Biodiversity in the Phanerozoic: a reinterpretation

Shanan E. Peters and Michael Foote

Abstract.—Many features of global diversity compilations have proven robust to continued sampling and taxonomic revision. Inherent biases in the stratigraphic record may nevertheless substantially affect estimates of global taxonomic diversity. Here we focus on short-term (epoch-level) changes in apparent diversity. We use a simple estimate of the amount of marine sedimentary rock available for sampling: the number of formations in the stratigraphic Lexicon of the United States Geological Survey. We find this to be positively correlated with two independent estimates of rock availability: global outcrop area derived from the Paleogeographic Atlas Project (University of Chicago) database, and percent continental flooding. Epoch-to-epoch changes in the number of formations are positively correlated with changes in sampled Phanerozoic marine diversity at the genus level. We agree with previous workers in finding evidence of a diversity-area effect that is substantially weaker than the effect of the amount of preserved sedimentary rock. Once the mutual correlation among change in formation numbers, in diversity, and in area flooded is taken into consideration, there is relatively little residual correlation between change in diversity and in the extent of continental flooding. These results suggest that much of the observed short-term variation in marine diversity may be an artifact of variation in the amount of rock available for study. Preliminary results suggest the same possibility for terrestrial data.

Like the comparison between change in number of formations and change in sampled diversity, which addresses short-term variation in apparent diversity, the comparison between absolute values of these quantities, which relates to longer-term patterns, also shows a positive correlation. Moreover, there is no clear temporal trend in the residuals of the regression of sampled diversity on number of formations. This raises the possibility that taxonomic diversity may not have increased substantially since the early Paleozoic. Because of limitations in our data, however, this question must remain open.

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Introduction

Temporal variation in taxonomic diversity is a fundamental feature of the fossil record that continues to motivate a wide range of paleontological and biological research. Although estimates of diversity are known to be sensitive to sample characteristics (Hurlburt 1971), the shape of Phanerozoic biodiversity based on compilations of taxonomic first and last appearances is now generally taken at face value, and diversity patterns are commonly explained biologically.

Twenty-five years ago, however, there was still debate over the basic patterns of Phanerozoic biodiversity. A central question was whether diversity has increased or remained largely stationary since the Cambrian (e.g., Valentine 1970, 1973; Raup 1972, 1976a,b; Seilacher 1974; Gould 1975; Sepkoski 1976, 1978; Bambach 1977; Sepkoski et al. 1981). The consensus today (Miller 2000) is that such debates

were largely resolved by Sepkoski et al. (1981) in an influential paper suggesting that the time-independent correlation of different measures of marine diversity overcomes biases in the fossil record and signifies a real evolutionary pattern. Sepkoski (1993) later verified the pattern by demonstrating stability with accumulating knowledge and taxonomic and stratigraphic revision. Adrain and Westrop (2000) also showed that taxonomic and stratigraphic errors in Sepkoski's genus data are randomly distributed, at least for Ordovician and Silurian trilobites, and interpreted this as evidence that large-scale patterns can be accurately represented in global diversity data compiled by nonspecialists.

Despite broad acceptance of the empirical pattern of global diversity through the Phanerozoic, there are reasons to suspect that some aspects of the pattern may be artifacts of the stratigraphic record (Miller 2000; Smith 2001). Raup (1972, 1976b) concluded that the appar-

ent increase in diversity since the Cambrian may be more illusory than real. His evidence was intuitive; the number of taxa sampled in a time interval must to some extent depend on the quantity of exposed sedimentary rock. Raup (1976b) showed that species diversity at the system level is correlated with rock area and volume and that much of the variance in diversity could be explained by secular variation in the amount of sedimentary rock. However, this point was lost in the 1981 consensus paper (Sepkoski et al. 1981), and such arguments concerning first-order biases largely disappeared from the literature (but, for example, see Signor 1982; Sepkoski 1994; Rosenzweig 1998; Alroy 2000; Miller 2000; Alroy et al. 2001; Smith 2001).

Here, with an emphasis on short-term variation and with finer stratigraphic resolution than that available in Raup's (1976a,b) data, we return to his original observation that sampled marine diversity correlates with the amount of sedimentary rock.

Diversity and Number of Sedimentary Formations

Ideally, the global marine outcrop area and volume of every depositional environment in each time interval could be measured and compared with estimates of diversity. Raup (1976b) used such area and volume estimates at the system level of stratigraphic resolution, but compiling such data would be extremely difficult at finer temporal resolution. Alternatively, a large number of points on continental surfaces could be selected randomly, and the rock type and age could be identified at each of those points. Composite stratigraphic sections could also be generated for the region around a randomly chosen point, but even this exercise would present many difficulties. To circumvent some of these problems, we used the number of marine formations as a proxy for the amount of rock representing epochs from the Early Cambrian to the Pleistocene (see Appendices 1 and 2 for explanation of epoch usage). Wignall and Benton (1999) used a similar approach in studying the Lazarus effect across the Permian/Triassic boundary.

To estimate the number of marine formations,

we counted every sedimentary formation formally recognized by the United States Geological Survey (USGS) in the Lexicon of Geologic Names (Keroher et al. 1967), which covers the United States and its territories. The USGS online Lexicon (http://ngmdb.usgs.gov/Geolex/geolex_home.html; 75% complete as of January 2001) could have been used for this purpose. This source, however, includes igneous rocks, nonmarine units, sequence names, subsurface units, and other geologic terms not directly related to the marine record available for paleontological sampling. Formations were chosen as the sampling unit because they have a formal definition (lithologically distinct and mappable on a 1:24,000 scale) and represent a commonly used unit in the hierarchy of stratigraphic nomenclature. Beds, members, groups, etc. were excluded to avoid double counting and because some of these units may be erected on the basis of fossil content.

In compiling data from the Lexicon, 2065 formally recognized and temporally resolved Phanerozoic sedimentary formation entries were examined. Most entries contain a number of bibliographic references, each of which is typically accompanied by a brief summary. Age, lithology, and thickness are usually summarized, and fossil content and environmental interpretations are commonly addressed as well. Approximately 6% of the entries contained only references and gave no data on the formation. We excluded a small number (32) of formations with maximal reported thickness less than 10 feet (3.05 m). Sixty-three percent of the entries we examined contained lithologic descriptions but did not explicitly state whether the unit was terrestrial or marine. These entries required environmental interpretation. Generally, lithologic descriptions were sufficient to allow the general environment of deposition (marine vs. terrestrial) to be inferred confidently. In situations where this distinction was unclear, either because no explicit environmental interpretation was given in the Lexicon or because the lithologic descriptions were inadequate, we assumed the formation to be of marine (including brackish and tidal) origin. In cases where a formation is known to span more than one epoch, we included it in the formation count for each rel-

evant epoch. A total of 1429 marine formations representing one or more epochs were identified. If we include only the 454 formations that are explicitly reported as marine, the correlations between sampled diversity and number of formations are stronger than those reported here, albeit not significantly so. Thus, our protocol of assigning formations with uncertain environment of deposition to the marine realm does not appear to bias our conclusions.

Sampled genus diversity in each time interval was estimated using Sepkoski's global database of marine animals and microfossils (Sepkoski 1996, 1997, 2000; personal communication 1998). Because Sepkoski's data do not provide information on occurrences within observed stratigraphic ranges, it is impossible to determine the total number of taxa actually sampled in an interval. However, given only first and last occurrence data, total sampled diversity can be bracketed. The minimal number of genera actually sampled in an epoch is equal to the number of genera with first and/or last appearance in that epoch. The maximum is equal to the minimum plus the number of through-ranging genera (i.e., those with first appearance before the epoch and last appearance after the epoch). The maximum is the number typically reported as total diversity for an interval of time.

