The ties linking rock and fossil records and why they are important for palaeobiodiversity studies

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Abstract: A correlation exists between the quality of the rock record and the diversity of fossils recorded from that rock record but what drives that correlation, and how consistent that correlation is across different environments, remain to be determined. Palaeontologists wishing to investigate past diversity patterns need to first address issues of geological bias in their data.

The fossil record provides the only empirical evidence of how life has diversified over geological time, but it needs to be interpreted with caution. For many years the history of diversity was estimated simply by summing up the numbers of taxa (species, genera, families) palaeontologists have recorded from successive geological time intervals, or extrapolated from their first and last occurrences in the geological record. This time series approach led to what is now a classic view of how diversity has changed over time (Sepkoski *et al.* 1981; Benton 1995; Sepkoski 1997). Such counts take the fossil record at face value, or assume that biases or errors are randomly distributed in such a way that the overall effect is negligible. We now realize that this is only a first, crude, approximation that may be subject to a number of strong biases that arise because of the nature of the sedimentary rock record.

Time series analysis requires that sampling be carefully controlled for best results. Ideally data should be collected so that sampling from each time interval is uniform, or at least sampled fairly using the 'shareholder quorum' subsampling method (Alroy 2010). Otherwise apparent changes in diversity may arise for spurious reasons, for example, because (a) a time intervals being sampled are of variable duration (longer time intervals = more recorded diversity), or (b) a time interval has been more intensively sampled (more localities/specimens/habitats/formations sampled = more recorded diversity). While for a biological survey it is easy to plan a sampling strategy that will give approximately equal effort and coverage for observations, palaeontologists are faced with a much more difficult task. Firstly, the time bins they work with are irregular and highly variable in their duration. For example, the durations of one of the most widely used time scales has intervals spanning two orders of magnitude (Gradstein *et al.* 2004). Secondly, and much more critically, palaeontologists are collecting from an already incomplete and highly biased set of rocks, which in turn skew the range of taxa and habitats that can be sampled (**Zuschin et al. 2011**). Bluntly put, we cannot sample what is not preserved in the rock record, although phylogenetic and molecular approaches can attempt to compensate (Pol & Norrell 2006; Bininda-Emonds *et al.* 2007; Wills 2007; **O'Connor et al. 2011**). So while it may be possible to standardize for sampling effort from the rock record that remains, those rocks might provide a far from uniform sample of the sediments and palaeoenvironments that were originally present.

Palaeontologists cannot therefore assume uniform sampling of the fossil record and must try to assess how the rock record they have to work with has affected their ability to sample evenly, and then develop methods that compensate appropriately for this variation. In recent years therefore palaeobiodiversity studies have become more probabilistic in their approach, concerned with establishing confidence limits around estimates that try to correct for uneven sampling (Alroy *et al.* 2001, 2008) and testing empirical patterns against model predictions (Foote 2001; Smith & McGowan 2007; McGowan & Smith 2008). If we are to improve our estimates of biodiversity over time then sampling parameters need to be better quantified and we need to better understand the complex interrelationship between rock and fossil records. This is no simple task and requires a more systematic approach to recording culture as well as better documentation of the variables (**Benton et al. 2011**).

Figure 1 summarizes the problem as we see it. Palaeontologists estimate past diversity from remains preserved in the rock record. As with any
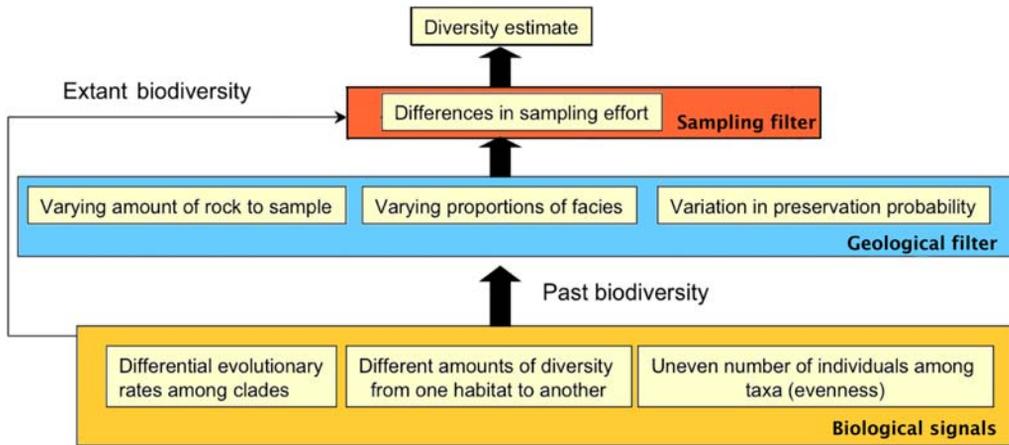
Fig. 1. Schematic flow chart showing how the sampled diversity estimate that palaeontologists have to work with represents a filtered signal of the original biological diversity record from the geological past.

