there is no veil line in the distribution (i.e. a minimum octave below which no species is represented; see Preston 1948, 1962; also, e.g., Koch 1978). The relative abundance, n_R, is

$$n_R = \frac{2^R}{\sum_{r=-\infty}^{\infty} y_r\, 2^r} \tag{4}$$

This is also the probability that any species will be collected at random, given its octave abundance. In practice, Eq. (4) need be calculated only to the limits of r at which y_r rounds to unity. If there is a veil line, Eq. (4) underestimates n_R but only trivially if the veil is well to the rarer side of the mode. Signor (1982, 1985) assumed that there was no veil line.

If N individuals are sampled randomly from the lognormal distribution, then the number of individuals expected for a species in the Rth octave is

$$N\, n_R \tag{5}$$

Signor (1978, 1985) noted that not all species in the *Rth* octave will be sampled unless Expression (5) is large relative to y_R. If N is substantial, the sampling distribution of individuals among species in any octave should be approximately Poisson, so that the probability of randomly collecting any given species in the *R*th octave is

$$1 - \exp(-N\, n_R) \tag{6}$$

Thus, the expected number of species, S_R, sampled from the *R*th octave is

$$S_R = y_R[1 - \exp(-N\, n_R)] \tag{7}$$

and the total number of species, S, expected in a large sample is simply

$$S = \sum_{R=-\infty}^{\infty} S_R \tag{8}$$

With this algebra, only two of the following three variables need be known to perform the inverse calculation of Phanerozoic species diversity:
N = number of individuals in the sample,
S = number of collected species in the sample.
y_T = total number of species that lived in the ecosystem.

The value of the third variable can always be calculated by successive approximation, iterating through Eqs (1) to (8). Thus, Signor (1982, 1985) computed standing species diversity in each geologic period with the following algorithm:

(1) Estimate the total number of species, y_{Cz}, that lived during the whole of the Cenozoic. This can be approximated knowing (a) the number of potentially fossilizable species alive in the oceans today, (b) the average longevity of these species, (c) the duration of the Cenozoic Era, and (d) the relative magnitude of diversity increase during the Cenozoic.

For example, if the number of living, fossilizable marine species is 100,775 (Valentine 1970), the average species longevity is 6.5 million years (Durham 1967), the duration of the Cenozoic is 65 million years (Lambert 1971), and the diversity increase during the Cenozoic is a factor of five (i.e. from 20% to 100% modern diversity), the total number of fossilizable species integrated over the Cenozoic is approximately

$$\begin{aligned} y_{Cz} &= (65\,\text{myr}/6.5\,\text{myr})\,[(0.2+1.0)/2]\ 100{,}775\ \text{species} \\ &= 604{,}650\ \text{species} \end{aligned} \tag{9}$$

[A five-fold diversity increase during the Cenozoic is probably a reasonable guess even if Cretaceous diversity were moderately high, given the severity of the Maastrichtian mass extinction (see species-level estimate in Sepkoski 1989).]

Tab. 1. Data used in the analysis of Signor's model for the inverse calculation of Phanerozoic species diversity. Paleontologic interest units, outcrop area, and sedimentary rock volume provide estimates of relative sampling intensity (see text).

Geologic system	Number of fossil marine species [1]	Paleontologic interest units [2]	Outcrop area [3] (× 10^4 km^2)		Sedimentary rock volume [4] (× 10^5 km^3)
			total	marine	
Tertiary	40,226	1060	2041	1245	1150
Cretaceous	21,967	760	1680	1462	560
Jurassic	12,380	260	312	253	620
Triassic	5,747	130	360	216	450
Permian	6,810	160	284	264	400
Carboniferous	15,006	300	396	226	530
Devonian	12,394	290	333	303	680
Silurian	5,525	200	207	~186	370
Ordovician	10,928	260	175	~158	440
Cambrian	8,274	150	248	~223	440

1. From Raup (1976a: Tab. 3), with insects (nonmarine) removed. His 'undifferentiated' data were distributed among geologic periods in proportion to resolved data.

2. From Sheehan (1977) without change; include interest in marine invertebrates and animal-like protists only.

3. From Raup (1976b), after Blatt & Jones (1975); 'total' includes marine and nonmarine sedimentary rocks. whereas 'marine' is corrected with data from Knoll et *al.* (1979) (see text); marine areas for the Cambrian to Silurian are guesses.

4. From Raup (1976b), after Gregor (1970); includes both marine and nonmarine sedimentary rocks.

(2) Estimate the total number of fossils sampled (i.e. collected and identified or described) from Cenozoic rocks. The estimate of y_T in step 1 is sufficient to compute Eqs (1) to (4). The Cenozoic sample size, N_{Cz}, can be calculated by successive approximation through Eqs. (5) to (8) until the number of sampled species in Eq. (8) equals the actual number counted by Raup (1976a).