Sampled genus diversity and number of marine sedimentary formations through the Phanerozoic are depicted in Figure 1. Many features of the diversity curves seem to be predicted by the number of formations, including the sudden declines in diversity at the end of the Ordovician and the end of the Paleozoic, the steady Mesozoic rise in diversity, and the gradual Cenozoic decline in minimum sampled diversity. In interpreting this figure, it is important not to conflate diversity and taxonomic rates, which respond differently to sampling heterogeneity (Foote 2000a,b). For example, the fact that low diversity in the Early Triassic may be an artifact of sampling does not mean that there was no significant turnover at the end of the Paleozoic (Raup 1978; Foote 2000b).

Perhaps the most conspicuous failure of number of formations to predict diversity con-

cerns maximum sampled diversity toward the end of the Cenozoic, which increases while the number of formations and minimum sampled diversity decrease. Because turnover rates are low in the Cenozoic (Raup and Sepkoski 1982; Van Valen 1984; Sepkoski 1998) and because many late Cenozoic genera are still extant (Raup 1972, 1979), there is an increasing chance for genera to contribute to the known diversity of an epoch without actually being sampled in that epoch. We will return below to the ''Pull of the Recent'' (Raup 1972, 1979) and the Cenozoic discrepancy between minimum and maximum estimates of sampled diversity. For the moment, we note that this discrepancy largely disappears when we consider epoch-to-epoch changes (i.e., first differences) in the two diversity curves (Fig. 1B).

Figure 2 further illustrates the relationship between epoch-level changes in the number of marine formations and changes in sampled genus diversity. We emphasize first differences mainly because we are interested in short-term diversity variation, but also for analytical reasons. First differences reduce the effect of autocorrelation in each time series (Kendall and Ord 1990), and the effect of long-term trends in the nature of the data. Such trends include the proportion of rock types (carbonate vs. clastic), the geographic distribution of rocks (tropical vs. extratropical), and the relationship between the number of formation names in the United States and the global amount of sedimentary rock. There is a strong positive correlation between change in diversity and change in the number of marine rock formations over the Phanerozoic (Fig. 2). Moreover, the relationship between change in estimates of sampled diversity and change in formation names is strong when the mutual positive correlation each variable has with change in interval length is factored out in a partial correlation (for minimum sampled diversity $r_{partial} = 0.74$, $p < 0.0001$; for maximum sampled diversity, $r_{partial} = 0.70$, $p < 0.0001$). Two features of the correlation are particularly striking. First, there is no obvious secular trend in the relationship. The Paleozoic data are distributed in much the same way as the Mesozoic and Cenozoic data. Second, few substantial changes in diversity occur without
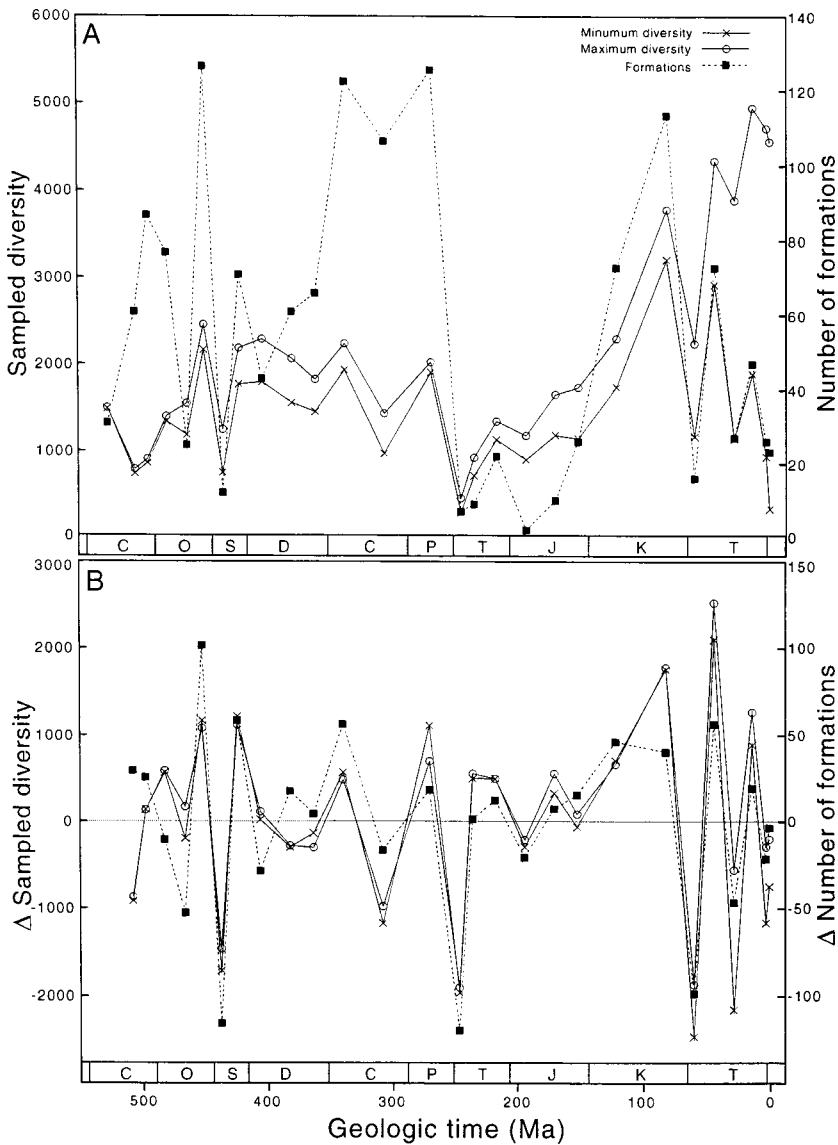
FIGURE 1. Number of marine formations in the USGS Lexicon and minimum and maximum sampled global marine genus diversity of animals and microfossils through the Phanerozoic. Data are presented at the epoch level of resolution (see Appendix). A, absolute numbers. B, first differences (value for given epoch minus value for previous epoch).

concurrent changes in the amount of record. This is seen in the concentration of points in the first and third quadrants of Figure 2. One point that deviates substantially from this tendency is that for the Middle Cambrian, evident in the lower right of Figure 2. Although the number of formations increases from the Early to the Middle Cambrian, diversity declines greatly primarily because of extinction in the Archaeocyatha, a group that may have

more finely subdivided genera than many other taxa in Sepkoski's database (Sepkoski 1978).

