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LETTERS

Environmental determinants of extinction selectivity in the fossil record

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The causes of mass extinctions and the nature of biological selectivity during extinction events remain central questions in palaeobiology. Although many different environmental perturbations have been invoked as extinction mechanisms[1–3], it has long been recognized that fluctuations in sea level coincide with many episodes of biotic turnover[4–6]. Recent work supports the hypothesis that changes in the areas of epicontinental seas have influenced the macroevolution of marine animals[7,8], but the extent to which differential environmental turnover has contributed to extinction selectivity remains unknown. Here I use a new compilation of the temporal durations of sedimentary rock packages to show that carbonate and terrigenous clastic marine shelf environments have different spatio-temporal dynamics and that these dynamics predict patterns of genus-level extinction, extinction selectivity and diversity among Sepkoski's Palaeozoic and modern evolutionary faunae[9]. These results do not preclude a role for biological interactions or unusual physical events as drivers of macroevolution, but they do suggest that the turnover of marine shelf habitats and correlated environmental changes have been consistent determinants of extinction, extinction selectivity and the shifting composition of the marine biota during the Phanerozoic eon.

One of the most striking features of the Phanerozoic fossil record of marine animals is a shift in the relative taxonomic richness of clades that first appeared early in the Palaeozoic era. Sepkoski summarized this transition by identifying three evolutionary faunae, each composed of Linnaean classes with covarying diversity trajectories[9], broadly similar ecologies[9–11], and comparable mean rates of taxonomic turnover[12]. The Palaeozoic evolutionary fauna, which is typified by low-biomass, epibenthic suspension feeders, was dominant during the Palaeozoic (Fig. 1a) and has higher and more variable rates of extinction (Fig. 1b) than the modern evolutionary fauna, which is typified by mobile infaunal suspension feeders and grazers[9–12] (see Methods). Selective extinction with respect to evolutionary fauna is prominent at the end-Permian mass extinction, but other time intervals also show differential rates of extinction (Fig. 1b).

Explanations for the transition between the Palaeozoic and modern evolutionary faunae have focused on biological interactions. For example, Sepkoski modelled evolutionary fauna diversity dynamics using coupled logistic equations that assume negative ecological interactions[12], but tests of this hypothesis fail at the genus level[13,14]. The diversification of the modern evolutionary fauna and the decline of the Palaeozoic evolutionary fauna has also been linked to increasing predation intensity during the Phanerozoic[15,16], but this hypothesis is not supported by genus occurrence data[17], nor does it predict the observed extinction selectivity (Fig. 1b). High rates of Palaeozoic evolutionary fauna extinction at the end-Permian mass extinction have been attributed to ecological factors and causally linked to the rise of the modern evolutionary fauna[12,13,18–20], but this does not explain longer-term shifts in evolutionary fauna dominance or selective extinction in other time intervals (Fig. 1).

Here I explore the hypothesis that patterns of extinction and extinction selectivity among the evolutionary faunae are linked, by means of differential environmental tolerances, to spatio-temporal dynamics in two types of marine shelf environments: those with sediments derived from the physical erosion of land (siliciclastics), and those with sediments precipitated as calcium carbonate (carbonates),

