

1 *Bicentennial Review*

2 **Marine diversity through the Phanerozoic: problems and prospects**

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6 **Abstract:** The fossil record provides direct evidence of how diversity has changed over time, but cannot be
7 taken at face value. Diversity curves constructed from counting taxa in the rock record are seriously biased by
8 unevenness of geographical and stratigraphical sampling effort, inequality in the rock record available for
9 sampling, and inconsistent taxonomic practice. Sample standardization removes some bias, but does not
10 overcome more general incompleteness problems. Modelling that accounts for potential biases is a newer
11 approach but needs accurate estimates of rock record and consistent taxonomic data. Uncertainty remains over
12 whether the steep rise in diversity over the last 100 Ma is real or reflects sampling bias. The repeated rise and
13 fall of marine diversity over time correlates closely with the areal extent of sedimentary deposits and
14 independent estimates of the quality of the fossil record, implying a common driving factor, namely
15 tectonically mediated sea-level change. However, whether changes in diversity are primarily biological in
16 origin, or reflect sampling artefact, remains contentious. There is a distinct possibility that many of the
17 apparent rises and falls in diversity over the Phanerozoic, including most of the ‘mass extinctions’, arise either
18 partially or entirely from rock record bias.

19 Ever since Phillips (1860) first sketched out the history of
20 diversity, palaeontologists have been turning to the fossil record
21 for insight into how life on Earth has changed over time.
22 Whereas Phillips based his sketch on an intuitive knowledge of
23 the British rock record, later workers, starting with Newell (1952,
24 1967) and Raup (1972), have employed a quantitative approach,
25 counting the numbers of taxa described from each time interval.
26 A major landmark was reached with the publication of Sepkoski's
27 marine family database and diversity curve (Sepkoski 1982).
28 This summarized the distribution of nearly 3500 families through
29 72 time intervals, and provided the first detailed picture of
30 marine diversity through the Phanerozoic (Fig. 1b). Later refinement
31 of the family-level curve (Sepkoski 1993) and replication
32 of the data gathering by a consortium of specialists (Benton
33 1993) made little discernible impact on the shape of the
34 Phanerozoic marine diversity curve (Benton 1995; Fig. 1b).
35 Meanwhile, Sepkoski had begun an even more monumental task,
36 compiling data on the distribution of marine genera. His
37 compendium of genus ranges was eventually published posthumously
38 (Sepkoski 2002; Fig. 1a), although results using these
39 data began appearing from 1986 onwards (Raup & Sepkoski
40 1986; Sepkoski 1996, 1997).

41 Thus for 140 years palaeontologists have striven to establish
42 the pattern of diversity change through the Phanerozoic by
43 documenting the stratigraphical occurrence of fossils in the rock
44 record with ever-increasing precision. However, precision is not
45 the same as accuracy and these estimates are ultimately only as
46 reliable as the rock record from which the fossils are extracted.

47 The first doubts concerning the reliability of diversity curves
48 based on a direct reading of the fossil record surfaced when
49 Raup (1976) began exploring the quality of the rock record
50 through time. He gathered data on the volume of sedimentary
51 rock preserved at Epoch level and noted that the Phanerozoic
52 diversity curve seemed to follow the rise in the volume of

1 sedimentary rocks that have been preserved. He concluded that
2 the rise in diversity towards the present day need not be real but
3 might simply be an artefact of a steadily improving rock record.
4 This created an initial flurry of concern, and set one of the key
5 research agendas for the next decade, but in 1981 the problem
6 was ‘solved’ when Sepkoski *et al.* (1981) showed that the same
7 Phanerozoic diversity curve was recovered from a variety of
8 approaches (species-level data, genus-level data, family-level
9 data, trace fossil data, and comparative community diversity).
10 Amazingly, Sepkoski *et al.* never addressed whether all five sets
11 of data could have been distorted by the same basic rock and
12 sampling biases.

13 As a result of the Sepkoski *et al.* (1981) paper, taxon counting
14 became generally accepted as the preferred method for documenting
15 Phanerozoic diversity patterns, and potential problems
16 were given little consideration over the next decade. However, by
17 the mid-1990s researchers were again starting to think about
18 potential biases and their effect on the fossil record. The
19 pioneering work by Holland (1995) highlighted the important
20 control sequence stratigraphic cycles had on fossil sampling
21 patterns, and the careful analysis by Miller & Foote (1996) of
22 Ordovician diversity patterns threw the spotlight on problems of
23 sampling bias. However, for the most part, such problems were
24 seen as fine tuning or regional, not ones that would seriously
25 affect the overall shape of the Phanerozoic diversity curve.

26 In 2001, however, the reliability of a Phanerozoic marine
27 diversity curve based on raw taxonomic counts came under
28 concerted attack. Smith (2001) and Peters & Foote (2001), using
29 different metrics, highlighted the existence of a major systematic
30 bias in the outcrop area of sedimentary rocks through time. Both
31 showed that the rock record varied over time and found a strong
32 and significant correlation between the amount of rock at outcrop
33 and sampled diversity. Alroy *et al.* (2001) were also concerned
34 about the effect of collection biases on the Phanerozoic diversity

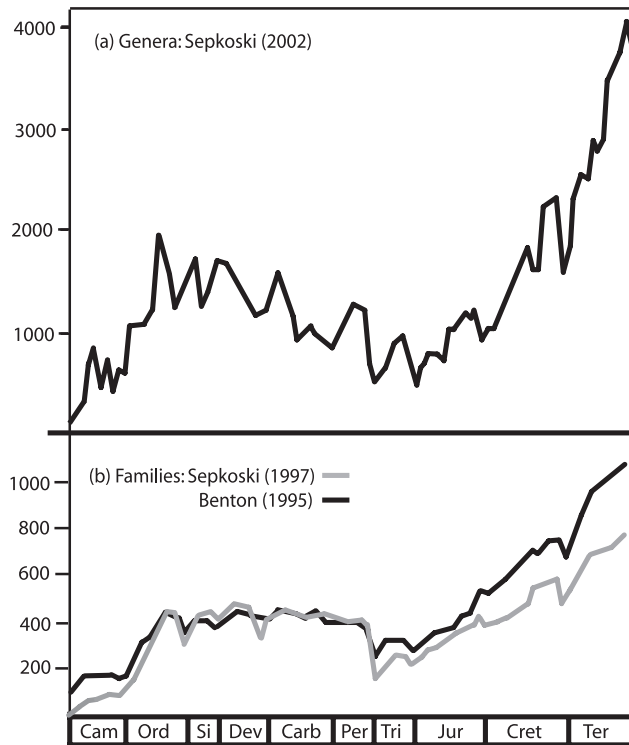


Fig. 1. Phanerozoic diversity curves derived from counting the number of taxa present in each stage, with range interpolation. **(a)** Genus-level diversity, from Sepkoski (2002). **(b)** Family-level diversity from Benton (1995) and Sepkoski (1997).

1 curve, and used species lists drawn from a large database of
 2 fossil localities to standardize for sampling effort. The revised
 3 Phanerozoic diversity curve seemed to them to be very different
 4 from the Sepkoski curve. Jackson & Johnson (2001) raised a
 5 third issue concerning geographical bias and the poor representa-
 6 tion of high-diversity, low-latitude marine faunas in current
 7 databases. Their recent collections from rocks in a small part of
 8 the Caribbean had shown unexpectedly high levels of diversity
 9 amongst Plio-Pleistocene invertebrates. Because the best-
 10 described regional faunas of this time interval lay outside the
 11 tropics, Jackson & Johnson (2001) concluded that new data were
 12 needed to overcome geographical biases and obtain a true
 13 indication of how marine diversity had changed. Finally, Smith *et*
 14 *al.* (2001) provided an empirical case study showing how biases
 15 in habitat representation in the rock record could seriously distort
 16 global marine diversity curves. Since then, a steady stream of
 17 papers have appeared questioning and probing Phanerozoic
 18 marine diversity patterns.

19 In this review I shall briefly explain the problems that face
 20 palaeontologists wishing to estimate marine diversity through
 21 time, review some of the techniques currently being developed to
 22 overcome these problems, and end by looking at a couple of
 23 aspects of the Phanerozoic marine diversity curve that are now
 24 under intense scrutiny.

25 What is wrong with the way marine diversity has been 26 estimated in the past?

27 Prior to 2001 Phanerozoic diversity curves were constructed from
 28 a simple count of numbers of taxa recorded in any given time
 29 interval (usually the 72–77 stage-level intervals of Sepkoski

1 (1982) and Benton (1993)). Compilations at any taxonomic level
 2 can be used to construct diversity curves, but Robeck *et al.* (2000)
 3 demonstrated that using more finely subdivided taxonomic group-
 4 ings produced a more precise view of underlying diversity in the
 5 rocks. Furthermore, although there will always be a certain
 6 amount of error in taxonomic compilations, Sepkoski (1993) and
 7 Adrain & Westrop (2000) both demonstrated that such error was
 8 random and thus did not pose a serious problem to this approach.

9 The fossil record is of course notoriously incomplete, so to
 10 compensate for this a technique called range interpolation has
 11 been employed. Range interpolation removes some problems of a
 12 patchy fossil record by assuming that a taxon is present in each
 13 time interval between its first and last occurrence, whether or not
 14 it has actually been found in those time intervals. Because the
 15 fossil record is dominated by organisms with mineralized
 16 skeletons, the history of those taxa with hard parts is taken as a
 17 proxy for all marine diversity. The exact ratio of mineralized to
 18 unmineralized taxa is unimportant so long as it has remained
 19 broadly similar throughout the Phanerozoic. By assuming that
 20 sampling is more or less uniform through time, the relative
 21 numbers of taxa described from each time interval (or that cross
 22 boundaries between intervals) can be used as a measure of how
 23 diversity has changed.

24 This taxon-counting approach is simple to employ and seem-
 25 ingly robust to certain potential problems, but makes the
 26 following three critical assumptions: (1) all time intervals are
 27 equally well sampled; (2) preservation potential is uniform over
 28 time; (3) taxonomists partition taxa in a uniform manner. Each
 29 unfortunately is beset with problems.

30 Sampling of the rock record

31 There are two aspects of sampling that need to be considered:
 32 geographical bias and variation in sampling intensity.

33 *Geographical bias.* Jackson & Johnson (2001) and Johnson
 34 (2003) argued that any diversity curve constructed simply from
 35 cataloguing the numbers of fossils already described was doomed
 36 to failure because well-studied parts of the world that contribute
 37 most to taxonomic compilations were not necessarily representa-
 38 tive of global diversity. Specifically, they found that the Neogene
 39 record of the tropics was woefully undersampled compared with
 40 temperate regions, a view later reinforced by Valentine *et al.*
 41 (2006).