These results suggest that relatively short-term fluctuations in diversity may depend considerably on variation in the amount of preserved sedimentary rock. Before accepting this interpretation, we must first evaluate the extent to which USGS formations correlate with independent estimates of the amount of
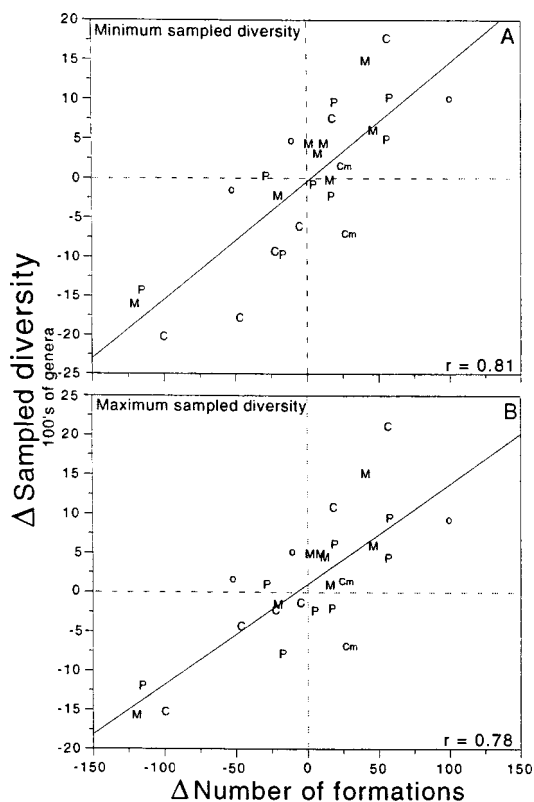
FIGURE 2. Epoch-to-epoch changes in number of marine formations and in minimum (A) and maximum (B) sampled global marine genus diversity (data from Fig. 1B). Abbreviations: Cm = Cambrian, O = Ordovician, P = post-Ordovician Paleozoic, M = Mesozoic, C = Cenozoic. Least-squares linear regression lines and product-moment correlation coefficients are indicated. Correlations are statistically significant at $p < 0.0001$. Regressions and correlations are similar if the four largest declines in diversity are omitted (results not presented). The strong relationship between number of formations and diversity suggests that short-term changes in Phanerozoic diversity may be strongly influenced by the amount of sedimentary rock available for sampling.

rock globally. We must also evaluate the possibility that fluctuations in the amount of continental flooding (i.e., habitable shelf area) drive changes in both diversity and the amount of preserved rock.

Formation Names As Proxies for the Marine Record

The foregoing analysis used the number of sedimentary formations as a proxy for the amount of preserved sedimentary rock. It seems intuitively reasonable that the number of formations representing a time interval reflects both the areal extent of sedimentary

rock and the total thickness and lithologic heterogeneity (i.e., environmental diversity) captured by the stratigraphic record. The amount of research conducted on a region may also be correlated with the number of named formations, because detailed stratigraphic investigation may uncover grounds for erecting formal lithologic units. The number of formations may thus provide a joint measure of the quantity of the record (Raup 1976b), research effort (Sheehan 1977), and lithologic variability. In analyses that consider only rock area or volume, geographically widespread and environmentally homogeneous units contribute substantially to estimates of the quantity of record even though they may contribute comparatively little to the number of formations. Conversely, intervals of time represented by relatively small outcrop area may preserve sections with much lithologic variation that may capture a wide range of environments. Although fundamental differences in various estimates of the quantity of record are expected, if the number of formations is a reasonable proxy, then formations should be at least weakly correlated with independent estimates of the quantity of marine rock.

The first expectation is that the amount of marine sedimentary rock preserved in the stratigraphic record should be influenced by the amount of continental crust flooded by ocean water. When a large proportion of continental crust is flooded (i.e., when relative sea level is high), marine sediments representing a variety of depositional environments may be widely deposited in settings with high, long-term preservation potential. When a smaller proportion of continental area is inundated, marine depositional basins are typically relegated to continental margins, and the probability of subsequent preservation and exposure is considerably lower (Holland 2000). Flooded continental area, however, is not a direct proxy for the amount of rock available for paleontological sampling. The processes associated with stratigraphic maturation, such as burial by younger sediments, erosion, and metamorphism, result in the preservation of a disproportionate amount of younger sediment (e.g., Gregor 1985; Wilkinson and Walker 1989; Wold and Hay 1993). This causes a time-

dependent relationship between the amount of marine sediment deposited and flooded continental area. For example, the Cambrian cratons were extensively flooded (Ronov 1978, 1994; Ronov et al. 1980), and there is much Cambrian sedimentary rock as a result. This rock, however, is primarily subsurface and unavailable for study. Nevertheless, because the degree of stratigraphic maturation is similar for superjacent epochs, we would expect short-term fluctuations in flooded area to be correlated with changes in the amount of exposed marine rock. We find this to be the case for United States formations. First differences in the percent of global continental area flooded (Appendix 2) (Ronov 1994) are indeed positively correlated with first differences in the number of marine formations in the USGS Lexicon ($r = 0.52$; $p < 0.01$). Absolute values from Ronov's (1994) continental flooding estimates are also positively correlated with the absolute number of formations in the Lexicon, but the correlation is predictably not so strong as for first differences ($r = 0.41$). These results suggest that the number of formation names in regions studied by the USGS is tracking global fluctuations in the amount of rock. Because there is evidence to suggest that fluctuations in continental flooding are approximately globally synchronous (Sloss 1976; Hallam 1977, 1984, 1992; Vail et al. 1977), patterns on one continent are likely to be similarly replicated elsewhere.

A more direct analysis is to compare absolute measures of exposed sedimentary rock area with the number of formations. Stratigraphic data compiled by the Paleogeographic Atlas Project (PGAP) at the University of Chicago were used to calculate marine rock area for several ages in the Mesozoic and early Cenozoic (Appendix 3). The PGAP data represent a comprehensive global survey of stratigraphic sections for use in paleogeographic reconstruction. Rock area measurements at the age level of resolution, calculated as the number of equal-area grids on continental surfaces occupied by at least one marine outcrop, were treated as samples from their respective epochs and were compared with the number of formations. Equal-area grids are $0.5° \times 0.5°$ at the equator; other grid sizes yield
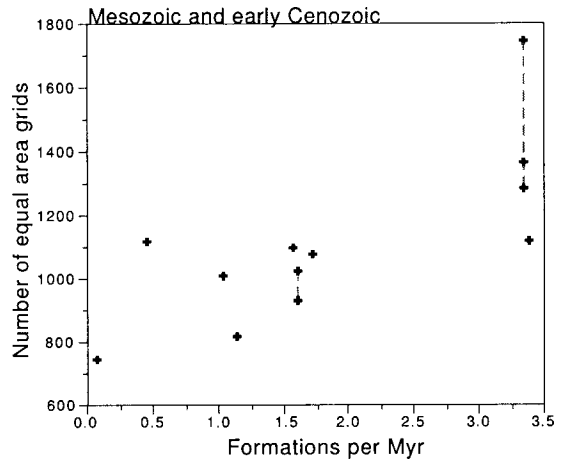

FIGURE 3. Number of marine formations and global rock area estimated as the number of equal-area grids occupied by at least one marine outcrop in the Paleogeographic Atlas Project database. Grid size is $0.5° \times 0.5°$ at the equator, and data are shown for the subset of epochs for which both measures are available (see Appendices 2, 3). Estimates of rock area are at the level of ages, which vary relatively little in duration. Because epochs, by contrast, vary by nearly an order of magnitude in duration, the number of formations is normalized by interval length. For two of the epochs, data on rock area are available for more than one age; these ages are connected by vertical dashed lines. The positive correlation suggests that the number of formations in the United States and its territories is a reasonable proxy for global outcrop area. See Table 1 for correlation coefficients.

similar results. Because the epochs of the Mesozoic and early Cenozoic vary in length from 6 Myr to 45 Myr, whereas the ages in the PGAP data are more uniform in duration, counts of rock formations in this analysis were divided by interval length. The PGAP data reflect the amount of rock exposed and available for study, so we expect stratigraphic maturation to have a similar influence on these data as on the number of formations. We therefore present a comparison between absolute values of each measure. If first differences are used, the correlation is similar. Figure 3 shows the relationship between the number of rock formations per million years and the number of equal-area grids occupied by marine outcrops in the PGAP global database. The Early Cretaceous epoch is represented by two ages in the PGAP data, and the Late Cretaceous is represented by three ages. Selecting a single age for each epoch therefore yields six possible combinations of ages within epochs. The corresponding correlations for these various

TABLE 1. Correlation between sampled marine formations (epoch-level) and exposed outcrop area (age-level) for nine Mesozoic and early Cenozoic epochs for which both measures are available (see Appendices 2, 3). Two epochs are represented by more than one age in the outcrop data; correlations are given for all possible combinations of representative ages. Because of gap in the distribution of data (Fig. 3), both product-moment correlation coefficient (r_p) and Spearman rank-order correlation coefficient (r_s) are shown.

