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Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies

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Patterns of origination, extinction and standing diversity through time have been inferred from tallies of taxa preserved in the fossil record. This approach assumes that sampling of the fossil record is effectively uniform over time. Although recent evidence suggests that our sampling of the available rock record has indeed been very thorough and effective, there is also overwhelming evidence that the rock record available for sampling is itself distorted by major systematic biases.

Data on rock outcrop area compiled for post-Palaeozoic sediments from Western Europe at stage level are presented. These show a strongly cyclical pattern corresponding to first- and second-order sequence stratigraphical depositional cycles. Standing diversity increases over time and, at the coarsest scale, is decoupled from surface outcrop area. This increasing trend can therefore be considered a real pattern. Changes in standing diversity and origination rates over time-scales measured in tens of millions of years, however, are strongly correlated with surface outcrop area. Extinction peaks conform to a random-walk model, but larger peaks occur at just two positions with respect to second-order stratigraphical sequences, towards the culmination of stacked transgressive system tracts and close to system bases, precisely the positions where taxonomic last occurrences are predicted to cluster under a random distribution model.

Many of the taxonomic patterns that have been described from the fossil record conform to a species–area effect. Whether this arises primarily from sampling bias, or from changing surface area of marine shelf seas through time and its effect on biodiversity, remains problematic.

Keywords: biodiversity; extinction; origination; sampling bias; fossil record

1. INTRODUCTION

Documenting how biodiversity has changed over geological time is one of the basic goals of palaeontology, and is essential if we are to place the current biodiversity crisis into historical perspective. Attempts to chart the history of biodiversity through the Phanerozoic started with Phillips (1860). He drew on his personal knowledge as palaeontologist for the British Geological Survey to construct a semi-quantitative figure showing the diversity of fossil assemblages through time (figure 1*a*). This is surprisingly close to our current best estimate and shows rising diversity towards the present, punctuated by two major dips in diversity coinciding with the Permo–Triassic and Cretaceous–Tertiary intervals.

More rigorous attempts to quantify Phanerozoic biodiversity did not begin until the late 1960s and early 1970s, and were spurred on by the publication of a compendium of taxonomic occurrence data at family level (Harland *et al*. 1967). Whereas Valentine (1969) was happy to use these data at face value as a record of past diversity, Raup (1972; see also Raup & Stanley 1971) was much more cautious. Raup was acutely aware of the potential biases within the rock record and how they might distort our perception of palaeodiversity. He pointed out that there was a close match between recorded species-level diversity (figure 1*b*) and surface area of exposed rock, and this led him to propose a very different taxonomic diversity curve, in which diversity rose rapidly during the Cambrian and then remained more or less constant.

Raup's work prompted a flurry of papers, some supportive (Raup 1976*a*,*b*; Sepkoski 1976, 1978), others critical (Bambach 1977; Sheehan 1977; Signor 1978), but the major protagonists eventually published a joint paper (Sepkoski *et al*. 1981) in which five estimates of diversity were presented (based on body fossil diversity at family, genus and species level, trace fossil diversity and taxonomic diversity within comparable communities). As all five estimates came up with basically the same pattern of change, Sepkoski *et al*. took this as corroboration and assumed that the pattern must be real. Although this effectively ended debate about rock record bias, these authors presented no reason to explain why the five estimates were considered to reflect a real pattern rather than all being subject to the same underlying bias, as Signor (1985, 1990) astutely pointed out. Indeed, all assume uniform sampling and preservation over time, a basic assumption that is questioned here.

Since 1980 the trend has been towards compiling more comprehensive and more accurate taxonomic databases from which to derive estimates of diversity. Foremost in

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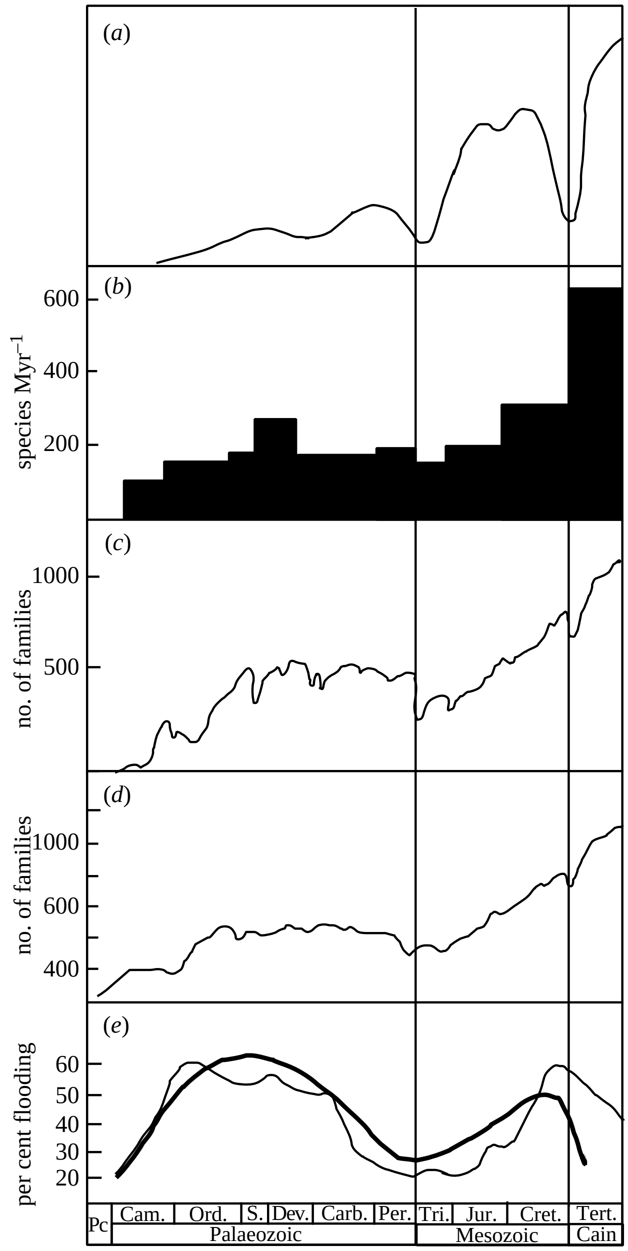

Figure 1. Estimates of Phanerozoic diversity. (*a*) From Phillips (1860). (*b*) Species of invertebrate from Raup (1972). (*c*) Marine families from Sepkoski (1993). (*d*) Marine families from Benton (1995). (*e*) Sea-level curve for the Phanerozoic (fine line) and percentage of platform flooding (heavy line) from Vail *et al.* (1977) and Worsley *et al.* (1986).

this endeavour has been Sepkoski, who set about compiling first- and last-occurrence data of marine taxa in the fossil record, first at family level (Sepkoski 1981, 1982, 1984), then at genus level (Sepkoski & Raup 1986; Sepkoski 1996, 1998). Sepkoski's diversity plot at family level (figure 1*c*) has become widely accepted as the definitive curve for marine organisms. Other compilations quickly followed for land plants (Niklas *et al.* 1980, 1985) and terrestrial vertebrates (Padian & Clemens 1985; Benton 1985, 1989). Subsequently, an independent database listing first and last occurrences of taxa at family level was compiled by a team of specialists (Benton 1993). Although this had some advantages over the Sepkoski compendium, in that individual contributors had in-depth knowledge of the group they were covering, primary data were drawn from the same resources as used by Sepkoski. Analysis of the Benton database (Benton 1995) not surprisingly therefore gave very similar estimates of Phanerozoic diversity (figure 1*d*).

The fact that the Phanerozoic marine diversity curves of Benton and Sepkoski are very similar and that they have proven to be very robust against compilation errors (Sepkoski 1993) has given growing confidence to the idea that they depict the true history of biodiversity. Consequently, over the past two decades attention has shifted to the analysis and interpretation of smaller-scale rises and falls in diversity over time-scales of tens rather than hundreds of millions of years (Myr). In particular peaks of last occurrences have been interpreted as evidence for mass extinction (Raup & Sepkoski 1982, 1984, 1986; Sepkoski & Raup 1986), and peaks of first appearance as evidence for adaptive radiations (Benton 1996; Sepkoski 1998).

However, if there are systematic biases affecting the nature of the rock record, then raw taxonomic counts will give a poor estimation of underlying diversity. It is therefore essential that potential biases affecting the rock record are properly accounted for if we are to obtain accurate estimates of palaeodiversity. Here I shall review the growing evidence that the fossil record is indeed subject to large-scale biases and explore the implications of this for biodiversity studies.

2. ESTIMATING BIODIVERSITY IN THE GEOLOGICAL PAST

Palaeodiversity is estimated from the fossil record in a very straightforward way that requires few assumptions. First a compilation of the known ranges of taxa is drawn up. Such data are now readily available from sources such as Sepkoski (1982) and Benton (1993). In most studies the family or genus is the chosen taxonomic level of focus. Diversity is then simply estimated by counting the numbers of higher taxa present in each time interval (usually stage). Each taxon is assumed to be present between its first and last occurrence, even if it has not been recorded from the intervening strata, and last occurrences are inferred to be lineage extinctions.

Taxonomic compilations provide the simplest and most direct means of estimating diversity levels in the geological past, but they are not error free. Specifically, this approach makes five assumptions about the nature of the taxonomic data and sampling regime. If these do not match reality then palaeobiodiversity estimates could be seriously awry. It is, therefore, worth considering whether these assumptions are realistic in the light of current knowledge.