(3) Estimate the sample size, N_i, for an earlier geologic period. Signor did this by assuming that sample size is a simple function of estimated sampling intensity, I_i, for the ith period relative to the estimate for the Cenozoic, I_{Cz} (see Tab. 1). That is,

$$N_i = \frac{I_i}{I_{Cz}} N_{Cz} \tag{10}$$

For example, the Cretaceous sample size using paleontologic interest units (Tab. 1) would be 760/1060 = 0.72 as many individuals as in the Cenozoic sample (see below).

outcrop area; these range from 40% for the Cenozoic, Triassic, and Carboniferous, to approximately 20% for the Jurassic, 15% for the Cretaceous, and 10% or less for the Permian and Devonian. Assuming that these proportions are broadly applicable to the world as a whole (a very big assumption) and that 10% is an adequate estimate for the Silurian to Cambrian, I computed global marine outcrop area (Tab. 1) and solved Signor's model. The results showed an enhanced rise in Cenozoic diversity, due entirely to the greater shrinkage of Cenozoic outcrop area relative to most other systems. Any more accurate estimate of marine outcrop area that similarly diminished Cenozoic area would have a comparable effect on modeled diversity. Because the rough estimate used here produced results virtually identical to paleontologic interest units, I will accept Signor's selection of interest units as the best measure of relative sampling intensity. (I agree with him that rock volume is not a good measure: much sedimentary rock is concealed in the subsurface, accessible only to deep drilling, and large volumes reside in orogenic foredeep deposits that often are rather sparsely fossiliferous.)

Biological variations upon the model

Questions can be asked about Signor's (1982, 1985) assumptions concerning random abundances of species and random sampling of fossils. For example, Nee *et al.* (1991) have argued that large species assemblages are not lognormally distributed but rather left skewed with many more rare species than predicted by Preston's (1948, 1962) random model. They suggest instead that species-abundance distributions may be more consistent with Sugihara's (1980) model of sequential niche division. [Alternatively, it could be that censuses over very large areas add together local lognormal distributions and therefore accumulate excess numbers of allopatric rare species, which tend to be rather localized; common species, on the other hand, tend to be more widespread (see Brown 1984; Rabinowitz *et al.* 1986).]

Sugihara's (1980) species-abundance model cannot be fit to data in the manner of the lognormal distribution. However, the lognormal distribution can be altered to make it left skewed. I interpolated abundance classes between all octaves to the left of the mode and adjusted species numbers in Eq (1) accordingly, making the distribution about as skewed as the data presented by Nee *et al.* (1991). [This exercise was strictly heuristic, since it violated assumptions underlying May's (1975) derivation of Eq. (3).] Signor's inverse calculation was then performed with the altered distribution. The results were virtually identical to the unaltered model, with a rise of 7.5 in estimated Cenozoic diversity using paleontologic interest units as the measure of relative sampling intensity.

I also altered the model in a second way. Signor (1982, 1985) incorporated all species present over the whole of a geologic period into a single lognormal distribution. However, ecological applications of the lognormal distribution have involved communities of contemporaneous species, and there is no reason to believe the same algebra should apply to species summed over tens of million years. It might be more reasonable to establish the model distributions in Eqs (1) to (3) for a single instant in time and then to integrate it over the geologic period of interest. However, evolutionary complication arise here: there seems to be a nonrandom relationship between species' abundances and their extinction rates. Widespread and abundant species tend to have lower extinction rates and therefore greater longevities than their rarer counterparts (Bretsky 1973; Boucot 1975; Sheehan 1982; Brown 1984; Jablonski 1986a, b; Erwin 1989).

I modeled this relationship in a crude fashion. The range of abundances from rarest to commonest species was divided into k classes, each with an approximately equal number of octaves. The longevity, d_i, for species in the ith abundance class was then computed as

$$d_i = i\,\bar{d}\,\frac{k}{\sum_{j=1}^{k} j} \qquad (11)$$

where $\bar{d}$ is the average longevity of species. This equation yielded a mean of d_i that equalled $\bar{d}$. Numbers of species, y_R, in each octave for a given instant were calculated as in Eq. (1). Integrated over time, the number of species in an octave in the ith longevity class became

$$y_{R,i} = \frac{T}{d_i}\,y_R \qquad (12)$$

where T is the duration of the geologic period. Since species with greater longevities accumulate more individuals, the relative abundances (Eq. 4) were now computed as

$$n_{R,i} = \frac{i\,2^R}{\sum_{j=1}^{k} \sum_{r=i_n}^{i_x} y_r\, i\, 2^r} \qquad (13)$$

where i_n and i_x are the minimum and maximum octaves in the ith abundance class. These manipulations right skewed the abundance distribution, producing excess numbers of rare species and increased abundances of common species. The manipulations also permitted standing diversity to be estimated directly rather than needing to normalize total numbers of species to period durations.

These modifications add a little more biology to the model while making it a little less random. The changes also slightly alter Signor's observation concerning the Cenozoic rise in diversity. With nine longevity classes, the