Age Representing Lower Cretaceous	Age Representing Upper Cretaceous	r_p	r_s
Aptian	Maastrichtian	0.713	0.550
Aptian	Coniacian	0.692	0.550
Aptian	Cenomanian	0.714	0.550
Valanginian	Maastrichtian	0.699	0.500
Valanginian	Coniacian	0.677	0.500
Valanginian	Cenomanian	0.703	0.500

FIGURE 4. Number of equal-area grids (as in Fig. 3) occupied by at least one marine outcrop in the PGAP stratigraphic database and minimum and maximum sampled marine genus diversity for several ages in the Mesozoic and early Cenozoic (see Appendix 3). A, Absolute numbers. B, First differences (value for given age minus value for previous age; linear product-moment correlation for minimum diversity is 0.63, for maximum diversity 0.68; both correlations significant at $p < 0.04$).

combinations are summarized in Table 1. The PGAP estimate of global outcrop area is positively correlated with number of marine formation in the USGS Lexicon. Together with the positive correlation between number of formations and percent flooding, these results suggest that the number of sedimentary formations in the United States and its territories is an acceptable proxy for the quantity of rock globally.

Figure 4 shows minimum and maximum sampled marine genus diversity at the age level of resolution, derived from Sepkoski's data as for our epoch-level analysis, and the number of equal-area grids occupied by marine outcrops in the PGAP data (see Appendix). Absolute values and first differences in outcrop area and sampled genus diversity are positively correlated (Fig. 4). Although both map area and the number of formations are likely to be imperfect proxies for heterogeneity in the stratigraphic record, the two estimates are mutually correlated and both are positively correlated with sampled genus diversity. Because the formation-name proxy we are using is imperfect, however, we would expect the correlation between change in amount of rock in the United States and change in global sampled diversity to underestimate the correlation that would be obtained if a more robust global estimate of rock were used. The effect of available sediment on sampled diversity is therefore likely to be stronger than that documented in Figures 1 and 2.

A recent study by Smith (2001) reports results consistent with our positive correlation between changes in sampled diversity and changes in number of formations. Using a different measure of the amount of marine rock in the post-Triassic of Great Britain and France (the number of geological quadrangle maps containing marine rocks of a given age), Smith found a positive correlation between detrended maximum genus diversity and amount of rock. We will return to Smith's

study below. For the moment, we note that our results do not appear to be very sensitive to the particular proxy for the amount of preserved rock.

Diversity-Area Effect

The correlation between diversity and number of marine formations (Figs. 1, 2) suggests that epoch-to-epoch changes in biodiversity may largely reflect variability in the amount of rock from which fossils are collected. It is nevertheless possible that these two quantities are positively correlated because each is independently affected by another factor. Perhaps the most obvious candidate is the proportion of the continents inundated by the oceans (Schopf 1974; Simberloff 1974; Sepkoski 1976; Flessa and Sepkoski 1978). Here we follow these authors and test the hypothesis that fluctuations in the area of shallow marine seas may have caused changes in diversity that are independent of the quantity of the marine record.

We first took residuals of the regression of change in minimum sampled diversity on change in number of formations. These residuals reflect variance in diversity change that is unexplained by concurrent change in the number of formations. We then took residuals of the regression of change in proportion of continents flooded on change in number of formations. Finally, we calculated the regression of the diversity residuals on the flooding residuals. This is qualitatively the same as calculating the partial correlation of diversity on flooding with number of formations held constant, and the resulting correlation coefficient is quantitatively identical to the corresponding partial correlation coefficient. We used this indirect procedure to enable the graphical representation of Figure 5, which shows a weak positive residual effect of change in area of flooding on change in diversity.

Change in continental flooding potentially accounts for 14% of the variance in the change in diversity residuals ($r = 0.38$). By contrast, the partial correlation coefficient for change in diversity versus change in formations with change in continental flooding held constant is equal to 0.73. This indicates that more of the variance in change in diversity is attributable
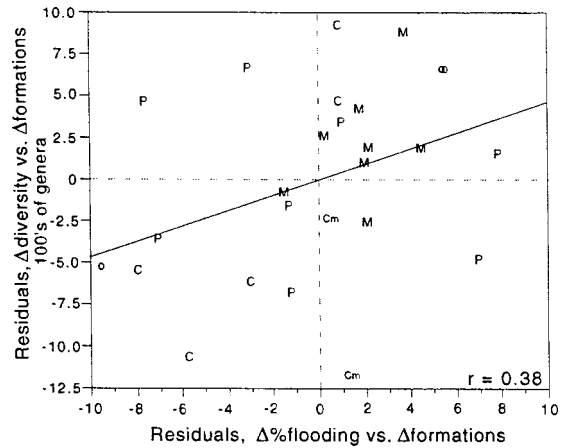

FIGURE 5. Diversity-area effect. Plot shows residuals of regression of change in continental flooding versus change in number of formations (abscissa) and residuals of regression of change in diversity versus change in number of formations (ordinate). Abbreviations are as in Figure 2. Linear product-moment correlation between residuals is marginally significant ($p = 0.058$), and the value of r^2 (0.14) suggests that less of the variation in diversity is attributable to area flooded than to the amount of preserved sedimentary rock; the corresponding partial correlation coefficient for diversity versus formation names with continental flooding held constant is equal to 0.73 ($p < 0.0001$). Line shows least-squares linear regression.

to change in formations, regardless of whether diversity residuals on flooding or diversity residuals on formations are examined. Following the method of Sepkoski (1976), we also calculated a stepwise multiple regression of diversity residuals first on marine formations alone and then on marine formations plus flooding. Including flooding as an additional independent variable increases the correlation from 0.81 to 0.84, and therefore potentially explains approximately 5% more of the total variance in changes in diversity than does number of formations alone. (Including interval length as a third independent variable increases the correlation to 0.89; this suggests that interval length has as great an effect on estimates of diversity as does continental flooding.)

Flessa and Sepkoski (1978) have cautioned against using analyses such as the foregoing one as unequivocal evidence for diversity-area effects. It is possible that change in continental flooding explains residual variation in the regression because high sea level can result in the preservation and recovery of a greater pro-

portion of the environmental mosaic, rather than simply a greater areal extent. In other words, continental flooding may be correlated with facies representation, an aspect of the number of formations that we are not considering in this analysis. Thus, although we are suggesting that the diversity-area effect is not very strong in our data, it is even possible that our analysis overestimates this effect. In agreement with Sepkoski (1976), we find that more of the variation in diversity is potentially attributable to variation in the amount of available rock than is potentially attributable to area effects. This result also suggests that the correlation between fluctuations in diversity and sea level that many workers have noted (e.g., Hallam 1992; Hallam and Wignall 1999; Brezinski 1999; O'Dogherty et al. 2000; Pegel 2000) may in part be driven by associated changes in the quantity of marine rock (see Jablonski 1980 for further discussion of facies-related problems with inferring the biotic effects of sea-level change). It is of course possible that our inability to detect a strong diversity-area effect is due to the fact that we have data only on sampled diversity, not true diversity. Our partial-correlation analysis should be able to reveal the relative strengths of the correlations between available sediment, extent of flooding, and sampled diversity, but data on true global diversity would be required to test the diversity-area effect conclusively.

