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LETTER

Ecological interactions on macroevolutionary time scales: clams and brachiopods are more than ships that pass in the night

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Abstract

Competition among organisms has ecological and evolutionary consequences. However, whether the consequences of competition are manifested and measureable on macroevolutionary time scales is equivocal. Marine bivalves and brachiopods have overlapping niches such that competition for food and space may occur. Moreover, there is a long-standing debate over whether bivalves outcompeted brachiopods evolutionarily, because brachiopod diversity declined through time while bivalve diversity increased. To answer this question, we estimate the origination and extinction dynamics of fossil marine bivalve and brachiopod genera from the Ordovician through to the Recent while simultaneously accounting for incomplete sampling. Then, using stochastic differential equations, we assess statistical relationships among diversification and sampling dynamics of brachiopods and bivalves and five paleoenvironmental proxies. None of these potential environmental drivers had any detectable influence on brachiopod or bivalve diversification. In contrast, elevated bivalve extinction rates causally increased brachiopod origination rates, suggesting that bivalves have suppressed brachiopod evolution.

Keywords

Capture-recapture, fossil, geochemical proxy, Ornstein-Uhlenbeck model, Phanerozoic, Red Queen, sea level, stochastic differential equations (SDEs), time series.

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INTRODUCTION

Living organisms influence the survival, fecundity and hence fitness of other organisms via interactions such as competition, facilitation, mutualism, parasitism and predation (Thompson 2005), modifying the ecological backdrop in which the evolutionary theatre is being played (Chave 2013). However, whether such ecological interactions have persistent and measurable effects on macroevolution (Jablonski 2008) is challenging to assess. The challenge stems from the inherent difficulties of estimating evolutionary rates and inferring ecological interactions with incomplete and uneven data, and accounting for other potential drivers of evolution on a geological time scale. Consequently, a dominant perspective among paleontologists is that while ecological interactions have their effects on short time scales, long-term evolution is driven by environmental changes (Benton 2009), most prominently, mass extinction events (Gould & Calloway 1980; Raup 1986). Several recent studies have found statistical relationships between various paleoenvironmental proxies and measures of biological diversity or evolutionary rates over the Phanerozoic (Cardenas & Harries 2010; Hannisdal & Peters 2011; Mayhew *et al*. 2012; Melott *et al*. 2012). For instance, Cardenas & Harries (2010) found significant correlations between changes in the origination rates of marine organisms and several paleoenvironmental proxies (^{87}Sr/^{86}Sr, δ^{34}S and eustatic sea level) which they interpreted as indicators of nutrient availability, leading the authors to suggest that times of higher marine nutrient levels promoted diversification. When diversity dynamics are examined independently of physical environmental drivers, however, they exhibit biological regulation, as evidenced by intervals of high origination rates following intervals of high extinction rates (Lu *et al*. 2006; Alroy 2008; Harnik & Lockwood 2011). This association may result from diversity-dependent dynamics within a clade, where interspecific competition influences speciation and extinction via species richness (Rabosky 2013). Interactions among distantly related lineages occur frequently in contemporary ecosystems and may also modulate the diversification of clades over geological time (Jablonski 2008) as suggested by Red Queen processes (Van Valen 1973; Voje *et al*. 2015).

Clades that are ecologically similar may evolutionarily outcompete one another, as proposed for dinosaurs and mammals (Meredith *et al*. 2011), multituberculate mammals and rodents (Van Valen & Sloan 1966) and cyclostome and cheilostome bryozoans (Sepkoski *et al*. 2000). In the marine realm, competition has been implicated in the post-Permian decline of brachiopods and rise in the taxonomic richness (Sepkoski 1981) and abundance (Clapham & Bottjer 2007) of bivalves. These two clades overlap in their feeding ecology and habitat preferences. Consequently their ‘double-wedge’ diversity dynamics have been interpreted by some as competitively ‘superior’ bivalves gradually replacing ‘inferior’ brachiopods (see references in Gould & Calloway 1980). In their seminal paper, Gould & Calloway (1980) reconsidered the diversity dynamics of bivalves and brachiopods, specifically whether local, intraspecific competition could be extrapolated to interspecific competition and macroevolution. Their conclusion, based on counts of fossil genera, was that brachiopods and bivalves were largely 'ships that pass in the night', independently evolving clades that did not contribute substantially to the macroevolutionary dynamics of the other group (Gould & Calloway 1980). Instead, it was a single event, the Permian mass extinction, which led to the low taxonomic richness of brachiopods in the post-Paleozoic and present day (Gould & Calloway 1980). More recently, others have argued for a 'middle ground' of these views. Miller & Sepkoski (1988) used coupled logistic equations to argue that interspecific competition and mass extinction events both left their mark on bivalve diversification whereas others favour predation and physical disturbances as overriding forces in shaping bivalve macroevolutionary history (Aberhan *et al.* 2006; Stanley 2008). There is even a return to a view of bivalve 'superiority', with the suggestion that bivalves have been using resources that have never been available to brachiopods (Payne *et al.* 2014).