42 European and North American data certainly contribute dis-
 43 proportionately to taxonomic compilations, simply because fossil
 44 collecting has been intensely pursued in those regions for much
 45 longer (Kidwell & Holland 2002). However, extreme unbalance
 46 in sampling between, say, Indo-Pacific faunas and those of
 47 temperate North America is no problem if this bias applies
 48 equally to all time intervals through the Phanerozoic.

49 Unfortunately, continental plates have migrated out of the
 50 tropics over time (Allison & Briggs 1993; Walker *et al.* 2002;
 51 Fig. 2). Because diversity is highest in the tropics, a long-term
 52 trend of decreasing diversity could be created artificially simply
 53 because the well-studied parts of the world have shifted over time
 54 from equatorial to temperate latitude through plate migration.
 55 Indeed, some palaeontologists are starting to factor out this bias
 56 from their analyses (e.g. Bush & Bambach 2004; Crampton *et al.*
 57 2006b). On the other hand, the smaller-scale rises and falls in
 58 diversity from stage to stage that have been taken as the
 59 signatures of mass extinction and radiation cannot be explained
 60 by such slow changes in the positions of continental blocks
 61 (Smith 2001).

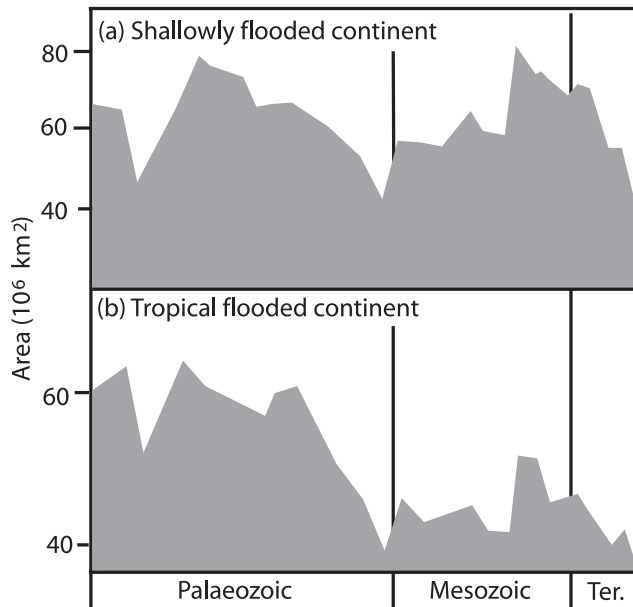


Fig. 2. Estimated surface area of continents flooded by marine incursions over the Phanerozoic, from Walker *et al.* (2002). (a) All continents. (b) Continental blocks lying within 30° of the equator.

1 *Sampling efficiency.* If some time intervals are less well sampled
 2 than others for whatever reason, then simple taxon counting fails
 3 as a reliable proxy for diversity. A rise in numbers of fossil taxa
 4 collected and recorded might simply be due to better preservation,
 5 more outcrop availability and/or more collection effort. Miller & Foote (1996) and Alroy *et al.* (2001) correctly identified
 6 this as a major concern, and have been at the forefront of
 7 developing methods that can overcome such sampling problems.

9 *The rock record as an unbiased sample*

10 Various lines of evidence (gap analysis: Foote & Sepkoski 1999;
 11 Crampton *et al.* 2006a; Fara & Benton 2000: collector curves:
 12 Benton 1998; Paul 1998: phylogenetic trees: Benton *et al.* 2000)
 13 suggest that palaeontologists have done a passably good job in
 14 exploring surface outcrops for their fossil content, at least in
 15 better-studied parts of the world. Of course, there is a strong
 16 geographical bias to these databases as discussed above; yet for
 17 any one region, rocks at outcrop have probably been approxi-
 18 mately equally well sampled over the Phanerozoic. But are those
 19 rocks themselves an unbiased subset of past sedimentary depos-
 20 its? It is this aspect that Smith (2001), Peters & Foote (2001,
 21 2002), Smith *et al.* (2001), Crampton *et al.* (2003, 2006a) and
 22 Peters (2005, 2006a) have all expressed concern about. What
 23 these studies highlight is that the amount of sedimentary rock
 24 preserved has fluctuated significantly over time, as has the nature
 25 of the sedimentary environments captured.

26 Rock record bias has been calculated in two ways. Smith
 27 (2001) estimated post-Palaeozoic rock outcrop area for western
 28 Europe by counting the number of geological maps with outcrops
 29 assigned to each of the 42 stages (an equal grid sampling
 30 method) (Fig. 3). Peters & Foote (2001) used the number of
 31 named formations from a lexicon of geological names as a proxy
 32 for both rock extent and habitat heterogeneity (Fig. 4). Both
 33 found that the rock record showed a strong and worryingly close
 34 match to sampled diversity. More detailed study of the New

1 Zealand record later found that measuring rock outcrop area was
 2 a more accurate estimator of number of fossil localities sampled
 3 (Crampton *et al.* 2003), whereas the number of formations might
 4 be a better estimator of habitat heterogeneity (Crampton *et al.*
 5 2006a).

6 Computer simulation studies (Holland 1995, 2000; Holland &
 7 Patzkowsky 1999), backed up by detailed field studies (Patzkows-
 8 ky & Holland 1996; Gale *et al.* 2000; Smith *et al.* 2001;
 9 Crampton *et al.* 2006a), have provided a broad understanding of
 10 how sequence stratigraphic packaging of sediments, driven by
 11 lower-order cycles of marine onlap–offlap, can bias perceptions
 12 of marine diversity. Transgressive phases to early highstand leave
 13 a good record as sediment accommodation space increases with
 14 rising sea level. In highstand phases accommodation space is
 15 low, progradation rates are high and much of the shelf tends to
 16 be covered in coarse-grained sediments, especially in siliciclastic
 17 systems, creating less conducive conditions for fossil preserva-
 18 tion. Late highstand and regressive phases leave the poorest
 19 record, as the last sediments to be deposited are the first to be
 20 exposed and eroded from perched positions. Productivity of the
 21 carbonate factory is governed by the aerial extent of shallow
 22 illuminated sea floor and also varies through a sequence cycle,
 23 affecting preservation potential. Crampton *et al.* (2006a) ob-
 24 served the best preservation of molluscan faunas in mid-cycle
 25 (around time of maximum flooding) at the top of transgressive
 26 systems tract intervals, and poorest preservation towards the end
 27 of highstand system tract intervals (Fig. 5). Lower-order se-
 28 quence cycles certainly play an important role in determining
 29 diversity patterns on a regional scale, but probably do no more
 30 than cause faunas to migrate across the shelf, passing in and out
 31 of the windows of preservation afforded to palaeontologists.

32 Highest-order cycles, driven by tectonic processes (primarily
 33 sea-floor spreading, mantle plume related phenomena, and con-
 34 tinental assembly and disassembly: Dewey & Pitman 1998), are
 35 more complicated to interpret (see below). This is because major
 36 onlap–offlap cycles across continental blocks concurrently
 37 change the surface area of shallow marine habitats and the
 38 surface area of sedimentary deposits that eventually are pre-
 39 served in the rock record. This creates distinct cycles of marine
 40 sediment abundance through the Phanerozoic that clearly follow
 41 higher-order sequence stratigraphic cycles (Figs 3–5).

42 Changing proportions of marine sedimentary rock preserved at
 43 outcrop mean that palaeontologists have been dealt a biased deck
 44 of cards before even a single fossil is collected. Thus, even if
 45 diversity had remained constant over the Phanerozoic, the fact
 46 that successive time intervals preserve greater or lesser amounts
 47 of sedimentary rock at outcrop can create variation in the
 48 numbers of fossils recorded through time.

49 Change in the proportion of onshore to offshore sediments
 50 preserved in the record is probably as important as changes in
 51 the volume of rock preserved (Smith *et al.* 2001; Crampton *et al.*
 52 2003, 2006a). The diversity of macrofossils preserved in the rock
 53 is a function of both the original biological diversity gradient and
 54 changing preservational potential across the shelf, controlled by
 55 sedimentation rates (e.g. Kidwell & Baumiller 1990). The ratio
 56 of onshore to offshore sediments is also affected by the angle of
 57 the continental shelf and thus varies through transgressive–
 58 regressive cycles and according to tectonic setting. The diversity
 59 of the New Zealand molluscan fauna drops in late highstand
 60 intervals (Crampton *et al.* 2006a), probably because of dilution
 61 by high sediment delivery in this siliciclastic setting (Cooper
 62 *et al.* 2006). A similar marked drop in diversity is recorded over
 63 the Cenomanian–Turonian boundary, when high-diversity faunas
 64 in oligotrophic onshore facies became displaced by lower-

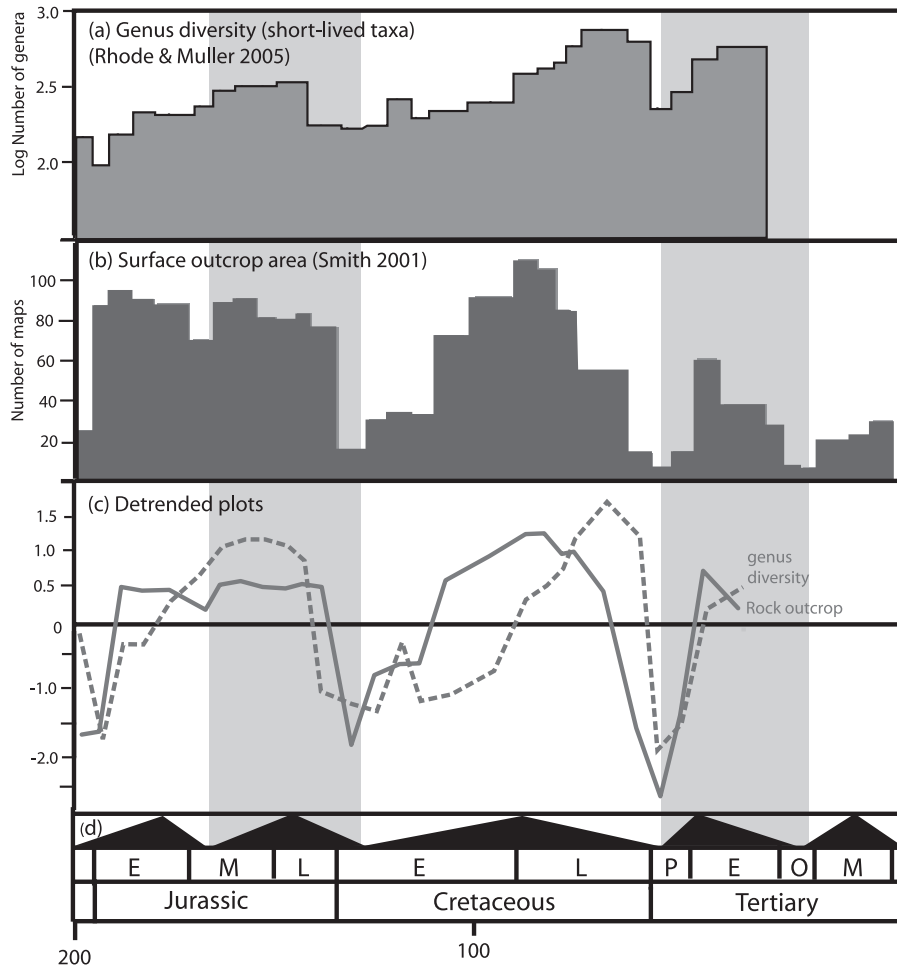


Fig. 3. Global marine genus diversity v. rock at outcrop record for western Europe (France, England and Wales) since the late Triassic. (a) Log diversity of genera whose taxonomic duration is 45 Ma or less (data from Rhode & Muller 2005). (b) Marine sedimentary rock at outcrop, based on number of 1:63 360 (UK) and 1:80 000 (France) geological maps, from Smith (2001). (c) Detrended plots of genus diversity and rock at outcrop diversity (from Smith & McGowan 2005). (d) Second-order sequences in western Europe, from Hardenbol *et al.* (1998).