The Phanerozoic Increase in Diversity

We have shown that short-term changes in fossil diversity are strongly correlated with changes in the amount of record. It is possible to obtain such a result regardless of whether diversity increased, decreased, or remained stationary over the course of the Phanerozoic. To evaluate long-term trends, we need to consider absolute estimates of diversity and the quantity of sedimentary rock, rather than first differences. Before doing so, we need to address the divergence between our minimum and maximum brackets on sampled diversity during the Cenozoic.

Because Cenozoic turnover rates are low, the majority of genera inferred to exist during any given epoch may not actually have been sampled during that interval. Given average genus-level origination and extinction rates on the order of 0.025 per lineage-million-years (Lmy) (Foote 2000a) and an average epoch length of about 10 Myr, nearly 80% of genera in the maximum estimate of sampled diversity would be expected to be extant both before and after each Cenozoic epoch. The empirical data (Fig. 1) bear this out in rough terms. How many of these through-ranging genera are likely actually to be sampled during an epoch? Previous estimates of preservation probability for marine invertebrates (Foote and Raup 1996; Foote and Sepkoski 1999) suggest that the figure is no more than about one-half on average. This would suggest that maximum sampled diversity during the Cenozoic, even in the absence of the Pull of the Recent (Raup 1972, 1979), could represent nearly a two-fold exaggeration of true sampled diversity. The exaggeration is much less in the Paleozoic and Mesozoic, when turnover rates are higher and epochs are generally longer. The exaggeration should be greater for the Pliocene and Pleistocene, because of their short duration.

Another reason to think that maximum diversity overestimates sampled diversity in the Cenozoic is that genera preserved before an epoch and extant today add to the tally for that epoch, regardless of whether they have any fossil record after their first appearance (Raup 1972, 1979). This problem is worst for the Pliocene and Pleistocene and decreases in importance further back in time. The magnitude of the Pull of the Recent can be explored using Sepkoski's genus data. Extant genera in the database include a flag, indicating whether they are known to have a Plio-Pleistocene fossil record. Although it is not clear how completely Sepkoski searched for Plio-Pleistocene records of extant genera, we can gain a rough idea of the effect of the Pull of the Recent by omitting those genera not flagged by Sepkoski. Diversity tabulations for the remaining genera are presented in Table 2. These figures suggest that a large proportion (roughly half) of fossil genera extant today lack any fossil representatives over the past 5 Myr and that sampled diversity may in fact be declining through the Cenozoic. Although in-

TABLE 2.   Effect of removing Recent genera not known to have a Plio-Pleistocene fossil record.

| | Raw data | | Culled data | |
Epoch	Minimum diversity (no. of genera)	Maximum diversity (no. of genera)	Minimum diversity (no. of genera)	Maximum diversity (no. of genera)
Paleocene	1175	2249	992	1693
Eocene	2933	4360	2318	3189
Oligocene	1145	3905	900	2489
Miocene	1896	4971	1495	3154
Pliocene	936	4736	936	2919
Pleistocene	322	4577	322	2263

completeness in Sepkoski's treatment of the data makes this inference uncertain, the estimated proportion of unpreserved through-ranging genera is consistent with other estimates (Foote and Raup 1996; Foote and Sepkoski 1999).

The combined effects of low turnover rate, interval length, and proximity to the Recent

FIGURE 6.   Modeling of combined effects of interval length, low turnover rate, and proximity to Recent, based on equations from Foote (2000a). Upper curves show expected ratio of maximum sampled diversity to true sampled diversity; lower curves show expected ratio of minimum sampled diversity to true sampled diversity. Interval lengths correspond to durations of Cenozoic epochs (Appendices 1, 2). All taxa still extant in the Recent are assumed to be known from the Recent. Baseline model: origination and extinction rates constant at 0.025 per lineage-million-years (Lmy); preservation rate constant at 0.05 per Lmy. High-sampling model: preservation rate constant at 0.1 per Lmy. Increasing-diversity model: origination rate constant at 0.057 per Lmy, to yield eightfold diversity increase. These results suggest that the best estimate of true sampled diversity is approximately halfway between the minimum and maximum values for the Paleocene–Miocene (Fig. 1, Appendix 2). True sampled diversity in the Plio-Pleistocene is probably greatly overestimated by maximum sampled diversity.

can perhaps be better appreciated with the help of simple mathematical modeling (Foote 2000a) (Fig. 6). An obvious approach is to ask how estimates of diversity would behave through the Cenozoic if diversity were in fact constant. The baseline calculations for this exercise use constant origination and extinction rates of 0.025 per Lmy, rates typical of the Cenozoic. Preservation rate was set to 0.05 per Lmy, corresponding to a probability of 0.4 that a genus alive during all of a 10-Myr epoch will be preserved at least once during that epoch. As stated above, this is empirically realistic. If diversity is truly constant, then true sampled diversity is about midway between the minimum and maximum estimates from the Paleocene through the Miocene. In the Pliocene and Pleistocene, maximum diversity overestimates sampled diversity by about a factor of four and a factor of eight, respectively, whereas minimum diversity underestimates sampled diversity by about 58% and 64%, respectively. These results are broadly consistent if other model parameters are assumed (Fig. 6). For example, even if preservation rate is much higher than we think is realistic (0.1 per Lmy), maximum diversity exaggerates sampled diversity by about threefold and fivefold in the Pliocene and Pleistocene. Most important, the results do not depend on modeling diversity as constant. Even if we assume an eightfold exponential diversity increase through the Cenozoic, maximum diversity in the Pliocene and Pleistocene exaggerates sampled diversity by threefold and sixfold. If we use the midpoint between minimum and maximum diversity as an estimate of sampled diversity through the Miocene, and if we adjust Plio-
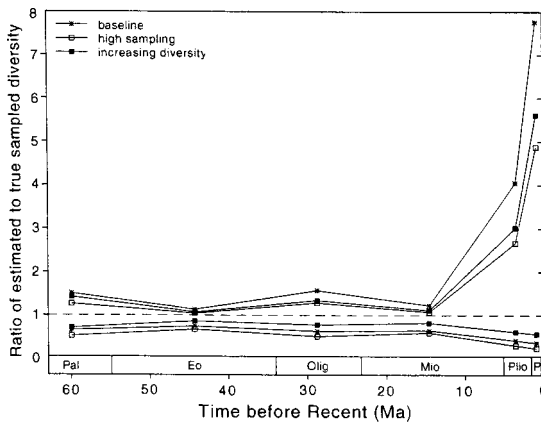
cene and Pleistocene diversity according to the conservative model results, we are left to conclude that there is no conspicuous increase in sampled diversity after the Late Cretaceous (Fig. 1, Appendix).

Thus, several lines of reasoning suggest that much of the divergence between minimum and maximum diversity estimates in the Cenozoic reflects low turnover and the Pull of the Recent, and that the true increase in sampled diversity, if there even is one, is likely to be much smaller than that which is suggested by the maximum diversity tabulation. This is especially true in the late Cenozoic, where minimum diversity is more likely than maximum diversity to be a reasonable proxy for sampled diversity. We will nevertheless present analyses involving both diversity estimates.

Figure 7 shows the relationship between the absolute number of formations in the USGS stratigraphic Lexicon and the minimum and maximum sampled diversity in Sepkoski's genus database. For minimum diversity, the two variables are positively correlated, whether epoch length is ignored or held constant via partial correlation ($r = 0.63$; $r_{partial} = 0.49$). Although the relationship between number of formations and diversity is weaker for absolute numbers than for first differences, and although there are limitations in the data, as we discuss below, the positive correlation suggests that the long-term pattern of diversity change through the Phanerozoic may require reevaluation. For maximum diversity, the high Cenozoic values, which may well be largely spurious as we discussed above, make the overall correlation with number of formations very weak (Fig. 7B).

