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Cyclicity in the fossil record mirrors rock outcrop area

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In a recent article, Rohde & Muller (Rohde & Muller 2005 *Nature* 434, 208–210) identified a strong 62 Myr cyclicity in the history of marine diversity through the Phanerozoic. The data they presented were highly convincing, yet they were unable to explain what process might have generated this pattern. A significant correlation between observed genus-level diversity (after removal of long-term trends) and the amount of marine sedimentary rock measured at a surface outcrop in Western Europe is demonstrated. This suggests that cyclicity originates from long-term changes in sedimentary depositional and erosional regimes, and raises the strong possibility that the cyclicity apparent in the record of marine fossils is not a biological signal but a sampling signal.

Keywords: Phanerozoic diversity patterns; cyclicity; quality of fossil record

1. INTRODUCTION

In a recent article, Rohde & Muller (2005) identified a strong 62 Myr cyclicity in the history of marine diversity through the Phanerozoic. This was based on an analysis of Sepkoski's (2002) compendium of first and last occurrences of marine genera in the fossil record. The data they presented were highly convincing, yet they were at a loss to explain what might have generated this pattern. Several potential processes able to generate cyclicity in diversity were evaluated, including cometary impacts, vulcanism, sea-level and climatic change, but the relevant geophysical records showed no cyclicity of comparable duration. They also considered whether cyclicity was simply reflecting variation in the quality of the fossil record and used the number of named geological formations over time (Peters & Foote 2001) as a measure of rock record bias. Again no compelling match emerged, although they noted that poor resolution might be obscuring any correlation in the case of rock record bias. However, a correlation is known to exist between observed genus-level diversity (after removal of long-term trends) and the amount of marine sedimentary rock at a surface outcrop (measured in a higher resolution study) for the more recent part of the geological record (Smith 2001). Here we demonstrate that the data of Rohde & Muller could be explained by a rock outcrop bias.

2. MATERIAL AND METHODS

Data on the diversity of genera with a duration of less than 45 Myr (their 'short-lived genera') were taken directly from Rohde & Muller (2005 and their associated supplementary material). For comparison with the high-resolution rock record data only those taxa from the Upper Triassic (Norian) to the Middle Eocene (Lutetian) were considered. This time-interval encompasses two complete 62 Myr cycles in the Rohde & Muller analysis.

The surface outcrop area of marine sedimentary rocks in western Europe was calculated for 39 stages or epochs from the Late Triassic to the Pliocene by using the British Geological Survey 1:63 360 (1 inch) series maps and the French Geological Survey 1 : 50 000 series maps. For each time-interval the number of map quadrats where marine sediments of the appropriate age outcrop provides a measure of the outcrop area available to palaeontologists. The primary data are provided in table 1. Sequence stratigraphic architecture for Western Europe is taken from Hardenbol *et al.* (1998). The cross-correlation test was implemented using the programme SYSTAT v. 5.2 (Systat Inc. 1992).

3. RESULTS

Figure 1 shows the global diversity of short-lived genera and the rock outcrop area for Western Europe, set against the primary and secondary sequence stratigraphical architecture (figure 1*c*). The variable nature of marine sediment deposition and erosion created by transgressive–regressive cycles has left a clear signature in the rock record at outcrop and this closely follows the palaeodiversity curve (figure 1*a*). When the two series are log-transformed and the weakly opposing long-term trends removed by plotting residuals, a tight correspondence between the shape of the two curves becomes immediately apparent (figure 1*b*). The fit between these two curves was tested by regression analysis and cross-correlation and found to be highly significant ($p=0.002$; figure 2). In fact, for reasons that remain unclear, the match was slightly stronger when the two curves were one step out of lag, indicating that the genus-level diversity was best predicted by the preceding rock outcrop area. The value of the cross-correlation coefficient at lag $0=0.554$, while at lag$+1$ the cross-correlation coefficient $=0.681$. Squaring these values provides an estimate of the amount of variation in diversity explained by changes in the rock record (lag $0=0.307$, lag$+1=0.464$), with the preceding rock area explaining about 15% more of the variation in diversity than contemporaneous rock area. The degree of correlation was much stronger than that previously found based on a comparison of total genus-level diversity and extending to the Pliocene, which had cross-correlation values of about 0.4 at lag 0 and lag$+1$ (Smith 2001). Based on these cross-correlation values, the amount of variation in diversity explained by rock area is only around 0.16. The current study explains 2–3 times more of the observed variance in palaeodiversity.