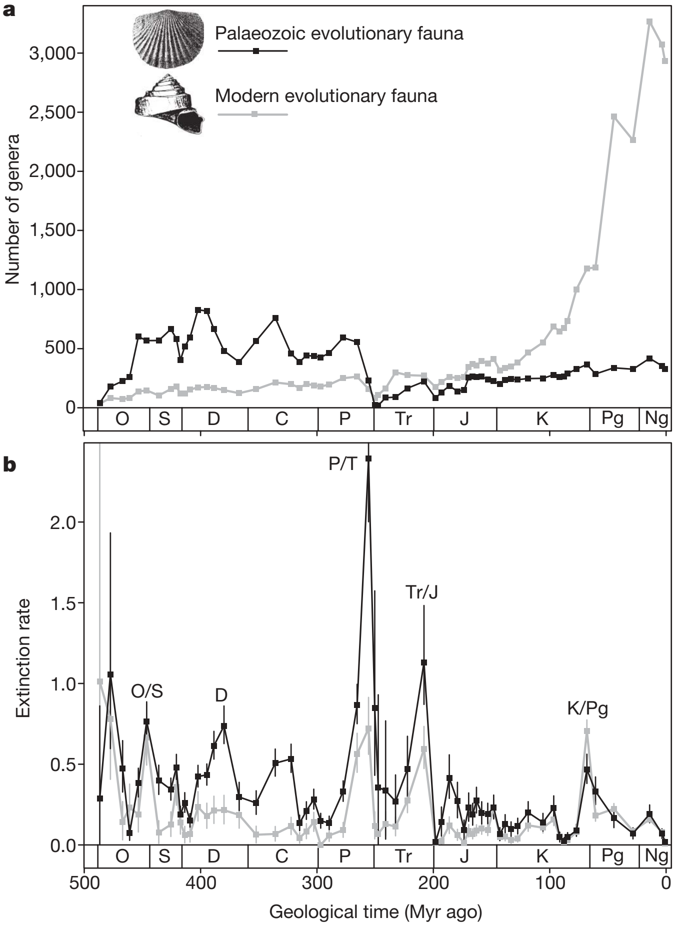

Figure 1 | Palaeozoic and modern evolutionary fauna genus diversity and extinction. a, Total number of genera. **b**, Per-capita, per-interval extinction rates. Error bars show 95% binomial confidence limits. Major mass extinctions are labelled (O/S, end-Ordovician; D, late-Devonian; P/T, end-Permian; Tr/J, end-Triassic; K/Pg, end-Cretaceous). O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; Ng, Neogene. Myr ago, million years ago.

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either inorganically or in association with biological activity, mainly photosynthetic algae[21]. Carbonate and siliciclastic environments are easily recognized in the rock record and differ markedly in terms of average substrate characteristics and nutrient levels[21], factors that are expected to influence the relative success of the Palaeozoic and modern evolutionary faunae[10,11,22]. The carbonate–siliciclastic distinction is also important because biological preferences for these environments have been linked empirically to different macroevolutionary trajectories[23,24].

To test the environmental determinant hypothesis, I first used the Paleobiology Database to determine whether or not Sepkoski's evolutionary faunae occur preferentially in carbonates or siliciclastics (Methods; see also Supplementary Information). In agreement with the average ecological characteristics of their constituent genera[9,11], most Palaeozoic evolutionary fauna genus occurrences (59% of 96,403) are from carbonate environments, which tend to have low nutrients and firm substrates[21], whereas most modern evolutionary fauna genus occurrences (61% of 134,833) are from siliciclastics, which tend to have higher nutrients and softer substrates. Thus, it is possible that differential turnover between these two environments has contributed to extinction selectivity during the Phanerozoic eon.

To quantify the sedimentary record in a way that permits direct comparison to macroevolutionary patterns, I compiled the temporal ranges of 3,940 gap-bound carbonate and siliciclastic rock packages at 541 locations in the United States (see Methods). The total number of packages is comparable to taxonomic diversity but is an area- and temporal-continuity-weighted measure of rock quantity[25]. Rates of package truncation are analogous to rates of taxonomic extinction[26] but reflect instead area-weighted rates of environmental truncation.

Shelf carbonate packages decline in number from a maximum in the Ordovician to minima in the Triassic and Recent (Fig. 2a). This long-term trajectory was influenced by the northwards drift of Laurentia from tropical to mid- and upper latitudes during the post-Palaeozoic era[27]. However, even after accounting for an overall reduction in tropical shelf area and unequal latitudinal sampling, there remains a significant decline in the global shelf area of carbonates relative to siliciclastics[28].

