Are global Phanerozoic marine diversity curves truly global? A study of the relationship between regional rock records and global Phanerozoic marine diversity

Alistair J. McGowan and Andrew B. Smith

Abstract.—The consensus view that the amount of rock available for sampling does not significantly and systematically bias Phanerozoic marine diversity patterns has broken down. How changes in rock availability and sampling intensity affect our estimates of past biodiversity has been investigated with a variety of new approaches. A number of proxies for the amount of rock available for sampling have been used, but most of these proxies do not rely directly on evidence from large-scale geological maps (maps that cover small areas) and accompanying memoirs. Most previous map-based studies focused on single regions or relied on small-scale synoptic maps. We collected data from published geological maps and memoirs from western Europe, Australia, and Chile, which we combined with COSUNA data from the United States to generate the first multiregional data set for investigating whether the global Phanerozoic marine diversity record is a true global record, or is instead biased toward North America and Western Europe as has long been suspected. Both short and long-term trends in variation in the amount of outcrop display limited correlation among the regions studied. A series of diversification models obtained better matches to observed fossil diversity from the European and U.S. records than for the Chilean and Australian records, further supporting suspicions that the global Phanerozoic diversity curve is disproportionately influenced by European and U.S. fossil data. These results indicate that future research into Phanerozoic marine diversity patterns should not continue to apply global eustatic curves as a proxy for rock at outcrop, but should use regional data on rock occurrence.

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Introduction

The “Sepkoski Curve” of Phanerozoic marine diversity (Sepkoski et al. 1981; Sepkoski 1993) has, for over two decades, been a major catalyst for research efforts into the history of life on Earth. This curve was widely accepted as a reliable summary of Phanerozoic marine diversity following Sepkoski et al.’s (1981) demonstration that five different methods of measuring diversity all agreed. However, after years of general acceptance of the Sepkoski Curve, numerous studies have revived the concern, first expressed by Raup (1972, 1976), that variation in the amount of rock available to sample for fossils systematically biases diversity estimates and the consensus view has broken down (Peters and Foote 2001, 2002; Smith 2001, 2007; Crampton et al. 2003, 2006a,b; Peters 2005, 2006a,b; Smith and McGowan 2005).

Variations in the amount of preserved sedimentary rock in the geological record have formed the subject of two related research programs. One has used the large-scale stratigraphic architecture of the rock record, controlled in part by sea-level change, for global stratigraphic correlation. This approach, discussed early in the last century by Chamberlin (1909), came to maturity through the work of Newell (1962, 1967) and Sloss (1963), and had its first culmination in the Vail et al. (1977) global sea-level curve.

The other program has linked the spatial distribution of sedimentary deposits to the amount of habitable area available for marine organisms through time. Chamberlin (1909) recognized the potential link between major sea-level falls and extinctions. Newell (1967) proposed that a relationship might exist between major paleontological turnover events and the loss of epicontinental seas during intervals of sea-level lowstand. The mathematical formalization of the relationship between habitable area and diversity (the species-area relationship) by MacArthur and Wilson (1967) provided a theoretical framework for quanti-
tative analyses of the relationship between available rock and diversity. Raup (1972, 1976) applied the species-area relationship to the relationship between the amount of rock, as a proxy for area, and diversity throughout the Phanerozoic. These early studies found a strong, positive correlation between the amount of rock available to sample and diversity.

Determining the causal factor(s) responsible for this positive correlation between rock availability and diversity is crucial for how we interpret changes in the marine diversity curve. One possibility is that diversity simply tracks the amount of available rock, and observed changes in diversity over time are due to sampling bias. The other suite of explanations emphasizes biological and/or ecological causes. The species-area effect assumes that as habitat area changes, biological processes, ranging from changes in the variety of habitats to relative levels of provinciality, will result in changes in diversity (see Rosenzweig 1995 for a summary). Peters and Foote (2001) and Peters (2005) proposed a hybrid “common cause” hypothesis to express the idea that a common driver of biodiversity and rock outcrop may exist, inducing a correlation between the two, but downplaying a direct, causal link between sampling and diversity.

Such ideas are also important for the interpretation of last occurrences in the fossil record. Johnson (1974) proposed the idea of perched faunas, taxa that appear in epicontinental seas during transgressions, only to disappear from the fossil record during regressions. Either last occurrences are genuine extinction events due to ecological pressures associated with the loss of habitable area, or these disappearances are an artifact of the lack of rock from the appropriate areas or habitats to sample and should be regarded as “apparent extinctions.”

Sepkoski’s curve was based on global first and last occurrences of taxa, but such records have a spatial, as well as a temporal, context. Given the history of geological research, the rocks of western Europe and North America are likely to yield a disproportionate number of these first and last occurrences (Kidwell and Holland 2002). This strong spatial bias is important because the completeness of regional rock records will vary because of differences in their tectonic and climatic histories (Kidwell and Holland 2002: Fig. 1C). Furthermore, the intersection of genuine biological processes with changing spatial sampling may introduce additional systematic biases. Allison and Briggs (1993) and Walker et al. (2002) highlighted the shift of well-sampled regions such as North America and western Europe from tropical to temperate latitudes through time as a possible source of bias in the fossil record.

Whatever the underlying cause(s), long-term trends in marine biodiversity, as deduced from fossil collection curves, are expected to follow eustatic sea-level change to some extent. However, some authors have questioned whether a common global response to continental flooding should always be expected because of the complex interaction between regional tectonics, sediment input, and onlap-offlap cycles (Dewey and Pittman 1998). As we have no reason to believe that the global rock record is anything other than a sum of regional records, it is reasonable to expect different rock accumulation histories from different regions. However, if our sample of rock is biased toward certain regions, then the global biodiversity curve will be dominated by the signal from those regions.

Our aim in this paper is to provide a quantitative assessment of regional Phanerozoic rock records and examine how rock bias might have affected long- and short-term diversity trends. We address two key questions:

1. Is there a coherent global rock record signal driven by eustatic sea-level cycles or does each region have its own independent history?
2. If the Phanerozoic diversity curve is influenced by sampling bias driven by the quality of the rock record, do the European and/or North American rock records predict Sepkoski’s curve better than Southern Hemisphere or summed global rock records?