1 diversity faunas, as sea levels rose and stratified oceanic condi-
 2 tions became more widespread across the continental shelf (Gale
 3 *et al.* 2000; Smith *et al.* 2001). Thus perceived diversity and the
 4 environment of origin of major clades (Jablonski & Bottjer 1991)
 5 are both potentially affected by changes in the proportion of
 6 onshore–offshore marine habitats captured by the rock record in
 7 any given time interval.

8 Changes in the extent of continental flooding affect both the
 9 absolute amount of sediment deposited over the cratons and the
 10 geographical extent of the habitats that those sediments capture,
 11 and so could affect biological diversity just as much as sampling,
 12 as is discussed more fully below.

13 Fossil preservation

14 The fossil record is palpably incomplete and, even within groups
 15 such as bivalve molluscs that might be expected to have good
 16 preservation potential, maybe a quarter of all taxa never enter the
 17 fossil record (Cooper *et al.* 2006; Valentine *et al.* 2006).
 18 However, incompleteness of the record is no hindrance to the
 19 construction of Phanerozoic diversity curves so long as preserva-
 20 tion potential is more or less uniform over time. Problems will
 21 arise only if there are some time periods where preservation is
 22 better than others, as that will obviously bias the numbers of taxa
 23 collected.

24 Changes in preservation potential may be driven intrinsically
 25 by biological evolution, or extrinsically by, for example, changes
 26 in ocean chemistry (Peters 2006a). An example of an intrinsic

1 change is provided by echinoids. The evolution of a rigidly
 2 sutured skeleton in the Mesozoic greatly enhanced the preserva-
 3 tion potential of echinoids and coincides with a marked improve-
 4 ment in the quality of their fossil record (Smith 2007). It is
 5 likely that other groups have undergone similar strengthening of
 6 their skeletons through the Phanerozoic (e.g. Bush & Bambach
 7 2004), which could bias the Phanerozoic diversity curve. How-
 8 ever, there has been no quantitative assessment of the likely
 9 magnitude of this effect. Migration off-shelf and onto the
 10 continental slope and ocean basin could introduce a systematic
 11 bias in the other direction, creating a poorer fossil record towards
 12 the present (e.g. Smith 2004).

13 Shell composition has long been suspected as having a major
 14 biasing effect on preservation (e.g. Bush & Bambach 2004);
 15 indeed, Valentine *et al.* (2006) found that taxa with more reactive
 16 shell chemistry and structure have a much poorer fossil record.
 17 Aragonite-shelled molluscs, for example, are expected to be
 18 more readily lost through dissolution than their calcite-shelled
 19 relatives. There is certainly ample evidence that some low-
 20 diversity assemblages were in fact normal diversity communities
 21 that have lost their aragonitic components through dissolution
 22 (Cherns & Wright 2000; Wright *et al.* 2003). If aragonite
 23 preservation potential varies over time this could pose a serious
 24 systematic bias for molluscs. Indeed, Erwin (1993) cited the lack
 25 of silicified faunas in the Early Triassic as the principal reason
 26 why gastropods had an exceptionally poor record at that time.
 27 This explanation is, however, not universally accepted (e.g.
 28 Frasier & Bottjer 2005), and neither Kidwell (2005) nor Cooper

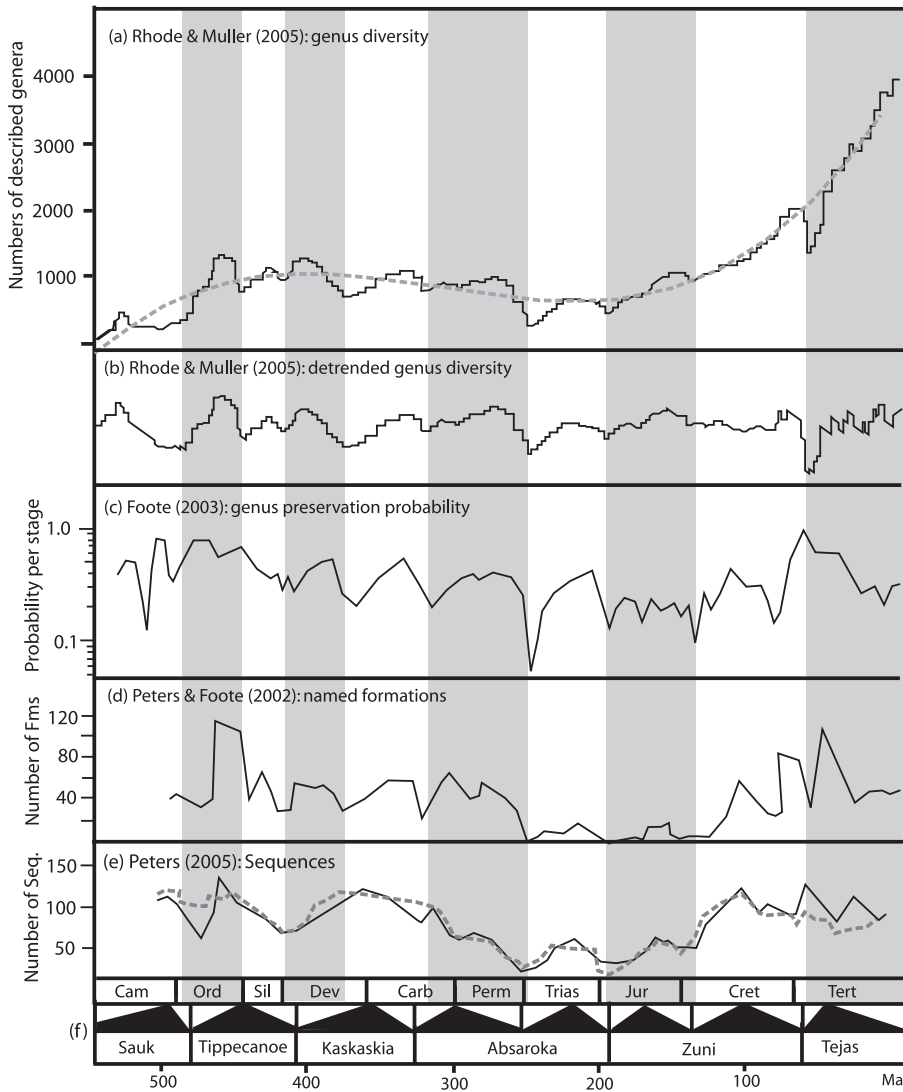


Fig. 4. Global marine genus diversity plotted against various rock record and sampling bias estimates for the Phanerozoic. **(a)** Global marine genus-level diversity taken from Sepkoski (2002) with single occurrences and poorly dated occurrences removed. Geological time scale revised and smooth trend curve (dashed) added by Rhode & Muller (2005). **(b)** As **(a)** but data detrended. **(c)** Estimated genus-level sampling probability per stage based on analysis of first and last occurrences of genera, from Foote (2003). **(d)** Number of marine formations in the USGS lexicon, from Peters & Foote (2001). **(e)** Number of marine sedimentary rock sections in North America based on the COSUNA charts (continuous line), from Peters (2005), and number of through-ranging gaps in deposition (dashed line), from Peters (2006a) **(f)** Major sequence stratigraphic cycles of North America, based on Sloss (1963).

1 *et al.* (2006) could find evidence for major large-scale bias over
 2 time in molluscan preservation. Furthermore, the relative com-
 3 monness of a mollusc in the fossil record bears no correlation to
 4 the robustness of its shell (as measured by size, thickness,
 5 reinforcement and mineralogy) (Behrensmeyer *et al.* 2005).

6 Therefore the preservational bias created by shell composition
 7 and durability on Phanerozoic diversity patterns is apparently
 8 weak and largely random, even though it may be highly signifi-
 9 cant in bed-to-bed comparisons and on a regional scale. Kidwell
 10 (2005) speculated that this was possibly because each time
 11 interval manages to capture an adequate range of taphonomic
 12 settings.

13 *Taxonomic practice*

14 Taxonomic data are messy. Taxa of the same rank cannot strictly
 15 be considered equal or even equivalent, as different taxonomists
 16 may have applied very different recognition criteria when erect-
 17 ing them. Although earlier studies (e.g. Adrain & Westrop 2000)
 18 found no evidence that taxonomic errors and arbitrary taxonomic
 19 splitting of lineages was systematically biased, Ausich & Peters
 20 (2005) provided some evidence to the contrary. Using Ordovi-
 21 cian–early Silurian crinoids as an example, they showed that

1 there was a preferential bias against extending taxonomic names
 2 across the major Epoch boundaries. This creates an underestima-
 3 tion of early Silurian biodiversity and an overestimation of rates
 4 of extinction in the late Ordovician.

5 Studies that look at rates of occurrence or standing diversity
 6 through time are relatively immune to taxonomic problems, as
 7 only the presence of hidden synonymy (morphologically indis-
 8 tinguishable taxa being given different names) might inflate
 9 estimates. However, serious problems arise when last occurrences
 10 of taxa are equated with extinction. Last occurrences of taxa are
 11 not necessarily extinctions, but could represent arbitrary cuts
 12 (pseudoextinctions) of a continuous lineage imposed by taxono-
 13 mists engaged in chopping up long branches (Smith & Patterson
 14 1988). At genus level maybe a third of last occurrences represent
 15 such pseudoextinctions (Patterson & Smith 1989).