biological survey, variation of sampling effort of the surviving rock record needs to be factored out. But this rock record has already passed through a geological filter that has altered and distorted not only the rock area that survives to sample, but also the proportions of facies and the preservational quality of its fossil record. Were this geological filter to remain approximately constant over time there would be little problem of interpreting the biological signal. However, it is far from uniform with amounts of rock to sample, proportions of facies represented by those rocks and preservation potential all varying from one time interval to the next. To interpret observed changes in sampled biodiversity estimates correctly we must therefore first understand the role of the geological filter.

Variability of the rock and fossil records

Fossil record

All clades rise and fall in diversity over time according to whether speciation or extinction is proceeding faster. Such change can take place rapidly, during mass extinction events and adaptive radiations, or gradually so as to define a long-term rising or falling trend over time. At any one time standing diversity also varies in different habitats and latitudes, and some taxa are much more numerous than others. These, of course, are the biological signals that palaeobiologists wish to isolate. However, superimposed on this comes variation in preservation potential. This varies markedly amongst taxonomic groups but remains relatively invariant within groups over time. Many of the best fossil records belong to microfossil groups

such as coccolithophorids and planktonic foraminifera, where specimens can be collected in abundance against a Milankovitch time scale (20 Ka) (e.g. Dunkley-Jones *et al.* 2008; Ebra *et al.* 2010; **Lazarus 2011**). For many other groups, however, fossil records can be patchy and incomplete at best. Amongst clades with a mineralized skeleton, the worst fossil record must surely be that of birds. Fountaine *et al.* (2005) compiled a total of just 121 specimens recorded from Mesozoic sediments, which encompass 98 species and 70 genera of fossil birds. Thus, over 80% of species and almost 60% of genera are known only from single specimens. Clearly the chances that any new fossil find will represent a new species or new genus are very high, particularly if it comes from a new location or time interval (Benton 2008).

While some groups clearly have better fossil records than others, so long as preservation potential in each group remains approximately similar over time there should be no problem. Changes to preservation potential can occur, as for example with the evolving robustness of the skeleton in echinoids (Smith 2007) or bivalves (Kidwell & Holland 2002; Behrensmeyer *et al.* 2005). However, for the most part, the preservation potential of major higher taxa changes so slowly that it can have little role to play in creating short- and medium-term fluctuations in sampled diversity. It is also unidirectional rather than cyclical. So, while preservation potential is variable amongst taxonomic groups it is unlikely to confound biodiversity studies except in generating simple long-term trends.

Lagerstätten pose a particular problem for the analysis of diversity patterns. The record of groups with low preservational potential or multi-element

skeletons that are prone to rapid post-mortem disarticulation, such as insects and vertebrates, may be largely confined to such deposits. As Lagerstätten are non-randomly distributed through time, both at coarse (Allison & Briggs 1993) and fine scales (e.g. Brett *et al.* 2009), this could seriously distort biodiversity counts. Improving our understanding of how Lagerstätten are distributed within a sequence stratigraphic framework (e.g. Brett *et al.* 2009) and taking Lagerstätten distribution into account when analysing diversity (e.g. **Benson & Butler 2011**), are important areas for future development.

Rock record

Palaeontologists collect fossils from the rocks that are available to them at outcrop or from drill cores, and for the most part have done this effectively. There are, never the less, spatial and temporal biases to this sampling (Smith 2001) with the record of Europe and North America dominating global databases. While these are easy to compensate for by standard procedures such as rarefaction and subsampling (e.g. Alroy *et al.* 2008), a deeper, more pernicious problem remains: the rock record being sampled is itself a biased sample of what once existed.