In addition to having different long-term abundance trajectories, carbonates have higher and more variable rates of truncation than siliciclastics (Fig. 2b). This is an important distinguishing characteristic that can be attributed to two main factors: (1) shelf carbonates form over a narrower bathymetric range than siliciclastics; and (2) carbonate environments are subject to negative interactions with siliciclastics because terrigenous sediment input can preclude or dilute carbonate production[21]. Thus, increases in terrigenous sediment supply, which can be driven by sea-level fall, tectonic uplift and climate change, can result in the selective elimination of carbonate environments relative to siliciclastics. Volatility in carbonates may also be enhanced by more direct linkage to climate via temperature and seawater chemistry[18,21].

A visual comparison of evolutionary fauna macroevolutionary patterns (Fig. 1) and the macrostratigraphy of their preferred shelf environments (Fig. 2) suggests numerous similarities, and these are borne out statistically. Palaeozoic evolutionary fauna extinction rates, de-trended to emphasize short-term variability, are significantly positively correlated with carbonates but not siliciclastics (Table 1). The opposite is true for the modern evolutionary fauna, although the correlations are generally weaker and both carbonates and siliciclastics may be important during the Palaeozoic. On longer timescales, the replacement of the Palaeozoic evolutionary fauna by the modern evolutionary fauna (Fig. 1a) is mirrored by the temporal replacement of carbonates by siliciclastics (Fig. 2a).

Despite the fact that sedimentary data from North America are being compared to genus data that are ostensibly global, more than 55% of the variance in interval-to-interval changes in Palaeozoic evolutionary fauna extinction rates during the Palaeozoic is predicted by interval-to-interval changes in rates of carbonate truncation (Fig. 3). Results are similar when only those genera occurring in North America are used to calculate evolutionary fauna rates (Table 1), when genus extinction is adjusted to account for variable and incomplete sampling[26] (Table 1), when variation in interval duration is factored out via partial correlation, when correlations are calculated for arbitrary stretches of geological time, and when analysis is confined to the Palaeozoic (see Supplementary Information). Thus, not only is the prominent biological selectivity at the end-Permian mass extinction reproduced by the selective truncation of carbonate environments, but it is reproduced in a way that is statistically robust and consistent with the environmental and biological selectivity observed in many other time intervals, including the end-Ordovician, late Devonian and mid-Carboniferous extinctions.

The ability of the sedimentary rock record to predict macroevolutionary patterns might seem to constitute prima facie evidence for a geologically controlled sampling bias in fossil data, but three observations allow this hypothesis to be discounted. First, adjusting genus extinction rates to account for variable and incomplete preservation[26] does not change the overall environment–evolutionary fauna relationship (Table 1). Second, analyses of the aggregate sedimentary and fossil records show that sedimentary hiatus durations do not predict rates of genus extinction[8], and hiatus durations are similarly uncorrelated with evolutionary fauna extinction rates. Third, if sampling bias was a dominant factor, correlations between sedimentary and fossil data would be comparable for all groups of taxa, yet extinction in the Palaeozoic evolutionary fauna is more strongly correlated with