Data and Methods

Data Collection from Maps. —To estimate variations in the amount of rock at outcrop
through time we used the geological map series of national geological surveys to provide a series of equal area sampling grids within each country. Maps, and accompanying sheet memoirs, published by the geological surveys of the United Kingdom, Chile, Australia, France, and Spain provided data on rock at outcrop, and whether the rocks were marine or terrestrial, fossiliferous or non-fossiliferous. Some maps occasionally contained multiple formations of the same type (e.g., two marine formations from the same time interval), but these were only counted as a single occurrence. Peters and Foote (2001, 2002) and
Crampton et al. (2003) have shown that the number of formations may provide a better measure of the range of environments sampled during an interval. By noting only whether marine rocks of a given age outcrop on a map we remove the potential for a confounding correlation between habitats and area. However, marine and terrestrial outcrops from the same time intervals were counted separately for each map area to provide a means of tracking the relative proportions of marine and terrestrial rock.

Rocks were defined as fossiliferous if there was a report of fossils of any type (recovery of microfossils was sufficient to classify rocks as fossiliferous) and the type(s) of fossils were noted in our records (see Smith 2001). Poorly dated rocks were those we could not assign to stage level on the basis of statements in the memoirs or fossil content.

Number of Maps and Areal Extent.—The countries vary greatly in their land area and the number of geological maps that cover that land area. The extent of coverage of each country is given in Table 1. None of the countries were covered completely, but incomplete coverage is a common problem even in studies of modern biodiversity. The maps can be regarded as analogous to quadrats used in ecological surveys. Rock outcrops are highly heterogeneous in their spatial distribution. For example, within England, Shropshire has rocks exposed that range in age from the Silurian to the Jurassic (3487 km²), whereas in Northamptonshire (2364 km²) only Jurassic rocks outcrop. We should not expect rock at outcrop through time to show a simple linear relationship to the relative land area examined among countries either.

Differences in Map Scales and Numbers of Maps.—Differences exist in the protocols and data used to construct geological maps. The European maps are based on data collected by geologists covering a large part of the mapped area on foot, whereas the Australian maps made extensive use of aerial photography because of the difficulties of fieldwork in the Australian interior. The interpretations of the aerial photography were validated by a number of geological transects within each map area (Major 1973).

The various national geological surveys also publish their maps at different scales. Sutherland (1996) discussed the effects of varying the size of quadrats. As quadrat size increases, the likelihood of encountering the object or taxon of interest increases, and large quadrats result in a higher frequency of occurrence. We assessed the impact of differences in scale, using a set of 817 1:50,000 and 117 1:80,000 geological maps of France (Smith and McGowan 2007). In effect the same geology was covered with two different, only partially overlapping, grids with cells of different sizes. As expected, despite almost an order of magnitude difference in the numbers of maps, the rock record curves derived from the two compilations varied in amplitude but not shape. Log10-transformation of the number of maps is used to dampen the influence of extreme values and makes the two curves more similar. Thus the

<table>
<thead>
<tr>
<th>Country</th>
<th>Scale</th>
<th>No. of maps</th>
<th>Land area (km²)</th>
<th>Estimated coverage</th>
</tr>
</thead>
<tbody>
<tr>
<td>England and Wales</td>
<td>1:63,630/1:50,000</td>
<td>220</td>
<td>262,351</td>
<td>63%</td>
</tr>
<tr>
<td>Spain</td>
<td>1:50,000</td>
<td>173</td>
<td>499,542</td>
<td>17%</td>
</tr>
<tr>
<td>Australia</td>
<td>1:250,000</td>
<td>262</td>
<td>7,617,930</td>
<td>57%</td>
</tr>
<tr>
<td>Chile</td>
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<td>28</td>
<td>748,800</td>
<td>30%</td>
</tr>
<tr>
<td></td>
<td>1:100,000</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1:250,000</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>France</td>
<td>1:50,000</td>
<td>817</td>
<td>545,630</td>
<td>80%</td>
</tr>
<tr>
<td></td>
<td>1:80,000</td>
<td>117</td>
<td></td>
<td>44%</td>
</tr>
</tbody>
</table>
scale of the maps affects the size of the peaks and troughs but not their position in time.

COSUNA Data.—We have also considered the COSUNA data of Childs (1985) as used in Peters (2005, 2006a,b). The COSUNA (Correlation of Stratigraphic Units of North America) data set consists of a series of 541 generalized stratigraphic columns that synthesize information from individual stratigraphic sections and borehole data from an area of around 260 km², although there is no uniformity in the area or number of sections that contribute to each individual generalized section (see Childs 1985 for further information). These data are qualitatively different from map and memoir data because they include subsurface as well as outcrop data. We used the number of sections where marine rock was encountered in each interval, as given by Peters (2005: supplementary data file).

Diversity Data.—The genus diversity data were downloaded from Sepkoski’s Online Marine Genus Database (http://strata.ummp. lsa.umich.edu/jack/index.php), based on his 2002 compendium. In the notation of Foote (2000) diversity is calculated as the sum of singletons \(X_{11}\), taxa that have their last occurrence within the bin \(X_{10}\), taxa that have their first occurrence with the interval \(X_{10}\), and through-ranging taxa \(X_{00}\). Per-interval extinction counts, which we regard as “apparent extinctions,” are the sum of singletons \(X_{11}\) and taxa that have their last occurrence in the interval \(X_{00}\). The 71 intervals used in this study are based, with some modifications, on the Gradstein et al. (2004) time scale. In all plots where a time axis is used, the length of geological intervals corresponds to the number of bins within that period, not absolute time, as this study is not concerned with rates. Because of differences between global and North American regional stage names, the values for several stages had to be combined and an average diversity calculated. Some additional data for Cenozoic intervals were derived from the supplementary data of Rohde and Muller (2005) that are based on Sepkoski (2002).

