Macrostratigraphy and macroevolution in marine environments: testing the common-cause hypothesis

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Abstract: Quantitative patterns in the sedimentary rock record predict many different macroevolutionary patterns in the fossil record, but the reasons for this predictability remain uncertain. There are two competing, but non-mutually exclusive, hypotheses: (1) similarities reflect a sampling bias imposed by variable and incomplete sampling of fossils, and (2) similarities reflect environmental perturbations that influence both the patterns of sedimentation and macroevolution (i.e., common-cause). Macrostratigraphy, which is based on the quantitative analysis of hiatus-bound rock packages, permits variation in the rock record to be expressed in terms of rock quantity and, more importantly, spatiotemporal continuity. In combination with spatially-explicit fossil occurrence data in the Paleobiology Database, it is now possible to more rigorously test alternative hypotheses for similarities in the rock and fossil records and to start distinguishing between geologically-controlled sampling bias and the common-cause hypothesis. Here we summarize results from measuring the intersection of Macrostrat and the Paleobiology Database. Our results suggest that patterns in the fossil record are not dominated by large-scale stratigraphic biases. Instead, they suggest that linkages between multiple Earth systems are driving both spatiotemporal patterns of sedimentation and macroevolution.

Darwin (1872, p. 289) famously described the stratigraphic record as 'a history of the world imperfectly kept.' This pessimism towards the stratigraphic record of evolution was articulated for the specific purpose of explaining why palaeontologists had failed to sample the innumerable intermediate forms that Darwin expected in his particular formulation of the theory of evolution by natural selection. Although this view of life is demonstrably misguided and macroevolutionary theory, such as punctuated equilibrium (Eldredge & Gould 1972), now accounts for the abundant non-continuous patterns of evolution that are observed in the fossil record, many palaeobiologists remain skeptical about the fidelity of the fossil record. In particular, there is concern that observed patterns of diversity, origination, and extinction in the fossil record are artifacts of the variable quantity and quality of the Phanerozoic sedimentary rock record. This bias-oriented perspective is rooted in the pervasive and strong positive correlations that have been documented between many different tabulations of rock quantity and diversity (Gregory 1955; Raup 1976; Smith 2001; Smith *et al.* 2001; Peters & Foote 2002; Crampton *et al.* 2003; McGowan & Smith 2008; Wall *et al.* 2009). Although past diversity can only be sampled from the incomplete rock and fossil records, it may also be the case that variability in the rock record both reflects and controls fundamental changes in Earth systems that in turn directly and/or indirectly influence the macroevolutionary history of life. This alternative interpretation of the observed co-variation between the fossil and rock records is known as the common-cause hypothesis; that is, there is a common set of processes that have similarly shaped both stratigraphic patterns and biological evolution.

The common-cause hypothesis has been discussed, if not formalized, by geologists for many decades. Sloss (1963) recognized that the large-scale variability and nature of the preserved stratigraphic record on the craton primarily reflects tectonically-driven cycles in continental flooding, and not the destruction of sedimentary rocks by erosion and metamorphism (see also Melott & Bambach 2011; Meyers & Peters 2011). Similarly, Newell (1952) proposed that mass extinctions, the large die-offs that he first described as such (Bambach 2006), were driven by sea-level fluctuations that resulted in the geographical spread of unconformities (e.g. Simberloff 1974). The common-cause hypothesis has not, however, been tested with quantitative data until very recently.

Initial tests of the common-cause hypothesis against the null hypothesis of stratigraphic and preservation-induced sampling bias have been made using an integration of Macrostrat (http://macrostrat.org) and the Paleobiology Database

(PaleoDB; http://paleodb.org). Macrostrat contains a summarization of the rock record for several different geographical regions, including (as of February 2011) North America, the circum-Caribbean, New Zealand, and the deep-sea. Macrostrat is continually growing and improving, but here we use data consisting of 15 773 formation-level lithostratigraphic units from a spatial array of 831 stratigraphic columns in the USA, Canada, Caribbean, eastern Mexico and northern South America (Fig. 1).

The PaleoDB is global in scope and contains fossil occurrences that are reported in the primary literature and by individual field investigators. Because both the PaleoDB and Macrostrat contain information on geographical location and basic lithostratigraphic data (Fig. 1a, b), PaleoDB fossil collections located in the study area are matched to specific units in Macrostrat on the basis of time and lithostratigraphy (see Peters & Heim 2010 for full descriptions of the matching procedures). In essence, the fossil record, at least as represented in the PaleoDB, has been returned to its original stratigraphic context, at least as captured by Macrostrat. With this unique integration of large-scale stratigraphic and palaeobiologic data, the common-cause hypothesis can be more rigorously tested against the null hypothesis of stratigraphic bias. Here we explore a few of these tests using the analytical framework of macrostratigraphy.