The quality of the sedimentary record varies markedly amongst environmental settings, with some environments, such as cratonic highlands and deep-sea basins, which represent over 50% of the surface area of the planet at present, being much less commonly represented in the geological record than others. However, in marked contrast to the fossil record, the sedimentary rock records from individual settings also show marked temporal variability at all time-scales. At the very largest scale, major plate tectonic cycles of plate accretion and dismemberment generate changes in ocean basin volume that drive sea-level changes on cratons of up to 150 m amplitude (Dewey & Pitman 1998; Miller *et al.* 2005). These sea-level cycles drive major changes to the relative proportions of terrestrial and marine sediments being deposited over the continental blocks, with marine sedimentary rocks dominating the rock record at times of highstand (Smith 2001; Smith & McGowan 2007). Over much shorter time intervals of 10–100 Ka, changes in land-locked ice drive sea-level oscillations of up to 150 m amplitude by altering the volume of water in the ocean basins (Miller *et al.* 2005). Finally, at intermediate time-scales of 10–50 Ma there is growing evidence that mantle cell cycles create regional sea-level changes of somewhat smaller amplitude (Lovell 2010; Petersen *et al.* 2010) through thermal uplift. All these processes directly affect the quality and nature of the rock record that is laid down by affecting uplift and erosion as well as accommodation space and thus sediment accumulation rates. When sea-level in the past was close to, or below, current levels the resulting rock record available to geologists is dominated by terrestrial sediments deposited in flood plains and continental basin environments. As a consequence there is only a highly restricted set of localities where marine rocks of those time intervals and their fossils can be investigated on land. Conversely, when sea-level stood much higher than present-day levels, as in the early Late Cretaceous, terrestrial and marginal marine deposits are relatively sparse. Note, however, that the link between sea-level change and habitable marine shelf area can be complex. Wyatt (1995) for example showed that, due to hypsometry, a drop in sea-level in the late Ordovician actually resulted in an increased surface area of shallow marine settings.

A further complicating factor is the degree of post-depositional compaction and alteration which sediments have undergone, as this affects how easily and effectively sampling can be carried out (Hendy 2009). The probability of preserving and sampling small and/or delicate fossils (and thus recording higher diversities) is higher in fine-grained, poorly consolidated sediments than in older sequences subjected to tectonic and thermal alteration. Finally, the chemical composition of the skeleton significantly affects the chances of a fossil surviving in the rock record and can seriously bias both land and deep-sea records (e.g. **Cherns & Wright** 2000, **2011**).

The evidence that sedimentary rock and fossil records are intimately linked

Recent efforts to calculate global diversity patterns after standardizing for collecting effort (Alroy *et al.* 2001, 2008) recover a Phanerozoic diversity curve that is different to that using raw sampled diversity. This suggests that the actual and potential collecting effort in different parts of the geological column is a significant factor in shaping our sampled diversity. But it does not tell us whether palaeontologists have unevenly sampled the rocks that are available at outcrop, or whether sampling has been relatively uniform, but those rocks provide a non-random sample of what once existed.

That a positive correlation exists between areal extent of sedimentary rocks on land and sampled diversity has emerged from a number of studies. These include studies that estimate the surface outcrop area of terrestrial or marine sedimentary rocks from geological maps and their accompanying memoirs (Ramp 1976; Smith 2001; Crampton *et al.* 2003; Smith & McGowan 2007;

McGowan & Smith 2008; Barrett *et al.* 2009; **Wall et al.** 2009, **2011**) or counts of the numbers of named formations (Peters & Foote 2001; Crampton *et al.* 2003; Benson *et al.* 2009; Mannion *et al.* 2010; **Benson & Butler 2011**). In all cases a statistically significant positive correlation has been demonstrated linking the rock and fossil records, both in marine and terrestrial environments.

One drawback of some of these studies is that they match rock and fossil diversity records that are not directly comparable. Most commonly regional rock record compilations have been tested against global diversity estimates (Smith 2001; Peters & Foote 2001; Smith & McGowan 2007; McGowan & Smith 2008; Benson *et al.* 2009). Global rock record outcrop estimates are available (Ronov 1978) but are compiled at a much coarser time-scale compared to diversity estimates (see Wall *et al.* 2009). However, not all studies suffer from this problem. **Crampton et al.** (2003, **2011**) compare fossil and rock record data from exactly the same geographical region and Peters & Heim (2010) have now combined the Paleobiology Database (a database of taxonomic lists of fossils with accompanying geological and spatial data: http://paleodb.org) with Macrostrat (a database of rock outcrop in North America: http://macrostrat.geology.wisc.edu) to compare North American rock and fossil records directly (**Peters & Heim 2011**). **Lloyd et al.** (**2011**) have a comparable deep-sea rock and fossil database for the central and North Atlantic and adjacent regions, and **Upchurch et al.** (**2011**) have compared regional rock outcrop estimates with regional dinosaur diversities. Where data from rock and fossil records are collected from exactly the same geographical region the evidence for a link between rock and fossil diversity records is generally strengthened for both short and long-term trends.

One additional complication has arisen recently in the use of geological maps to directly estimate the area of exposed rock available to sample for fossils (e.g. Uhen & Pyenson 2007; Wall *et al.* 2009). Dunhill (2011) has shown that, for a series of 50 sites within England and Wales, the area of rock outcropping and the amount of rock exposure (i.e. rock that is not covered by superficial deposits and one could literally stand on) is not well correlated. This finding makes it much more difficult to apply simple species-area reasoning to local diversity fluctuations in the fossil record at small scales. However, such variation becomes negligible for large-scale studies that simply ask what proportion of a large landmass has rocks that yield fossils of a particular age, and present day exposure and historic exposure patterns may be very different.