It is tempting to interpret the residuals (Fig. 8) of the absolute diversity versus rock formation regression biologically, as others have done (e.g., Rosenzweig 1995), but there are several reasons to be cautious in this exercise. First, how well the number of U.S. formations approximates global rock amount may vary systematically over time. For example, if we focus on minimum sampled diversity (Fig. 8A), most Mesozoic epochs preserve more genera than predicted by the number of marine rock formations in the USGS Lexicon.

FIGURE 7. Number of sampled marine formations and minimum and maximum sampled marine diversity for Phanerozoic epochs (data from Fig. 1A). Abbreviations are as in Figure 2. Correlation for minimum diversity is positive and significant, but weaker than that for first differences in these quantities. Note that the Cambrian, Ordovician, post-Ordovician Paleozoic, Mesozoic, and Cenozoic all have both positive and negative residuals. For maximum diversity, the regression line has a slope near zero and the correlation is not significant. See text and Figure 5 for explanation of the divergence in Cenozoic maximum and minimum sampled diversity estimates. Lines show least-squares linear regressions.

Rather than reflecting high diversity, this may represent the poor North American record for much of the Mesozoic. The near lack of correlation between number of formations and maximum diversity implies that the residuals from the trend (Fig. 8B) yield essentially the same time series as the maximum diversity estimate itself (Fig. 1A).

Second, differences in the character of the sedimentary record can also have pronounced effects on sampled diversity, as Raup (1976b) discussed. Ronov (1978) and Ronov et al. (1980) demonstrated short and long-term fluc-
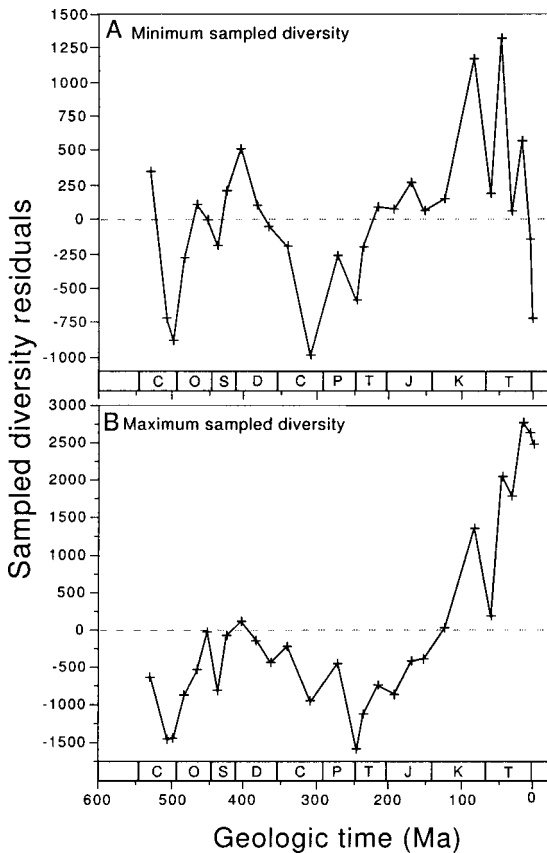
FIGURE 8. Temporal pattern in the residuals from the regressions of Figure 7. See text for discussion.

tuations in the proportion of sediment types through time, and our compilation of formation names shows a substantial decline in carbonates relative to siliciclastics through the Phanerozoic as well as epoch-to-epoch changes in dominant lithofacies (results not presented). In addition, Allison and Briggs (1993) documented a decrease in representation of tropical environments through the Phanerozoic. Diagenetic and taphonomic factors may also be differentially distributed through time (e.g., Kidwell and Brenchley 1994; Schubert et al. 1997; Cherns and Wright 2000), increasing the probability of preservation and recovery in frequently unconsolidated Late Cretaceous and Cenozoic sediments. Finally, Sepkoski's global diversity data include taxa, such as the Foraminiferida, that have many deep-sea genera. Submarine strata (sediments preserved only on today's ocean floor) are not covered in the USGS Lexicon but increase in abundance during the Mesozoic and Cenozoic (from 0% ocean floor coverage in the Lower Jurassic to nearly 100% coverage in the Recent). Thus, we are not in a strong position to determine to what extent the residuals in estimated sampled diversity reflect limitations inherent in the use of U.S. formation names and to what extent they reflect true diversity anomalies.

The result presented in Figure 8A differs from that of Raup (1976b: Fig. 6), who found a downward trend in residuals of global species diversity against rock area, a trend that is especially evident in his analysis of U.S. map area. It is unclear to what extent this discrepancy reflects our use of different taxonomic data, a different level of temporal resolution, or a different proxy for the amount of sediment available for sampling. The result presented in Figure 8B is, however, congruent with that of Smith (2001), who also found a discrepancy between the post-Triassic increasing trend in maximum diversity (equivalent to his ''standing diversity'') and the declining trend in rock area in Great Britain and France. Smith (2001) interpreted this discrepancy as evidence for a real increase in diversity, but it is possible, as we argued above, that the Cenozoic increase in diversity is highly inflated. Only if we accepted maximum diversity in the Cenozoic as our estimate of true sampled diversity—a decision that would require us to ignore the biasing effects of turnover rate, interval length, and the Pull of the Recent—would we have a compelling reason to argue that there has been a substantial tendency for diversity to increase since the Cambrian. Thus, although it is not possible to rule out a long-term increase in biodiversity through the Phanerozoic, the data studied here do not suggest such a finding.

The heterogeneity in the nature of the record that hinders long-term analysis of the correlation between diversity and number of formations is less important in analyzing changes from one epoch to the next. Nevertheless, such variability would also pose similar problems if we were to evaluate residuals from the regression of diversity change on change in number of formations (Fig. 2).

Discussion

Although paleontologists are still concerned about artifacts in the apparent timing and magnitude of turnover events and changes in global diversity (e.g., Signor and Lipps 1982; MacLeod and Keller 1991; Ross and Ross 1995; Miller and Foote 1996), the very reality of such changes has been widely accepted since the publication of the consensus paper of Sepkoski et al. (1981). Sampling effects continue to be explored in smaller-scale studies (e.g., Raymond and Metz 1995; Alroy 1996, 1998; Johnson 1998; Aguirre et al. 2000; Kullman 2000), but there have been relatively few recent efforts (e.g., Miller and Foote 1996; Alroy et al. 2001; Smith 2001) to assess the role of sampling in global metazoan diversity. We suspect that this is in part because diversity compilations often prove remarkably robust to added knowledge (Sepkoski 1993) and taxonomic revision (Adrain and Westrop 2000), and because aspects of the pattern are sometimes borne out similarly in different regions (Miller 1997, 1998). The stability of paleontological databases, however, does not provide clear evidence for the accuracy of the signals they reveal, because variation in the character of the record is still an issue. Recent modeling work by Holland (1995, 2000) and Holland and Patzkowsky (1999) has shown that, at the third-order sequence level, stratigraphic architecture can be important in shaping patterns of first and last occurrences. Similarly, the results presented in this paper suggest that, even if paleontologists visited every marine outcrop all over the world and perfectly identified and described all of the specimens they contain, an inaccurate picture of diversity would still emerge because of temporal variations in the quantity of exposed sedimentary rock. Short-term fluctuations in diversity are shown to be particularly prone to this type of bias.