(a) *Error in the taxonomic database is randomly distributed*

Because of new discoveries and ever-changing taxonomic concepts, no database can be free of error. Error arises from changing views of taxonomic composition (i.e. what species are included in the higher taxonomic categories being used) and changes to the stratigraphical ranges of those taxa through new discoveries or refined correlation. However, so long as error is randomly

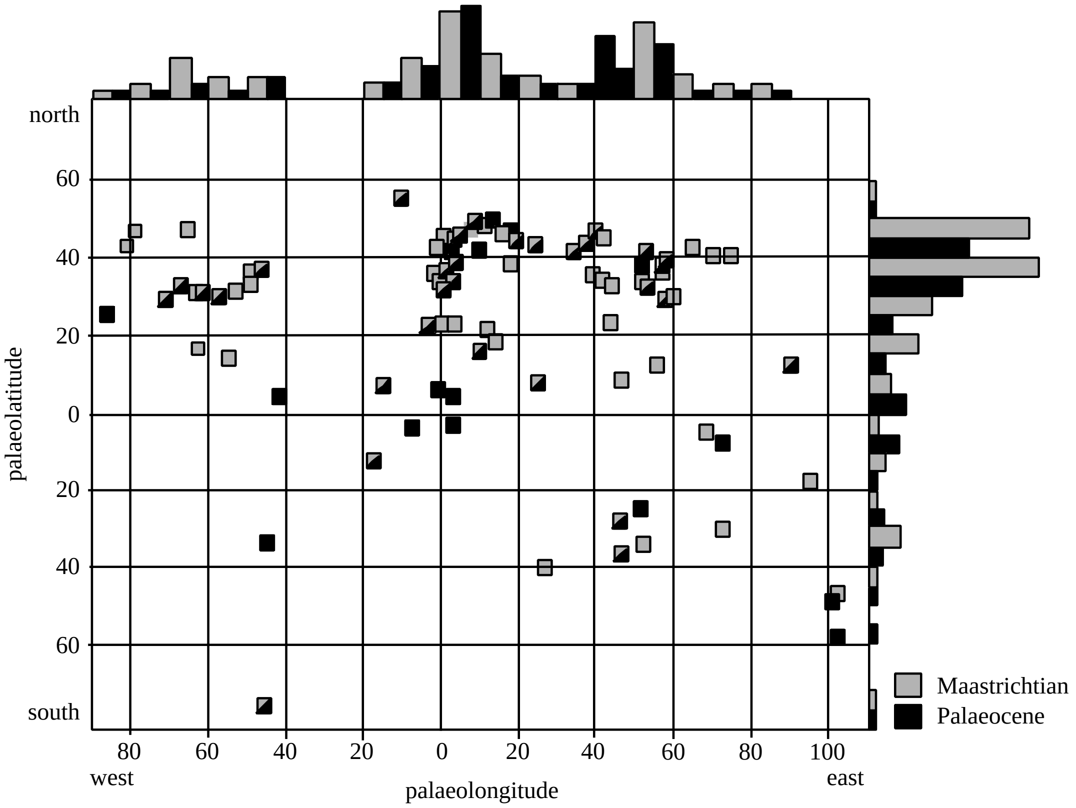

Figure 2. Palaeogeographical distribution of all sedimentary formations that yield echinoid faunas of Maastrichtian and Palaeocene age (data from Smith & Jeffery 2000). Localities have been placed on the palaeogeographical reconstruction of Scotese *et al.* (1988) for the end Cretaceous; bar charts at the top and right-hand side show the relative proportions of fossil localities partitioned into 10° blocks of palaeolongitude and palaeolatitude.

distributed, it can only act to degrade any underlying signal and will not create an artificial one (Raup 1991). This indeed seems to be the case. Sepkoski (1993), despite changing almost a third of his family entries and altering times of origination and/or extinction for 35% of the remaining families over a period of ten years, found that the basic diversity pattern remained unchanged. Adrain & Westrop (2000) came to a similar conclusion. In their work on Ordovician trilobite faunas they made extensive stratigraphical and taxonomic revisions, altering many of the entries listed in the Sepkoski database. Yet, despite this, no significant change in the overall pattern of trilobite diversity over time resulted. As many taxonomic ranges were extended as were shortened. It is therefore safe to conclude that stratigraphical and taxonomic biases in large data sets are effectively random in distribution and thus cannot be responsible for creating trends in diversity patterns.

(b) *Higher taxa are a suitable proxy for species-level diversity*

Data on taxonomic diversity can be compiled at species level (e.g. Raup 1976*a*; Niklas *et al.* 1985), but it is generally accepted that species preservation is too serendipitous for species counts to capture true underlying diversity patterns with any accuracy. Robeck *et al.* (2000, p. 186) found that 'when sampling is poor, counting species results in one of the worst correlations with underlying lineage diversity'. Consequently, higher taxonomic units are used as a proxy for species in diversity counts. Because higher taxonomic units generally involve range interpolation between first- and last-occurrence data, small-scale fluctuations in sampling can be compensated for. However, this requires that there is, on average, a constant relationship over time between the number of species that are included in taxa of a given rank.

In fact, the number of species that are included in family-level taxa varies systematically over geological time (Flessa & Jablonski 1985). Families in the Early Phanerozoic have, on average, many fewer species than families in the Tertiary, and this presumably leads to an increasing overestimation of species diversity as one goes back in time. As extinction and origination are often quoted as per cent extinction or origination with reference to standing diversity, any bias in standing diversity estimate will also affect these metrics, making levels of extinction and origination appear proportionally larger back through time. The weak trend towards declining extinction and origination rates observed over the post-Palaeozoic (documented below, § 5(c)) is probably attributable to this bias, as proposed by Flessa & Jablonski (1985). However, the strongly rising trend shown by diversity over the same time interval is counter to this bias and thus if anything, is underestimated.

(c) *Data are globally representative*

The quality of databases has been steadily improving and both Sepkoski (1982 *et seq.*) and Benton (1993) compiled taxonomic information on a global scale. Yet simply for historical reasons, North America and Europe remain much more densely and effectively sampled than other parts of the world. Figure 2 shows the distribution of sedimentary formations that are known to yield Late Cretaceous and Early Palaeocene echinoids, plotted against palaeolatitude and palaeolongitude. The dominance of sites in the Northern Hemisphere, and especially Western Europe and North America, is striking. Thus even though taxonomic data are drawn from around the world, areas where there has been a long tradition of fossil collecting tend to dominate and drive diversity, origination and extinction patterns. This is very clearly seen in the compilation of first occurrences of marine invertebrate orders published by Jablonski & Bottjer (1990). Out of the 49 records listed, 33 (67%) were from Western Europe and the vast majority of those were from France or England.

This geographical bias in taxonomic databases poses no real problem for diversity studies at medium and small time-scales. For example, an identical bias affects Maastrichtian and Palaeocene sampling and so cannot be responsible for any change in diversity recorded across the Cretaceous–Tertiary boundary. However, over longer intervals of geological time the configuration of continents has altered significantly with respect to the palaeoequator (Allison & Briggs 1993). As marine diversity may be most directly correlated with solar energy (Roy *et al.* 1998) any shift of the well-studied Northern Hemisphere regions from temperate to tropical or polar could create an apparent change in diversity, counterbalance a real change in diversity or enhance a trend artificially.

On the other hand, Europe and North America have remained at more or less the same palaeogeographical latitude since the Early Cretaceous, while taxonomic diversity has increased dramatically. The rising trend shown by taxonomic diversity cannot therefore be explained by geographical bias.

(d) *The nature of the taxa being counted is irrelevant*

Large taxonomic databases will inevitably include a mixture of different kinds of taxa. For diversity counts it makes no real difference whether the taxonomic units being used are monophyletic, paraphyletic, polyphyletic or a mixture of any of the above (Smith 1994). Even when species are randomly partitioned into higher taxa those higher taxa can be used to estimate original standing diversity so long as sampling is effectively uniform. Robeck *et al.* (2000) have demonstrated that taxon size and number are much more important factors in determining whether the underlying pattern of sampled diversity is captured accurately.

However, the nature of the taxonomic units being counted becomes critical when it comes to interpreting changes in diversity and last appearances (Smith 1994). Major gaps in distribution may be used by taxonomists as convenient break-points for subdividing continuous lineages. This has the effect of underestimating the gappiness of the record (by counting two discrete taxa rather than a single taxon with a sampling gap) and leads to overestimation of the number of lineages becoming extinct. Thus changes in diversity are captured by any sort of taxonomic data, but discriminating between changes that reflect underlying biological rises and falls in diversity from those that represent sampling artefacts requires additional information in the form of a phylogenetic hypothesis (Smith & Patterson 1988; Smith *et al.* 2001).

(e) *Sampling is either uniform or varies in a complex and random way*

Taxon counts estimate the diversity of fossils as sampled over time. If sampling and preservational biases can be assumed to be uniform over time, then sampled diversity will accurately reflect real biological patterns of diversity. Alternatively, if sampling and preservational biases can be assumed to fluctuate randomly over time, then the errors introduced will dampen and blur any underlying signal without creating an artificial pattern. Problems arise if there is some sort of systematic bias created by cyclical trends in sampling and preservation. Diversity counts based on mixed (monophyletic and non-monophyletic) taxa would then tend to mirror the quality of the fossil record rather than underlying diversity.

Two independent lines of evidence suggest that there may be major biases affecting the fossil record over time-scales of 10–50 million years (Myr), these being gap analysis and sequence stratigraphical modelling.

(i) *Gap analysis*

If the fossil record were uniformly sampled then gaps in the ranges of taxa should be randomly distributed over time. Conversely, if sampling quality fluctuates over time then we may expect some clustering of gaps during less-well-sampled time intervals.

Several workers have analysed the distribution of taxonomic range gaps through geological time. Smith (1988) demonstrated that the Late Cambrian has a particularly poor fossil record for echinoderms. He found that between 72 and 82% of lineages inferred to have passed through this time interval were still unsampled, whereas the fossil record was estimated to be much more complete for both the Middle Cambrian and the Early Ordovician. Some of this may be due to errors in the phylogenetic hypothesis, but it is unlikely that a discrepancy of this size is entirely artificial. Subsequently, considerable effort has been put into searching outcrops of Late Cambrian age in North America and Australia with only a small resultant increase in diversity (Smith & Jell 1990; Sprinkle & Guensburg 1995). This implies that the low taxonomic diversity is not due to a lack of collecting effort, but reflects a biased rock record in which sedimentary environments that favour fossil preservation are underrepresented at certain times.