Macrostratigraphy

Macrostratigraphy (Peters 2006*a*; Hannisdal & Peters 2010) is a recent development in quantitative stratigraphy that takes advantage of spatially explicit stratigraphic data, which can be summarized quantitatively using a variety of metrics, most of which relate to the spatiotemporal extent and continuity of the sedimentary rock record. Fundamental to the approach is that any geographical location, the rock record can be divided into a succession of sediment packages that are bound by temporal gaps. These gap-bound rock packages can be defined on any criteria, including the hiatuses that occur at unconformities or lithological contacts, which may or may not correspond to temporal hiatuses. For example, if the dynamics of carbonate environments need to be quantified separately from those of siliciclastic environments, a sandstone unit separating two limestone units at a location would constitute a gap, even if sedimentation were in fact temporally continuous through the whole succession and there were no hiatus (Peters 2008). In the analyses presented here, marine sedimentary packages are based on hiatuses in all types of marine sedimentation that are resolvable at a temporal resolution of *c*. 1–3 Ma.

The advantage of partitioning the stratigraphic record into gap-bound packages is that time series for the number of sedimentary packages, rates of package initiation and rates of package truncation can be derived, yielding macrostratigraphic quantities that are quantitatively identical to, and also analogous to, macroevolutionary quantities, such as taxonomic richness and rates of origination and extinction (Peters 2006*a*, *b*; Hannisdal & Peters 2010). Rock package initiation and truncation rates are quantities that reflect the spatial rates of translation, as well as expansion and contraction,
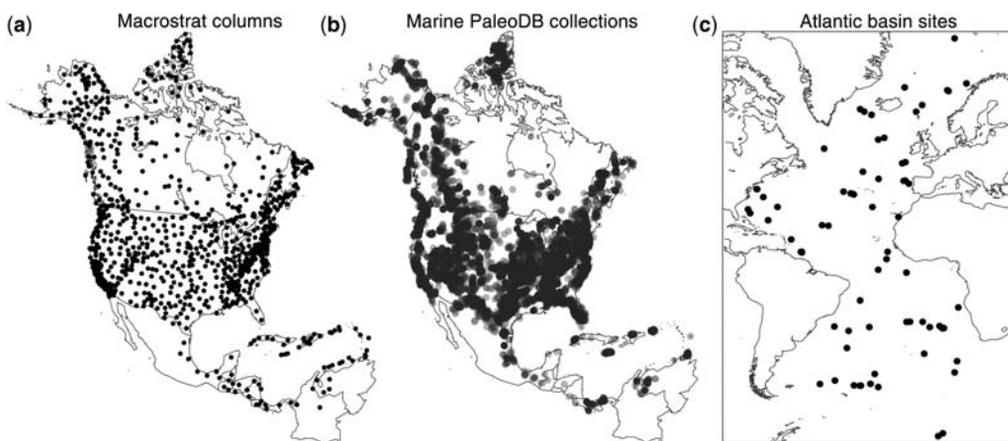

Fig. 1. Maps of continental coverage area and the Atlantic Ocean basin. (**a**) Map showing the 831 locations of stratigraphic columns used here. (**b**) Map of the marine PaleoDB collections. PaleoDB points are transparent so that dark areas indicate many stacked collections. (**c**) Map showing the locations of the ODP/DSDP/IODP core locations used for the deep-sea. All cores were drilled from the sediment surface down to or very near basaltic seafloor.

respectively, of sedimentary environments through time. With paired measures of the geological and fossil records, quantitative tools can be used to interrogate how these systems respond to each other and to covarying environmental changes.

For all of the analyses presented here, only marine packages and marine fossil genera are used. Future work will address the non-marine rock and fossil records (Rook *et al.* 2010). The temporal gaps that define marine packages are hiatuses at unconformities and gaps in marine sedimentation that occur at environmental transitions between marine and non-marine environments. The average duration of the marine packages used here is 26 Ma, which corresponds to *c.* 2nd order stratigraphic sequences (Vail *et al.* 1977) and, remarkably, to the average duration of marine invertebrate genera in the PaleoDB (e.g. 29 Ma in Anthozoa, 24 Ma in Rhychonellata).