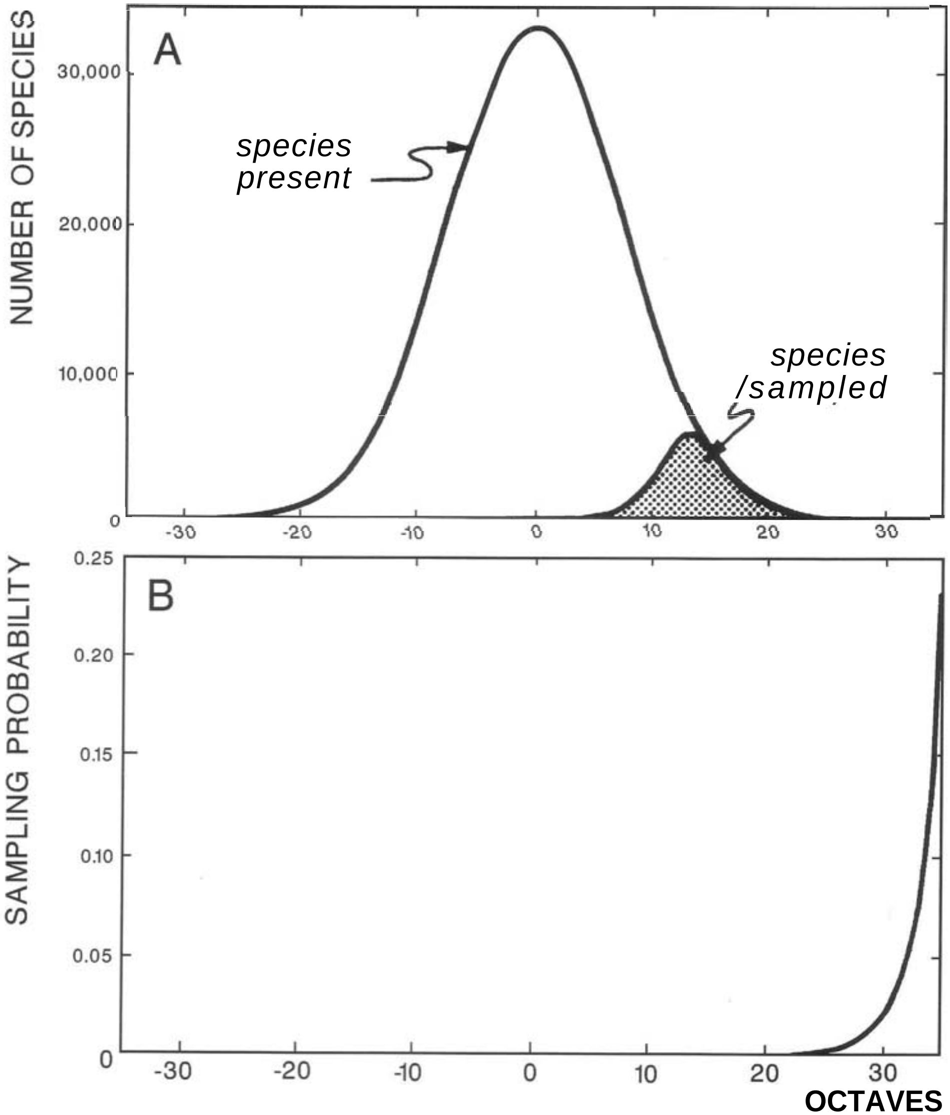


Fig. 3. Outcome of random sampling of species in Signor's (1982, 1985) model. ☐A. The Cenozoic species-abundance distribution for a total of 604,650 species ('species present') and the sampled distribution ('species sampled') of 40,226 fossil species (Tab. 1). More than 99% of sampled species come from the upper half of octaves, and all of the most abundant species are collected. ☐B. Probability of sampling a Cenozoic species as a function of its abundance (**Eq.** 4). This probability becomes extremely small below the upper dozen octaves.

estimated rise in Cenozoic diversity falls from a factor of 7.5 to 6.0, using paleontologic interest units.

The reason for the small differences in this and the left-skewed model is that all models end up sampling primarily from the right tail of the species-abundance distributions. Figure 3A illustrates the sampling of

Cenozoic species governed by Eq. (7). In the unmodified model, 99.97% of sampled species in the Cenozoic come from the upper half of the octaves. Furthermore, 90% of sampled individuals come from the most abundant 0.5% (= 215) of the sampled species, which constitute 0.04% of total species. This situation is an exaggerated example of the real situation found by Koch (1978). He intensively sampled Cenomanian fossils from the Cretaceous Interior Seaway of North America and compared the species' abundance distribution of his amalgamated collections to the distribution from previously published collections. The comparative pattern in this actual exercise is very similar to the model pattern in Fig. 3A, with one important difference: Koch (1978) posited a veil line just to the rare side of the lognormal mode, below which no species could be observed. Signor's (1982, 1985) assumption that no veil line exists posits *a* large number of very rare species beyond the reach of sampling.

The two modified versions of Signor's model change the distribution of sampled species only minuscully. This aspect of the model is a direct consequence of Eq. (4), which makes the probability (= n_R) of picking up and identifying a specimen of a species in the rarer octaves infinitesimally small if the range of octaves is large (i.e. y_T is large) (Fig. 3B). Alternative models of species abundances, such as the log series and broken stick (see Magurran 1988), hardly change this situation, since all predict highly skewed abundances and very large numbers of rare species.

Is paleontologic sampling random?

Two questions might be asked about the modeled sampling in Eqs (7) and (10): (a) Is sampling really uniform through time, such that ratios of estimated intensities relative to the Cenozoic are appropriate? (b) Do paleontologists really collect and identify fossils at random?

Altering Cenozoic sampling intensity.—The manner in which sample sizes are calculated in Eq. (10) assumes that there are no secular changes in the richness of fossil samples or the way in which they are obtained. There are several reasons to doubt this. First, Bambach (1977) observed that local fossil assemblages in the Cenozoic are on average about twice as rich as older assemblages (Fig. 1C). Thus, half the outcrop area or half the paleontologic field effort might be needed to produce a given diversity of fossils. Second, many fossiliferous Cenozoic units, especially in siliciclastic facies, are comparatively uncemented, and aragonitic fossils are not uncommon, as recognized by Signor (1978). Thus, more individuals can be sampled per unit of outcrop area or unit of paleontologic field effort.