Erwin (1993) undertook a similar taxonomic range gap analysis for gastropods through the Permo–Triassic. He found that there was a large increase in the proportion of taxa missing from the record during the Early Triassic and attributed this to preservational failure and especially to the drop in the number of silicified assemblages. Gastropods are aragonitic-shelled and thus highly prone to be lost from the rock record unless silicified. Cherns & Wright (2000) have recently stressed the problem of silicification biases in the fossil record.

On a larger scale, Paul & Donovan (1998) applied range gap analysis to families of Palaeozoic echinoderms and found striking fluctuations in the proportion of gaps through time. They pointed out that mass extinctions were generally followed by sharp increases in the proportion of unsampled taxa, bearing out Erwin's (1993) gastropod data.

Two explanations have been advanced for why gaps in taxonomic ranges cluster immediately after mass extinctions: either taxa are present in much lower abundance after an extinction event and thus are less likely to be sampled (Wignall & Benton 1999) or the drop in diversity reflects sampling or preservation artefacts (Twitchett 2000). The obvious taphonomic bias of the fauna that disappear (Twitchett 2000) and the fact that the taxa that temporarily disappear are predominantly found in habitats that also disappear from the fossil record for extensive periods of time (Smith *et al.* 2001) is clear evidence that the latter explanation is correct. Taxon absences arise because of lack of habitat continuity and/or changing preservational opportunity in the fossil record, not as a result of fluctuating abundance within a uniformly sampled habitat.

(ii) *The stratigraphical distribution of fossils*

The biases imposed by sequence stratigraphical architecture on the nature of the fossil record are now reasonably well documented, thanks to the efforts of Brett, Patzkowsky and especially Holland. Holland (1995*a*,*b*) used computer modelling to examine the predicted distribution of fossils within sequence bundles. He was able to show that peaks of origination and extinction could be generated by sequence architecture even when none originally exist. Specifically he noted that first occurrences and last occurrences of taxa tend to cluster around major flooding surfaces purely from sampling considerations. Stacked sequence bundles in a deepening or shallowing trend will tend to reinforce this pattern, especially if there is erosion and increased duration of hiatus at a sequence boundary. Using a similar numerical approach Holland & Patzkowsky (1999) have also shown that there are significant differences in the preservation potential of sediments from different basinal settings and at different times in a stacked depositional sequence. There is a growing body of field observations to support the basic premise that sequence stratigraphical architecture controls faunal diversity patterns, at least on a local or regional scale (Patzkowsky & Holland 1996, 1999; Brett 1995, 1998; Goldman *et al.* 1999; Smith *et al.* 2001).

The implications are obvious. Before we can start to interpret changes in taxonomic diversity at a scale of stage level (i.e. changes over time intervals of *ca.* 5–30 Myr) we must be sure that these changes are not simply driven by sequence architecture. Holland (1995*a*,*b*) noted that extinction events, such as at the Permo–Triassic boundary, commonly coincide with major flooding surfaces in the transgressive systems tract. He raised the valid question as to whether last occurrences were clustered because of biological events or sedimentary controls on preservation and distribution. 'The sequence models suggest that there should exist horizons characterized by the abrupt last occurrences of many relatively shallow-water taxa and the abrupt first occurrence of many relatively deep-water taxa. If the fossil record were read literally, this pattern might be misinterpreted as a mass extinction followed by a major radiation . . .' (Holland 1995*b*, p. 18).

One such interval is the Cenomanian–Turonian boundary. Smith *et al.* (2001) dissected the distribution of last-occurrence data in terms of basinal setting and sequence stratigraphical framework and demonstrated a tight correlation between faunal change, preservation potential and sea level. Although faunal changes at that interval had previously been taken as evidence for a mass extinction and subsequent radiation, Smith *et al.* (2001) were able to demonstrate that faunal replacement patterns were those predicted if sequence depositional architecture was the controlling factor.

3. SAMPLING QUALITY OF THE FOSSIL RECORD

If the fossil record has been sampled efficiently then estimates of palaeodiversity from taxon counts are more likely to be accurate and reliable than if we have only sampled a small proportion of the available fossil record. So how good is our knowledge of the fossil record? The past 150 years have witnessed an exponential growth in the intensity of palaeontological collecting, and have brought us to a point where our sampling of the fossil record on the whole appears to be really very good if we confine ourselves to taxa that possess a heavily mineralized skeleton. Although early estimates suggested that less than 10% of species were preserved in the fossil record (Newell 1959; Valentine 1970; Signor 1985), more recent findings suggest that we have achieved surprisingly high levels of completeness, especially in well-studied parts of the world.

Three lines of evidence support this view: gap analysis, historical sampling curves and frequency-distribution analysis. Gap analysis estimates completeness as the number of time intervals that the taxon is missing from divided by the total number of time intervals between its first and last occurrence. Using this approach Paul (1982, 1998) estimated that between 70 and 80% of the record of Palaeozoic cystoid families were sampled at stage level, while Harper (1998) found more than 90% of bivalve families have a continuous record at stage level.

The construction of collection curves for fossil taxa provides a second measure of completeness. Maxwell & Benton (1990), Benton & Storrs (1994) and Benton (1998) have applied this approach to a number of vertebrate clades. For a well-studied group such as European dinosaurs the data fall on a logistic curve, implying that the great proportion of fossil taxa expected from these outcrops have been collected. Palaeontologically less-well-explored countries such as China, however, remain undercollected (Benton 1998).

A somewhat related approach is to ask how many new taxa have been described from newly made collections, as opposed to revision of museum material already collected (Paul 1998). For bivalves and echinoderms this approach suggests that around 60% of species, 90% of genera and maybe 95% of families are already known (Paul 1998; Harper 1998) and that new collections largely resample the known fossil record.

The third approach uses frequency-distribution data of taxonomic ranges (Foote & Raup 1996). This technique uses empirically determined sampling patterns, specifically the relative frequency of taxa confined to a single time interval to those in two or three successive time

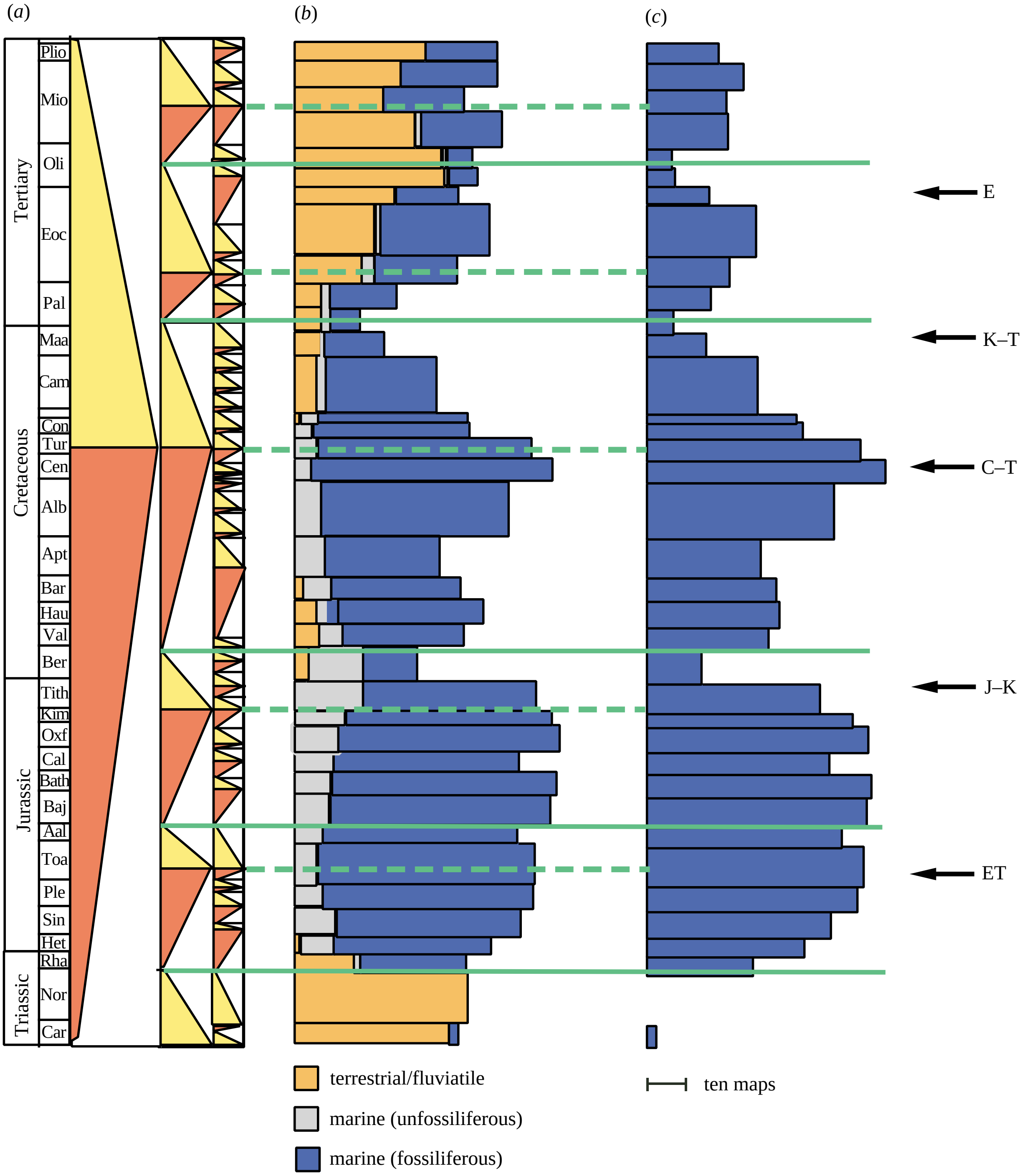

Figure 3. Sequence stratigraphical framework and surface area of sedimentary rock cropping-out in France and England. (*a*) First-, second- and third-order sequence stratigraphic cycles determined for Western Europe (from Hardenbol *et al.* 1998). Solid green lines, second-order sequence bases; dashed green lines, second-order flooding surfaces. (*b*) Sedimentary rock outcrop area measured as numbers of geological maps (1:63 360 UK series, 1:50 000 French series) with outcrops of that age. Sedimentary rocks are partitioned into terrestrial/fluviatile, marine with fossils, and unfossiliferous marine or metasediments. (*c*) As (*b*), but with only fossiliferous marine sedimentary rocks plotted. Arrows indicate the five major mass extinction events (ET, Early Toarcian; J–K, end Jurassic; C–T, Cenomanian–Turonian; K–T, Cretaceous–Tertiary; E, end Eocene.

intervals, to provide an estimate of the average completeness. For Late Cambrian–Early Ordovician trilobites from Oklahoma and European bivalve species completeness was estimated at 90%, while Ordovician-to-Devonian crinoid genera and Cenozoic mammal species of North America had slightly poorer records (70 and 60%, respectively). When applied to global databases similar ranges of completeness emerged for many fossil groups with a robust skeleton (Foote & Sepkoski 1999).