4. DISCUSSION

This observation, that about half the variance in genus-level diversity can be explained by the rock outcrop area, is important because the amount of rock at outcrop could provide a simple explanation for why we see variation in genus-level diversity: sampled diversity is highest when there is most rock available at an outcrop and palaeontologists can sample across a wider range of local communities and

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Table 1. Rock outcrop area based on number of map quadrats with marine sedimentary rocks of the appropriate age at an outcrop.
(Sediments are listed separately for France and the UK; log genus diversity, log rock outcrop area and the residuals of log genus diversity (ResLogGen) and log rock outcrop area (ResLogMap) are also given. Abbreviations for epochs follow Sepkoski (2002).)

epoch	France map area (marine sediment)	UK map area (marine sediment)	combined map area (marine sediment)	log genus diversity	log map area	ResLogGenus	ResLogMap
Lut	25	13	38	2.779	1.580	0.418	0.094
Ypr	19	40	59	2.711	1.771	0.078	0.704
Tha	15	0	15	2.480	1.176	−1.354	−1.345
Dan	7	0	7	2.384	0.845	−1.866	−2.482
Maa	13	1	14	2.831	1.146	1.235	−1.503
Cam	25	30	55	2.883	1.740	1.697	0.435
San	34	50	84	2.782	1.924	1.147	1.001
Con	35	50	85	2.699	1.929	0.715	0.977
Tur	46	60	106	2.646	2.025	0.489	1.250
Cen	54	55	109	2.595	2.037	0.275	1.249
Alb	42	49	91	2.423	1.959	−0.725	0.954
Apt	26	46	72	2.348	1.857	−1.091	0.585
Bar	29	4	33	2.322	1.519	−1.141	−0.551
Hau	30	4	34	2.431	1.531	−0.315	−0.546
Val	26	4	30	2.260	1.477	−1.306	−0.759
Ber	12	4	16	2.255	1.204	−1.219	−1.682
Tit	41	35	76	2.267	1.881	−1.025	0.477
Kim	47	36	83	2.528	1.919	0.784	0.565
Oxf	50	30	80	2.538	1.903	0.971	0.478
Cal	41	40	81	2.533	1.908	1.060	0.460
Bat	51	40	91	2.519	1.959	1.090	0.590
Baj	50	38	88	2.486	1.944	0.999	0.507
Aal	44	26	70	2.403	1.845	0.579	0.143
Toa	49	39	88	2.334	1.944	0.247	0.436
Ple	48	42	90	2.348	1.954	−0.327	0.434
Sin	42	53	95	2.212	1.978	−0.327	0.477
Het	34	53	87	1.987	1.940	−1.733	−1.526
Nor	25	0	25	2.201	1.398	−0.156	−1.578

also stand a better chance of capturing rarer taxa. We note that cyclicity was evident only in short-lived taxa, not in long-lived taxa. This is significant because short-lived genera are those most likely to reflect biases in the fossil record. One way to test our hypothesis would be to look at taxa that are restricted to single stratigraphic levels. Such taxa were either originally rare or had strongly restricted habitat preferences and their distribution is even more likely to reflect biases in the rock record. We predict that the correspondence between diversity and rock outcrop area should be even more pronounced in these taxa if sampling were indeed the underlying cause.

There are two reasons why we observed a stronger correspondence between rock outcrop area and the diversity curve than in a previous study (Smith 2001). First, this analysis considered only short-lived genera and omitted the long-lived taxa that failed to display cyclicity in the Rohde & Muller (2005) analysis. Second, the most recent part of the record was not included. Rohde & Muller noted that cyclicity was less regular in this part of the geological column and previous workers (Alroy *et al.* 2001; Peters & Foote 2001) have observed that the 'pull of the Recent' has significantly distorted the biodiversity curve over this time-interval. Both this study and the earlier analysis of Smith (2001) found a small lag between the cross-correlation of rock outcrop and diversity. At present this remains unexplained, but we note it is evident only in the Cretaceous cycle and not the Jurassic cycle.

Of course, global diversity has been compared here with only a small part of the world's rock record. However, there are good reasons for believing that the rock record of Western Europe is a suitable proxy for making this comparison. First, Sepkoski's genus-level data is dominated by occurrences in North America and Europe and, second, very similar patterns of rock record bias have been shown to exist in North America using a different approach (and different data; Peters & Foote 2001). Hardenbol *et al.* (1998, p. 6) note that major transgressive–regressive cycles in western Europe 'reflect the response of the western portion of the Eurasian Plate to major plate tectonic phases in the opening of the Atlantic Ocean. These major tectonic phases affect the volume of ocean basins and hence global sea-level, and thus produce synchronous tectono–eustatic major transgressive–regressive cycles which are essentially identical for Tethyan and Boreal realms'. That implies that patterns of rock record bias seen in Western Europe are likely to be repeated elsewhere in the world.