Evidence that effective sampling of Cenozoic fossils may indeed be high comes from Raup (1976b: Fig. 5). His regression of fossil species diversities on total outcrop area gives the Cenozoic a large positive residual (which increases if strictly marine outcrop area is substituted). The double-logarithmic regression indicates that total Cenozoic outcrop area would need

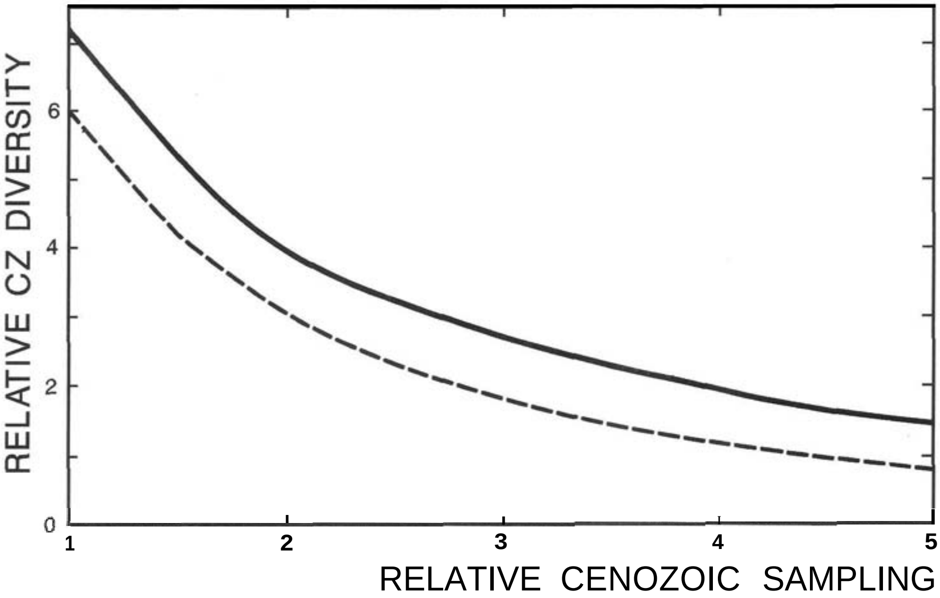


Fig. 4. Calculated Cenozoic species diversity relative to the average of the earlier Phanerozoic as a function of the relative effectiveness of Cenozoic sampling (**Eq.** 10). Diversities were calculated using the parameter values in Fig. 2 with sampling intensity measured by paleontologic interest units (Tab. 1). **A** relative effectiveness of 2 indicates that the Cenozoic is sampled twice as intensively as suggested by raw interest units. The solid curve is for Signor's original model; the dashed curve is for the model with variable species longevities.

to be nearly doubled in order to predict fossil diversity correctly. Conversely, it seems to indicate that twice as many species have been sampled per unit of outcrop area from Cenozoic sedimentary rocks as from older rocks.

I performed calculations with Signor's inverse model assuming that effective sampling of the Cenozoic is greater than what is suggested in Tab. 1. This alteration markedly reduced calculated diversity in the Cenozoic relative to the Paleozoic and Mesozoic (Fig. 4). For example, if effective Cenozoic sampling is twice that suggested by paleontologic interest units, the Cenozoic rise declined from a factor of about 7 to a factor of 4 in the unmodified model, and to about a factor of **3** in the version with variable species longevities. With yet greater sampling efficiency in the Cenozoic, the calculated rise declined further, reaching equity in the modified version of the model at efficiencies of about 4.

Biased modes of sampling. — The fundamental assumption that underlies Eq. (7) is that for 70 years (or more) paleontologists have collected and identified (or described) individual fossils at random. There are various reasons to suspect this:

(1) Large animals are often easy to observe and collect even though they may not be numerically abundant. A deer standing in a meadow in bloom is far more visible than the myriad insects flying around it. Indeed, a far