All three approaches are encouraging in that they suggest that our sampling of fossils from the rock record is now really rather good. However, all are concerned primarily with how well sampled our rock record is, not how complete or representative that rock record is of what once existed. Furthermore, the extent to which we have sampled the available rock record is much less important than whether we have sampled uniformly over time. Sampling uniformly at 30 or 90% efficiency should generate identical diversity curves. However, if there are major temporal biases in the rock record then our sampled fossil record will be equally biased, even if we have sampled the available rocks with 100% efficiency. As extinction and origination peaks are generally resolved to stage level, can we assume that the preservational bias and sampling at stage level remain effectively uniform? Sepkoski & Raup (1986, p. 6) claimed that '[taxonomic] data for the most part are uniformly sampled over the entire fossil record, permitting unbiased estimates of long-term extinction patterns and allowing comparisons of patterns from one geologic interval to another'. This claim is critical to the whole taxic approach, yet it has never been tested.

4. SYSTEMATIC BIAS IN THE POST-PALAEOZOIC ROCK RECORD

Raup (1972, 1976*b*) was the first to consider seriously the problem of sampling bias in the fossil record. He showed that there was a remarkably strong correlation between rock volume or surface outcrop area and apparent species diversity. Raup considered various possibilities and concluded that the simplest explanation was that recorded species diversity reflected sampling effects rather than true underlying biodiversity trends. The more rock surface sampled, the more specimens collected, and the more specimens collected the more species recorded. Younger rocks are, in general, less indurated than older rocks (making fossil collecting easier) and offer a larger outcrop area, so even under uniform diversity, the expectation is for apparent diversity to increase towards the present. Furthermore, older sedimentary rocks are more likely to be metamorphosed and their fauna eradicated. Statistical tests by Raup (1976*b*) and Sepkoski (1976) strengthened the support for this correlation. Although both Raup and Sepkoski subsequently recanted this view in favour of a direct reading of the fossil record (Sepkoski *et al.* 1981), the questions raised about sampling bias have never been tackled properly.

Raup's (1972, 1976*a*,*b*) pioneering analysis of rock-record bias had to make several simplifications. First his species database was for invertebrates and protists in general and, although dominated by marine species, it included non-marine molluscs and insects. Second, his estimates of rock volume and surface outcrop did not distinguish marine from non-marine and did not take any account of the degree of diagenesis or metamorphism that affected those rocks. Finally, data were compiled at the level of geological era and provide a rather crude picture in comparison with subsequent taxonomic databases that have been compiled at stage level. For comparison with current taxonomic databases a more refined estimate of surface outcrop area has therefore been assembled.

Surface outcrop data have been compiled using the British Geological Survey 1:63 360 (1 inch) series maps and the French Geological Survey 1:50 000 series maps. I have focused on the time interval from the Late Triassic to the Plio–Pleistocene, dividing this interval into the 40 stages or epochs used by Sepkoski for his taxonomic database. For each map I have recorded whether sedimentary rocks of those 40 time intervals crop-out, and if so, whether they are terrestrial, fluvio-lacustrine or marine. The associated sheet memoir was used to establish whether the sedimentary rocks of each time interval cropping-out had yielded an invertebrate fauna. Unfossiliferous sedimentary units, such as heavily dolomitized limestones and metasediments in tectonic nappes, were recorded separately. In total, data were compiled for 254 French maps and 345 UK maps. Surface area of outcrop was then expressed simply as the number of map areas in which rocks of each of the 40 time intervals were recorded. Although slightly less accurate than measuring surface outcrop area directly from each map, this method has the distinct advantage of providing quantitative information on the distribution of fossiliferous deposits and on the palaeoenvironmental setting of exposed rocks. The first-, second-, and third-order sequence stratigraphical framework for Europe is taken from Hardenbol *et al.* (1998).

When map area is plotted against time (figure 3*b*) a cyclical trend is evident, with terrestrial deposits predominating in the Triassic and later Tertiary, at times of low sea level, and marine deposits being particularly well represented during the Jurassic and the Cretaceous. This corresponds to the first-order sequence cycle of Hardenbol *et al.* (1998) and the post-Palaeozoic supercycle of Fischer & Arthur (1977) and Fischer (1984).

When marine deposits alone are plotted then cyclicity at a finer scale is evident, with marked drops in outcrop area recorded at the Triassic–Jurassic, Jurassic–Cretaceous and Cretaceous–Tertiary boundary intervals and during the Oligocene (figure 3*c*). These cycles, for the most part, coincide with Hardenbol *et al.*'s (1998) second-order depositional cycles. However, two second-order sequence stratigraphical cycles have been distinguished in the Jurassic but only one major cycle is apparent in surface outcrop area. This suggests that the importance of the two Jurassic cycles might have been overemphasized by sequence stratigraphers relative to those in the Cretaceous and Tertiary.

Overall there is a clear trend towards smaller sedimentary rock outcrop area through time. This is evident from plotting rock outcrop area against time (figure 4*a*). The Pearson correlation coefficient is 0.67 and the regression coefficient is strongly negative ($y = 0.994x + 48.98$) and significant at the $p < 0.005$ level ($r^2 = 0.472$). This is because there is a marked reduction in preserved outcrop area during the regressive phase of the first-order depositional cycle. To remove this trend the residuals from the regression analysis were plotted and used in all further analyses (figure 5*a*).

To test whether the pattern conformed to a random walk the detrended data were subjected to a Wald–Wolfowitz runs test (Wilkinson *et al.* 1992) with a cut point of zero. This rejected the hypothesis of a random walk at $p = 0.001$. The data can therefore be considered as defining a cyclical time-series.

To explore the structure of this time-series the autocorrelation signal resident in the detrended data was plotted (figure 6*a*). There is a very strong dependence in the residuals with a cycle duration of 12 time intervals and a barely significant negative autocorrelation at six steps.

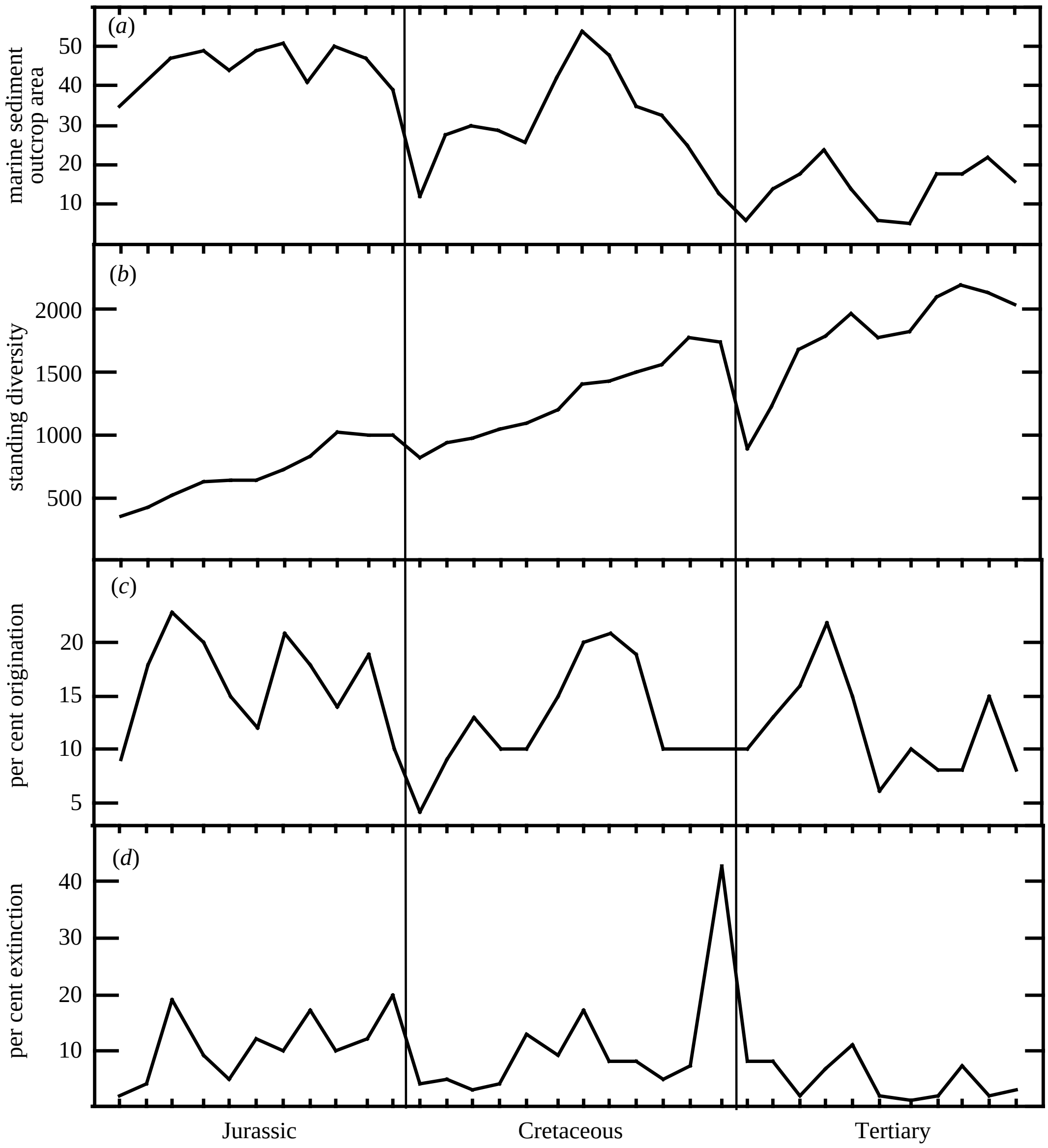

Figure 4. Plots of (*a*) marine sediment outcrop area; (*b*) generic-level standing diversity (from Sepkoski 1996); (*c*) per cent origination at generic level (from Sepkoski 1998); (*d*) per cent extinction at generic level (from Sepkoski 1996), all plotted against geological stage from the Hettangian to the Plio–Pleistocene.