Common Cause v. sampling bias

A frequent criticism of the fidelity of the fossil record is that it is biased by temporal heterogeneity in the quantity and quality of preserved sedimentary rock. A simple characterization of the bias hypothesis predicts that observed diversity should be high for intervals of time with a large quantity of preserved rock (e.g. rock volume, outcrop area) and low for time intervals with less preserved rock because rock quantity determines the number of fossils recovered and, therefore, diversity estimates (Raup 1979; Smith 2001; Smith *et al.* 2001; Peters & Foote 2001, 2002; Crampton *et al.* 2003). Another version of the bias hypothesis was formalized in a sequence stratigraphic framework by Holland (1995), who demonstrated that taxon first appearance datums (FADs) will be artificially concentrated at sequence bases and maximum flooding surface whereas last appearance datums (LADs) will cluster at sequence tops and maximum flooding surfaces. In both cases, it is the presence of a temporal gap in the sampling of taxon ranges that promotes the artificial clustering of FADs and LADs at discrete and predictable stratigraphic levels.

Holland's (1995) unconformity bias hypothesis is explicitly testable using macrostratigraphic data because the recognition of packages is based on hiatuses in sedimentation and, therefore, potential gaps in the sampling of taxon ranges. Thus, both the 'gappiness' and the 'rockiness' of the sedimentary rock record can be simultaneously quantified using the principles of macrostratigraphy. Contrary to the predictions of the sampling bias hypothesis, changes in the mean durations of the hiatuses that bound marine sedimentary rock packages do not predict changes in the magnitude of origination or extinction in the fossil record (Fig. 2). If sampling bias were the dominant driver of patterns of extinction and origination in the fossil record, then, all else being equal, long gaps in sampling should be associated with bigger artifactual rate pulses on either side of that gap. This is, however, not what we observe. Instead, it is the spatial extent of the unconformities that define package boundaries that predicts a significant amount of the variability in rates of genus extinction and origination (Fig. 3). The spatial extent of an unconformity can be related to the magnitude of the causal environmental change (e.g. retraction of a large epicontinental sea).

The common-cause hypothesis is an alternative to the bias hypothesis that invokes either direct or indirect links between the physical environmental changes that are reflected in the spatial extent of
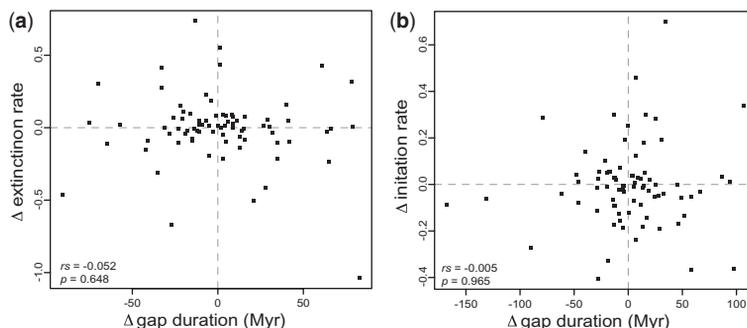