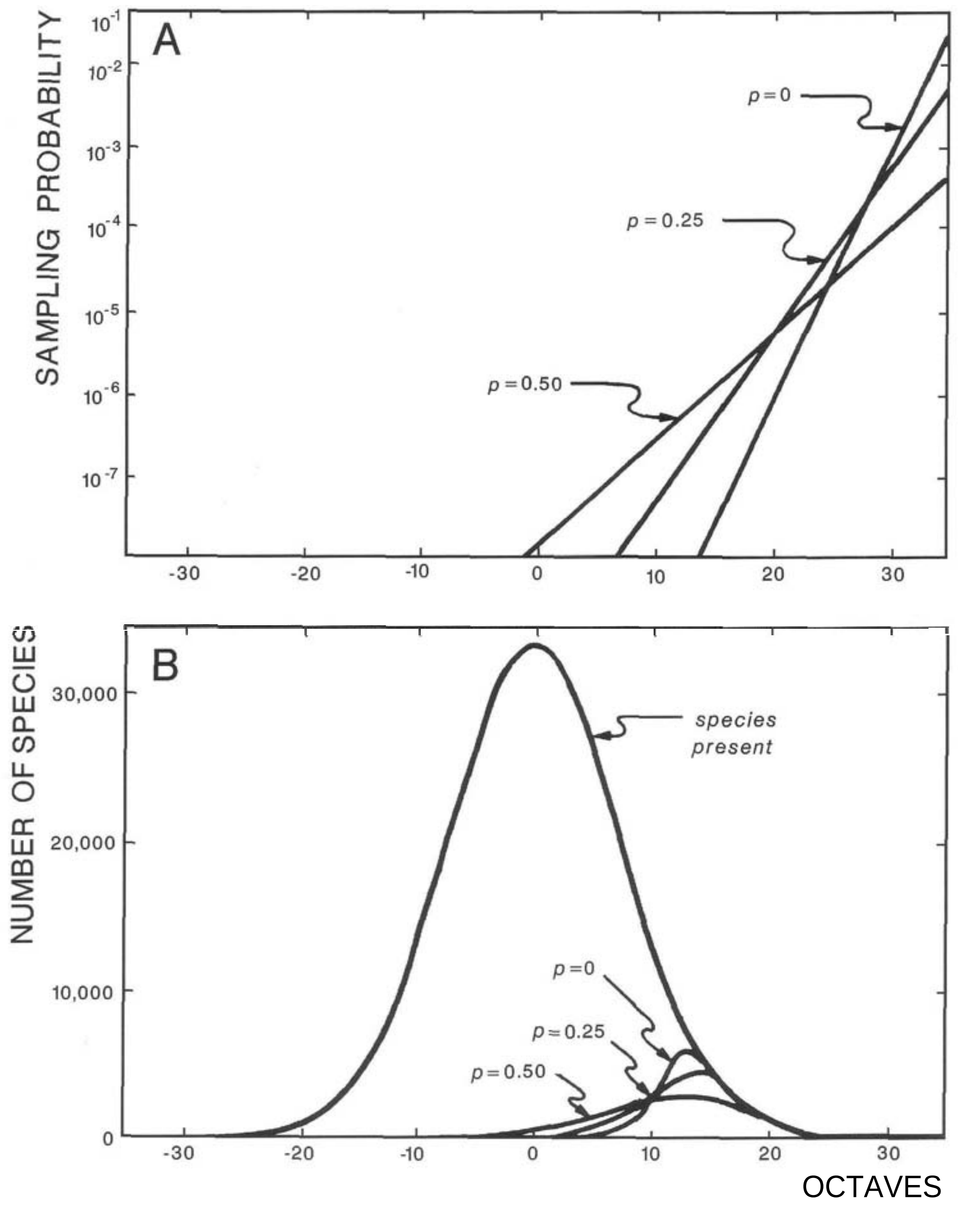


Fig. 5. Effects of introducing a bias toward sampling rarer species. ❑A. Probability of sampling a species as a function of its abundance (octave) on logarithmic axes. The curve for completely random sampling ($p = 0$) is equivalent to Fig. 3B. Increased sampling bias toward rarer species as a result of conditioning on common species (p= 0.25, 0.50) enhances the probabilities of collecting species in lower octaves, although species in the highest octaves retain the greatest chances of being collected. ❑B. Distribution of sampled species in the Cenozoic Era (cf. Fig. 3A). As sampling bias toward rarer species increases, more species near the modal octaves are sampled.

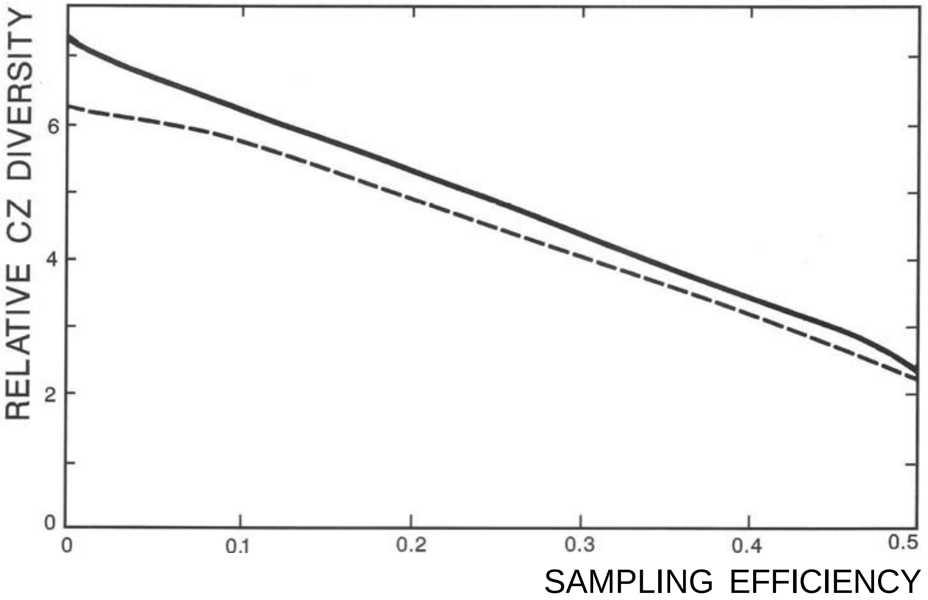


Fig. 6. Calculated Cenozoic species diversity relative to the average of the earlier Phanerozoic as a function of bias toward sampling of rarer species (*p* in Eq. 14). The solid curve is for Signor's original model: the dashed curve is for the model with variable species longevities.

larger proportion of the estimated species diversity of living mammals has been described than of insects (e.g. Mayr 1969; May 1988). An inverse relationship between size and abundance exists but is certainly not perfect (Damuth 1981; Brown & Maurer 1987; May 1988; Morse *et al.*, 1988). Still, this could lead to more collecting from the smaller octaves of a lognormal distribution than assumed in the random sampling model.