5. SEQUENCE STRATIGRAPHY, ROCK RECORD BIAS AND POST-PALAEOZOIC DIVERSITY PATTERNS

It is clear from § 4 that our ability to sample the fossil record cannot be considered uniform over time. The match between surface outcrop area and sequence stratigraphy is striking, with both first- and second-order cycles leaving a clear signature on the post-Palaeozoic rock record. The surface outcrop area of marine sedimentary rocks that is preserved changes predictably according to sequence stratigraphical structure, as does the ratio of terrestrial to marine sediments (figure 3). Stacked regressive phases result in a relatively poor marine fossil record but a good terrestrial record, while extended highstand intervals are associated with a poor terrestrial rock record. Thus even if diversity had been effectively uniform over time, the heterogeneity of the sedimentary record would create apparent fluctuations in diversity simply through sampling and the species–area effect. Alternatively, changing surface area of shallow marine seas through time could be driving biological diversity patterns. In either case a relationship between outcrop surface area and species diversity is expected.

So what evidence is there that surface area effects are influencing diversity patterns? Here I test whether there is correlation between rock outcrop area and tabulated taxonomic diversity in the fossil record. Diversity data for marine animal genera were taken from Sepkoski's compilation. Per cent extinction (100 × number of originations/standing diversity) and standing diversity (number of recorded genera per time interval) were taken from Sepkoski (1996) and per cent origination (100 × number of extinctions/standing diversity) from Sepkoski (1998).

(a) *Standing diversity and outcrop area*

A plot of standing generic diversity against time (figure 4*b*) shows a strong rising trend over time. This

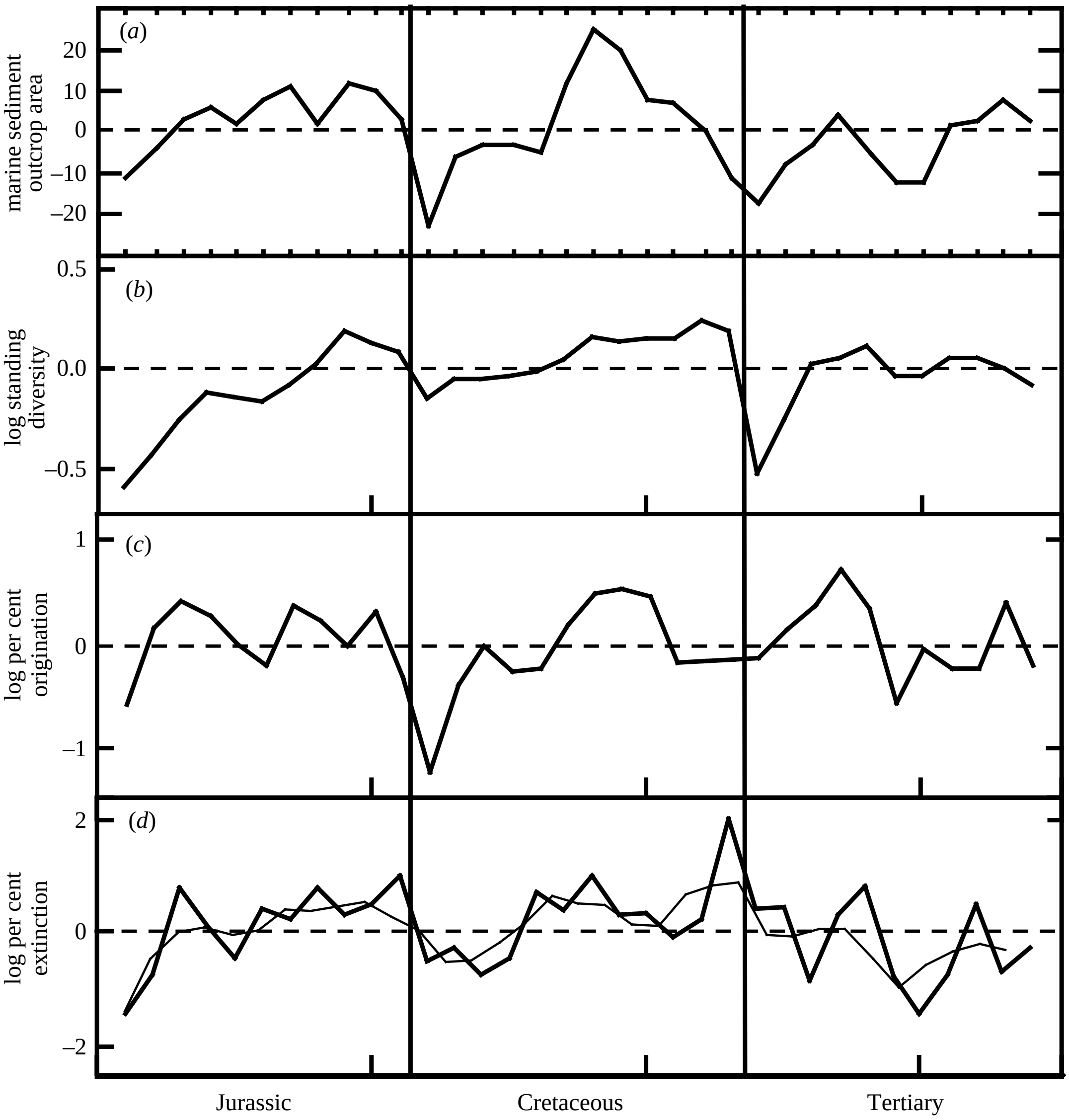

Figure 5. Detrended plots of (*a*) marine sediment outcrop area; (*b*) log generic-level standing diversity (from Sepkoski 1993); (*c*) log per cent origination at generic level (from Sepkoski 1998); (*d*) log per cent extinction at generic level (from Sepkoski 1996), all plotted against geological stage from the Hettangian to the Plio–Pleistocene. In each case, data were recast as residuals from a regression against time (geological stages treated as an ordered series). In (*d*) the fine line is a three-point moving average weighted (1, 2, 1).

contrasts with the declining trend in rock surface outcrop area over the same time interval. Superimposed on this overall trend is a series of small rises and falls in diversity, with a major drop immediately following the Cretaceous–Tertiary boundary. The Danian and to a smaller extent, Thanetian, stand out as outliers against an otherwise very clear trend. A regression analysis of these data gives a strong positive correlation ($r^2 = 0.889$ and a probability significant at $p < 0.0005$).

Diversity data were first transformed to logarithms, in order to reduce variation in amplitude, and then recalculated as residuals from regression on time to remove the temporal trend. A plot of detrended data (figure 5*b*) was investigated using the Wald–Wolfowitz runs test (Wilkinson *et al.* 1992) with a cut point of zero. The hypothesis that this pattern represents a random walk can be rejected with high confidence ($p < 0.005$). Furthermore, this time-series closely matches the detrended plot of rock outcrop area in appearance.

The structure of this time-series was explored in more detail using autocorrelation analysis (figure 6*b*). A plot of autocorrelation lag closely resembles a similar plot derived from rock outcrop surface area and is suggestive of a cyclical pattern, with strongest negative correlation some 7 and 16 time intervals offset. Smoothing the trend using a three-point weighted running average markedly improves the cyclicity signal of the autocorrelations. Cross-correlation was used to test how well points on one time-series predict the position of points on a second time-series. A cross-correlation plot comparing detrended diversity and surface area shows a strong and significant correlated peak at lag 0 and at a lag of −1 (figure 7*a*). Standing taxonomic diversity is therefore significantly