Fig. 2. Macroevolutionary rates for marine organisms v. hiatus durations in marine sedimentation. (**a**) First differences in change in genus origination rate v. first differences in mean duration (millions of years, Ma) of hiatuses that terminate in the previous time interval. (**b**) First differences in change in extinction rate v. mean duration of hiatuses initiating in the following interval. Rate excursions are not correlated with the durations of the hiatuses that define package boundaries but they are correlated with the spatial extent of those hiatuses (Fig. 3). This result is not consistent with an unconformity-induced sampling bias.
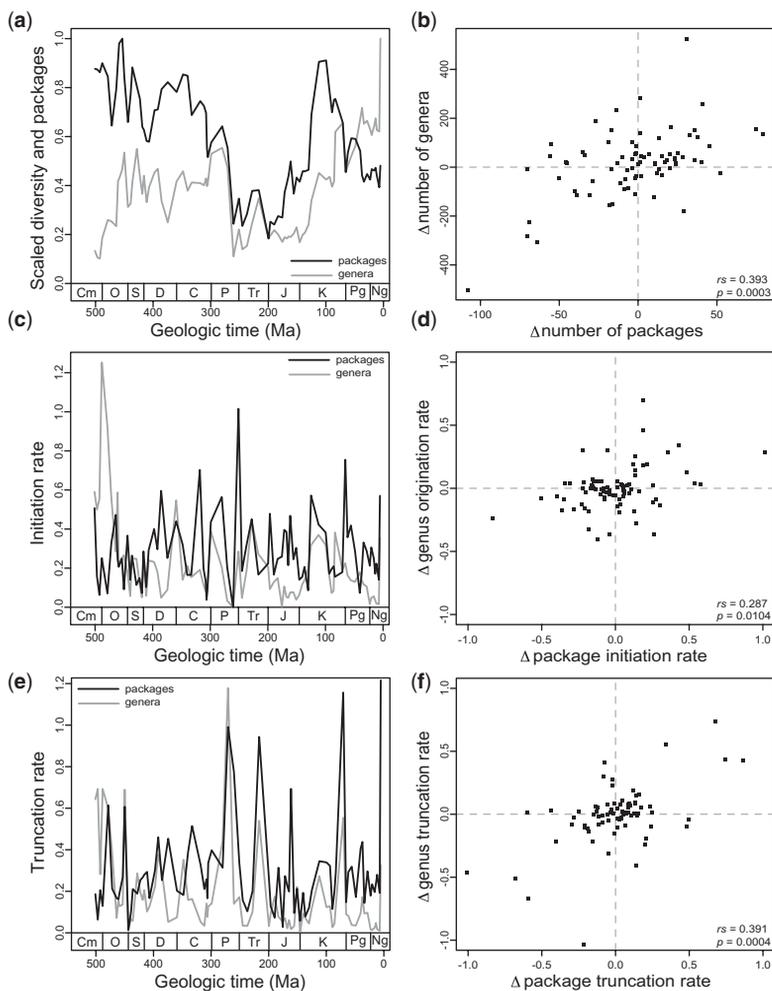
Fig. 3. Macrostratigraphy v. macroevolution. (**a**) Time series of the number of marine genera and packages. Points are plotted at interval bases. (**b**) First differences of the data presented in (a) with the Spearman rank-order correlation coefficient (ρ) and p-value in the bottom left. (**c**) Per capita, per interval regional origination rates for marine genera and per capita, per interval rates of marine package initiation. Plotting conventions same as for (a). (**d**) First differences of the data presented in (c). Plotting conventions same as for (b). (**e**) Per capita, per interval regional extinction rates for marine genera and per capita, per interval rates of marine package truncation. Plotting conventions same as for (a). (**f**) First differences of the data presented in (e). Plotting conventions same as for (b). Time-scale abbreviations are as follows: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; Ng, Neogene.

unconformities, variability in rock quantity and biological evolution. Of course, it is likely that both common-cause mechanisms and stratigraphically-controlled sampling biases have influenced the fossil record of marine animals. Isolating and quantifying the relative magnitude of sampling and common-cause are non-trivial. Crampton *et al.* (2003), found that the aerial extent of outcrop in a region is a good predictor of sampling effort and taxonomic richness in the fossil record. However, they could not attribute the area-diversity relationship

strictly to bias. In modelling expected extinction rates based on observed outcrop area, Smith & McGowan (2007) found that many small fluctuations in the number of marine genera could be explained by outcrop area, but that mass extinctions could not.

Previous work (Peters 2005, 2006*b*, 2008; also Heim & Peters 2011) has focused on macroevolutionary rates because they are less sensitive to variations in sample size than tallies of taxa and because changes in taxonomic richness reflect shifts in the balance between rates of origination and extinction

(Foote 2000); a given change in diversity may be driven by a change in origination, extinction, or some combination of the two. One of the most compelling results that supports the common-cause hypothesis, and that is not consistent with a simple sampling bias, is the asymmetry in the ability of macrostratigraphic quantities to predict genus origination v. genus extinction, a result to which we return here.

Asymmetry in the relationship between macroevolution and macrostratigraphy

If the fossil record of extinction and origination were dominated by an unconformity-related stratigraphic bias, then both origination and extinction should be similarly positively correlated with variability in the rock record (Holland 1995) and the magnitude and timing of intervening hiatuses should predict apparent turnover pulses. This is, however, not observed when comparing macroevolutionary and macrostratigraphic rates (Figs 2 & 3; Table 1). Extinction rates are significantly positively correlated with sediment truncation rates (Fig. 3e, f), but origination rates do not strongly covary with sediment initiation rates (Fig. 3c, d). The discrepancy between origination and extinction suggests that macroevolutionary rates are not determined by a straight-forward sampling bias that is due to the clustering of taxon FADs and LADs at unconformities (Holland 1995; Fig. 2).