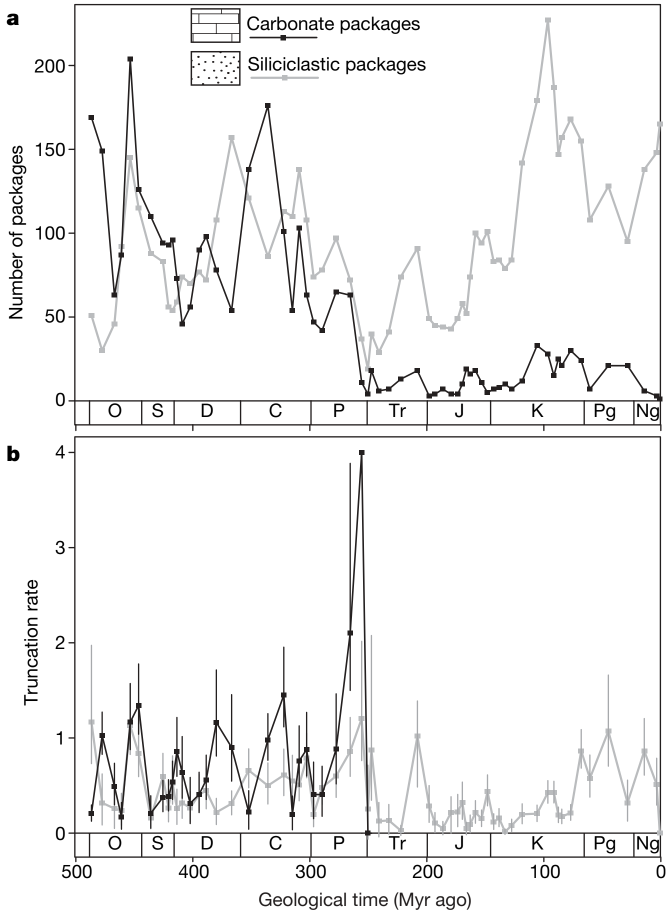

Figure 2 | Carbonate and siliciclastic macrostratigraphy. **a**, Total number of packages, an area- and temporal-continuity-weighted measure of rock quantity. **b**, Per-package, per-interval truncation rates, an area-weighted measure of environmental truncation. Error bars show 95% binomial confidence limits. There are too few carbonate packages in the post-Palaeozoic to reliably calculate truncation rates.

Table 1 | Spearman rank-order correlation coefficients

Lithofacies	Raw extinction rates	Corrected extinction rates	North America extinction rates
Palaeozoic evolutionary fauna			
Carbonate*	0.752‡	0.686‡	0.747‡
Siliciclastic	0.204 (NS)	0.106 (NS)	0.157 (NS)
Modern evolutionary fauna			
Carbonate*	0.265 (NS)	0.061 (NS)	0.547†
Siliciclastic	0.409†	0.451†	0.406†

Data are de-trended (first differences) time series of genus extinction rates and environmental truncation rates. Raw extinction rates are face-value extinction rates in Sepkoski's compendium (Fig. 1b). Corrected extinction rates are extinction rates corrected for variable and incomplete sampling (mean of 194 pulsed model iterations[26]). North America extinction rates use only genera occurring in North America according to the Paleobiology Database (~30% of genera used to calculate raw extinction rates). Cross-correlations for carbonate–siliciclastic, 0.116* (NS); Palaeozoic–modern evolutionary faunae, 0.675 ($P < 0.0001$). NS, not significant ($P \geq 0.1137$).

* Carbonate rates are constrained only in the Palaeozoic (Tremadocian–Guadalupian; $n = 27$). The last Permian stage (Tatarian) is omitted because of limited carbonate packages; including it strengthens the correlation between carbonate and Palaeozoic evolutionary fauna (raw extinction rates $r = 0.778$). Correlations for siliciclastics include Tremadocian–Pliocene ($n = 62$).

† $P \leq 0.0043$.

‡ $P \leq 0.0002$.

carbonate truncation than the modern evolutionary fauna is correlated with either environment.

The inability of sampling bias to explain adequately environment–evolutionary fauna correlations leaves two alternative hypotheses. First, it is possible that genus last occurrences are taxonomic artefacts, and that the observed correlations reflect a tendency among systematists to arbitrarily truncate continuous lineage segments during times of environmental turnover. Although conceivable, this hypothesis is unlikely because short-term variability in rates of extinction would persist even if most lineages were artificially truncated, provided that true lineage extinctions also result in genus last occurrences (see Supplementary Information). The second, much more probable, hypothesis is that both evolutionary fauna turnover and shelf sedimentation share a common cause. The most plausible mechanism is sea-level change and the resultant expansion and contraction of epicontinental seas, phenomena which are intimately linked to tectonics via crustal uplift and subsidence, and to global climate via temperature and continental ice volume.