Construction of Smoothed Data Series.—Smoothed data series were constructed by taking a nine-point moving average of the values in each data series. A nine-point average was used as the nearest odd multiple of 7 Myr (the average stage length) that exceeded the length of most second-order sequence cycles (~50 Myr). Data were thus averaged over approximately 63 Myr. The smoothed data series thus runs from the Late Cambrian to the Aquitanian (basal Neogene), as the first and last four points in the time series have to be excluded in such a smoothing operation.

Cross-correlation of Data Series.—To compensate for unevenness of the time bins used, the cross-correlation correction outlined by Kirchner and Weil (2000a,b) was implemented. This combines data from time bins by amalgamating all bins that lie within the lag time plus or minus half of the lag time, rather than using only bins at exactly the lag separation as is the case in standard time series analysis. The Python computer code for these calculations is available on request from the corresponding author. Short-term variation was assessed by subtracting the nine-point moving average curve from the raw data, and the resulting residuals were used as the data for the cross-correlations.

Development of Models Relating Rock Availability and Observed Diversity.—Separate models were developed for each of the major geographical areas (Europe, Australia, Chile, and United States) to study the relationship between rock availability and diversity. \(\log_{10}\) diversity was used in these models to dampen the effects of extreme points and to remove the non-normality from the raw data series (see Raup 1976). First, the time series for rock and the time series for diversity were each sorted separately from lowest value to highest value. This forces a near-perfect correlation between rock at outcrop and diversity, which becomes our null hypothesis of what sampled diversity would be recovered if true diversity had been constant throughout the Phanerozoic, and only the amount of rock at outcrop determines variation in sampled diversity. Our assumption of statistically uniform increase in sampled diversity for a given increase in rock availability is conservative given our limited data.

A model of the form \(y = m x + c\), based on the ranked data, was then applied to the rock
series in the correct (original) time series order. As the plots are in log-log space, the degree of fit of straight-line equations gives some insight into whether there is a power law relationship between rock availability and genus diversity, which is the standard species-area plotting technique (Rosenzweig 1995). This is Model I, which attempts to explain all variations in diversity as the result of variation in the amount of rock sampled with diversity held constant.

**Development of Taxonomic Diversification Models.**—Using a regression analysis of the residuals from Model I we developed long-term diversification models to investigate the support for a range of long-term trends in diversification. Model II fits a linear regression to the residuals from Model I and represents steady diversification from the Cambrian to Pliocene. Model III splits this long-term diversification into three phases based on major inflections in the residuals. Separate linear regressions are then fitted to each phase. By comparing the improvement in fit as more parameters are added using the Akaike Information Criterion (AIC), we can determine the relative support for the each model.

**Results**

**Regional Patterns of Rock at Outcrop.**—Absolute counts of European, Australian, and Chilean map quadrats with marine and terrestrial rocks at outcrop are shown in Figure 1. The absolute amount of rock at outcrop does not show a simple exponential decay; instead there are major cycles. These cycles are not synchronous among the three regions. The amount of poorly dated rock generally decreases through time, but there is no simple, uniform progression from large amounts of poorly dated rock in the early Paleozoic to almost no poorly dated rock in the Neogene.

The numbers of European, Australian, and Chilean map quadrats with marine rock are plotted in Figure 2. We used both Spearman’s rank and Kendall’s τ tests to compare patterns between each pair of regions. Spearman’s rank correlation provides information on whether highs and lows in rock at outcrop are significantly correlated. Kendall’s τ provides information on whether the rock availability is fluctuating synchronously between two regions (Hammer and Harper 2006).

Table 2 reports correlations between the time series of the marine quadrats and the time series of marine quadrats where fossils
Table 2. Spearman’s rank correlation test and Kendall’s τ test results comparing the time series of all map quadrats containing marine sediments with the time series of map quadrats containing fossiliferous marine sediments at outcrop.

<table>
<thead>
<tr>
<th></th>
<th>Spearman</th>
<th>p-value</th>
<th>τ</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>U.K.</td>
<td>0.95</td>
<td>&lt;0.01</td>
<td>0.87</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Spain</td>
<td>0.87</td>
<td>&lt;0.01</td>
<td>0.81</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>France</td>
<td>0.99</td>
<td>&lt;0.01</td>
<td>0.95</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Australia</td>
<td>0.97</td>
<td>&lt;0.01</td>
<td>0.89</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Chile</td>
<td>0.95</td>
<td>&lt;0.01</td>
<td>0.92</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

are collected from at least one outcrop within the map area from each time bin. If factors such as diagenetic loss of fossils or failure to collect fossils were a major influence on the fossil record, then cases should exist in which there were many quadrats with marine rock at outcrop, but few that yielded fossils. Such cases would reduce the strength of correlation between rock and diversity. However, all regions show strong positive correlations between marine rock and fossiliferous marine rock, so for the subsequent analyses we show results for marine rock only.

We tested whether the rock outcrop time series for each region sampled were sufficiently similar to be considered as sampling the same underlying signal. A high level of congruence among the rock outcrop time series for the three European countries is evident (Table 3), but with some mismatch. In particular, Pleistocene glaciation has removed most of the post-Eocene U.K. rock record, relative to the French and Spanish records. No Northern versus Southern Hemisphere pattern was detectable. Chile shows significant correlations with Spain and France for both tests, but not with the United Kingdom. Australia shows a significant correlation with France, although the Kendall’s τ result indicates that as rock at outcrop is increasing in France, it is decreasing in Australia, and vice versa. Importantly, Chile and Australia show no significant correlation, ruling out a north-south split in the regional data.

Results of analyses, including the COSUNA data, are shown in Table 4. Significant Spearman’s rank correlations were found between the United States and Australia and between the United States and Chile. However, the Kendall’s τ results indicate that the rock records of Australia and the United States are rising and falling together while those of Chile and the United States are in antiphase. Both tests indicate significant, positive correlations between Chile and Europe.

The results above consider correlation among regional rock records with no time lag. Cross-correlation analyses were performed to examine whether any significant correlations exist among the regions at time lags ranging from 5 to 60 Myr. All cross-correlation analyses show cycles of positive and negative correlation, but few of the correlations are significant (Fig. 3) and the significant correlations do not cluster around particular lag times.