When the timing of the FADs and LADs for genera occurring in the study area (Fig. 1) are based on their global fossil occurrences in the PaleoDB, rather than only those occurrences within the target regions (Fig. 3), the asymmetry between origination and extinction is strengthened (Table 1). Rates of origination based on the globally-determined genus FADs are not correlated with macrostratigraphic rates of initiation, whereas the correlation between

extinction and truncation for the global fossil data remains virtually unchanged (Table 1).

Because the PaleoDB is a continuously growing database of published fossil occurrences, it is also possible that incomplete sampling has influenced the observed asymmetry in the predictability of rates of origination and extinction. As published collection records are entered into the PaleoDB, new taxa are added and the stratigraphic ranges of previously entered taxa may be extended. Using the creation date field for collections in the PaleoDB, the correlations between macroevolutionary patterns and macrostratigraphic quantities were calculated for each year of the PaleoDB between 1998 to February 2011 (Fig. 4). The strengths of the correlations between taxonomic turnover rates and macrostratigraphic rates increased sharply between 1998 and 2000, as the PaleoDB rapidly matured. Since then, the correlations appear to be approaching an asymptote and are not changing rapidly or strongly systematically. This result suggests that our knowledge of the relationship between macroevolution and macrostratigraphy is relatively mature and that the relative strengths of the correlations are not likely to change markedly by the addition of new fossil data in the next several years. Ongoing improvements and additions to Macrostrat may, however, have a large quantitative effect, but that effect is anticipated to strengthen, not weaken, any statistical similarities, and to do so in a way that similarly influences both extinction and origination.

Distribution of fossils within hiatus-bound sediment packages

The stronger correlation between sediment truncation and generic extinction suggests that there are systematic differences in the distribution of fossils, FADs and LADs within sedimentary rock packages. To test this hypothesis, the relative locations of

Table 1. *Macrostrat–macroevolution results for three different data sets. Spearman rank-order correlation coefficients for first differences on time series of genus diversity, origination and extinction compared to the analogous macrostratigraphic quantities. The Sepkoski (2002) global genus compendium is compared to the macrostratigraphy of North America (Peters 2005). The Paleobiology Database data are in comparison to the macrostratigraphic data for the same region (Figs 1 & 3) and for the same set of genera with global, rather than regional, FADs and LADs. A global compendium of Planktonic foraminifera genera are also compared to the macrostratigraphy of the Atlantic Ocean basin (Peters et al. 2010)*

	USA, Sepkoski's global genus compendium	Paleobiology Database (regional)	Paleobiology Database (global)	Atlantic Basin, Planktonic Foraminifera
Diversity	0.51	0.39	0.24**	0.46
Origination	0.36	0.29	−0.01*	0.27
Extinction	0.50	0.39	0.42	0.55

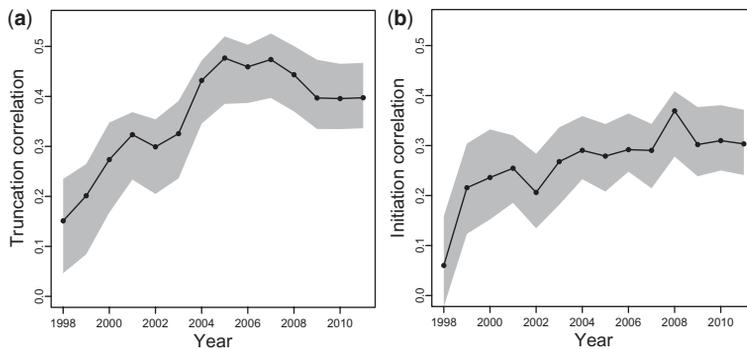All *p*-values < 0.01, except *$p = 0.93$, **$p = 0.03$.

Fig. 4. Evolution of the macroevolution–macrostratigraphy correlations with increased sampling in the PaleoDB. New palaeontological data has been continuously entered into the PaleoDB since 1998, thus adding new taxa and extending the ranges of existing genera. (**a**) Time series of the Spearman rank-order correlation coefficient based on first differences between marine genus origination rate and marine package initiation rates. The gray field is a 95% bootstrap confidence interval and the slope of the linear regression through the data is given in the upper left. (**b**) Correlations between genus extinction and package truncation as the sampling in the PaleoDB increased. Plotting conventions are the same as in (a).