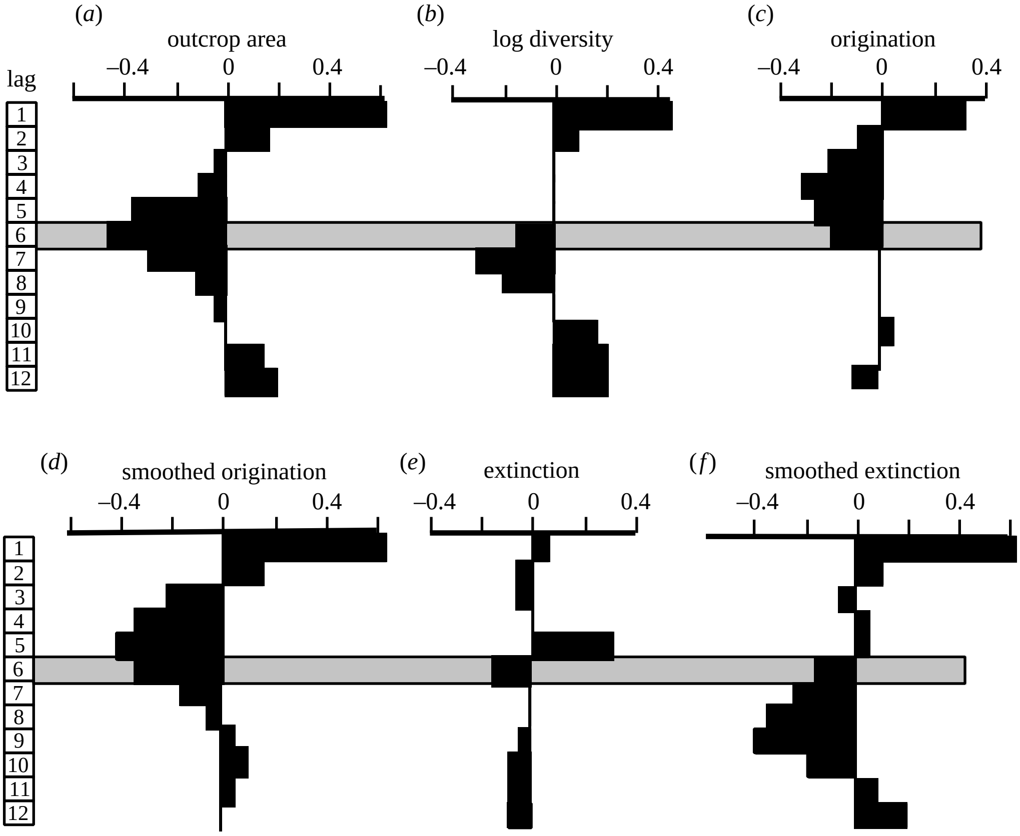

Figure 6. Autocorrelation charts for (*a*) marine sediment outcrop area; (*b*) log standing diversity; (*c*,*d*) generic originations; (*e*,*f*) generic extinctions; all plotted against time (geological stages treated as an ordered series). Charts depict how strongly correlated points on the time-series are to those one, two, three . . . , etc., time-units removed. Stippled band is for reference only.

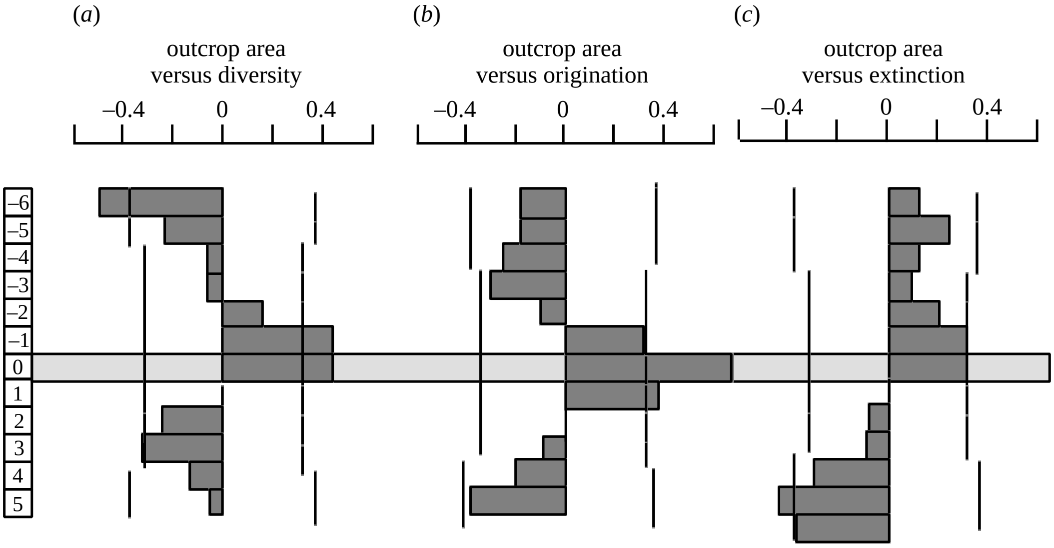

Figure 7. Cross-correlation charts for marine sediment outcrop area versus (*a*) standing diversity; (*b*) generic originations; (*c*) generic extinctions; all plotted against time (geological stages treated as an ordered series). Charts indicate the degree of match between two time-series plots at various degrees of lag. Lines indicate two standard errors about the mean. Stippled band is for reference only.

correlated to the surface outcrop area observed in that stage and the immediately preceding stage.

(b) *First-occurrence patterns and outcrop area*

Per cent origination plotted against time shows a wide scatter of points with a slight decline towards the present (figure 4*c*). Regression analysis gives a non-significant negative correlation ($p = 0.054$) of $y = -0.171x + 16.89$. The data were transformed into logarithms and detrended prior to further analysis (figure 5*c*). A runs test suggests that these data are more structured than expected from a random walk (Wald–Wolfowitz runs test; $p = 0.026$).

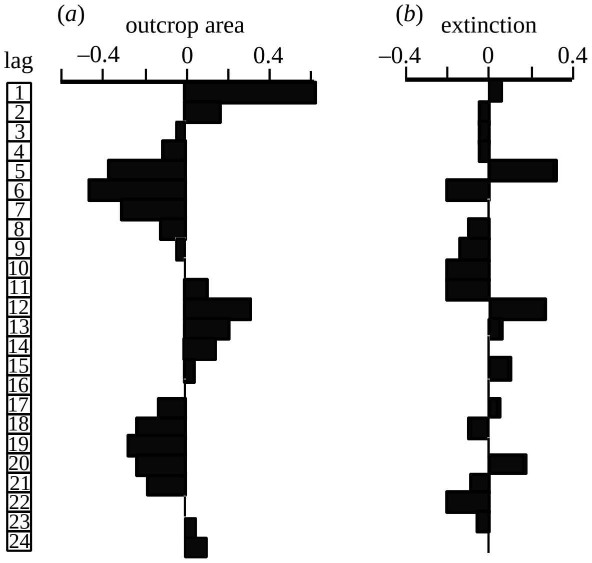

Figure 8. Extended autocorrelation charts for (*a*) marine sediment outcrop area; (*b*) generic extinctions; plotted against time (geological stages treated as an ordered series). Extinction peaks appear to coincide with rock outcrop area maxima and minima.

The detrended series shows a very close match to the surface outcrop area time-series (figure 5*a*,*c*). Cross-correlation analysis shows a strong and highly significant positive correlation with rock outcrop area, with no lag (figure 7*b*). A plot of autocorrelations suggests only that there is a small and non-significant negative correlation after a lag of four time intervals (figure 6*c*). Smoothing the data with a 1, 2, 1 weighted three-point moving average increases the autocorrelation but not to levels of significance.

(c) *Last-occurrence patterns and outcrop area*

Per cent extinction plotted against time shows a wide scatter of points, with the Maastrichtian extinction datum forming a prominent outlier (figure 4*d*). If this point is excluded, there is a trend towards lower extinction rates towards the present (regression equation of $y = -0.207x + 11.74$; $r^2 = 0.161$, $p = 0.021$). A runs test on the log residuals is not significant (Wald–Wolfowitz runs test; $p = 0.108$), so the pattern of extinctions effectively conforms to a random-walk model. This is confirmed by autocorrelation, which, after transforming to logarithms and detrending, showed little evidence of autocorrelation at stage level (figure 6*e*). However, there are small though non-significant peaks at every five or six time intervals, corresponding to the 27 Myr periodicity suggested by Raup & Sepkoski (1982). The peaks coincide with maximum and minimum rock surface area (figure 8).

Cross-correlation between the detrended but unsmoothed extinction curve and rock outcrop area identifies two positions at which significant correlations are to be found (figure 7*c*). There is a significant positive correlation at a lag of 0 and −1 and a significant negative correlation at a lag of +5.

6. DISCUSSION

Twenty-five years ago the burning issue in palaeontology was whether counts of taxa from the fossil record reflected sampling artefact or true biological diversity. At that time Raup (1976*b*, p. 295) was so confident that sampling was driving diversity curves that he suggested that 'the burden of proof lies with those who would argue that diversity was indeed higher in the Cretaceous and Tertiary than at other times in the Phanerozoic'.

It is now evident from the data presented here that the general trend of increasing taxonomic diversity since the Late Triassic at family or genus level runs counter to the influence of sampling biases and can therefore be considered a robust estimate for how biodiversity has changed over time. However, the same cannot be said for the long-term Palaeozoic diversity curve or for smaller-scale trends of origination and extinction during the post-Palaeozoic.

Before discussing the general implications of this finding it is worth considering three possible factors that may limit the generality of conclusions that can be drawn from my analysis. First, rock area has been measured for only a small part of Western Europe, second this study has looked only at the post-Triassic record of that area, and third the analysis deals only with shallow-water marine invertebrates, which form a small fraction of the total global biodiversity.

Although data are compiled from only a limited area it seems almost certain that first- and probably second-order cycles of sequence stratigraphical architecture are the result of worldwide changes. Hardenbol *et al.* (1998, p. 6) referred to second-order cycles as major transgressive–regressive (MTR) cycles and pointed out that they 'reflect the response of the western portion of the Eurasian plate to major plate tectonic phases in the opening of the Atlantic Ocean. These major tectonic phases affect the volume of ocean basins and hence global sea level and thus produce synchronous tectono-eustatic MTR cycles which are essentially identical for Tethyan and boreal basins'. Consequently, the biases I have identified in the rock record of France and England are likely to be repeated in many other places. Furthermore, as pointed out above (§ 2(c)), a surprising number of first and last occurrences are of Western European taxa, simply because the geology of this region is so extensively known.