Table 3. Comparison of rock outcrop area among regions studied, using Spearman’s rank correlation and Kendall’s τ tests. The upper right area of each part of the table (above the matrix diagonal) reports the correlation value, and the bottom left area (below the matrix diagonal) reports the p-values. Spearman’s rank correlation test compares ranks. Kendall’s τ compares whether two data series are significantly in phase (positive values) or antiphase (negative values).

<table>
<thead>
<tr>
<th></th>
<th>U.K.</th>
<th>France</th>
<th>Spain</th>
<th>Australia</th>
<th>Chile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spearman</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U.K.</td>
<td>N/A</td>
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<td>0.42</td>
<td>−0.04</td>
<td>0.13</td>
</tr>
<tr>
<td>France</td>
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<td>0.78</td>
<td>−0.28</td>
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<tr>
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<td>0.26</td>
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<td>&lt;0.01</td>
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</tr>
<tr>
<td>Kendall’s τ</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<tr>
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<td>&lt;0.01</td>
<td>0.90</td>
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</table>
TABLE 4. Comparison of rock outcrop area among regions studied, using Spearman’s rank correlation and Kendall’s τ tests. The three European countries are combined, and the United States is represented through the COSUNA data.

<table>
<thead>
<tr>
<th></th>
<th>Europe</th>
<th>Chile</th>
<th>Australia</th>
<th>U.S.A. (COSUNA)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spearman</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>−0.17</td>
<td>−0.11</td>
</tr>
<tr>
<td>Chile</td>
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<td>−0.10</td>
<td>−0.49</td>
</tr>
<tr>
<td>Australia</td>
<td>0.16</td>
<td>0.44</td>
<td>N/A</td>
<td>0.42</td>
</tr>
<tr>
<td>U.S.A. (COSUNA)</td>
<td>0.39</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>N/A</td>
</tr>
<tr>
<td><strong>Kendall’s τ</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>&lt;0.01</td>
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</table>

**Figure 3.** Cross-correlation analysis of residuals after the subtraction of the nine-point moving average from the observed amounts of marine rock at outcrop among the four regional data sets at lags from 0–60 Myr in 5-Myr increments. An asterisk indicates significance at p < 0.05.
The residuals do show some cyclicity but do not vary in phase (Fig. 4). The similarities between Chile and Europe are further emphasized by this plot, as are the similarities between the U.S. and Australian rock record. There is therefore little evidence for coordinated cycles of short-term variation (~50 Myr) in the amount of rock at outcrop among the different regions.

Comparison of Observed and Predicted Diversity Based on Rock at Outcrop in Western Europe.—The differences between the observed global diversity for each interval and the diversity predicted from the availability of western European rock at outcrop are shown in Figure 5A, with the equation shown in Table 5. Deviations from the diversity predicted by the model described above had to be explained by factors other than rock at outcrop.

The assumption that diversity has remained constant through the Phanerozoic, with changes in observed diversity being driven entirely by differences in rock at outcrop, is highly unrealistic, so we modified the assumption of constant diversity by developing two models based on linear regressions of the residuals against time. Model II simulates a constant Cambrian–Pliocene diversity rise (+0.014 log units per interval). Model III (developed in Smith and McGowan 2007) has three phases with different diversification rates: Cambrian–Mid-Devonian rise (+0.02 log units per interval), Mid-Devonian–Triassic fall (~0.04 log units per interval) and Early Jurassic–Pliocene rise (+0.03 log units per interval). Figure 5D shows the model diversification trajectories superimposed on the residuals. Model II (steady long-term diversification) shows some improvement in fit (Fig. 5B), but there is a dramatic improvement in fit with Model III three-phase model (Smith and McGowan 2007) (Fig. 5C). The AIC values allow us to ascertain whether the addition of the extra parameters is justified by the improvement in fit (Table 6). The negative ΔAIC values for Models II and III indicate that the extra parameters added are justified in both models, but the difference in the evidence ratios of the
two models, which express the probability that a given model is the best model (Johnson and Omland 2004), is not high enough for us to be sure that we should prefer Model III over Model II.

Variants of Model I, based on the map data compiled for each country, were also developed for Australia and Chile, using the protocols outlined above and the map data for each country (Table 5) and the resulting curves are shown in Figure 6A,B.

If a single global marine diversity signal through time exists, we should be able to detect similar diversification trends from the rock records of all regions. A separate rock model is required for each region, as the coverage among areas is different and likely to follow different slopes. We then applied Mod-

**Table 5.** Equations of rock versus diversity for each of the regions studied in the form $y = mx + c$. Significance and $r^2$ values are reported.

<table>
<thead>
<tr>
<th>Region</th>
<th>Equation</th>
<th>Correlation</th>
<th>p-value</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
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<td>Europe</td>
<td>$y = 0.4763x + 2.1552$</td>
<td>0.31</td>
<td>&lt;0.01</td>
<td>0.10</td>
</tr>
<tr>
<td>Australia</td>
<td>$y = 0.5017x + 2.636$</td>
<td>0.03</td>
<td>N.S.</td>
<td>0.00</td>
</tr>
<tr>
<td>Chile</td>
<td>$y = 0.4861x + 2.8834$</td>
<td>0.24</td>
<td>0.05</td>
<td>0.06</td>
</tr>
<tr>
<td>COSUNA</td>
<td>$y = 1.0644x + 0.8861$</td>
<td>0.55</td>
<td>&lt;0.01</td>
<td>0.30</td>
</tr>
</tbody>
</table>
els II and III, based on European residuals, to the Australian and Chilean rock models to assess the improvement in fit and determine whether the same diversity patterns could be recovered in all regions (Fig. 6C,D). Model II does little to improve the match between observed and predicted diversity in either Chile or Australia. When Model III is applied to Chilean and Australian data the match improved, but not to the same degree as for Europe (Fig. 6E,F).