PaleoDB fossil collections within each of the marine packages in Macrostrat was determined (Peters & Heim 2011). All packages that span more than one geological stage and that contain more than one lithostratigraphic unit were scaled to unit duration and then divided into 100 equal-duration increments. That is, time was uniformly distributed within the constituent units of the package. Finally, the number of PaleoDB collections in each of the time increments was tabulated and then scaled to the maximum value in that package. This process was performed on all fossiliferous packages and an average occupancy curve for fossil collections was calculated for various time intervals (Fig. 5a).

To generate an expected window of collection occupancy (i.e., a null distribution), fossil collections were randomized within packages multiple times. The randomization envelope is not flat, indicating that there is a non-uniform distribution of lithostratigraphic units within marine packages, possibly due to changing environmental heterogeneity during the evolution of *c.* 2nd-order sedimentary sequences, a hypothesis which we hope to soon test with field data. It is also, however, possible that this modal null distribution reflects the inherent binning scheme used here. Regardless of the reason for the modal null, this provides the expected pattern under a model of randomly distributed fossil collections.
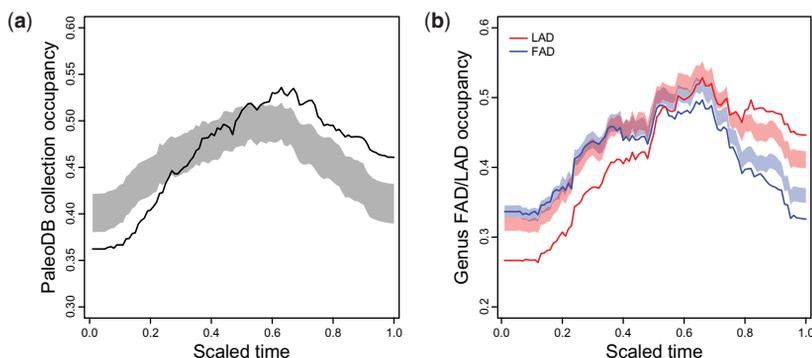

Fig. 5. Stratigraphic occupancy of marine fossils. (**a**) Mean Phanerozoic distribution of fossil collections within hiatus-bound sedimentary packages. Shaded regions are 95% confidence limits around the expected mean occupancy based on 1000 bootstrap randomizations of fossil collections within hiatus-bound sedimentary packages. (**b**) Mean stratigraphic distribution of generic first and last appearance datums in marine sediment packages. Shaded regions encompass all outcomes for 1000 randomizations of FADs and LADs among collections within packages. Null distributions differ because packages that contain FAD- and LAD-defining collections are a partially overlapping subset of all fossil-bearing packages.

These results indicate that PaleoDB fossil collections occur more frequently than expected in the top 40% of package durations and less frequently than expected in the bottom 25% of package durations. This result is difficult to explain without more refined environmental and lithological data, but one hypothesis is that fossil distribution is related to changing environmental characteristics of marine shelves during the evolution of large-scale, *c*. 2nd-order transgressive–regressive cycles. Alternatively, the pattern could be driven by changes in mean sediment accumulation rate, such that rates are initially high during the accommodation formation phase of 2nd-order successions, and then decrease as the basin fills, allowing more frequent beds that contain rich concentrations of skeletal remains to be formed at the top of packages (Kidwell 1989, 1991, 1993; Banerjee & Kidwell 1991; Abbott 1997; Abbott & Carter 1997).

The stratigraphic distribution of generic FADs and LADs was calculated using the same procedure described above for PaleoDB fossil collections (Fig. 5b). LAD occupancy is not markedly surprising in light of the asymmetrical relationship between origination and extinction and macrostratigraphy; LADs are in fact preferentially located in the top of packages, and they are found at package bases less frequently than expected due to chance alone. The FAD results are in some ways more interesting. FADs are more uniformly distributed within packages, but are much less common near package tops than expected under a model of random distribution.

The fact that FADs occur only rarely at package tops is curious given that the majority of fossil collections are found in the top 40% of packages. If a simple sampling bias were a dominant component of the reason for the rock-fossil similarities documented here, then recovering more fossils should result in more FADs and more LADs. The discrepancy between FAD and LAD distribution within packages indicates that there is a tendency for FADs and LADs to reflect some other attribute of packages than simply the preservation of fossil occurrences that might identify range end-points. Instead, it is likely that differences in the distribution of lineage origination and extinction within package durations reflect a macroevolutionary response to the palaeoenvironmental changes that occur during the formation and maturation of 2nd-order sedimentary sequences. This is, we believe, *prima facie* evidence for a complex common-cause relationship between sedimentation and macroevolution that involves process-response lags and biological responses to the evolution of shelf environments during large-scale draining and flooding of epicontinental seas.