16 The trend recently has been to treat databases compiled at
 17 finer taxonomic resolution (e.g. genus level) as more reliable
 18 than those at a high taxonomic resolution (e.g. family or order).
 19 This largely stems from the study by Robeck *et al.* (2000), which
 20 showed, using computer simulation, that the finer the taxonomic
 21 category used in a study the more precise a view of underlying
 22 diversity resulted. However, their computer simulations only
 23 explored the accuracy of methods assuming that the preserved

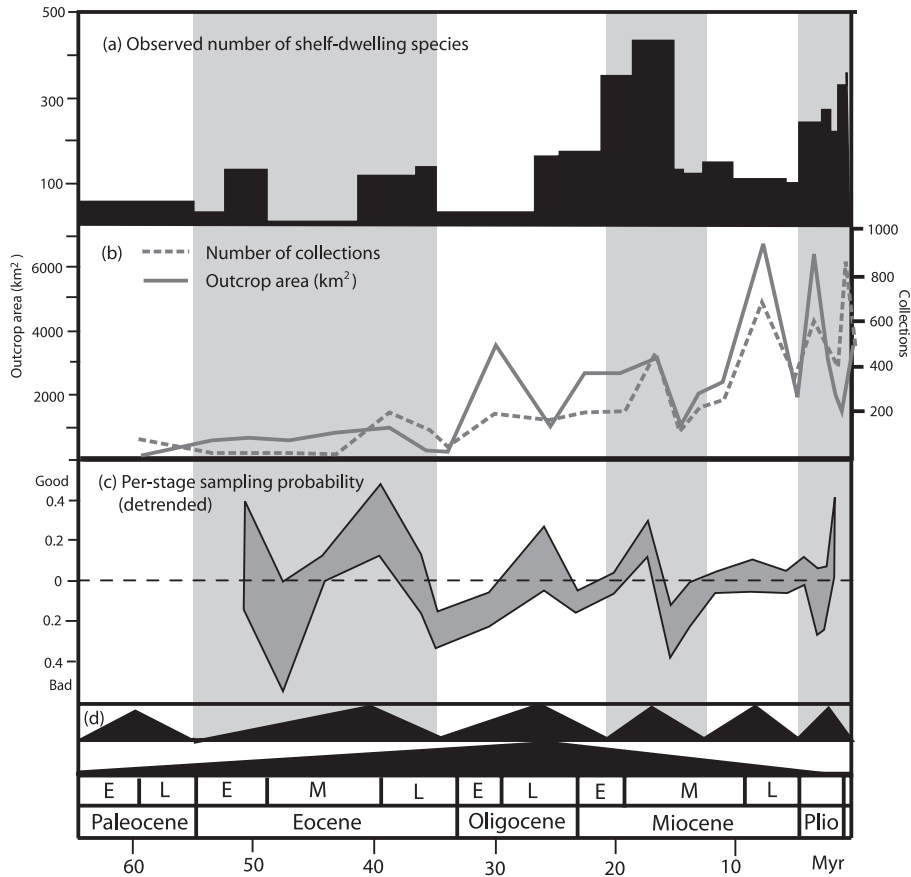


Fig. 5. Molluscan species diversity in New Zealand since the Eocene v. various sampling biases. (a) Number of species recorded. (b) Number of collections in the New Zealand Record File (green dashed line) and surface outcrop area of sedimentary rocks in New Zealand (red line). (c) Maximum and minimum per-stage sampling probability (detrended) based on gap analysis and inverse survivorship modelling. (d) Major sequence stratigraphic cycles. (a) and (b) from Crampton *et al.* (2003); (c) and (d) from Crampton *et al.* (2006a).

1 fossil record was an unbiased representation of true underlying
 2 biodiversity. Reduced to absurdity, species counts give the best
 3 estimate of how many species can be collected at outcrop, but
 4 species data are also the most affected by biases in the rock
 5 record. As the focus of study moves down the taxonomic
 6 category from order to family to genus to species, the average
 7 taxon duration declines, with the result that a greater proportion
 8 of taxa come to have durations equal to or shorter than the
 9 sizeable gaps in the rock record separating sediment bundles
 10 (Peters 2006a, b). Therefore, deriving diversity curves from
 11 higher taxa with longer average duration should help to smooth
 12 out some of the rock bias that affects genus-level databases.

13 Finally, higher taxa are being used as a proxy for numbers of
 14 species that existed in each time interval. Naturally, one would
 15 want the average number of morphospecies assigned to a higher
 16 taxon such as a genus or family to be constant through time.
 17 Unfortunately, this is not the case. Plotting numbers of described
 18 species and families through time (see Fig. 7) shows that
 19 significantly more species are assigned to a Neogene family than
 20 to a Palaeozoic family (Flessa & Jablonski 1985). Why this
 21 should be so is still unclear, but, if we want to use higher taxa as
 22 a measure of species diversity, then we also need to correct for
 23 this bias.

24 New approaches to overcome biases of the fossil record

25 In the face of overwhelming evidence that the fossil record is
 26 seriously biased by a wide range of factors, two approaches are
 27 currently being developed to try to improve diversity estimates:

1 sample standardization and modelling that incorporates informa-
 2 tion about variation in the quality of the fossil record.

3 Sample standardization

4 Both Jackson & Johnson (2001) and Alroy *et al.* (2001)
 5 recognized that sampling unevenness could be seriously biasing
 6 the Phanerozoic diversity curve, and that data standardization
 7 was needed. However, they did not agree on what that standardi-
 8 zation procedure should be. Jackson & Johnson (2001) and
 9 Johnson (2003) argued that palaeobiologists should be applying
 10 standard ecological approaches that use abundance data to
 11 determine comparable measures of sampling completeness
 12 through rarefaction. Furthermore, they believed that new data
 13 needed to be gathered to remove biases in global coverage. From
 14 the number of specimens collected and the number of species
 15 those specimens represent one can easily determine how many
 16 species we would expect to find in each sample if a standard
 17 number of specimens were collected. This provides a clear and
 18 unambiguous way of comparing alpha diversity where sampling
 19 has been very unequal. The problem is that insufficient data of
 20 this form are yet available to allow a global biodiversity curve to
 21 be constructed.

22 Alroy *et al.* (2001) opted for a different form of standardiza-
 23 tion, one that made best use of the available published literature.
 24 They used two methods, both of which employed randomized
 25 subsampling of taxonomic lists. The first involved rarefaction of
 26 individual taxonomic occurrences in the database, as previously
 27 employed by Miller & Foote (1996). The second method drew
 28 entire taxonomic lists and counted numbers of taxa added. For

1 each time interval a list of fossiliferous localities is compiled,
 2 along with a list of the taxa that each locality has yielded.
 3 Drawing localities at random from this pool until a predeter-
 4 mined number of species is reached and repeating many times
 5 provides a relative measure of taxonomic diversity.

6 Both sample size standardization and subsampling of taxo-
 7 nomic lists are methods for removing uneven sampling and
 8 thereby allowing meaningful comparison of average taxonomic
 9 diversity between time intervals. However, subsampling of
 10 taxonomic lists makes a number of unrealistic assumptions that
 11 are not met by real data, and can be strongly influenced by the
 12 spatial organization of the diversity they encompass (Bush *et al.*
 13 2004). More critically, all methods of standardization simply
 14 remove the biases created by local incompleteness within known
 15 collections, they do not tackle the larger problem of general
 16 incompleteness, where faunas are not preserved in the first place
 17 (Foote 2001, 2003).

18 *Modelling large-scale preservation bias*

19 Instead of trying to standardize for sampling differences through
 20 time, an alternative approach is to estimate how preservation
 21 potential has varied and use this to adjust the raw diversity curve.
 22 This has been successfully applied to extinction studies where
 23 there are good data on sampling and species diversity, and a
 24 variety of methods can be employed to establish the relative
 25 completeness of the fossil record for each time interval (see
 26 Crampton *et al.* 2006a, and references therein). The raw taxon
 27 count is used to construct an initial diversity plot, which is then
 28 subsequently modified through applying correction factors based
 29 on the quality of the fossil record. However, this approach has
 30 yet to be applied to the global Phanerozoic marine diversity
 31 curve.

32 There are numerous papers that have tried to assess the quality
 33 of the fossil record (e.g. Foote & Sepkoski 1999; Benton *et al.*
 34 2000), but these look at the record as a whole rather than stage
 35 by stage. Currently, four methods can provide the sort of high-
 36 resolution temporal data on the quality of the fossil record that
 37 are needed: gap analysis, ghost range analysis, modelling of
 38 origination and extinction patterns, and rock record analysis.

39 *Gap analysis.* Paul (1998) summarized how gap analysis can be
 40 used to determine the relative quality of the fossil record. Put
 41 simply, between the first and last occurrence of a taxon there will
 42 be time intervals when it has been captured (i.e. preserved,
 43 collected and identified) and time intervals where it has yet to be
 44 recorded (gap). The ratio of gap to known record gives a measure
 45 of the quality of the fossil record specific for that time interval.
 46 Periods with a high gap to observed ratio have comparatively
 47 poorer fossil records than periods with proportionally fewer gaps.
 48 A plot of the ratio of gap to observed distributions through the
 49 Phanerozoic provides an estimate of how successful we have
 50 been at capturing the taxa that are known to range through time
 51 intervals. This was the approach used by Paul (1998) to plot the
 52 quality of the Palaeozoic fossil record as exemplified by
 53 echinoderms, and was one of the techniques used by Crampton
 54 *et al.* (2006a) in assessing the New Zealand fossil record of
 55 Cenozoic molluscs (Fig. 5c). It has also been used to explore the
 56 quality of the Jurassic to Eocene continental fossil record of
 57 vertebrates (Fara & Benton 2000; Fara 2002). However, this
 58 method cannot take account of any missing range beyond the
 59 first and last recorded appearance of a taxon, and also takes no
 60 account of pseudoextinction: name changes imposed by taxono-
 61 mists onto a single lineage typically coinciding with a major

1 preservation gap. To take account of these two problems we need
 2 a different approach.

3 *Ghost lineage analysis and molecular clocks.* The construction
 4 of phylogenetic trees encompassing large numbers of taxa
 5 provides an alternative method for estimating the relative quality
 6 of the fossil record over time. Phylogenetic relationships amongst
 7 taxa are constructed without reference to their stratigraphic
 8 occurrence, being based solely on the distribution of morphologi-
 9 cal characters. Yet when the resulting cladogram is optimized
 10 and calibrated against the observed stratigraphical distribution of
 11 fossils, the resultant tree identifies periods of time when lineages
 12 must have existed even though they have not yet been found
 13 (Norrell 1992). Counting both the inferred and observed ranges
 14 in such calibrated trees compensates for missing parts of the
 15 fossil record much better than range interpolation, as it allows
 16 for some range extension beyond first and last occurrence datum
 17 points. Treating plesiomorphic taxa that are stratigraphically
 18 older than their sister group as potential ancestors avoids
 19 spurious range extensions (Smith 1994; Lane *et al.* 2005).