Europe may have a good fit once rock at outcrop and long-term diversity trends are accounted for, but the marine rock record for the Permian–Triassic interval is poor to nonexistent in the European countries we gathered rock record data from (Smith and McGowan 2007). COSUNA has information on rock at outcrop and in the subsurface, and there is much more Permian and Triassic marine outcrop in the United States, so we also investigated the performance of the COSUNA data in predicting the shape of the marine diversity curve.

Figure 7 shows the performance of the COSUNA data in matching the global diversity curve, using the relationship given in Table 6. Model I has a much better fit to Sepkoski’s diversity curve than the predictions derived from European rock at outcrop. When Model II, based on the European rock record, is applied to the COSUNA data, the strength of correlation is comparable to that of the European record when Model III is used (Fig. 5C). When Model III, based on European data, is used the correlation between rock and diversity decreases.

Separate taxonomic diversification models were developed for the residuals from the COSUNA data, and the resulting correlations between the predicted and observed curves are shown in Figure 8A,B. The residuals, and the regressions associated with diversification models, are shown in Figure 8C,D and provide further evidence of the differences in the rock records among regions. Whereas the western European residuals yield three clear points of inflection (Fig. 5D), the pattern of residuals from the COSUNA-derived Model I are more complex, so we investigated a wider range of diversification models (Fig. 8C).

In the COSUNA version of Model III shown, the first phase of the model runs from the Cambrian to the Mid-Triassic, but with a lower diversification rate. The second phase runs from the Mid-Triassic to the Late Cretaceous, with very low diversification rate. The final phase, which commences during the Late Cretaceous, has a similar per-interval diversity increase as the European model. An alternative Model III placed the end of the first phase in the Pliensbachian, but this model had a slightly lower $r^2$ value (0.63) and a lower AIC. A five-step model (Model V; $r^2 = 0.77$) is the preferred model, judging from the AIC evidence ratios, despite the increase in parameter number (Table 6).

The Paleozoic portions of Models III and V, based on COSUNA residuals, are similar, but the Cretaceous–Neogene section differs no-
Correlations between predicted and observed diversity for Australia and Chile. Individual models reported in Table 6 were developed to relate rock outcrop area for each country to genus diversity. A, Australian Model I result. B, Chile Model I. C–F Models of long-term diversity change developed for the European residuals (Models II and III) added to the results of the independent regional rock models for Australia (C, E) and Chile (D, F).
noticeably between Models II and III/V, with diversity in this interval being underestimated by Model II and overestimated by Models III and V.

**Identification of Cycles in Rock Record.**—Residuals from the smoothed data series through time for each region are plotted in Figure 9. Major negative residuals were treated as system bases, and we assumed that major sedimentary cycles ran between these system bases. Although the Mesozoic–Cenozoic record of marine rock at outcrop of Europe shows good agreement with sequence stratigraphic data from Hardenbol et al. (1998) (see Smith 2001), it is evident from Figure 9 that the cycles across the four regions are neither global nor in phase. Even the cycles picked from COSUNA and European data are not congruent until the Cretaceous, probably because the COSUNA data cover the whole United States, not just the Atlantic Coast area influenced by the opening of the Atlantic. Surprisingly, the cycles picked from the COSUNA data do not show a close fit with the zonation of the cratonic interior of the United States developed by Sloss (1963) based on sedimentary packages and orogenic events. Sloss (1963) picked seven cycles, whereas our analysis of the COSUNA data suggests six major cycles.

Cumulative curves for the amount of marine rock outcropping in each region through time (Fig. 10A–D) highlight the major cycles of rock accumulation. The smooth cumulative curve for COSUNA data reflects the different nature of the COSUNA data, which capture information about rock at depth because of the incorporation of subsurface data, rather than information about the amount of rock exposed at the earth’s surface. Clearly the major cycles are not synchronous in different parts of the world. The two paleogeographic maps included in Figure 10E,F are presented to illustrate
one clear instance of temporal mismatch in maximum flooding events. Australia shows maximum flooding for the Cretaceous in the reconstruction for 120 Ma, while flooding had yet to peak in the United States and Europe. The 90-Ma reconstruction shows that flooding of the Australian craton had waned greatly, while the interior of the Canada and the United States are extensively flooded.

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rock availability and number of extinctions (Fig. 11A). Intuition might suggest that as gap originations increase and rock availability decreases, taxonomic last occurrences (TLO) should increase and this can be seen in some cases. However, some TLO peaks are found during times when gap originations are decreasing and rock availability is increasing.

We performed cross-correlations at a range of lags from 0 to 60 Myr for TLOs versus gap originations (Fig. 11B) and TLOs versus rock availability (Fig. 11C). There was no significant correlation between gap originations and number of TLOs at a lag of 0 Myr, a significant negative correlation at 10 Myr, and a significant, positive correlation at 60 Myr. However, at a lag of 0 Myr there is a significant negative correlation between rock availability and TLO, as expected. Positive correlations between rock availability and TLO are present also at 20–30 Myr offsets.

**Discussion**

*Quantifying the Phanerzoic Rock Record.*—To date, five major approaches have been used to quantify the rock record available to paleontologists. Each has its own advantages and disadvantages.

1. Number of named formations.—Wignall and Benton (1999), Peters and Foote (2001, 2002), Wang and Dodson (2006), and Crampton et al. (2003) have all used counts of the number of named geological formations within a time interval as a measure of how good the rock record is. Although the number of formations in a time interval may give a better measure of habitat heterogeneity than a simple measure of rock outcrop area (Crampton et al. 2006a), and represents a relatively easy type of data to compile, the approach has a number of drawbacks.

Formation counting assumes that formations are equivalent entities and have been named consistently. Where formations are the result of the mapping efforts of individual national geological surveys, this assumption is likely to be valid. For example, the U.S. Geological Survey has a standard definition of a formation, reproduced by Peters and Foote (2002) as “lithologically distinct and mappable at a scale of 1:24,000.” Globally, however,
it is doubtful whether the naming of formations is sufficiently uniform. Russian mapping uses a mixture of biostratigraphic and paleomagnetic data rather than lithological units. The Russians also made extensive use of boreholes, up to one borehole per km² (R. Twitchett personal communication 2007). Russian formation data have more in common with COSUNA data than with British Geological Survey map and memoir data.