The alternative hypothesis for the asymmetry in the FAD–LAD distribution with gap-bound packages is that the biological meaning of genus first and last appearances are disjunct. If, for example, taxonomists tend to artificially truncate continuous lineages at unconformities and then artificially lump lineages on the other side of unconformities, then it is conceivable that the result shown in Figure 5 could be an artifact of taxonomy. Although we strongly suspect that this is not the case, a more rigorously phylogenetic approach to the identification of lineage range end points would be highly advantageous to testing the common-cause hypothesis.

Deep-sea macrostratigraphy

Marine sedimentation on the continents is controlled by the extent to which the continents are flooded by shallow seas. Thus, eustatic sea-level and continental freeboard are the dominant mechanisms involved. Sedimentation in the deep-sea is, however governed by a completely different set of rules. Here we compare deep-sea sedimentation patterns to macroevolutionary patterns in surface-dwelling plankton.

Data on the lithology, thickness, and temporal distribution of deep-sea sediments were recovered from published Ocean Drilling Program, Deep Sea Drilling Program and Integrated Ocean Drilling Program scientific reports. Hiatuses in sedimentation at each site were identified wherever one or more nannofossil zones were missing entirely or not represented by a measurable thickness of sediment. A total of 249 hiatus-bound sediment packages composed of 3692 lithological units were recognized from 73 suitably drilled Atlantic sites (Fig. 1c). (Suitable sites have continuous core recovered from the sediment–water interface down to or very near basaltic basement rock.)

Planktonic foraminifera are abundant in the global ocean and play an important role in understanding the history of the oceans, but relatively little is know about the factors that have governed their macroevolutionary history. First differences in planktic foraminiferal diversity are significantly positively correlated with changes in the number of deep-sea sediment packages (Table 1; Peters *et al.* 2010). The correlations remain when the correlation imposed by the variable durations of calcareous nannofossil zones is removed by partial correlation. The only systematic departure from the statistical relationship between foraminifera diversity and the number of packages occurs during the late Eocene through the Oligocene, a time which also represents the most dramatic climate transition in the past 200 Ma (Zachos *et al.* 2008).

First differences in planktic foraminifera per-capita species/genus extinction rates are also

significantly positively correlated with first differences in rates of deep-sea sediment package truncation. Rates of planktic foraminifera species/genus origination, by contrast, are less strongly positively correlated with rates of package initiation, though the correlation is significant. Thus, similarities between changes in planktic foraminiferal diversity and changes in the number of sediment packages reflect more the congruence in rates of sediment truncation and lineage extinction than they do rates of origination and package initiation.

These new results for the deep ocean are remarkably similar to those for the continental shelves. Like the shelf results, these new results for the deep-sea indicate that the macroevolutionary history of planktic foraminifera is linked causally to the oceanographic factors that govern spatiotemporal patterns of sedimentation. In the deep-sea, such changes are related to oceanographic factors, including surface water nutrient loads, the strength and pathways of ocean circulation and bottom currents (Keller & Barron 1983; Lyell 2003), and the age and source of deep water and the position of the calcium carbonate compensation depth (Van Andel 1975). The mechanisms that govern sedimentation in the deep-sea are radically different from those that govern sedimentation on the shelves, and yet the quantitative linkages between macroevolution and sedimentation are similar. This too, is compelling evidence for a causal, common-cause link between patterns of sedimentation and macroevolution, though many outstanding questions remain about the relative roles of sampling, taxonomic practice, and common biological response to environmental perturbations that manifest in the rock record.