(2) Human perception is often attracted to the unusual object. For example, this *italicized* word can be spotted far more quickly on the printed page than would be predicted from the random expectation requiring looking at half of **all** words on average. I suspect that people's perception is not a search image for A (where A is the common object), but rather an expectancy of A and a search image for Not A. My grandfather, John Sepkoski (Jan Szczepkowski), had this; he could find a four-leaf clover in an unkempt lawn with remarkable swiftness by not seeing all the three-leaf individuals. Many paleontologists probably do something similar, as suggested by (a) the many cases in which the rare specimen is described ('A new species from the ABC Formation') or the unusual fauna is monographed; (b) paleoecologic surveys that assess taxa on a 'rare-common-abundant' scale which is approximately logarithmic (e.g. Sutton et *al.*, 1970; McGhee 1976), with search devoted to finding rarer species once the more common ones have been identified; and (c) rules for gathering random collections by bulk sampling, quadrat counts, etc. that are codi-

fied in a number of texts and review papers, in large part to control common human behavior and discourage highgrading collections with rarer species.

It is not enitrely clear how such a bias toward rarer species might best be incorporated into Signor's inverse calculation. For the sake of simplicity, I have assumed that the bias is proportional to abundance. Thus, if R is the more abundant octave, the sampling efficiency *in* octave $R\text{-}1$ might be $p\%$ greater, and the efficiency in $R\text{-}2$ similarly $p\%$ greater than in $R\text{-}1$, etc. This assumption alters the effective relative abundance, n_R', of a species from Eq. (4) to

$$n_R' = \frac{(1+p)^{-R}\,2^R}{\sum\limits_{r=-\infty}^{\infty} (1+p)^{-r}\,y_r\,2^r} \tag{14}$$

In a large sample, n_R' would approximate the probability of picking up a specimen of a species in the Rth octave, given that the collector has been conditioned to the more common species. But, this collector's sample would still contain more specimens of the commoner species, so long as $p < 1$. This is illustrated in Fig. 5A, which graphs Eq. (14)for several values of p. In terms of the inverse calculation, the effect of biased sampling efficiency is to spread the collection of species out so that slightly more are sampled around the modal octave (Fig. 5B).

The substitution of Eq. (14) for Eq. (4) in the versions of the model decreases the apparent Cenozoic rise in calculated diversity, and decreases it dramatically as p approaches 0.5 (Fig. 6). With paleontologic interest units used to estimate sampling, a 10% bias in sampling efficiency decreases the estimated Cenozoic rise from a factor of 7 to 6 in the unmodified model; with a bias of 25%, the rise reduces to a factor of 4.5 to 5; and with a 50% bias, the factor is around 2. It should be noted that in no case does this manipulation destroy the correlation between sampled diversity and sampling intensity, since sampled diversities always equal Raup's (1976a) numbers which, in turn, correlate with paleontologic interest units, outcrop area, etc. (Raup 1976b; Sheehan 1977).

Fig. 7. Empirical patterns of taxonomic diversity for marine animals ☐A–B. Stage-level data for families from Sepkoski (1992b) and for genera from an unpublished, active compilation described in Sepkoski (1988, 1989). These two ranks display similar temporal patterns although mass extinctions appear more severe among genera (as expected from Raup 1979b) and the Cenozoic rise appears more pronounced. OC. The heavy curve for species diversity is from Raup (1976a), the same as in Fig. 1B. The stippled field represents a possible range of values calculated from Signor's inverse model. The lower bound is Signor's unmodified calculation (Fig. 1A). The upper bound is somewhat arbitrary and was calculated with the same parameter values but using the model with variable species longevities, 100% more effective sampling in the Cenozoic, and 10% bias toward sampling rarer species. Upon rescaling, the empirical data for genera or families could fall within these bounds.

Discussion

The exercises reported above probed assumptions about randomness in the elegant inverse calculation of species diversity performed by Signor (1982, 1985). The random components of the model were extracted, rebuilt, and reinserted in order to determine how they affect the calculation. In general, however, randomness was never entirely eliminated but merely constrained under some further deterministic considerations. Thus, for example, biological components of the model were changed from fossil species abundances reflecting small additive random factors in the environment to a slightly more constrained subdivision of niches or resources and to a situation in which rare, endemic species tend to survive less time than widespread, abundant species. Sampling components were altered from completely random sampling of surviving rocks or by armies of indiscriminant paleontologists to biased sampling in which Cenozoic fossils are more readily collected or rarer fossils are more actively sought. The modified models were far from rigidly structured; the particular species or their characteristics within a time period or abundance class were not specified.

This tinkering with assumptions of randomness proved the model robust in some respects and very sensitive in others. Changes in biological assumptions hardly changed the inverse calculation, in large part because only the more abundant tail of the species abundance distribution (whatever its shape) was being sampled, for the most part. However, changes in assumptions about this sampling did alter the calculation and always in the same direction, toward higher pre-Cenozoic diversities. This suggests that paleobiologists should be careful when modeling the collection phase of their craft (or, in my case, other paleontologists' collecting). Random models of sampling may be appropriate when considering limited clades over intervals of tens of million years; however, these models should be investigated to determine sensitivities about the uniformity of fossiliferousness in sedimentary horizons and formations (e.g. Raup 1989; Sepkoski & Kendrick 1993). On much larger scales, other deterministic or biasing factors should be tested for sensitivity, such as Raup's (1979a) 'pull of the Recent'.