During intervals where sedimentary units are more finely subdivided (e.g., those dominated by cyclothems or interbedded volcanic and sedimentary units), this might lead to an inflated estimate of the number of formations. Conversely, for thick, monotonous formations that are richly fossiliferous, this approach will lead to underestimates of diversity. The areal extent of formations is not considered in counts of formations. Peters and Foote (2002)

Figure 10. A–D, Cumulative curves charting the increase in rock through time for the four regions. Note difference in y-axis scales. The arrows indicate inflections in the accumulation, which mark major drops in the addition of extra rock. E, F, Two Cretaceous paleogeographic maps illustrate asynchrony in major flooding events in Australia and United States/Europe. E, Early Cretaceous (120 Ma) showing major flooding of the Australian interior, but Western Interior Seaway (WIS) and major European flooding has not yet peaked. F, Mid–Late Cretaceous (90 Ma) showing major flooding of the WIS and Europe, while the Australian craton has now drained.
reported a good correspondence between outcrop and number of formations whereas Crampton et al. (2003) found such correlations, at best, relatively weak. Crampton et al. (2003) reported stronger correlations between number of fossil collections and number of formations. However, their reported correlation between number of formations and species diversity was not significant. Without additional data it is impossible to determine the area/volume of outcrop, or to distinguish between fossiliferous and non-fossiliferous portions of a formation either horizontally or vertically.

2. Equal area sampling.—Used by Smith (2001), Smith and McGowan (2005, 2007). This approach uses geological maps as a sampling grid and determines whether rocks of a certain age outcrop on a particular map. A further, more conservative, refinement is to use the sheet memoir to check whether fossils have been recorded from outcrops in the area, rather than assuming that a formation known to be fossiliferous somewhere within its range yields fossils wherever it occurs. A key aim is to mimic the discovery process of both rock and fossils by field collection. With information on which map areas did and did not con-
tain fossils, it is possible to draw a distinction between map areas with no rock at outcrop and map areas with unfossiliferous rock at outcrop. Such data have more potential for further analysis than either counts of fossiliferous formations or number of collections, both of which count only successes in collection of fossils.

Unfortunately not all national geological surveys provide accompanying memoirs for published maps, and collection of these data is time consuming. Variation in the scales of published maps and differences in the collection, recording, and publication of primary geological and paleontological data remain causes for concern.

3. Fossil locality counts.—Counting the number of localities within a region that have yielded fossils of a specific age provides a direct measure of the relative fossiliferousness of the rock record through time. Fara (2002) used this method, as did Crampton et al. (2003, 2006a,b). This method has the advantage of directly measuring the number of localities sampled within each interval, and such collection data have been key in efforts to apply sample-standardization to paleodiversity analyses (Alroy et al. 2001), a parallel development in attempts to correct for sampling biases.

However, in order for a locality to be added to the data set, fossils must have been collected from the locality. Therefore, except for cases in which detailed bed-by-bed collecting or bulk sampling have been carried out, the number of localities approach will always have the problem that we do not know the number of “failures to collect” at outcrop. If the number of localities sampled, irrespective of whether or not fossils were recovered, were routinely reported this would be useful and generate data that would be more amenable to analysis with ecological techniques (Jackson and Johnson 2001). The number of localities collected from cannot alone provide data on how wide a range of habitats have been sampled, although additional geological data available from Paleobiology Database records, for example, can help to correct for such biases as demonstrated by Kowalewski et al. (2006).

4. Digitization of large-scale maps.—Raup (1976) (with data from Blatt and Jones 1975), Sloss (1976), Ronov (1994), Vermeesch (2003), and Crampton et al. (2003) used digitization of very small-scale (>1:100,000) geological and paleogeographic maps to estimate changes in sedimentary rock availability. Such an approach provides rapid coverage of large areas, and can provide estimates of the amount of rock volume deposited by multiplying area data by estimates of sedimentation rate.

However, the information derived from such maps does not always take account of lithological data that would indicate that the presence and/or preservation is unlikely, e.g., dolomitized carbonate deposits. Temporal resolution of small-scale geological maps is often limited to epoch or period, which prevents detailed study of stage-level fluctuations that are the routine level of analysis for most studies of marine biodiversity in the fossil record. This makes it more difficult to establish causal relationships between rock availability estimated from small-scale maps and short-term variations in diversity. Paleogeographic maps in particular may bear little relationship to the amount of rock preserved at outcrop. Finally, as the units of measurement are often millions of square kilometers, variation in estimates of changes of depositional area over short periods is small, leading to relatively “flat” trend lines through time. As digitization does not necessarily measure rock at outcrop, its results should be considered as estimates of the extent of depositional systems and the total potential rock area available during the time of deposition.

5. Analysis of distribution of hiatuses.—Peters (2006b) analyzed the distribution of sedimentary hiatuses in the COSUNA data as a measure of rock-record quality. The COSUNA data contain detailed information on gaps in the record, and can be corrected to take account of the areal extent of gaps. However, some of the records of available rock and hiatuses in the COSUNA data are subsurface. It is not clear how appropriate subsurface data are as a proxy for rock available for paleontological sampling. The distinction between the rock at the surface and rock that may exist in the subsurface, but is effectively inaccessible for the collection of marine macrofossils, is
an important one. We would expect subsurface data, including seismic data, to overestimate the amount of rock available to collect from, especially in the older parts of the rock record.

Global versus Regional Signals.—Raup’s groundbreaking studies of the relationship between the amount of rock and marine diversity (Raup 1972, 1976) used small-scale maps at epoch or even period level. His studies identified the possibility that a bias existed, but the spatio-temporal scales he used are too coarse for the questions that are currently being addressed. Early studies tended to extrapolate from regional data sets (U.S.R., U.S.) to global patterns without demonstrating that such scaling-up was justifiable.