Discussion

The weight of evidence currently suggests that many patterns in the macroevolutionary history of the marine fossil record are not best explained by sampling artifacts in fossil preservation alone. Sampling bias at unconformities predicts that taxonomic origination rates and extinction rates should be covary in similar ways with the sampling bias induced by sampling failures at unconformities. Remarkably, the correlations between origination and initiation are much weaker than extinction and
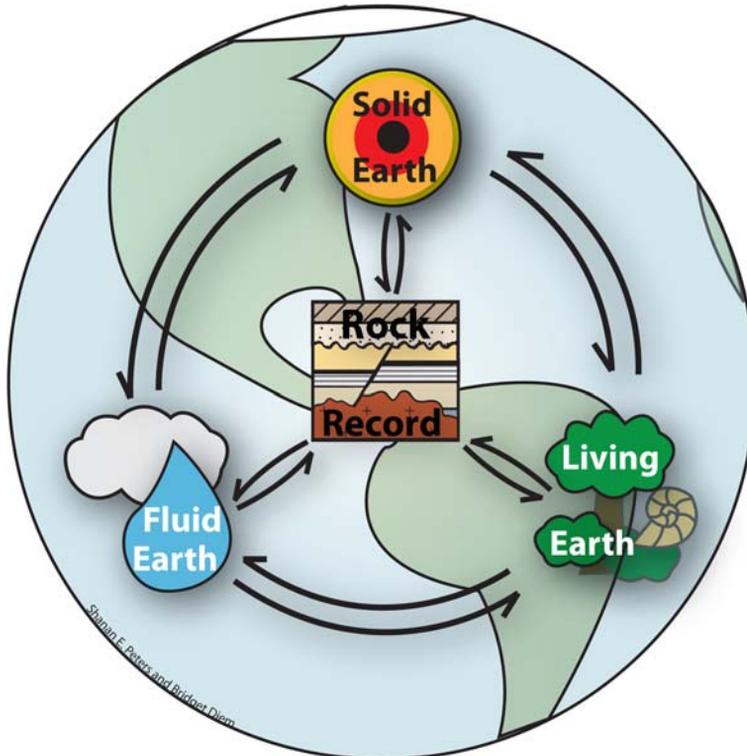

Fig. 6. Our view of the Earth systems process connections that are operating in our new formulation of the 'common-cause' hypothesis.

truncation across three different fossil data compilations (Table 1): Sepkoski's global genus compendium and the macrostratigraphy of North America (Peters 2005), the PaleoDB and macrostratigraphy of North America (Heim & Peters 2011), and global planktonic foraminifera and the macrostratigraphy of the Atlantic Ocean basin (Peters *et al.* 2010). Furthermore, the stratigraphic distribution of marine fossil collections within hiatus-bound packages, which is a direct measure of sampling effort, is not consistent with the hypothesis that sampling bias dominates macroevolutionary patterns. Fossil collections occur predominantly in the top 40% of packages, but genus FADs occur less frequently than expected in the top of packages and LADs even more frequent in the top of packages than expected.

These results suggest that the extinction of marine organisms is likely to be causally linked to many of the environmental changes that occur during contractions in the area of marine sedimentation, whereas origination is not linked in a similar way to the expansions in the area of sedimentation. Perhaps the origination of new lineages exhibits a lagged response to the environmental changes that occur when packages initiate, thereby dampening any process-response linkages in interval-to-interval changes in patterns of sedimentation and origination. Alternatively, originations may simply be more biologically deterministic and extinctions more environmentally deterministic. Further exploration of the specific drivers of taxonomic origination, extinction and marine sedimentation are needed. It is also absolutely imperative that differences in sampling intensity be explicitly taken into consideration and accounted for quantitatively. Our analyses accept the fossil record at face-value, and although there is some evidence to suggest that the fossil record of extinction has relatively high fidelity (Foote 2003), incomplete sampling distorts macroevolutionary patterns and, therefore, is expected to obscure, rather than to enhance, correlation with such macroevolutionary quantities as rates of truncation and initiation.

One of the goals going forward in stratigraphic palaeobiology should be to interrogate the exact mechanisms that are involved in driving similar sedimentary and biological responses. Simple changes in habitable area, the most direct common cause mechanism for marine shelf organisms, are unlikely to exert a strong control on the macroevolutionary history of marine life. Instead, common cause mechanisms are likely to involve numerous direct and indirect linkages and feedbacks between climate, tectonics, sedimentation, and biological evolution (Fig. 6). In the deep-sea, these linkages include seawater chemistry, ocean circulation, and surface water productivity, all of which respond to, and interact with, climate and tectonics. On the

continents these linkages include the draining and flooding of continents due to changes in climate and plate tectonics, which itself can perturb the climate cycle and alter global climate. Under this view of the common cause hypothesis, the sedimentary record is more akin to an integrative record of the direct and indirect linkages between Earth systems than it is a direct driver of macroevolutionary change. Testing this next-generation formulation of the common cause hypothesis will be exciting because it demands a much higher level of quantitative integration of biological, geochemical, and sedimentary data on large spatial and temporal scales than has ever before been accomplished. Assembling the requisite data, rigorously controlling for variability in sampling in ways that do not discriminate against a process-connection to variable quantities of fossils, and then integrating these data quantitatively will be rewarding.

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