Our analyses have focused on the correlation between marine genus diversity and the amount of marine rock available for sampling, but there is reason to suspect that diversity patterns in the terrestrial record might also be subject to strong stratigraphic bias (Smith 2001). Figure 9 shows global family diversity in
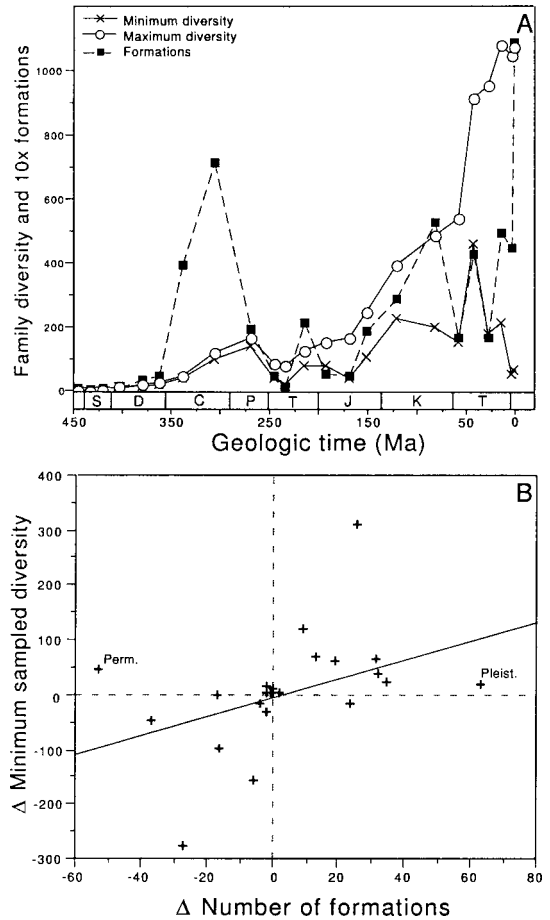

FIGURE 9. Number of terrestrial formations in the USGS Lexicon and minimum and maximum sampled family diversity in terrestrial animals (Benton 1993). Data are presented at the epoch level of resolution (see Appendix). A, Absolute numbers. B, First differences (value for given epoch minus value for previous epoch). Least-squares linear regression line is shown in B. To indicate the data points most affected by the fine stratigraphic subdivision of Carboniferous cyclothems and Pleistocene glacial deposits, the Permian and Pleistocene are indicated as Perm. and Pleist. respectively. See text for discussion.

terrestrial animals (Benton 1993; also accessible at http://ibs.uel.ac.uk/benton/foss2.html) and the number of formations in the USGS Lexicon confidently identifiable as continental in origin. As with marine genus diversity, there is a positive correlation between the number of continental formations and sampled terrestrial diversity when we consider either absolute values (Spearman rank correlation for maximum diversity is 0.78, and for minimum diversity 0.75) or, more appropriately, first differences

(Spearman rank correlation for maximum diversity is 0.44, $p = 0.02$; and 0.64, $p = 0.001$ for minimum diversity). Although the correlation between terrestrial family diversity and formations is not so strong as for marine genera and formations (in part because of the large number of named terrestrial formations in finely subdivided Carboniferous cyclothems and the profusion of named Pleistocene formations owing to the heterogeneity of glacially deposited sediments), these results suggest that stratigraphic heterogeneity in the continental record may also affect estimates of terrestrial diversity.

The fact that the number of USGS formations represents a predictor of sampled global diversity that is weaker for terrestrial data than for marine data might seem to be prima facie evidence that the terrestrial fossil record is more complete than that of the marine realm. However, such an interpretation does not necessarily follow from what we have presented. First, it is possible that the terrestrial formation-diversity correlation is weaker than the marine correlation simply because the terrestrial time series have more noise than the corresponding marine data. Second, it is possible that, in contrast to the marine realm (Table 1, Fig. 3), a sample of terrestrial formations from a single continent is not a reasonable proxy for the amount of rock globally. To explore this possibility, we compared terrestrial formations from the USGS Lexicon with global outcrop area of terrestrial rocks in the PGAP data, following the same procedure as for marine rocks (Table 1, Fig. 3). The corresponding correlations are essential zero, ranging from -0.18 to 0.09. One plausible reason that the United States alone is a fair proxy for the global marine record but not for the global terrestrial record is that, despite the importance of coastal deposits in the terrestrial data, the marine record is far more strongly dominated by eustatic variation in sea level than is the terrestrial record. That U.S. formations can predict any of the variation in sampled terrestrial diversity at the global scale is presumably a consequence of the fact that family diversity of the United States is an important component of global diversity. Be that as it may, we repeat our caution against interpreting the foregoing results as evidence that the terrestrial fossil record is more complete than the marine record.

Despite the correlation between the number of formation names in the USGS stratigraphic Lexicon and two independent measures of the amount of marine record, there are several potential problems with the formation-name proxy used in this study, to which we have already alluded. First, the number of formation names from only the United States and its territories has been compared with global diversity. Although the United States is heavily studied and undoubtedly contributes a large proportion of the data in Sepkoski's database, it is not the sole source of information. Other regions (e.g., Great Britain [Miller 2000]) may exhibit different patterns in the temporal distribution of marine formations. Smith (2001), however, presents congruent results using a different proxy for the amount of post-Triassic rock in Great Britain and France. Second, like many taxonomic databases, the formations sampled in this study probably contain some synonyms and incorrect age determinations. We suspect that these errors are randomly distributed in direction (as Adrain and Westrop [2000] showed for some taxonomic data), but there may be temporal heterogeneity in their frequency. For example, the number of Cambrian formation names may be artificially inflated because of spotty outcrop distribution and difficulties associated with correlation. Third, counting formations as a measure of the quantity of marine rock implicitly assumes that all formations are the same in some meaningful sense. It may nevertheless be the case that there are significant temporal differences in what constitutes a formation or in the per-formation probability of genus preservation. For example, because of the fine subdivision of cyclothems, it is conceivable that a given number of Late Carboniferous formations constitutes a smaller thickness and represents a narrower range of environments than does the same number of Eocene formations. Likewise, it is conceivable that Cenozoic units preserve a greater proportion of taxa than Paleozoic units because they have suffered less diagenetic loss of information (Miller 2000). Fourth, Phanerozoic-scale

trends in the dominant lithofacies (Ronov et al. 1980), changes in water-mass characteristics (Ziegler et al. 1998), or other environmental attributes may diminish the utility of the formations proxy. For example, tropical carbonates are relatively more common in the Paleozoic than in the Cenozoic, whereas the Cenozoic may have better representation of clastic shore-face sediments. This might tend to bias the Paleozoic toward higher diversity, although the taphonomic differences between clastic and carbonate sediments may serve to offset this particular effect (Best and Kidwell 2000). Fifth, the actual number of taxa sampled in a time interval is not known—it can only be constrained using stratigraphic range data. If there are secular trends in the proportion of through-ranging taxa that are actually sampled, then some aspects of the relationship between formations and sampled diversity may change. The small difference between the upper and lower bounds on sampled diversity in most epochs (Fig. 1, Appendix 2) suggests that there is relatively little error in our bracketing procedure. Nonetheless, tabulations of actual occurrences in faunal lists, such as the compilation of the Paleobiology Database (Alroy et al. 2001), should enable the number of sampled taxa to be determined more accurately than we have done in this analysis. This is especially important for constraining sampled diversity in the Cenozoic. Finally, it is possible that fossil abundance and therefore biological diversity influence the number of recognized sedimentary formations. Although we cannot test this possibility, we doubt that many formations recognized by the USGS are erected on the basis of fossil content (if for no other reason than that the Lexicon descriptions focus on lithologic data and only occasionally mention fossil content in the context of environmental interpretation or correlation).