Recent re-exploration of the rock record bias has been more nuanced. Most analyses have been regional rather than global in coverage (Smith 2001; Peters and Foote 2002; Crampton et al. 2003, 2006a,b) but have done much to convince paleontologists that the issue of rock record bias needed to be taken seriously. Previous to this study only Peters and Foote (2001) had attempted global coverage at stage level by sampling back issues of the Journal of Paleontology to generate an estimate of the number of fossiliferous formations worldwide. An equal-grid sampling strategy, based on the data held by the Paleogeographic Atlas Project, which used a variety of grid sizes, was also employed for 12 Mesozoic and Cenozoic intervals to verify the relationship between rock at outcrop and number of formations.

Our analyses indicate that we must move forward from the concept of a single global pattern of cratonic flooding, and by extension the concept that rock deposition and/or marine biodiversity is controlled by global eustatic cycles that occur in synchrony throughout the Phanerozoic (Hallam 1989, 1992). The areas sampled from western Europe do form a cohesive unit. However, even within this small area the correlation of the United Kingdom to France and Spain is not as strong as the correlation between the latter two regions. These differences are probably the result of the destruction of post-Eocene sediments and “sedimentary blanketing” by glacial deposits in the United Kingdom (Pleistocene glaciation had much less of an effect on France and Spain). However, we found little support for combining regional data, even from regions such as the United States and western Europe—which might, a priori, be expected to have closely matching diversity and geological histories—until the Cretaceous.

Chile and Australia do not form a cohesive “Southern Hemisphere” unit. The consistent negative correlation in long-term variation between the two regional records emphasizes this point. Rather, the large cratonic masses of North America and Australia seem to show more similarities, and contrast with the active accretionary margins of Chile and western Europe. The active tectonics of accretionary margins may well be overriding the contribution to sequence architecture made by sea-level change, whereas large-continental shield areas such as Australia may require particularly high relative sea levels to flood large amounts of the continental area.

Comparison of Performance of Diversification Models.—This paper has extended the use of linear models based on rock at outcrop, initially developed by Smith and McGowan (2007) for western Europe, to remove rock outcrop area bias from Sepkoski’s diversity curve. We have shown how simple correction factors might be developed to account for variations in long-term diversity and rock outcrop. Residual analysis of the models also provides an additional means of identifying mismatches between regional rock records and the global marine diversity curve. We have established that the resultant improvement in fit justifies the addition of extra model parameters (Table 6), but we find that differences exist in the major points of inflection in the predicted diversity curves between the COSUNA and western European data. We did not undertake maximum-likelihood analyses to establish the range of values that the long-term increase and decrease parameters might take on the predictive models. We offer these models as a preliminary investigation on which to base more sophisticated analyses in future.

One important issue that we have addressed is the relative contribution to the Sepkoski Curve made by countries such as Australia and Chile that represent large geo-
graphic areas but which have not been sampled as intensively as North America and western Europe. The poor correlations found between the marine rock record at outcrop and Sepkoski’s curve suggests that we cannot go to any area of the world and recover a standard high-resolution global diversity signal. This may partly be the result of the small numbers of maps available to override the imposed signal of the European long-term diversity model, although we tried to account for this by developing independent rock models for each country (Table 5). Model III plus the Chilean rock model does generate a strong correlation, which may be related to the marked increase in marine rock during the Jurassic and Cretaceous in both Europe and Chile (Table 3, Figs. 1, 2). Australia shows particularly marked departure from western European model during the Cambrian and Jurassic–Cretaceous.

Western Europe’s marine outcrop record provides reasonably good predictions of small-scale diversity trends once long-term diversity trends are accounted for (Smith and McGowan 2007). However, the lack of marine rock at outcrop during the Permian and Triassic in western Europe results in a very poor fit between diversity predicted from the rock record and observed diversity during this interval.

The COSUNA data set shows impressive initial fit to the constant diversity model (Fig. 7A), but the COSUNA data are of a different nature. In particular the use of subsurface data compensates for intervals lacking rock at outcrop during intervals of major craton flooding such as the Cambrian. The COSUNA data, with their vertical dimension, are more akin to an estimate of volume rather than area. Poor fit is concentrated in the Cenozoic, and some parts of the Paleozoic. A difference in the amounts of additional variance explained by the models developed for the United States and Europe has ramifications for the sorts of long-term diversification models we might accept (see Benton and Emerson 2007 for a review of possible models). Both COSUNA and European data support a real long-term diversification trend throughout the Phanerozoic, although at different rates (Model II results), and the results on Figures 5 and 8, and to a lesser extent Figure 6, lend support to there being two phases of diversification separated by a downward perturbation, but do not agree upon the timing of these episodes. The AIC values of the U.S. models indicate increased support for three- and five-phase models, but the timing of the different phases of diversity increase and decrease is different, although diversification rates in the final phases of both the European and U.S. models are very similar (around 0.03 log units per interval). The consistent outcome is that, as predicted, the European and North American rock records provide much better predictions of small-scale variations in the Sepkoski Curve than either Australia or Chile.

At present it is unknown what results an equal-area sampling study of the U.S. rock record would yield. The United States is a much larger area (about eight times that of the western European countries studied), but given the spatially heterogeneous nature of the rock record, it is unlikely that rock at outcrop would show a simple eightfold increase, as the example of the English counties of Shropshire and Northamptonshire illustrates.

Drivers of the Mismatch.—Rock outcrop is the end result of a variety of processes. If there is no accommodation space in a basin at a particular time then no sediments can be laid down and the creation of accommodation space is extremely heterogeneous in space and time. Even if sediments are deposited they must then be preserved, then exposed at the surface to enable mapping and collection of fossils. Peters and Foote (2001) and Vermeesch (2003) noted that that erosion is not the only process that can lead to lack of outcrop. Rocks may be present in the subsurface but covered by younger sediments. This “sedimentary blanketing effect” is particularly pronounced when even a relatively thin layer of younger sediments has been deposited across a large area. Stable cratonic areas are particularly vulnerable to this effect, as the flooding of North America by the Western Interior Seaway demonstrates. Mountain-building episodes can result in the exposure of rocks that would otherwise be buried. The loss of rock at outcrop cannot be regarded as a simple decay
function through time (Smith and McGowan 2007), nor is there spatial uniformity in the patterns of rock at outcrop, owing to the interaction of deposition, tectonics, and erosion to create outcrop (Raup 1972).