20 Phylogenetic trees constructed from molecular data or both
 21 morphological and molecular data can provide an additional
 22 estimate of origination times that is largely independent of the
 23 stratigraphic occurrence of fossils. Where morphological and
 24 molecular trees agree, multiple local (minimal age) fossil
 25 calibration points are used and methods that allow molecular
 26 rates of evolution to vary across the tree are employed, accurate
 27 and precise molecular estimates of divergence can be obtained
 28 (Near *et al.* 2005; Smith *et al.* 2006; Yang & Rannala 2006).
 29 Molecular clocks are limited in use to groups that have diverse
 30 extant representatives, but can be used as probes to test and
 31 compare the quality of their fossil record at Epoch level (e.g.
 32 Teeling *et al.* 2005; Smith 2007).

33 So far, phylogenetic trees and molecular phylogenies have
 34 been used only in small-scale studies and/or across a limited
 35 number of taxa (mostly terrestrial vertebrates). The construction
 36 of a Phanerozoic curve mapping the quality of the marine fossil
 37 record at stage level from phylogenetic and molecular data has
 38 yet to be attempted. However, given the rate at which high-
 39 quality cladograms and molecular phylogenies have appeared
 40 over the last decade it will not be long before such an attempt
 41 can be made. The advantage of this approach is that it should be
 42 more effective at picking up sampling and rock record bias than
 43 gap analysis (Lane *et al.* 2005).

44 *Rate modelling of originations and extinctions.* Foote (2001,
 45 2003, 2005) has been developing a sophisticated model-based
 46 approach that uses data on first and last occurrences of taxa to
 47 simultaneously estimate the most likely rates of origination,
 48 extinction and preservation for each time interval. His approach
 49 is to extrapolate the expected pattern of preserved first and last
 50 appearances corresponding to a given evolutionary model, start-
 51 ing from an initial specified time series of rates of origination,
 52 extinction and preservation. Optimization is used to find the set
 53 of rates that best predict the observed pattern of first and last
 54 occurrences.

55 Using this approach, Foote (2003) developed a curve for the
 56 rate of preservation (i.e. quality) of the fossil record through the
 57 Phanerozoic (Fig. 4c). He was also able to demonstrate that
 58 origination and extinction rates had varied over time, although
 59 the precise timing and duration of peaks in extinction or
 60 origination was sensitive to model assumptions. That is to say,
 61 we know that origination and extinction rates have varied in a
 62 way that is not directly predictable from sampling bias. However,

1 as noted by Foote, his approach still assumes uniformity of
 2 sampling with respect to environments and geography, and takes
 3 no account of taxonomic problems with the database such as
 4 pseudoextinction.

5 *Rock record.* A plot of how the rock record changes through the
 6 Phanerozoic can be used as a proxy for the quality of the fossil
 7 record. Counts of rock outcrop area or number of geological
 8 formations provide estimates of the number of fossiliferous
 9 localities and/or the environmental heterogeneity captured by the
 10 rock record at any one time interval. Smith (2001), Peters &
 11 Foote (2001, 2002) and Crampton *et al.* (2003) have all provided
 12 such estimates (Figs 3–5). An alternative approach is to measure
 13 the distribution of sedimentary hiatuses in the geological record
 14 (Peters 2006a). Reassuringly, the preservation rate plot of Foote
 15 (2003) and the rock record plot of Peters & Foote (2002),
 16 although derived from very different assumptions, show excellent
 17 agreement (Fig. 4c and d), which gives confidence to their
 18 approximate correctness.

19 As our knowledge of how the quality of the fossil record
 20 varies over time advances, more sophisticated methods will
 21 surely be used to correct the Phanerozoic marine diversity curve.
 22 The studies of Foote (2003), Bush & Bambach (2004) and
 23 Crampton *et al.* (2006a, b) hint at what might be achieved with
 24 high-quality datasets.

25 **Current controversies concerning the marine** 26 **Phanerozoic diversity curve**

27 So far I have discussed why traditional methods of estimating
 28 Phanerozoic marine diversity, although precise, are no longer
 29 considered accurate in the face of various biases. I have also
 30 outlined some of the alternative approaches that workers are
 31 turning to, to overcome these biases and derive more accurate
 32 diversity estimates. To end I want to highlight two aspects of the
 33 marine Phanerozoic diversity curve that are currently a matter of
 34 considerable debate: has marine diversity increased significantly
 35 over the last 100 Ma and what is driving cycles of diversity?

36 *Has taxonomic diversity risen steeply since the Mesozoic?*

37 One of the most striking features of the Phanerozoic marine
 38 diversity curves of Sepkoski and Benton is the dramatic rise in
 39 diversity that starts in the late Cretaceous and continues to the
 40 present day. This trend is apparent in all compilations that have
 41 used traditional methods of taxon counting (e.g. Fig. 1) and at all
 42 taxonomic levels, although it is at its most pronounced for
 43 genus-level data (Lane & Benton 2003). Furthermore, such a rise
 44 intuitively makes sense. Many important groups appear to have
 45 diversified greatly since the start of the Mesozoic, with origina-
 46 tion greatly outstripping any extinction (actinopterygian fishes,
 47 echinoids and starfishes, decapod crustaceans, corals, cheilos-
 48 tome bryozoans, neogastropods). Indeed, it is striking how the
 49 diversity curve tracks the rock record curve throughout most of
 50 Phanerozoic, but starts to diverge from the Late Cretaceous
 51 onwards very markedly (Fig. 6). No other time interval shows
 52 anything comparable. On the other hand, some analyses, after
 53 taking sampling into account, have suggested that diversity was
 54 either static or declining through the Cenozoic (Alroy *et al.*
 55 2001; Peters & Foote 2001; Crampton *et al.* 2006b).

56 There are several potential artefacts that could be creating this
 57 Cenozoic rise in diversity. Probably the most significant of these
 58 is what Raup (1972, 1976) dubbed ‘the pull of the Recent’.
 59 Traditional analyses, such as those of Sepkoski and Benton, use

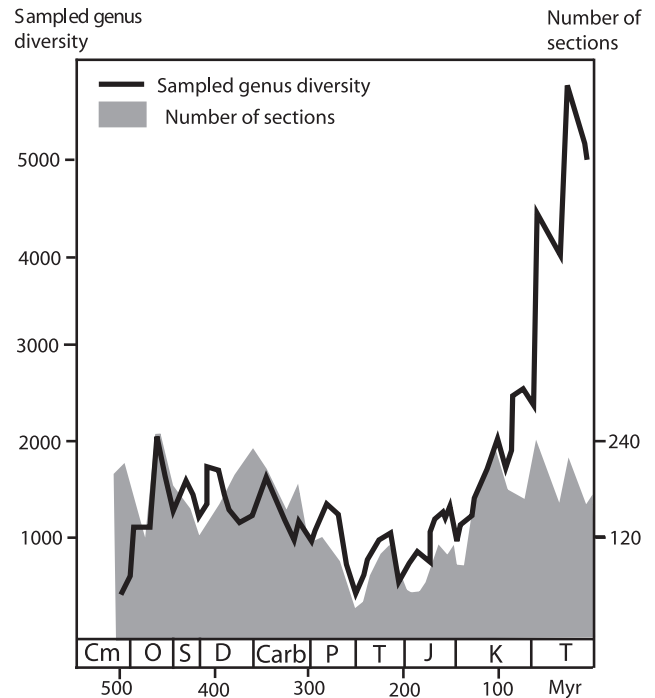


Fig. 6. Genus diversity and rock record curves (number of Formations in the US Geological Survey lexicon), showing divergence of genus diversity and rock record curves occurring from about 100 Ma (from Peters 2005).

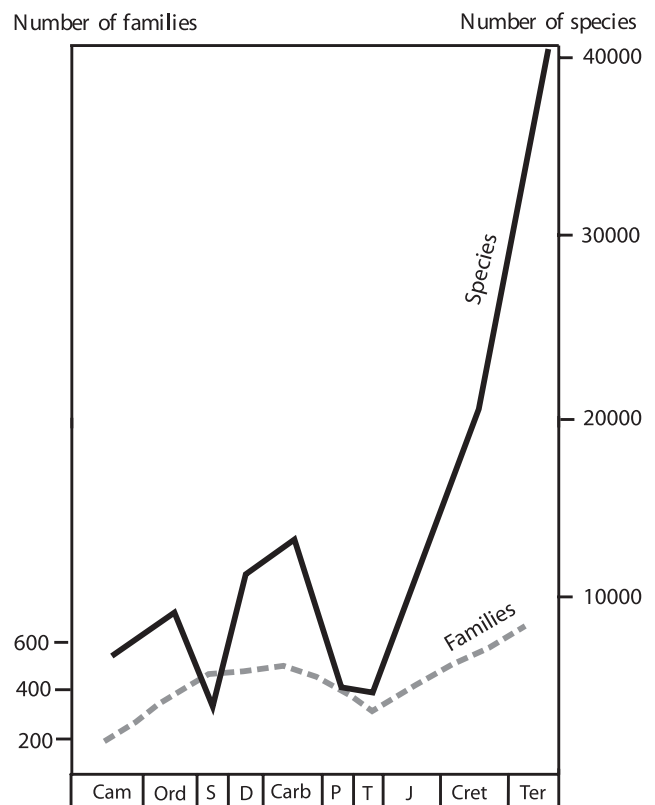


Fig. 7. Change in the ratio of species per family through the Phanerozoic (from Flessa & Jablonski 1985).

1 range interpolation to compensate for gaps in the fossil record.
 2 However, if there is one level (the Recent) where the biota is
 3 completely known (more or less) this will skew diversity counts.
 4 The closer in time we approach the Recent, the more taxa will
 5 have their ranges extended forward from their last fossil record
 6 to the Recent. Extinct taxa cannot benefit from this additional
 7 correction for missing record so the net result is an increase in
 8 the ratio of observed to inferred taxa towards the present day.

9 One way to ameliorate the problem of the ‘pull of the Recent’
 10 is to omit all Recent records so that taxon counts extend only to
 11 their latest fossil occurrence. A preliminary study by Sepkoski
 12 (1997) using this approach suggested that there might indeed be
 13 a small effect, but that the rise in overall diversity during the
 14 Cenozoic was not an artefact. Peters & Foote (2001) were
 15 sceptical of this result and re-examined Sepkoski’s genus-level
 16 data, removing all Recent taxa not recorded from the Plio-
 17 Pleistocene. They estimated that about 50% of extant genera with
 18 a fossil record were missing from rocks of the last 5 Ma. If true,
 19 this would be a major distorting bias, as it would greatly inflate
 20 estimates of sampled diversity in these youngest time intervals.
 21 Modelling by Peters & Foote (2001) suggested that the rise in
 22 diversity since the late Miocene was probably overestimated
 23 four- to eight-fold.