Patterns of sediment deposition and erosion on the continental shelf are a complex product of

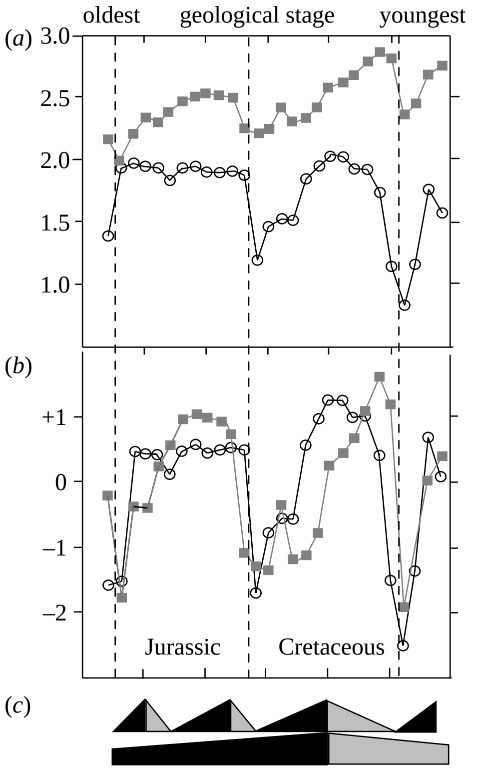

Figure 1. Plots of area of marine sediments exposed at an outcrop in Western Europe (France and the UK: open circles) and the numbers of short-lived (i.e. <45 Myr duration) genera (squares) plotted against geological stages from the Upper Norian to the Middle Eocene. (*a*) Log transformed plots that are not detrended, (*b*) detrended log transformed plots, (*c*) first and second order sequence stratigraphical cycles (from Hardenbol *et al.* (1998)). Black rising wedges: transgressive phases; light grey declining wedges: regressive phases. For details of time-scale and how sediment outcrop area was measured see Hardenbol *et al.* (1998).

interactions among regional tectonics and eustatic sea-level change. However, these processes, as well as affecting the rock record, also control the extent of continental shelf flooding, and thus directly influence biological diversity through a species/area effect (Rosenweig 1996; Peters & Foote 2001; Smith 2001; Smith *et al.* 2001). Clearly, both biological and rock record biases are likely to arise in tandem and there is an urgent need to collect data, such as that of Crampton *et al.* (2003), that can discriminate the relative importance of these two potential explanations of palaeodiversity curves.

Of course, this does not answer the question of what is driving the major cycles that create the first and second order sediment packages on our continental shelves in the first place. But it suggests that the answer lies in the mechanisms that control long-term cycles of sediment deposition and erosion, and raises the strong possibility that the 62 Myr cyclicity apparent in the record of marine fossils is not a biological signal but a sampling signal.

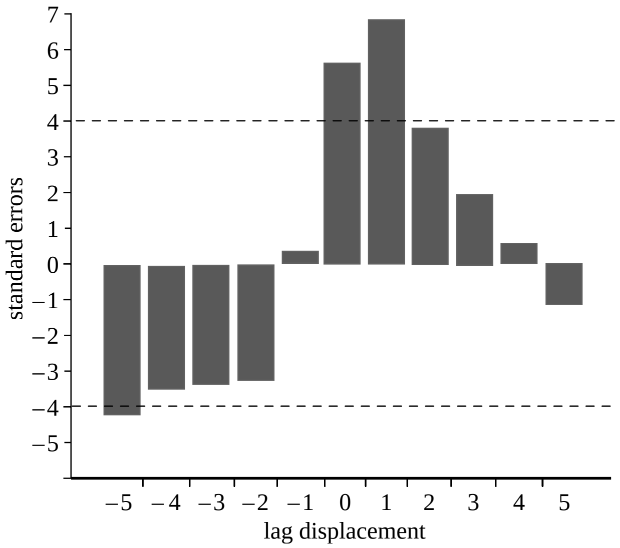

Figure 2. Cross-correlation plot of log transformed outcrop area of marine sediment regression residuals against log transformed, short-lived generic diversity regression residuals. Dashed line, 4 s.e.

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