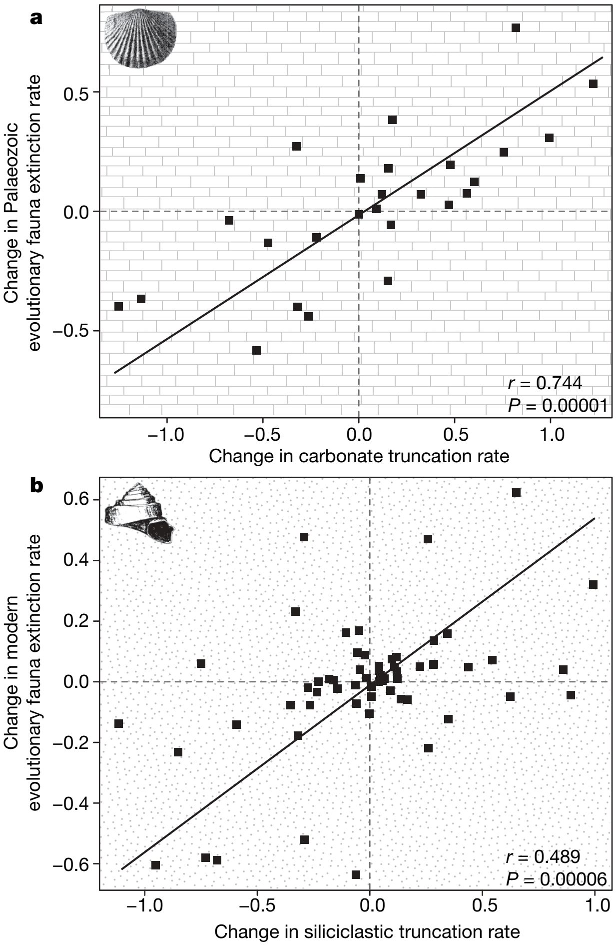

Figure 3 | First differences in evolutionary fauna extinction rates versus environmental truncation rates. a, Palaeozoic evolutionary fauna versus carbonate. **b**, Modern evolutionary fauna versus siliciclastic. Linear product-moment correlation coefficients, *P*-values and reduced major axis trend lines are shown. The last Permian stage is omitted in **a** owing to low numbers of carbonate packages (if included, $r = 0.815$). See Table 1 for rank-order correlations for all pairwise comparisons.

Whatever the reasons for the close statistical similarities between patterns of marine shelf sedimentation and rates of extinction among Sepkoski's Palaeozoic and modern evolutionary faunae, these results must affect our understanding of large-scale patterns in the fossil record. If the correlations reflect taxonomic artefacts, then extinction rate estimates, including those at the major mass extinctions, require substantial revision. If, instead, both selective biological extinction and differential environmental turnover share a common cause, then mechanisms for extinction and extinction selectivity gain important new constraints. Although the ultimate explanation is likely to be more complicated than a simple species area effect, these results do provide a substantial measure of support for the intriguing and long-standing hypothesis[5,6] that changes in the areas of unique epicontinental sea habitats, as well as correlated environmental effects, have consistently influenced rates of extinction, extinction selectivity, and the shifting composition of the marine biota during the Phanerozoic eon.

METHODS SUMMARY

Genus data derive from Sepkoski's global compendium[29] of marine animal genera (http://strata.geology.wisc.edu/jack). Only genera with both range endpoints resolved to one of Sepkoski's 63 post-Cambrian time intervals (stages) were used. The evolutionary faunae were based on Sepkoski[9] and partitioned as follows. A total of 8,009 genera from Bivalvia, Echinoidea, Gastropoda, Gymnolaemata and Malacostraca constitute the modern evolutionary fauna, and 7,460 genera from Anthozoa, Articulata, Asteroidea, Blastoidea, Crinoidea and Stenolaemata comprise the Palaeozoic evolutionary fauna. Together, these two evolutionary faunae include more than 70% of all post-Cambrian genera in Sepkoski's compilation.

To estimate environmental preferences, global genus occurrences were downloaded from the Paleobiology Database (http://paleodb.org) marine invertebrate working group on 7 September 2007. Multiple species from the same genus in a collection were grouped together and subgenera were kept separate. Of 308,865 genus occurrences, 256,481 (83%) could be assigned to one of three evolutionary faunae. Each collection was assigned to one of four lithologies (carbonate, siliciclastic, mixed, unknown) on the basis of the primary and secondary lithology fields (see Supplementary Information). Occurrences in mixed collections (those with primary and secondary lithologies from two different environments) were assigned one-half of an occurrence to each environment. Changing this protocol does not substantively affect the results.