Where does this exercise leave the question of the Phanerozoic history of species diversity? The best answer is, unresolved. Almost certainly, marine species diversity in the Cenozoic, or at least Neogene, was at an historical high, as all empirical measurements indicate (Signor 1990b; Sepkoski 1992a). But how much higher is an open question. Data for marine animal families and genera (Fig. 7) would suggest that the increase is lower than the factor of 7 or more obtained from Signor's (1982, 1985) original inverse calculation. Families exhibit twice as much diversity in the Neogene as the average for the post-Cambrian Paleozoic, and genera exhibit three times as much. Otherwise, the curves for the two taxonomic levels are rather similar in details. The progression from two to three down the Linnean hierarchy might suggest that species will exhibit even higher diversity in the Cenozoic. Furthermore, taxa above the species level are known to underestimate downward fluctuations in diversity (e.g. Raup 1979b), and they may damp upward fluctuations as well. On the other hand, as Raup (1979a) argued, genera should be more sensitive to the pull of the Recent, affected by such factors the ease of collecting from younger sediments, the gargantuan sample of living animals from the modern oceans, and the enhanced taxonomic understanding of, and discrimination among, extant taxa. Thus, the fact that they exhibit a relatively higher Neogene diversity than do families might be an artifact of sampling.

In Fig. 7C, I have provided a range of possibilities for the Phanerozoic history of marine species diversity, based on the considerations in this paper. The solid line is the empirical estimate derived from Raup (1976a). The lower bound around this curve was calculated with the unmodified inverse model, using Signor's (1982, 1985) favored parameters (average Cenozoic diversity of 60,000 species; mean longevity of 6.5 million years; paleontologic interest units). This curve mostly parallels Raup's empirical estimate but exhibits a much greater increase in the Cenozoic: more than seven times older diversity in contrast to the empirical three times. Because all plausible tinkerings with Signor's model decreased the Cenozoic rise, I have treated his curve as the lower possible bound.

The upper bound in Fig. 7C was calculated with the same parameter values and with modifications of the model that altered the randomness of sampling: 100% more effective sampling in the Cenozoic [which is suggested by Bambach's (1977) data and Raup's (1976b) Fig. 5] and 10% bias in sampling efficiency toward rarer species (which may not be small since abundance octaves are a logarithmic scale). These values may be conservative, although the resulting estimate of Phanerozoic species diversity looks little like the curves for genera and families. What cannot be resolved right now is whether the modified assumptions are bad or if the parameter values or even Raup's (1976a) counts of fossil species are faulty. Indeed, his data do not include the results of the last 30 years of very active paleontologic research. Until better empirical data and cleverer models are available, I do not think we have a solution to the problem of Cenozoic diversity increase.

Conclusions

Random, or stochastic, models can be extremely effective in paleobiology as argued by Hoffman (1981, 1988) and others. Monte Carlo simulation, using random number generators and probability values, can provide insight into the behavior of complex evolutionary systems, in which some complexity is treated as outcomes of probabilistic processes. Numerical or analytical calculations based upon probability theory can provide exact estimates of evolutionary expectations and their variance over geologic time scales. But both are extreme simplifications of nature, and the assumptions of randomness need to be tested and manipulated to determine how sensitive model solutions are. This may be particularly important with respect to probabilistic models of paleontologic sampling, since little is known about the probability of finding and recognizing a specimen of any fossil species and about how this probability might vary across taxa, time, and space.

The case study examined here involved the estimation of Phanerozoic species diversity and in particular the magnitude of increase of marine species toward the Recent. It illustrates how sensitive random models can be and how tenuous our knowledge of the history of species diversity is. Manipulations of equations attempting to describe how paleontologists collect and identify (or describe) fossil species radically changed calculations of the pattern of Phanerozoic species diversity and the amount of estimated Cenozoic increase. The substantive conclusion of this exercise is that we do not know for certain whether average species diversity in the Cenozoic was just a little greater than in the Paleozoic or an order of magnitude greater.

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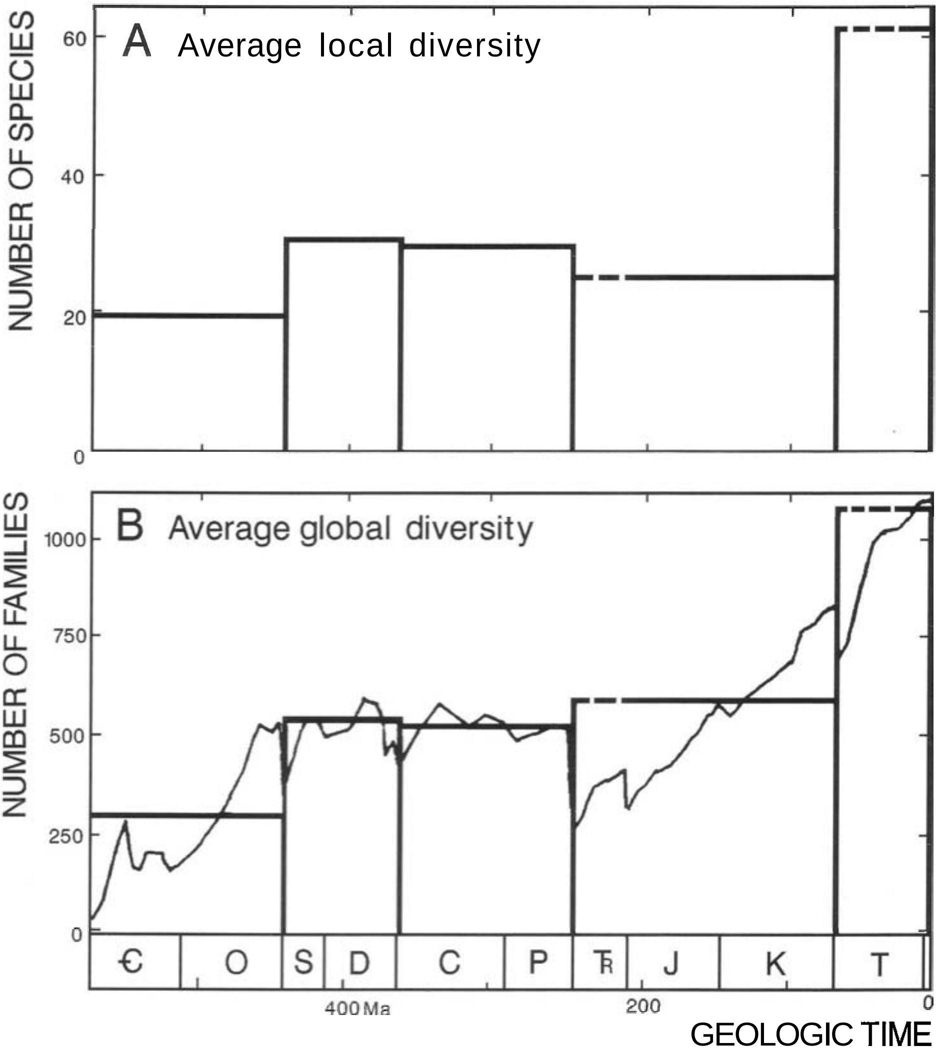