24 However, Jablonski *et al.* (2003) took a detailed look at
 25 Sepkoski’s molluscan generic database and found that only a
 26 small number of extant bivalves with a fossil record had no Plio-
 27 Pleistocene fossil record. The reason for this marked discrepancy
 28 was because Sepkoski’s data were not standardized or updated
 29 but simply took taxonomic records as originally published.
 30 Jablonski *et al.* corrected species taxonomic assignments and
 31 found that only 9% of extant taxa with a fossil record were not
 32 present in the Pliocene. Additional records from sources not
 33 consulted by Sepkoski reduced this figure to 5.4%. Thus the ‘pull
 34 of the Recent’ may not be such a problem if care is taken over
 35 taxonomic assignments.

36 Two additional factors might also act to artificially elevate
 37 marine diversity towards the Recent.

38 (1) There may still be an overall trend towards a better fossil
 39 record in younger rocks, simply because fossils are better
 40 preserved and easier to collect from younger, less lithified
 41 sediments. This seems to be the case in the most detailed
 42 analysis of sampling bias yet undertaken, that by Crampton *et al.*
 43 (2006a). They found that the probability of sampling fossil
 44 molluscs increased through the Cenozoic by between 20 and
 45 50%, most markedly in the Pliocene and Pleistocene (Fig. 5).
 46 They ascribed this to the greater ease of recovery of fossils from
 47 younger strata as well as to increasing surface outcrop area
 48 preserved.

49 (2) Cenozoic turnover rates are low compared with the
 50 Mesozoic and Palaeozoic and time intervals comparatively shorter,
 51 so a greater proportion of genera extend across several time
 52 intervals (nearly 80% survive through each Cenozoic epoch;
 53 Foote 2000). Consequently, Peters & Foote (2001) estimated that
 54 this could create a two-fold increase in genus diversity for the
 55 Cenozoic, and would have greatest effect on the Plio-Pleistocene,
 56 where durations are the shortest.

57 Countering these two biases are four biases that act in the
 58 opposite direction, leading to underestimation of global marine
 59 diversity towards the Recent.

60 (1) All measures of rock bias in the Phanerozoic (Peters &
 61 Foote 2001; Smith 2001; Crampton *et al.* 2003; Peters 2005)
 62 have demonstrated a marked reduction in outcrop area and/or
 63 sampled habitat heterogeneity through the Cenozoic (Figs 3–5).
 64 Thus even if sampled diversity levels rose slowly (e.g. Alroy *et*

1 *al.* 2001) or remained more or less uniform over time (Crampton
 2 *et al.* 2006b), this trend is maintained in the face of decreasing
 3 numbers of fossil localities and/or habitat heterogeneity. De-
 4 creased rock outcrop must surely ameliorate, to a large extent,
 5 any increase in the quality of preservation and ease of collection
 6 that also occurs towards the present.

7 (2) The average number of species assigned to a family has
 8 more or less doubled since the Jurassic (Fig. 7; Flessa &
 9 Jablonski 1985), so that counts of higher taxa will progressively
 10 underestimate species diversity towards the Recent. This could
 11 underestimate Neogene species diversity compared with mid-
 12 Jurassic species diversity by as much as a factor of two.

13 (3) There has been a shift of the well-studied parts of the
 14 world away from the tropical belt during the Cenozoic (Fig. 2).
 15 Estimates of diversity in which the tropical fauna is progressively
 16 undersampled would be expected to result in lower sampled
 17 diversity towards the present (Jackson & Johnson 2001; Bush &
 18 Bambach 2004).

19 (4) There may be a large-scale bias against aragonitic shell
 20 preservation towards the Recent as a result of increased depth of
 21 bioturbation (Bush & Bambach 2004), causing a one- to two-fold
 22 reduction in diversity (but see discussion above).

23 The preliminary analyses by Alroy *et al.* (2001) of their
 24 database of biotic inventories using various methods of standar-
 25 dization found comparable diversity levels in the Palaeozoic and
 26 Mesozoic–Palaeogene, and evidence of only a modest rise in
 27 diversity between the end of the Middle Jurassic and the end of
 28 the Palaeogene. They concluded that there was ‘only a weak
 29 Mesozoic–Cenozoic radiation’, much smaller than had been
 30 predicted from raw taxon counts. However, Bush *et al.* (2004)
 31 showed that one of the techniques being used was highly
 32 unreliable, and that the other methods actually produced results
 33 that were comparable with the Sepkoski curve (Fig. 8).

34 Diversity has three components, alpha diversity (diversity
 35 within communities), beta diversity (diversity added by different
 36 communities in a region), and gamma diversity (diversity added
 37 by different geographical regions) (Whittaker 1972). Bush &
 38 Bambach (2004) compared alpha diversity in the Palaeozoic
 39 (Late Ordovician to Late Devonian), with communities in the
 40 Late Miocene to Pleistocene. After correcting for various
 41 possible biases (changing palaeolatitude, aragonitic dissolution,
 42 and inequality in the proportional representation of onshore–
 43 offshore communities) they concluded that alpha diversity had
 44 increased by a factor of about 3–4 since the late Devonian,
 45 broadly comparable with the results of Sepkoski *et al.* (1981).
 46 Kowalewski *et al.* (2006) did the same for Jurassic and Neogene
 47 communities and also found that alpha diversity had increased,
 48 although not by as much as expected. These observations are
 49 important because, for diversity to remain static or decline in the
 50 face of rising alpha diversity, beta or gamma diversity must have
 51 declined. A decline in beta diversity could come about through
 52 progressively restricting the set of communities available for
 53 palaeontologists to sample at outcrop; for example, through
 54 progressive loss of deposits representing mid- to outer shelf on
 55 land as sea levels fell through the Cenozoic.

56 In summary, there are good reasons for believing that the
 57 practice of through ranging between first and last occurrence,
 58 and the increase in the quality of the fossil record towards the
 59 present could be responsible for overestimating the rise in
 60 sampled marine diversity during the Cenozoic. However, there
 61 are also factors that bias the curve in the opposite direction (i.e.
 62 underestimation of the rise in diversity), and the most powerful
 63 biasing factor towards overestimation, the ‘pull of the Recent’,
 64 has been demonstrated to be less of a problem than at first

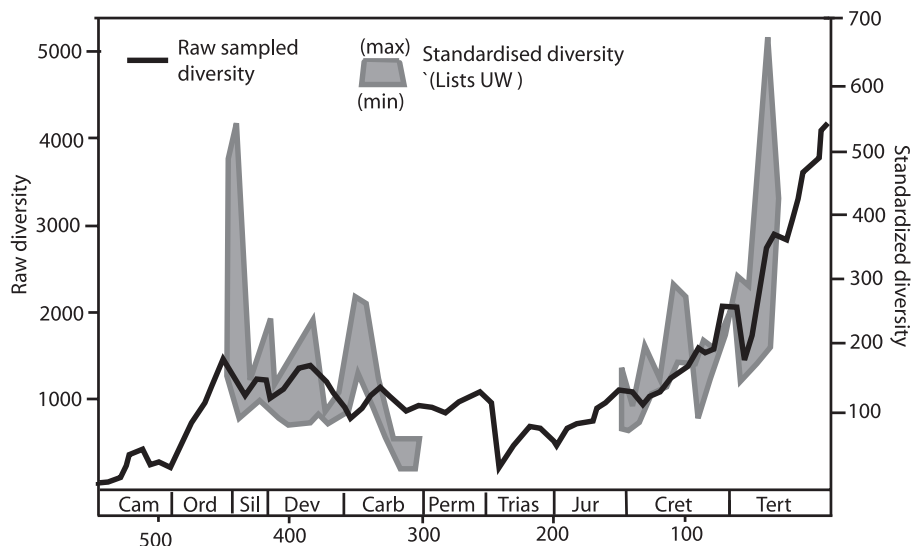


Fig. 8. Genus diversity through the Phanerozoic estimated from taxonomic counts without standardization (black line; from Sepkoski 2002) and from applying the lists unweighted method (UW) of Alroy *et al.* (2001), the method least affected by bias according to Bush *et al.* (2004). Maximum estimate is based on only those taxa found within the time interval; minimum counts are based on only those taxa that cross boundaries.

1 suspected. Habitat sampling is a key issue here because changing
 2 sea levels change the range of habitats and communities
 3 preserved on land for palaeontologists to sample; this effect
 4 could be artificially driving beta diversity and cannot easily be
 5 corrected for by undertaking more fieldwork. Because there are
 6 so many biases that need to be taken into account, it is not yet
 7 clear whether the rise in marine diversity towards the Recent is
 8 genuine or artificial.

9 *Cycles of extinction or cycles of non-preservation?*

10 The idea that taxonomic diversity might rise and fall episodically
 11 goes back to the catastrophists of the early 19th century.
 12 However, belief in a more regular pattern to extinction and
 13 origination is much more recent. Ager (1977) hinted at a 60 Ma
 14 cycle but thought it probably fortuitous, Thompson (1977)
 15 showed a *c.* 30 Ma cycle in vertebrate diversity, and Raup &
 16 Sepkoski (1984, 1986; see also Rampino & Haggerty 1995)
 17 advanced evidence of a 26 Ma cycle of extinction in marine
 18 invertebrates. The latest resurrection of this is that of Rhode &
 19 Muller (2005), who used Fourier spectral analysis to argue that
 20 the genus-level Phanerozoic marine diversity curve has a strong
 21 62 Ma cyclicity (Fig. 4b). However, like all previous claims for
 22 cyclicity, Rhode & Muller's 62 Ma periodicity turns out to be an
 23 artefact of data manipulation and the analytical method used
 24 (Omerbashich 2006).