Two first-order cycles are evident in plots of the ratio of terrestrial to marine rock in western Europe through time (Smith and McGowan 2007), and these correspond well to the tectonic supercycles of continental breakup and assembly highlighted by Fischer (1984). Similar first-order cycles are also evident in the Australian and Chilean rock records, but the timing of these cycles differs slightly. There is therefore a global signature that relates to global tectonics and the construction and disassembly of large continental masses. However, over shorter time scales, the lack of congruence among the regional rock records implies that regional rather than global processes are more important. Smith (2001) postulated that the breakup and flooding of regions plays a key role in determining regional sequence architecture, given that cycles of marine rock at outcrop in western Europe corresponded with the second- and third-order cycles of Hardenbol et al. (1998).

Viewing time series of paleogeographic maps, such as those of R. Blakey (http://jan.ucc.nau.edu/~rcb7/mollglobe.html) illustrates the potential for asynchronous flooding of major cratonic areas to generate distinct regional patterns of rock at outcrop. Two of Blakey’s maps are shown in Figure 10E,F as an example of this phenomenon.

Further investigation of paleogeographic maps of Australia compiled by Struckmeyer and Totterdell (1990) shows flooding of the eastern part of the continent during the Cambrian and Ordovician, followed by a long period of relatively little flooding, culminating in the long cycle (Cycle 5; Fig. 9C). The subsurface data on Cambrian and Ordovician rock available from COSUNA help to drive a positive correlation between Australia, which has much Cambro-Ordovician rock exposed at outcrop, and the United States. The dearth of Mid-Triassic to Mid-Jurassic rock in Australia is matched in the COSUNA data (Fig. 4).

**Taxonomic Last Occurrences and Stratigraphic Gap Originations.**—A strong positive correlation exists between genus extinction rates (last occurrence data) and changes in the rock record (Peters and Foote 2002; Peters 2005, 2006b; Crampton et al. 2006a). This is also evident in our data, where there is a significant positive correlation between cycles of rock outcrop area and taxonomic last occurrences, with TLOs peaking in phase and out of phase (Fig. 11A). However, the results from our analyses of gap originations and the number (not rate) of taxonomic last occurrences found no evidence of significant match between the two variables (Fig. 11B) at either 0 Myr lag or using first differences. A regression analysis on the first differences of the gap originations and extinction residuals had an $r^2$ of 0.03, indicating a poor fit between the series, similar to that reported by Peters (2006b).

The offset correlation between gap originations and TLOs is perhaps counterintuitive, but the cross-correlation results and careful examination of the time series in Figure 11 yield an understandable explanation. A significant negative correlation exists at a lag of 10 Myr, indicating that TLOs are at their lowest 10 Myr after peak numbers of gap originations. In terms of sequence architecture gap originations peak during second-order Regressive Systems Tracts and TLOs are at their lowest during the early stages of Transgressive Systems Tracts. The inset cartoon of sealevel cycles and gap and extinction peaks in Figure 11A presents this model visually and this pattern is at its clearest in the Mesozoic portion of the main figure.

Having significant peaks in TLOs that are both in phase and out of phase with the amount of rock at outcrop is also explicable. As expected TLOs peak as we move from a time interval with a good rock record to one with a poor rock record. However, there are also intervals where TLOs peak as we approach maximum flooding and rock outcrop area. Holland (1995) predicted these two phases of TLOs—one at system bases, corresponding to lows in the amount of rock, and another set of last occurrences during periods of maximum flooding.

**Conclusions**

To answer the questions set out in the introduction:
1. The global record of rock at outcrop is more than a simple response to eustatic sea-level fluctuations. Strong, positive correlations were found for rock at outcrop among the three western European countries studied, but this does not extend to the pre-Cretaceous United States. There is some evidence of an intercontinental correlation that can be related to long-term first- and, occasionally, second-order sea-level changes from the cross-correlation analyses. We have not been able to identify the most appropriate spatial scale at which to perform analyses, and this scale may shift with changing palaeogeographic and palaeotectonic regimes. Further progress in understanding the history of marine biodiversity should be focused on the construction of regional data sets, accompanied by information on tectonically and sedimentologically meaningful units. In a few cases, such as the Cenozoic of New Zealand, political, tectonic, and biodiversity regions meaningfully coincide. Beyond such serendipitous cases, a clear palaeogeographic framework should be established.

2. Models relating rock available for sampling, combined with taxonomic diversification models, do well at predicting the small-scale changes seen in the Sepkoski Curve for rock from western Europe and the COSUNA data sets. Chile and Australia do not perform as well, further emphasizing the regional biases of the first and last occurrence data used in the construction of Sepkoski’s genus-level database. The previously documented bias of the fossil record to North America and western Europe is further supported by these findings.

Having developed a simple set of models relating rock availability, and corrections based on residuals of these models, we would urge other researchers to take advantage of this approach. The rock prediction variable need not be the number of quadrats with rock at outcrop. Other predictor variables, such as number of collections, number of formations, or the preservation rates calculated by Foote (2003), could be used with this approach.

The failure of the number of gap origina-
ations to predict the number of taxonomic last occurrences, even when the possibility of a time lag was considered, is rather counterintuitive. We offer an explanation, and the topic needs further work to test the pattern in a more quantitative manner. The variation in whether gap originations and rock availability are increasing or decreasing in or out of phase with apparent extinctions could also be a source of further understanding about the relative roles of sampling and biological effects. An important aspect of future data collection will be the collection and inclusion of paleoenvironmental data to allow models to incorporate a habitat gain/loss component, as used by Smith (2001). We have demonstrated that the data and analytical techniques exist to replace global sea-level curves with regional studies that quantify proxies for rock at outcrop in more detail, providing a meaningful approach to studying mega-biases in the fossil record that are related to the variations in the rock record.

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