Fig. 8. Comparison of local, within-community species diversity with global familial diversity. ❑A. Histogram displaying Bambach's (1977) median values for local diversity in open-marine environments. Medians were determined for five coarse intervals of time, and data for the Triassic and Paleogene (dashed lines) were lacking. ❑B. Stage-level data for global familial diversity (light curve). The superimposed histogram displays average familial diversity over the coarse time intervals, with data from the Triassic and Paleogene excluded.

Appendix: Comments on Bambach's (1977) within-community species richness

The data illustrated in Fig. 1C are the best-resolved species diversities in Bambach's (1977) seminal study of within-community, or alpha, diversity. This study was a milestone in our understanding of the history of marine species numbers, which helped resolve debates about the qualitative pattern of Phanerozoic diversity increase (e.g. Sepkoski *et al.*, 1981). Barnbach compiled data on numbers of fossil species in benthic communities in three broad environmental zones: 'high-stress environments', 'variable nearshore environments', and 'open marine environments'. The majority of communities in his data base came from the open-marine zone, which is what is illustrated in Fig. 1C. In most of his analyses, Bambach lumped his data into five coarse time intervals so as to have sufficient sample sixes to distinguish statistically significant differences in median diversities among the zones and through time. The intervals were lower Paleozoic (Cambrian and Ordovician), middle Paleozoic (Silurian and Devonian), upper Paleozoic (Carboniferous and Permian), Mesozoic (Jurassic and Cretaceous; no Triassic data were available), and Cenozoic (data were almost entirely from the Neogene). Median numbers of species within open marine environments (Fig. 8A) exhibited low diversity in the lower Paleozoic, 60% greater diversity in the middle Paleozoic which held through the upper Paleozoic and Mesozoic, and 100% greater diversity in the Cenozoic.

In the absence of data with greater temporal resolution, Bambach (1977) may have overinterpreted the pattern of alpha diversity. He inferred two intervals of major, episodic increase: between the lower and middle Paleozoic, and between the Mesozoic and Cenozoic. With more highly resolved data on global diversity assembled subsequent to Bambach's study, it can be seen that his median alpha diversities are consistent with more gradual changes. Figure 8B illustrates stage-level familial data (Fig. 7A) with average diversity over the long time intervals superimposed. These averages are low in the lower Paleozoic, increase by 80% to the middle Paleozoic, change little into the Mesozoic (Triassic excluded), and then increase by 85% to the Neogene. This pattern is virtually indistinguishable from Barnbach's data, which, in more detail, exhibit the median value for the Ordovician exceeding that of the Cambrian, and the median for the Cretaceous exceeding the average of the Paleozoic (Fig. 1C).

Streszczenie

Rzeczywista liczba gatunkow współwystępujących w poszczegolnych horyzontach czasowych przeszłości moie być oszacowana w oparciu o znajomosd liczby zidentyfikowanych gatunkow kopalnych i liczby skamieniałości znalezionych w poszczegolnych jednostkach czasu geologicznego. Liczba zebranych skamieniałości jest proporcjonalna do stopnia rozpoznania oraz powierzchni zajmowanej przez osady jednostek geologicznych.

Rozumowanie umożliwiające takie szacunki oparte jest na założeniu lognormalnego rozkladu częstości gatunkow w stosunku do liczebności ich osobnikow i losowego charakteru oprobowania paleontologicznego. Zaburzenie lognormalnosci rozkladu nie wpływa istotnie na wiarygodność szacunkow. Nie jest również istotnym czynnikiem zaburzającym zróżnicowane trwanie gatunkow rzutujące na wyliczenia w oparciu o różnej wielkości jednostki geologicme. Istotnym problemem jest natomiast zdecydowanie nielosowy charakter opróbowania paleontologicznego, na przykład zmniejszający się udział czynników diagenetycznych w zachowaniu do dziś skamieniałości kenozoicznych tudziei skłonność badaczy do skupiania uwagi na rzadkich i niezwykłych skamieniałościach.