Most of the shortcomings outlined above should add noise to the relationship between number of formations and sampled diversity and may account for some of the residual variation. We can think of no reason, however, to suspect that such problems would combine to produce a strong spurious correlation between changes in these two quantities. The primary effect of the uncertainty in our proxy is to limit the extent to which inferences can be made. This is particularly true in the long-term analysis of diversity. To evaluate long-term trends more fully, we would require comparable global data that include not only number of formations but also information on thickness, paleolatitude, lithology, paleo-water mass characteristics, and diagenetic factors.

Although short-term variation in diversity seems to be strongly affected by variation in the quantity of available sedimentary rock, some patterns derived from taxonomic data are more difficult to bias by the amount of rock. For example, the existence and temporal succession of Sepkoski's (1981) Evolutionary Faunas, which consist of sets of taxa with covarying diversity patterns and which have characteristically different rates of evolution, are not likely to be artifacts of variation in the quality of the record. Similarly, if origination and extinction rates are appropriately measured, large-scale patterns such as the Phanerozoic decline in background rates (Raup and Sepkoski 1982; Van Valen 1984; Gilinsky and Bambach 1987; Sepkoski 1998) are likely to be robust (Foote 2000a). It is probable, however, that the magnitude of evolutionary radiations and mass extinctions is distorted by short-lived increases and decreases in the amount of sedimentary rock.

The distinction between the intrinsic quality of the fossil record that is actually preserved (local completeness) and the amount of rock preserved globally (global completeness) needs to be emphasized. Our analysis focuses on the effect of the latter. Using a separate compilation of families (Benton 1993), Benton et al. (2000) compared the hypothesized order of first appearances based on phylogenetic estimates with the timing of first appearances in the fossil record, concluding that there is little trend in completeness over the course of the Phanerozoic. Their analysis mainly concerns intrinsic completeness, however. There is no prima facie inconsistency between our results and those of Benton et al.

Finally, although we suspect that the correlation between number of formations and diversity largely reflects an artifact that must

be circumvented, we acknowledge that this correlation may partly reflect the independent influence of environmental heterogeneity on both true diversity and number of formations. Thus, it is conceivable that some of the signal we are interpreting as artificial is in fact biologically meaningful. We do not claim to have conclusively proven that the short-term variation in global taxonomic diversity through the Phanerozoic is in fact largely artificial; we only suggest that it may be so. Along with other authors (Miller 2000; Alroy et al. 2001; Smith 2001), we suggest that it would be wise to reopen the conversation on sampling and global diversity that seems to have been closed for the past 20 years. This discussion should also include mass extinctions (Signor and Lipps 1982; MacLeod and Keller 1991; Smith 2001), because most of them share at least one feature: they are associated with a decrease in the quantity of sedimentary rock available for paleontological sampling. Pronounced heterogeneity in the amount of rock and in facies representation at extinction intervals will distort the apparent magnitude and abruptness of these events.

Conclusion

The number of marine formations appears to be a reasonable proxy for the amount of available sedimentary rock and probably incorporates important factors, such as research effort and lithological heterogeneity, that area and volume estimates alone fail to capture. Judging from the strong positive correlation between epoch-level changes in the number of marine formations in the United States and its territories and in global genus diversity sampled from marine environments, it is likely that short-term fluctuations in diversity largely reflect changes in the quantity of marine sediments. The same may be true for long-term changes, but further work is required to test this possibility rigorously.

Acknowledgments

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Appendix 1

Data Used in Analyses

Sources of data are explained in the text. Epochs and durations correspond to those listed in the now outdated Geological Society of America (GSA) timescale (Palmer and Geissman 1999), with three exceptions: (1) The GSA timescale uses a regional subdivision of the Cambrian. We accepted the subdivision of Cambrian formations into Early, Middle, and Late epochs as given in the USGS Lexicon and treated these as corresponding with Sepkoski's Early Cambrian (Tommotian, Atdabanian, Botomian, and Tojonian), Middle Cambrian, and Late Cambrian (Dresbachian, Franconian, and Trempealeauan). We based Cambrian epoch durations on Bowring and Erwin 1998. (2) To attain a relatively even subdivision of the Silurian, the Wenlockian was included in the Late Silurian rather than the Early Silurian. (3) Because a large proportion (approximately 42%) of Permian formations were unassigned to epoch in the USGS Lexicon, the Permian was not subdivided. Redistributing Permian formations in proportion to the resolved data yields results congruent with those we present in the text. Because the USGS Lexicon does not use the same subdivision of the Ordovician as used in Sepkoski's taxonomic database or in the GSA timescale, we used the epoch definitions of GSA and assigned each formation on the basis of the correlation charts of Ross et al. (1982). In periods other than the Permian, temporally unresolved units (32 all told) were omitted. Distributing them in proportion to resolved units yields comparable results.

Appendix 2

Number of formations, estimated continental flooding, and sampled marine diversity.

Epoch	Interval length (Myr)	No. of marine formations	No. of terrestrial formations	Ronov (1994) % Flooding	Minimum diversity (no. of genera)	Maximum diversity (no. of genera)
Early Cambrian	33.0	31	0	30	1496	1506
Middle Cambrian	10.0	61	0	32	741	788
Late Cambrian	10.0	87	0	33	863	908
Early Ordovician	20.0	77	0	37	1344	1404
Middle Ordovician	12.0	25	1	39	1189	1554
Late Ordovician	15.0	127	1	34	2171	2463
Llandovery	15.0	12	0	28[1]	751	1251
Wenlock + Late Silurian	11.0	71	1	38[1]	1774	2192
Early Devonian	26.0	43	0	28	1800	2295
Middle Devonian	21.0	61	3	35	1562	2072
Late Devonian	16.0	66	4	33	1458	1831
Early Carboniferous	31.0	123	39	28	1940	2244
Late Carboniferous	33.0	107	71	25	974	1439
Permian	42.0	126	19	22	1912	2032
Early Triassic	6.0	7	4	17	287	454
Middle Triassic	15.0	9	1	18	714	927
Late Triassic	21.0	22	21	18	1138	1351
Early Jurassic	26.0	2	5	18	906	1186
Middle Jurassic	21.0	10	4	22	1189	1660
Late Jurassic	15.0	26	18	24	1149	1743
Early Cretaceous	45.0	73	28	24	1747	2307
Late Cretaceous	34.0	114	52	29	3220	3798
Paleocene	10.2	16	16	15	1175	2249
Eocene	21.1	73	42	18	2933	4360
Oligocene	9.9	27	16	9	1145	3905
Miocene	18.5	47	49	10	1896	4971
Pliocene	3.5	26	44	5	936	4736
Pleistocene	1.8	23	108	—	322	4577

[1] According to estimates by Ronov (1994) and Hallam (1992), Silurian sea level was at a maximum in the Wenlockian. Hallam (1992) indicates that continental flooding in the Liandovery was probably close to the Late Silurian maximum. Therefore, because we include the Wenlockian with the Late Silurian, the order of Ronov's (1994) Silurian data have been reversed.

Appendix 3

Exposed marine rock area and marine genus diversity.

Age	No. of equal-area grids	Minimum diversity (no. of genera)	Maximum diversity (no. of genera)
Induan	815	75	247
Norian	1005	725	996
Pliensbachian	741	342	802
Callovian	1113	392	1137
Tithonian	1073	515	1252
Valanginian	928	262	1049
Aptian	1018	468	1334
Cenomanian	1742	848	1862
Coniacian	1277	222	1637
Maastrichtian	1363	1351	2368
Thanetian	1095	609	1879
Lutetian	1103	510	2595