The conundrum

That rock and fossil records are intimately connected is therefore now well established, for both marine and terrestrial records. However, determining the mechanism that is responsible for generating this linkage remains surprisingly difficult. Climate change, mantle plume cycles and plate tectonic activity all act in concert to create cycles of sea-level change across cratons. This has two important consequences: it changes the relative amount of marine and terrestrial sedimentary rocks that end up being preserved in the geological record and it also changes the surface area of shallow marine and terrestrial habitats where organisms can live. These two factors (regional extent of sedimentary rock and regional extent of original habitat) change in concert: as the outcrop area of marine rock record expands with craton flooding, the surface area of marine habitats also expands, potentially driving speciation and leading to greater standing diversity. Conversely, as sea-level drops, the area over which marine sedimentary rocks are deposited becomes smaller, as does the habitat area for marine organisms driving extinction and leading to smaller standing diversity.

We are therefore faced with two linkage mechanisms acting in parallel. On the one hand the fluctuating quality of the rock record may be controlling sampled diversity directly through altering the potential collecting effort that can be made in each time interval. The more outcrop area and the more environmental heterogeneity that outcrop encompasses, the more biological diversity is likely to be recovered from a simple species/area consideration (Rosenzweig 1995). On the other hand, biological diversity will also be responding directly to sea-level change. The 'common cause' hypothesis (Peters 2005) thus predicts that species diversity and rock record will mirror one another because both macrostratigraphy and biodiversity respond independently and in concert to sea-level cycles.

In truth both sampling and common cause effects must act together to influence the fossil record that we have recovered from the rock record. The key question to be answered then is which, if either, of the two processes dominates? This may turn out to be a far from simple question, as the relative strengths of the two factors may be dependent on the environment, time-scale or geological period being studied (e.g. **Benson & Butler 2011**). For example we may find that sampling effects may dominate in forming small-scale, stage-to-stage, changes in sampled diversity, while common cause effects shape longer-term trends. It could even be possible that sampling effects dominate at certain periods while common cause effects drive biodiversity curves at other time periods.

How we test these ideas remains to be formulated but a start is now being made (Peters 2005; Hannisdal & Peters 2010; **Hannisdal 2011**; Wall *et al*. 2011). Peters (2006) found no correlation between the size of taxonomic loss and the duration of the succeeding sediment hiatus. However, as his null hypothesis assumed uniform diversity over time, all this proves is that there is more to the fossil record than pure sampling bias, something also shown by Smith & McGowan (2007). Peters & Heim (2010) also argued for common cause dominancy based on their demonstration that in North America last occurrences of marine taxa correlate more strongly to marine sediment package terminations than first occurrence rates correlate to sediment package originations. This, however, mirrors the asymmetry of the sediment packages themselves, which provide a relatively complete record of transgressive intervals but whose later parts are artificially truncated by non-deposition and erosion (thereby truncating generic ranges). The weak correlation between taxic and sediment package originations thus argues for a relatively weak sampling bias, while the stronger correlation between sediment trucations and taxic last occurrences argues for strong sampling bias within cycles of deposition.

Where next?

If we are ever to develop a more complete and accurate estimate of Phanerozoic biodiversity patterns then a first important step must be to develop a better understanding of the complex interaction between rock record quality and sampled diversity. This requires better documentation of the way in which the rock record changes over time as well as a more consistent recording strategy that takes account of both sampled diversity and sampling opportunity, comparable to that developed for North American Quaternary land mammals (**Barnosky et al. 2011**). To test these ideas thoroughly we probably need to turn to sedimentary depositional systems where sea-level is not the dominant driving factor of both biological opportunity and rock record quality. Here the deep-sea record offers such an opportunity.

For land-based records the Paleobiology Database Project (PaleoDB) represents a major advance in providing taxonomic occurrence data tied to specific outcrops. This offers the ability to analyse faunas from comparable habitats and to make partial corrections for collection effort. It is not the complete answer, however, as it only provides indirect estimates of alpha diversity (Bush *et al.* 2004) and in calculating regional or global diversity is not able to correct for the biases introduced by the missing rock record and habitat heterogeneity.

Standardizing for sampling effort without also standardizing for the proportion of rocks capturing different palaeoenvironments that are preserved in the geological record, will still produce misleading results. What is really needed is an equivalent database that can be used to measure the diversity and heterogeneity of the geological record. This would need a method to combine the digital data generated by geological surveys summarizing the aerial distribution of rock outcrops, with field evidence about the nature of the sedimentary environments those outcrops encompass. It would also need to be compiled at a temporal resolution equivalent to the PaleoDB. Then it would be truly possible to disentangle the signals coming from biodiversity and rock record.

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