25 The possibility that marine diversity has risen and fallen
 26 repeatedly on a regular basis over the Phanerozoic has, neverthe-
 27 less, intrigued palaeontologists. Although not strictly periodic,
 28 the regularity of this pattern suggests that marine diversity, rather
 29 than being the result of a complex, often haphazard set of
 30 biological and physical chance interactions, might be driven by a
 31 single recurring extrinsic factor. Furthermore, the long time scale
 32 of these cycles of diversity implies a major tectonic or extra-
 33 terrestrial driver of change. Rhode & Muller (2005), like others
 34 before them, sought to identify the driver by seeking to match
 35 the rises and falls in diversity against various geological and
 36 astronomical signatures, including $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (as a proxy for
 37 global climate change and biomass), time of emplacement of
 38 large igneous provinces, sea-level curves, ages of impact crater,
 39 and number of rock formations. Two of these showed weak
 40 correlation with marine diversity (emplacement of large igneous

1 provinces and the Exxon sea-level curve (Haq *et al.* 1987)) but
 2 the correlations were neither statistically robust nor convincing.
 3 Subsequently, Smith & McGowan (2005) demonstrated a highly
 4 significant correlation between rock outcrop area and genus
 5 diversity for the post-Palaeozoic (Fig. 3c). They showed that
 6 more than half the variance in genus-level diversity is explained
 7 by the amount of rock at outcrop. A similar close match is seen
 8 in the paper by Peters (2005), where a more refined database of
 9 stratigraphic sections was provided (Fig. 6). Basically, highest
 10 diversity is observed at times of widespread sediment deposition,
 11 whereas lowest diversity coincides with system bases when
 12 marine sediment at outcrop is at its lowest. Critically, peaks in
 13 the number of last occurrences of taxa mostly coincide with the
 14 transition from time intervals with a good marine rock record to
 15 those with a poor rock record (Smith 2001; Peters & Foote 2002,
 16 figs 3–5).

17 It is now clear that sampled marine diversity, as measured by
 18 taxon counts at genus, family and presumably species levels,
 19 fluctuates regularly through time. This recurrent signal is un-
 20 likely to have arisen simply by chance (e.g. Sepkoski 1989;
 21 Benton 1999), so some forcing mechanism seems to be involved.
 22 Furthermore, the high statistical correlation between amount of
 23 rock at outcrop and marine diversity rules out any of the
 24 postulated extraterrestrial drivers (periodic passage of the Solar
 25 System through space, oscillation of the Sun through the galactic
 26 plane, solar activity cycles, companion star effects or planet X;
 27 see Rhode & Muller (2005) for a succinct summary), as there is
 28 no plausible mechanism to link any of these extraterrestrial
 29 drivers to rock preservation at outcrop. There are, on the other
 30 hand, several potential geotectonic processes that work on the
 31 time scale required and that affect rock record through sea-level
 32 change (Dewey & Pitman 1998; Miller *et al.* 2005).

33 Changes in rock record, as measured by map outcrop area
 34 (Smith 2001; Smith & McGowan 2005), number of named
 35 formations (Peters & Foote 2001, 2002) or onset of stratigraphic
 36 gaps (Peters 2005, 2006a, b) correspond to second- and third-
 37 order sequence stratigraphic cycles (Figs 3–5). Consequently,
 38 they are best explained as a direct response to major cycles of
 39 craton flooding and draining. Sloss (1963) first recognized that
 40 major regional unconformities on the shelf (surfaces of erosion
 41 and non-deposition) divide the stratigraphic record into se-
 42 quences and provide the key to understanding eustatic change.

1 The sedimentary record ultimately preserved at outcrop during
 2 one of these cycles will depend upon the interplay of total
 3 surface area inundated by the sea, and length of time and severity
 4 of erosion following retreat of the sea. The amount of marine
 5 rock preserved should be greatest around the maximum flooding
 6 surface, when the continents are most extensively inundated, and
 7 will be at its lowest at around system base. However, the flooding
 8 record of continents is not a direct measure of eustatic change
 9 because variations in subsidence and sediment supply also influ-
 10 ence shoreline location (Dewey & Pitman 1998), and tectonically
 11 active regions may differ somewhat from stable cratons in their
 12 response (Crampton *et al.* 2006a).

13 There are three major drivers that control global sea-level
 14 curves on time scales of tens of millions of years (Dewey &
 15 Pitman 1998; Miller *et al.* 2005): (1) emplacement of large
 16 igneous provinces in the form of oceanic plateaux, which
 17 produces fast rises in sea level (at rates in the region of
 18 60 m Ma^{-1}) and slow falls as a result of thermal subsidence
 19 (10 m Ma^{-1}); (2) changes in ocean crust production primarily
 20 effected by variations in sea-floor spreading rates or ocean ridge
 21 lengths (100–300 m amplitudes at rates of 10 m Ma^{-1}); (3)
 22 continental collision and crustal shortening (amplitude 50 m at
 23 rates of up to 1 m Ma^{-1}). All three drivers are ultimately related
 24 to mantle plume activity; increased plume activity results in
 25 elevated sea-floor spreading rates and the emplacement of major
 26 volcanic provinces, all of which reduce ocean basin volume and
 27 force seas to rise and flood over the continents. Times of reduced
 28 plume activity result in ocean basin deepening, and general
 29 regression of seas from the continental blocks. In addition,
 30 variations in sedimentation rates can cause slow changes (60 m
 31 amplitude changes at rates of 10 m Ma^{-1}). Although glacial
 32 cycles can trigger massive changes in sea level they act over
 33 much shorter time scales than those of interest here (amplitudes
 34 of 200 m at rates of 20 m ka^{-1}).

35 The well-known *c.* 300 Ma Wilson cycle of continental accre-
 36 tion and fragmentation (Fischer & Arthur 1977), presumably
 37 linked to superplume development, is responsible for the two
 38 first-order sequence stratigraphic cycles of the Phanerozoic
 39 (Dewey & Pitman 1998, fig. 2) and is clearly expressed in the
 40 rock record by a major shift in the proportion of terrestrial to
 41 marine sediments (unpublished data) and in continental flooding
 42 (Fig. 2b). Thermal uplift, prior to rifting and break-up of a
 43 supercontinental block, causes sea level to drop and terrestrial
 44 sediment to be deposited across those areas of the continent that
 45 can today be sampled by geologists at outcrop. Sedimentation in
 46 shallow marine habitats still takes place, but over more limited
 47 areas on outer continental shelves or even upper slopes, areas not
 48 currently accessible to field palaeontologists. With plate rifting
 49 and dismemberment, continental trailing edges develop, which,
 50 as they sink, provide accommodation space for marine sediments
 51 to build through time. Maximum flooding is expected to coincide
 52 with maximum continental dispersal. Finally, towards the end of
 53 the cycle, as plates converge and coalesce there is net destruction
 54 of marine sediments through subduction, shortening and flexion
 55 of continental blocks at collision margins, all resulting in sea-
 56 level fall and enhanced erosion of the most recently deposited
 57 sediments.

58 Smaller-scale cycles of continental flooding and draining
 59 occurring over a time scale of tens of millions of years are
 60 superimposed over this primary cycle and consequently have
 61 different signatures depending upon where each falls in the first-
 62 order cycle. When first- and second-order flooding surfaces
 63 coincide there is a breakdown of shelf-edge fronts and stratified,
 64 oligotrophic oceanic conditions spread widely over the shelf, as

1 in the early Late Cretaceous (Gale *et al.* 2000). Conversely, the
 2 degree to which terrestrial sedimentation dominates at lowstands
 3 of lower-order cycles will be less as first-order cycles approach
 4 their maximum flooding surface than towards their start or end.
 5 The driver of these secondary cycles is less clear and possibly
 6 not a single factor. As the rate of ridge production has remained
 7 more or less uniform over the last 180 Ma (Rowley 2002), this
 8 cannot be responsible for driving the sea-level cycles. However,
 9 large igneous province emplacement possibly shows strong
 10 periodicity over parts of the Phanerozoic at about the correct
 11 wavelength (Prokoph *et al.* 2004). Furthermore, there is *prima*
 12 *facie* evidence for a link between the emplacement of major
 13 oceanic basaltic provinces and the onset of rapid sea-level rise,
 14 as, for example, in the Cenomanian (Kerr 2005). Evidence for
 15 cycles of sediment erosion comes from strontium, carbon and
 16 oxygen isotopes and shows a 30 Ma cyclicity (Prokoph & Veizer
 17 1999). In summary, a combination of plate assembly and
 18 disassembly on a time scale of *c.* 300 Ma, overlain by a second-
 19 order *c.* 30–100 Ma cycle of continental flooding and regression
 20 driven by changing ocean basin volume can best explain the
 21 cycles in rock record that have been observed. But can these also
 22 explain cycles in diversity?

23 *What causes the link between sampled diversity and rock* 24 *record?*

25 The connections between the primarily tectonic processes that
 26 alter sea level and marine diversity are complex (Fig. 9). Flood-
 27 ing of cratons increases the surface area of shallow marine shelf
 28 that organisms can inhabit, while also increasing the surface area
 29 over which marine sediments are deposited and ultimately
 30 become incorporated into the rock record. Regression reduces
 31 habitable shelf area and reduces the volume and surface area of
 32 previously deposited marine sediments from the rock record by
 33 erosion. Consequently, therefore, there are two competing and
 34 non-exclusive hypotheses that would explain the link between
 35 rock outcrop area and marine diversity: a biological and a
 36 sampling hypothesis (Peters & Foote 2001, 2002; Smith 2001;
 37 Peters 2005, 2006a).

38 *Biological hypothesis.* Diversity changes through speciation and
 39 extinction in response to increases and decreases in the surface
 40 area of shallow continental shelves. Shallow-water habitats (with-
 41 in storm wave base) are nutrient rich because of vertical mixing
 42 and/or lie within the ecologically important photic zone. They
 43 therefore support large and heterogeneous marine communities.
 44 As sea levels rise and seas start to spill across the continental
 45 shelves marine life diversifies to occupy the ever-increasing area
 46 of shallow-water habitats. Biodiversity later decreases as con-
 47 tinental shelf area covered by sea decreases through competition
 48 and extinction. Biodiversity also decreases at times of maximum
 49 flooding because that is when the waters covering large parts of
 50 the shelf become stratified as the sea floor becomes too deep to
 51 allow adequate nutrient recycling through storm mixing, and
 52 open ocean, oligotrophic conditions spread across much of the
 53 continents.