Macrostratigraphy is based on the temporal ranges of gap-bound rock packages compiled separately for different geographical locations[25]. The correlation charts of ref. 30 were used to compile the temporal ranges of surface and subsurface rock packages at 541 locations in the United States (see Supplementary Information). A total of 1,518 carbonate and 2,422 siliciclastic packages were recognized. Reference 26 describes the survivorship-based rate parameters calculated for both gap-bound rock packages and marine animal genera.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Genus data. Sepkoski's original definition[9] of the evolutionary faunae included nektonic and planktonic taxa, such as nautiloids and vertebrates. Here, only primarily benthic invertebrate classes are assigned an evolutionary fauna (see Methods Summary). Including classes with primarily planktonic or nektonic genera does not significantly alter the results (see Supplementary Information). Because the Palaeozoic and modern evolutionary faunae are not sufficiently taxonomically diverse to calculate rates in the Cambrian, all analyses are limited to the post-Cambrian.

Sedimentary package data. Macrostratigraphy is based on the temporal ranges of gap-bound rock packages compiled separately for different geographical locations[25]. For this analysis, temporal gaps in sedimentation fall into one of two categories: (1) those that constitute missing time (hiatuses); and (2) those that constitute missing environment. For example, a unit designated as carbonate but bracketed above and below by siliciclastics would constitute a single gap-bound carbonate package. Similarly, a unit designated as carbonate and bracketed by hiatuses would also constitute a single gap-bound carbonate package (see Supplementary Information). This definition of gaps means that the timing of environmental truncation may be controlled by non-deposition and/or erosional truncation of a longer-duration sediment package. Although the relative frequencies of package termination types cannot be measured at this time, it is likely that most of the environmental gaps recognized here reflect non-deposition rather than significant erosional truncation, if for no other reason than because marine sediments and gaps repeatedly accrue only in areas of low elevation and low net rates of erosion. To be recognized as a significant gap, hiatuses must span approximately one to three million years, although the ability to recognize such gaps varies temporally and spatially according to geological knowledge.

To partition sedimentary packages into carbonates and siliciclastics, the dominant lithologies and environmental data in ref. 30 were followed. Most rock units can be assigned to either carbonates or siliciclastics based on the charts, which reflect the dominant, rather than exclusive, lithology of the specified stratigraphic units. In the few cases where the dominant lithology was reported as mixed carbonate and siliciclastic, the unit was assigned to carbonates, although results are not sensitive to this procedure. It is not always possible to determine from the charts whether a unit was deposited in a marine or terrestrial setting, but in cases where terrestrial sediments could be identified they were excluded. The inclusion of an unknown quantity of terrestrial siliciclastic sediment may be responsible for the lower overall siliciclastic correlations (Table 1).

Although many Phanerozoic carbonates contain abundant animal skeletons, it is important to acknowledge that animal fossils are not required for the formation of carbonate sediments. A substantial fraction of the carbonate in modern shelf environments is produced by photosynthetic algae[21], and carbonates are abundant in similar shelf settings throughout the Proterozoic, long before animals with skeletons evolved. Thus, animal fossils tend to be found in carbonates that would probably have formed in their absence, just as fossils are found in siliciclastic sediments that would have accumulated with or without skeletal input.

Finally, it is worth noting that both Sepkoski's genus data and the macrostratigraphic data have numerous correlation, categorical and transcription errors. However, such errors should weaken, not inflate, the correlations reported here. Furthermore, the possibility that genus last occurrences are arbitrary subdivisions of continuous lineage segments does not demand that interval-to-interval changes in rates of genus extinction diverge statistically from true underlying rates of extinction, provided that true lineage extinction still results in a significant number of recognized genus last occurrences (see Supplementary Information).