Quantitative data have only been presented for the post-Palaeozoic, but there is no reason to believe that the Palaeozoic is any different (see § 6(a)). Phylogenies provide an independent means of estimating how good our fossil record is (Norell & Novacek 1992; Benton *et al.* 2000), since they provide an independent estimate of the order in which taxa ought to appear in the fossil record. However, it is difficult to transform these findings into a general guide to how complete the fossil record is. The fit is significantly better than random and, on a coarse scale, the fit of cladograms against stratigraphy for Palaeozoic, Mesozoic and Tertiary taxa shows no significant change (Benton *et al.* 2000). However, the Benton *et al.* analysis was at too coarse a level to give insight into secular changes in the quality of the fossil record over time-scales discussed here. All that can be said is that the problems of

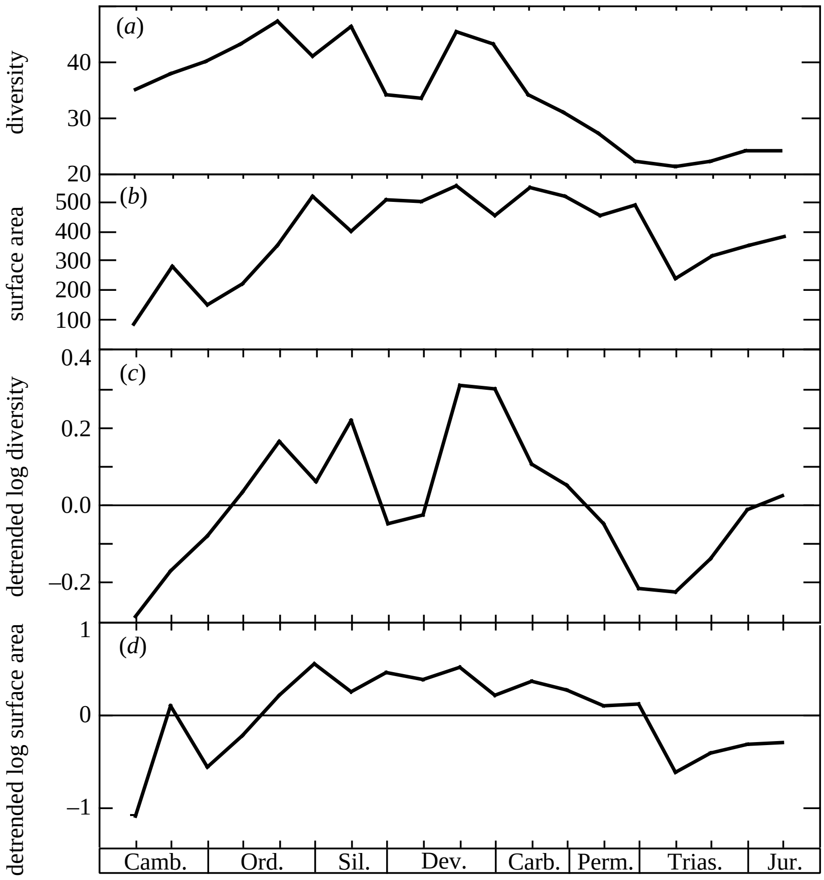

Figure 9. (*a*,*c*) Raw and detrended data on family-level taxonomic diversity (from Sepkoski 1993, fig. 4). (*b*,*d*) Raw and detrended data on area of continents covered by seas ($\times 10^6\,\mathrm{km}^2$) (from Ronov 1994, fig. 13). All data are plotted against time (geological eras and epochs treated as an ordered series) from the Early Cambrian to the Early Jurassic.

the rock record pointed out above almost certainly also apply to the Palaeozoic record, but are not necessarily any worse.

Finally, shallow marine invertebrates do account for only a small part of today's biodiversity but they are the overwhelmingly dominant constituent of the fossil record. Nor are terrestrial deposits immune from rock biases imposed by sequence stratigraphical architecture. It is therefore safe to conclude that the results are of general relevance to how we estimate Phanerozoic diversity.

(a) *Diversity in the Palaeozoic*

The Phanerozoic sea-level curve is composed of two first-order cycles (Vail *et al.* 1977; Fischer 1984; Worsley *et al.* 1986) with lowest surface area of continental shelf seas reached during the Cambrian, Permo–Triassic and present day (figure 1*e*). Comparison of diversity curves in the two first-order cycles suggests that the two are not comparable. In the post-Palaeozoic cycle there is clear decoupling of diversity from surface area, with diversity increasing relentlessly towards present-day levels even through the first-order highstand and lowstand system tracts, when outcrop surface area is declining. This decoupling is reassuring because it demonstrates that the observed taxonomic diversity could not be produced from sampling bias. In contrast Palaeozoic taxonomic diversity is either static or in decline during the first-order highstand and lowstand system tracts and more closely tracks inferred sea-level trend. At best this would suggest that diversity was increasing at a much slower rate during the Palaeozoic than in the post-Jurassic. However, there remains the strong possibility that the general Palaeozoic diversity curve is largely a reflection of rock outcrop area, as initially suggested by Raup (1972, 1976*b*).

The area of continental shelf covered by sea through the Phanerozoic was estimated by Ronov (1994) based on rock outcrop area. Although this is at a coarser resolution than the study presented here, it does provide an opportunity to test whether rock outcrop is correlated with apparent taxonomic diversity. Figure 9 plots area of continental shelf covered by sea and marine invertebrate family diversity from the Early Cambrian to the Early Jurassic. Log-transformed and detrended plots of the same are also provided. Although far from perfect, the two trends show some similarities and indeed a cross-correlation plot (figure 10) indicates significant correlation between the two. It is therefore likely that our current view of Palaeozoic diversity is also at least partially moulded by sequence architecture and MTRs.

(b) *Species–area correlation: a reflection of ecology or sampling?*

Evidence presented here shows that there is a strong species–area control on post-Palaeozoic diversity curves

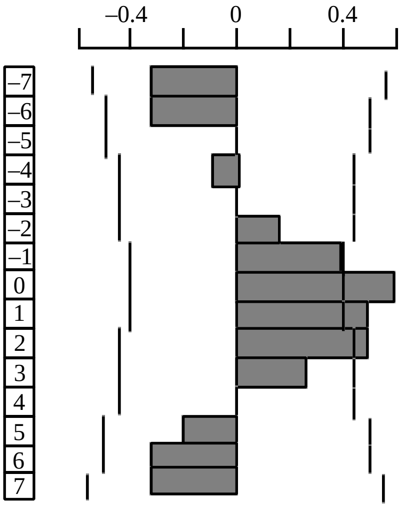

Figure 10. Cross-correlation chart for shelf sea area (from Ronov 1994) versus family diversity in the fossil record (from Sepkoski 1993) from the Early Cambrian to the Early Jurassic. The vertical lines indicate two standard errors about the mean.

that is superimposed onto the long-term trend. There are two contrasting explanations for why surface outcrop area and marine biodiversity through the post-Palaeozoic should be correlated. Variation in surface outcrop area could reflect original changes in the extent to which shallow seas covered cratonic blocks. The well-known species–area relationship means that a plot of diversity against surface area approximates well to a simple power function (Rosenweig 1996). Therefore, as surface area of continental shelf seas increases marine species diversity is also expected to increase.

Alternatively, the present-day surface-outcrop area may have little or no relationship to the original surface area of shelf seas and the species–area relationship observed may simply arise through sampling. The more rock exposed the more fossils that can be collected and the higher the perceived diversity of that time interval.

Disentangling which of these two classes of explanation is responsible for the correlation between rock outcrop area and taxonomic diversity is not simple because the two are intimately related. Increasing sea level floods more of the continental cratonic area, but also leads to an increase in the surface area of rock ultimately preserved at outcrop. So is the Cenomanian a time of high diversity because of the large surface area of rock outcrop that we have access to or because of the development of wide epicontinental seas at this time? Further complications arise because changing sea level also alters preservation potential of both fossils and palaeoenvironment, and marine diversity varies with water depth. Increasing average water depth over the continental shelves can alter the ratio of onshore to offshore habitats that enter the rock record and even result in reduced diversity being preserved in the fossil record (Smith *et al.* 2001).

Water depth affects preservational potential of fossils in several ways. The preservation of multiskeletal organisms such as arthropods and echinoderms is greatly enhanced by relatively rapid and final burial. Brett *et al.* (1997) provided a detailed classification and characterization of taphofacies that relates preservation potential to position within depositional cycles. Taken together with Kidwell & Baumiller's (1990) study, preservational conditions are probably at their optimum in transgressive system tracts when water depth is *ca.* 20–100 m. Aragonitic-shelled organisms such as gastropods and ammonites are rapidly lost in deeper-water settings by dissolution (Koch 1998) and even the more robust calcitic-shelled forms will degrade through bio-erosion if sedimentation and burial are too slow. Thus, although there are few hard data, it is intuitive that preservation potential will generally decrease in deeper water, while the high-energy near-shore environments are also expected to have low preservation potential because of breakage and abrasion.

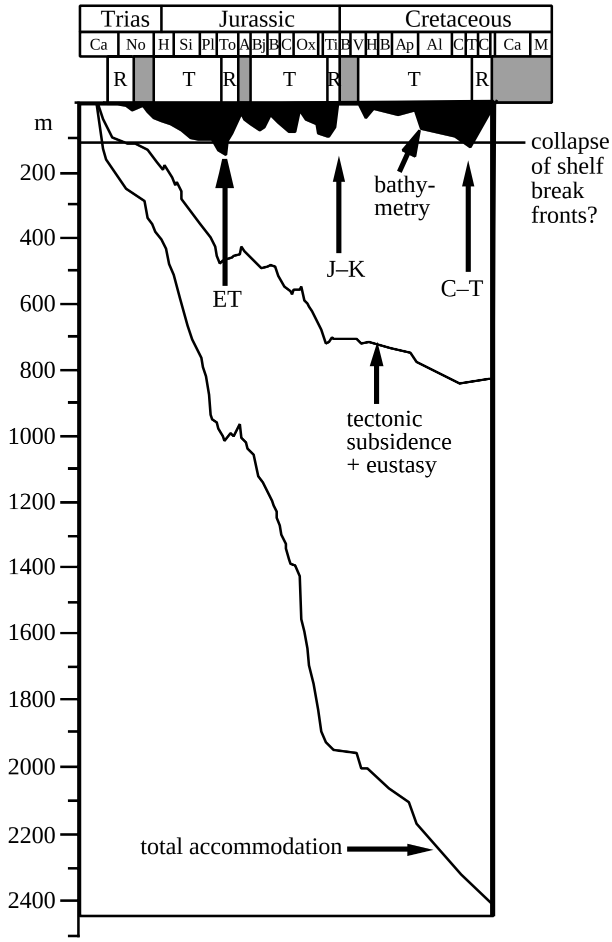

Figure 11. Water bathymetry and accommodation space history for the Paris Basin as determined from backstripping, modified from Jacquin & de Graciansky (1998). The horizontal line indicates the depth at which shelf-margin fronts might have broken down allowing stratified oceanic waters to replace mixed coastal waters. T, transgressive phase; R, regressive phase; black, no rock record; ET, Early Toarcian; J–K, end Jurassic; C–T, Cenomanian–Turonian.