54 *Sampling hypothesis.* Diversity changes only slowly in marine
 55 settings, as communities migrate across the shelf to keep pace
 56 with slowly changing sea levels, but the amount of rock that is
 57 preserved at times of continental flooding is much greater than at
 58 times of regression. The diversity of taxa sampled in any time
 59 interval is simply controlled by the amount of rock at outcrop
 60 that remains and the proportions of shallow- to deep-water

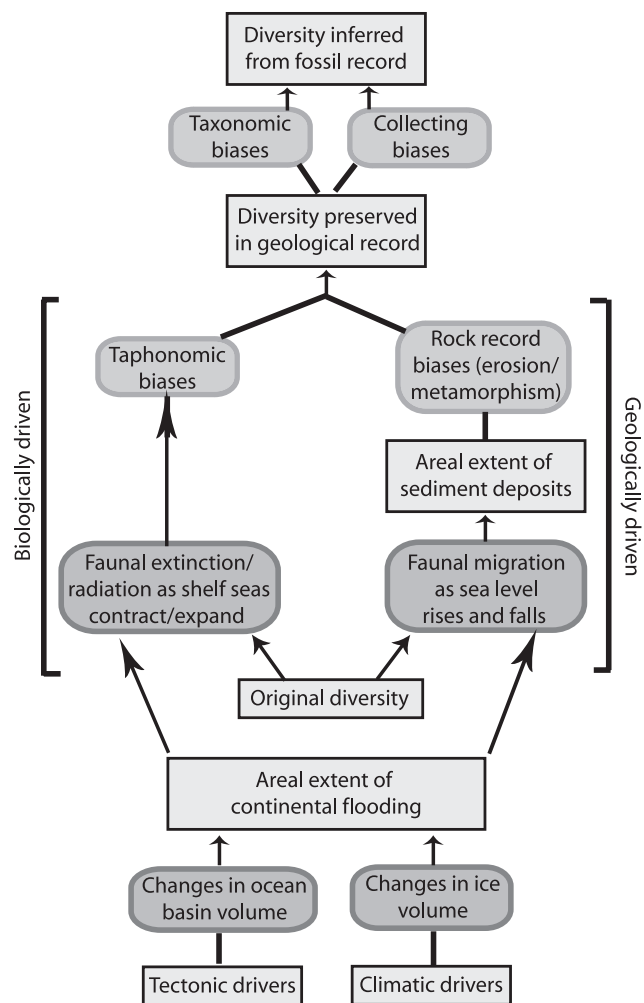


Fig. 9. Schematic flow chart showing the two ways in which tectonic and climatic drivers can alter sampled fossil diversity through sea-level change.

1 habitats sampled. With less rock preserved, a smaller range of
2 habitats will be sampled and fewer rare taxa discovered.

3 Of course, the truth probably lies somewhere between, with
4 both biological and sampling factors playing their part. But is it
5 possible to tell which has the upper hand in any one cycle? There
6 seems little doubt that the drop in diversity associated with the
7 continental accretion and formation of Pangaea at the end of the
8 Permian was real. It resulted in a fundamental reorganization of
9 marine community structure and the concomitant loss of major
10 clades (Erwin 2006; Wagner *et al.* 2006) on a scale seen at no
11 other time interval except possibly at the end of the Cretaceous
12 (Sepkoski 1981, 1997; Peters 2005). However, there is much less
13 certainty about whether marine diversity during other time
14 intervals really fluctuated significantly, despite all the claims
15 made for mass extinctions (e.g. Jablonski 2005).

16 To distinguish between the biological and sampling hypothe-
17 ses, Peters (2005, 2006a) compared the duration of genera with
18 the duration and timing of unconformity-bounded sedimentary
19 sequences, based on over 4000 sections at 541 North American
20 localities. He found that there was a strong and statistically
21 significant match between genus duration in the fossil record and
22 sequence duration in sections, both averaged over the entire

1 Phanerozoic and at the level of individual stages. Furthermore,
2 he showed that the proportion of genera having their last
3 occurrence in a stage was not correlated with the duration of
4 time encompassed by the overlying gap. Because the sampling
5 hypothesis predicts that the proportion of genera having their last
6 occurrence should increase as the duration of the overlying gap
7 increases, and genus duration should be independent of sequence
8 duration, Peters concluded that genus diversity was intimately
9 tied to habitat continuity within local depositional basins; that is
10 to say, that sea-level change drove both rock record and bio-
11 logical diversity independently. He also showed that rates of
12 genus origination and extinction were positively correlated with
13 the areal extent of hiatuses.

14 Peters (2005, 2006a) made a strong case for why the match
15 between marine biodiversity and rock record might be more
16 biological than sampling artefact in origin. However, there are
17 reasons for questioning his conclusions. First, Peters showed that
18 the average duration of a stratigraphic gap is around 100 Ma
19 whereas the average duration of a genus and a sequence is about
20 25 Ma. Therefore few if any genera are expected to span gaps in
21 individual sections, making the duration of the hiatus academic
22 to local survivorship (as demonstrated by the lack of correlation).
23 Second, Peters ignored the problem of pseudoextinction, which is
24 estimated to affect about one-third of genera in well-studied
25 groups (Smith & Patterson 1988) and probably more in strati-
26 graphically important groups such as ammonites and graptolites.
27 The disappearance of a genus along with marine sedimentation
28 in a region is no guarantee that it has not survived somewhere
29 else, only to be given a new name by taxonomists when its
30 descendants reappear at a later time. Indeed, taxonomists are
31 very likely to have used gaps in the rock (and fossil) record as
32 convenient and objective points to subdivide otherwise continu-
33 ously evolving lineages. Marine conditions continued uninter-
34 rupted throughout the Phanerozoic whether or not our biased
35 sample of rock deposits captures this. Therefore the correspon-
36 dence between average section duration and average genus
37 duration could equally well be explained as a reflection of
38 taxonomic practice if pseudoextinctions are clustered around
39 peak occurrences of gaps in the stratigraphic record. That
40 pseudoextinction might have a sizeable effect is suggested from
41 gap analysis at higher taxonomic level (Paul 1998), where it is
42 clear that time intervals when there are peaks of last occurrence
43 are followed by time intervals when there are elevated propor-
44 tions of missing fossil record.

45 Today the world's continental marine shelves represent the
46 most productive marine ecosystems but cover only about
47 $28 \times 10^6 \text{ km}^2$ or 0.1% of the Earth's surface (Carlton *et al.*
48 1999). Therefore one might expect major changes in sea level
49 that alter marine shelf area to be a driver of extinction. We can
50 test this assumption by turning to the Pleistocene fossil record.
51 Pleistocene glaciation cycles had a profound effect on sea level.
52 For example, the last glacial maximum at around 20 ka ago
53 caused sea levels to drop rapidly (1 cm a^{-1}) to $C. 120 \pm 5 \text{ m}$
54 below that of today (Miller *et al.* 2005). This shifted sea level
55 close to the continental shelf-edge, and did so an order of
56 magnitude faster than any tectonically driven sea-level fall. The
57 net result was a dramatic reduction in the area of shallow water
58 marine habitats, with those lying within the photic zone, the most
59 productive areas of all, shrinking to about 20% of their former
60 extent (Schaaf 1996). Yet Valentine *et al.* (2006) have shown that
61 bivalve genera were remarkably immune to Pleistocene sea-level
62 changes. Although there are major shifts in geographical range
63 (Valentine & Jablonski 1991), extinction at genus level was less
64 than 6%. Regional extinction was maybe three to four times

1 higher in high-latitude, isolated island regions, where the effects
 2 of glaciation were strong and latitudinal migration impossible
 3 (e.g. New Zealand: Crampton *et al.* 2006b). It is hard to think of
 4 a more extreme situation than having sea level drop to the
 5 continental shelf-edge so rapidly, and yet diversity at genus level
 6 changed only modestly. This and several other lines of evidence
 7 suggest that regression or transgression by itself cannot generate
 8 high levels of extinction in marine populations (see Gale *et al.*
 9 2000; Smith *et al.* 2001). Other factors, such as perturbation of
 10 primary productivity in the oceans, must be critical.

11 The concept that mass extinctions profoundly affected the
 12 history of life on Earth through the Phanerozoic dominated the
 13 last decade and a half of palaeontological research in the 20th
 14 century. Yet much of the evidence for such events (and their
 15 supposed cyclicity) came from taxon sampling that was neither
 16 standardized nor took account of variation in the rock record.
 17 There are, nevertheless, two time intervals when extinction is
 18 greater than predicted even after preservational and rock record
 19 biases (but not pseudoextinction or habitat biases) are taken into
 20 account. These occur at the Permo-Triassic and Cretaceous–
 21 Tertiary boundaries and stand as evidence that life has been
 22 affected by extraordinary events. Other postulated times of mass
 23 extinction are much less convincing, as they occur at times when
 24 the rock record at outcrop was also becoming markedly poorer
 25 and when pseudoextinction is likely to be most rife. This means
 26 that their precise duration, timing and even existence remain
 27 ambiguous (Foote 2003, 2005).

28 Summary and conclusions

29 The fossil record provides our only realistic means of estimating
 30 how diversity has changed through time. Currently, however, our
 31 understanding of Phanerozoic marine diversity patterns is in a
 32 state of flux. We know that past attempts to measure biodiversity
 33 through time are probably inaccurate because of several major
 34 systematic biases, although we are still unsure as to how
 35 profound an effect these will turn out to have had in distorting
 36 our view. The primary biases that blight current efforts to
 37 estimate Phanerozoic marine diversity are: (1) uneven sampling
 38 effort of rocks at outcrop both geographically and over time; (2)
 39 a cyclical systematic bias in the rock record from which we have
 40 to make our fossil collections, driven ultimately by episodes of
 41 tectonic activity; (3) taxonomic inconsistency, especially asso-
 42 ciated with interpreting the meaning of last occurrence data.
 43 More sophisticated methods of estimating diversity patterns are
 44 now being developed that can take sampling and rock record bias
 45 into account and are already challenging some long-held views.
 46 These approaches need to be combined with a deeper apprecia-
 47 tion of the nature of taxonomic data before we arrive at a
 48 definitive view of how marine diversity has changed over time.

49 It is possible that the Phanerozoic marine diversity curve will
 50 turn out to be very different from the one prevalent just a few
 51 years ago. The relentless rise in marine diversity through the late
 52 Cretaceous and Cenozoic may still be there, although once
 53 sampling artefact has been properly accounted for it will
 54 probably be seen to be flattening out over the last 60 Ma. More
 55 importantly, many of the marked stage-to-stage changes in
 56 diversity present in unstandardized data, and that provided the
 57 ‘bread and butter’ for ‘mass extinction’ hypotheses during the
 58 1980s and 1990s, may be no more than artefact. Only the end-
 59 Permian and end-Cretaceous events currently seem secure. Even
 60 if there are other periods of elevated extinction that cannot be
 61 explained solely by sampling bias (Foote 2003), there is growing
 62 evidence that changes in diversity are principally the result of

1 slow-acting tectonic events that control the temporal continuity
 2 of the geological record (Peters 2005), not catastrophes. And so
 3 we seem to be returning more or less full circle to the views of
 4 Newell (1952), who first produced cogent evidence in support of
 5 cyclical sea-level change as the primary driver of the marine
 6 fossil record. The critical question facing us now is whether it
 7 does this biologically, through altering the ecological landscape
 8 of shallow marine seas, or indirectly as a consequence of the
 9 volume of sedimentary deposits that enter the rock record.

10
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1. Spelling Norrell not as in ref. list. Which is the correct version?
2. Carlton et al. date not as in ref. list. Which is the correct year?
3. Alroy et al. - please give the first three authors before et al.
4. Cherns & Wright - please check the page range.
5. Dewey & Pitman - please give editor/s.
6. Newell 1967 - please give title of the Special Paper.
7. Smith 2007 - please update if possible.