Species diversity of benthic marine invertebrates is also depth related. Within level-bottom mud habitats total diversity is at its highest between 1000 and 2000 m water depth (Begon *et al.* 1996). However, because habitats are much more heterogeneous in shallow-water settings than at these depths, Gray *et al.* (1997) argued that shallow-water settings should have much higher diversities when all habitats are taken together. This is borne out by empirical data (Smith *et al.* 2001), which show that echinoid species diversity peaks at *ca.* 80–120 m in present-day open marine settings.

Preservation potential and diversity for common macroinvertebrates both peak in the range of 20–120 m water depth, so any change in the relative surface area of continental shelf seas within this depth range, either at the time of deposition, or as ultimately preserved in the fossil record, could create changes in apparent species diversity over time even if diversity remained constant. This is a real problem. Schaff (1996) demonstrated that dramatic changes to the surface area of the photic zone occurred during Pleistocene sea-level changes, and Smith *et al.* (2001) have shown that the relative ratio of onshore to offshore facies varies through time in response to sea-level changes in the Mid-Cretaceous.

The only realistic way to distinguish between sampling and biologically driven patterns is to gather phylogenetic information. The key here is the recognition of ghost lineages and the stratigraphical distribution of pseudoextinctions. Pseudoextinctions are created when continuous lineages are separated into a plesiomorphic grade and a derived clade, often using gaps in the fossil record as the convenient cut point. If sampling were the dominant factor, pseudoextinctions should be relatively common and concentrated at system boundaries and transgressive systems tract flooding surfaces. Conversely, if biological factors are responsible then we would expect extinctions of monophyletic clades to predominate over pseudoextinctions. However, if erosion and non-deposition create a large gap in the rock record, extinctions occurring in the unsampled interval will be smeared back in time to just before the hiatus, giving a mixed signal that is difficult to interpret.

As yet there are few studies that attempt to distinguish between biological extinction and pseudoextinction, although Paul & Donovan's (1998) observation that taxonomic gaps cluster after mass extinction events implies that sampling is probably a significant problem at those times. Smith *et al.* (2001) found a preponderance of pseudoextinction and a major gap in the record of shallow marine sediments at the Cenomanian–Turonian boundary. They concluded that sampling was the predominant cause of the peak of last occurrences at this time. By contrast, phylogenetic work on the Maastrichtian–Palaeocene echinoid fauna demonstrates that some 35% of taxa at generic level have no known Tertiary descendants (Smith & Jeffery 1998). Thus although sampling could conceivably play a major part in exacerbating the size of the apparent extinction event, there is a genuine extinction signal at the end Cretaceous. More phylogeny-based studies are urgently needed.

(c) *Mass extinction: a common thread?*

Of the five major mass extinctions of the post-Palaeozoic recognized by Sepkoski & Raup (1986) two occur towards the end of a prolonged sequence of stacked sea-level rise and three coincide with the terminal phase of a stacked regressive system tract (figures 3 and 8). Although this disparity suggests that there is no single underlying factor, these are the two intervals in a depositional cycle where computer modelling has predicted clusters of first and last occurrences are to be expected even in the absence of pulsed extinction (Holland 1995*a*). Furthermore, the major extinctions all share a number of important characteristics: they coincide with massive flood basalt outpourings, occur during unusually large and sharp sea-level excursions close to flooding surfaces in transgressive system tracts, are associated with strong positive δ^{13}C excursions, but without evidence for widespread anoxia in shelf areas, and take place through whole-scale community replacement, with a low-diversity fauna replacing high-diversity fauna and little continuity at species or genus level.

The end Jurassic, end Cretaceous and end Eocene extinction peaks each coincide with the terminal phase of a stacked regressive systems tract and are followed by intervals of minimal surface outcrop area (figure 3). There is therefore every reason to believe that extinction peaks at these times are enhanced or even largely generated by sampling artefact. By contrast, the Early Toarcian and end Cenomanian extinctions occur immediately before peak flooding, during a second-order transgressive systems tract. These provide much better opportunities for understanding events that lead up to mass extinctions, since surface area outcrop remains high throughout and there is no confounding sampling bias.

Both intervals coincide with sudden and rapid increases in continental shelf bathymetry, as deduced from backstripping (Jacquin & de Graciansky 1998) (figure 11). In both cases rapid sea-level rise coincides with, and was presumably triggered by, eruption of huge volumes of flood basalts—at least, they coincide very precisely with the initiation of major flood basaltic provinces. Gale *et al.* (2000) presented evidence that rising sea levels towards the end of the Cenomanian led to the sudden collapse of shelf-break fronts, thereby allowing the spread of stratified oceanic water across large areas of the continental shelf. Although oceanic and shelf marginal sediments show evidence of anoxia at this time, there is little evidence that anoxia played any role in driving extinction in mid- to onshore shelf areas where faunal turnover is greatest. It is more likely that, with stratification, nutrient recycling was severely reduced over much of the shelf area, triggering a collapse in primary productivity with cascading effects down the food chain. Inner shelf environments and their faunas were relatively unaffected, but were displaced far onto the craton where they formed perched deposits with little chance of entering the rock record. Over large areas therefore, diverse benthic fauna disappeared and were temporarily replaced by a low-diversity community migrating in from pre-existing oligotrophic settings. Inshore refugia ensured that most survived.

A similar explanation is applicable to the Early Toarcian event and may also apply to the end Permian and end Cretaceous events, where major transgressions are also thought to have resulted in rapid drowning of continental shelf areas (Hallam & Wignall 1997). Jin *et al.* (2000) have recently shown that faunal change at the Permo–Triassic boundary is almost identical in nature to that seen at the Cenomanian–Turonian and is accompanied by the same geochemical signatures. Thus a combination of genuine extinction, brought about through collapse of the primary food chain and community perturbation, and sampling artefact, brought about by the reduction in surface area of preserved onshore facies, characterize all mass extinctions. Again, unravelling the relative roles played by sampling bias and ecological perturbation will prove extremely difficult.

(d) *The terrestrial record*

So far I have focused on the effects of sequence architecture on the marine fossil record. But first-order cycles clearly have a strong effect on altering the ratio of terrestrial to marine sediments preserved in the rock record (figure 3). The most obvious manifestation of this is in the dearth of Late Cretaceous terrestrial vertebrate faunas worldwide. The major transgression of the Mid-Cretaceous replaced inshore and marginal marine settings with open shelf chalks of decidedly oligotrophic nature over vast areas. Terrestrial vertebrate remains from chalks are exceedingly scarce (Milner 2001), for obvious taphonomic reasons, and terrestrial and marginal marine deposits in Europe and most of the world are effectively absent until the Campanian. Consequently, outside Uzbekistan and one formation in the USA, mammal and bird fossil localities are unknown between the Early Cenomanian and the Early to Mid-Campanian (Foote *et al*. 1999; Le Loeuff & Buffetaut 1995). A similar sampling problem is evident in the fossil record of freshwater fishes (Peter Forey, personal communication). The return of marginal marine facies, shallow marine eutrophic shelf basinal facies and lacustrine deposits in the Early Tertiary is coincident with the return of deposits yielding diverse terrestrial faunas and an apparent explosive radiation of taxa.

No quantitative assessment of the terrestrial fossil record is attempted here, but it is clear that it too is seriously biased by sequence architecture.

7. CONCLUSIONS

Over the past two decades a vast amount of attention has been devoted to the interpretation of cyclical changes in taxonomic diversity measured over a time-scale of 10–50 Myr. This started with Raup & Sepkoski's (1984) analysis for periodicity of extinction, but quickly spread to encompass origination patterns and the study of rebound events after mass extinctions. These studies all start from taxonomic databases in which taxonomic and stratigraphical errors abound. But such errors are random and thus add only noise that will degrade an underlying signal. Furthermore, the approach does not need sophisticated taxonomy to provide a reliable answer. However, all such studies have assumed that taxonomic sampling is uniform over time.

For the post-Palaeozoic at least, the rock record is far from uniform. Our available rock record is now very well sampled palaeontologically, but that rock record is both incomplete and systematically biased over time. Evidence from gap analysis and empirical estimates of rock area suggest that sea-level changes exert a major bias on sampling and preservation. Sea-level changes that define sequence stratigraphical cycles of onlap and offlap also control sedimentary outcrop area, and much of the observed small-scale fluctuation in sampled diversity described in the palaeontological literature could be attributed to a species–area bias. The onus is now on those who wish to interpret taxonomic patterns in terms of mass extinctions and adaptive radiations first to demonstrate that sampling is not wholly or partially responsible for generating those patterns before invoking evolutionary scenarios.

The ideas presented here have grown out of discussions with Andy Gale (Natural History Museum, London) about Cenomanian sequence stratigraphy and its effect on faunas, and he has done much to educate me on the importance of sequence stratigraphy. I am very grateful for the positive criticism and helpful suggestions provided by two referees, Chris Paul and Mike Benton. This research was funded by UK Natural Environment Research Council grant GR3 11322.

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