Here, we re-examine whether ecological interactions between brachiopods and bivalves might have affected processes of diversification, by examining their origination and extinction dynamics, for the following reasons. First, although there is a revived interest in ecological controls on macroevolution (Rabosky 2013) and some indication that ecological controls are important in diversification patterns in the fossil record (Lu *et al.* 2006; Alroy 2008; Harnik & Lockwood 2011), most paleontological studies exclusively focus on physical environmental drivers (Cardenas & Harries 2010; Hannisdal & Peters 2011; Mayhew *et al.* 2012). There is hence a need to tease apart the contributions of ecological and environmental drivers to diversification in the same analytical framework (Ezard *et al.* 2011; Voje *et al.* 2015). Second, diversification estimates from the fossil record can be improved. While the observation of an individual of a taxon in the fossil record is proof that the taxon was extant then, the absence of any individuals of a taxon is not proof that it was absent. Although different approaches have been used to account for sampling variation in the fossil record (Alroy *et al.* 2001; Foote 2001, 2003; Alroy 2010), we favour state-space approaches because they simultaneously model 'process' (diversification) and 'observation' (sampling) (Clark & Bjørnstad 2004; Liow & Nichols 2010; King 2014). Third, we have recently developed time series analysis tools (Reitan *et al.* 2012) that can overcome many of the stumbling blocks encountered by previous paleobiological analyses, including unequal temporal sampling, mismatch between continuous processes and discrete measurements, variable uncertainty of estimates and inability to test for statistical causality (Granger 1969). The causality we describe here is a statistical property that mimics causality inferable from controlled laboratory experiments.

We examine the following possibilities: over macroevolutionary timescales, (1) brachiopod and bivalve genus-level diversification rates (extinction, origination, or both) are driven by one or more environmental drivers (e.g. temperature and sea levels). If they are driven by the same environmental driver(s), then any temporal coordination of diversification dynamics in these two clades might be mediated via such drivers. (2) Brachiopod and bivalve diversification rates affect one another, possibly because of ecological interactions between these two clades. (3) The diversification rates of the two clades are the result of an interaction between clade–clade dynamics and environmental drivers. We find that bivalves suppressed the origination of brachiopods and that the five paleoenvironmental time series that reflect climate, productivity, plate tectonics, volcanism and sea-level change had no influence on either clade's diversification rates.

METHODS AND DATA

Diversification estimates

We downloaded all available occurrences of brachiopods and bivalves found in marine sedimentary deposits from the Paleobiology Database (PaleoDB; downloaded 16 Dec 2014, see Supporting Information). We use the International Commission on Stratigraphy (ICS) time scale (Cohen *et al.* 2013). Our analyses span 86 temporally unequal stages from the Ordovician (485.4 million years ago) to the Recent. We first examined the age range of each observed occurrence (occurrence for short) and discarded those data that had a reported age range that was wider than the longest stage in the ICS time scale. We then assigned each remaining occurrence to one of the 86 stages using the mid-point of the reported age of the occurrence. Using these data, we tabulated the observation or non-observation of each genus in these stages.

We focus on genera rather than species because there is a greater consistency in taxonomic identifications across multiple workers at the genus level. Moreover, genus-level diversity dynamics for bivalves inferred using the PaleoDB are robust to taxonomic error (Wagner *et al.* 2007). There is also good evidence that a significant percentage of morphogenera are monophyletic (Jablonski & Finarelli 2009) and that species and genus-level diversification dynamics can be comparable (Liow & Finarelli 2014).

This genus observation data matrix served as the input data for parameter estimation using a capture-recapture model: the Pradel seniority model, or Pradel model for short (Pradel 1996). In essence, the Pradel model estimates the probabilities of origination, extinction and sampling simultaneously for a given data set of observed occurrences (see Supporting Information). Observations of fossils are a combination of the processes of true presence and the combined effect of sampling efforts, abiotic (e.g. erosion and sedimentation, biochemistry) and biotic factors (e.g. abundance, durability of identifiable remains). In a time interval where a set of fossil taxa is first observed, there is a high chance that some subset of these truly originated in an earlier time interval. Likewise, the last time interval in which any given fossil taxon is found has a good chance of not being the true last time interval in which it is extant (Liow & Nichols 2010). Hence, sampling parameters should be an integral part of any model that uses fossil occurrences to estimate diversification parameters. The parameters estimated here are genus origination, extinction and sampling probabilities, and their standard errors, based on a full time-varying model, as estimated using MARK (White & Burnham 1999) executed via RMark (Laake 2013) (Table S1). The global sampling rates we estimate reflect heterogeneous sampling processes occurring at finer spatial and taxonomic scales, and there is little reason to hypothesise that this heterogeneity will either systematically distort our diversification estimates for brachiopods and bivalves or our inference regarding their causal and correlative links.

Paleoenvironmental proxies

We used published time series of low latitude $\delta^{18}0$, low latitude $\delta^{13}C$, $\delta^{34}S$, $^{87}Sr/^{86}Sr$ (Prokoph *et al.* 2008) and eustatic sea level (a composite from Cardenas & Harries 2010) in our analyses. Each of these proxies has been linked to extinctions and biodiversity change in marine invertebrates, including brachiopods and bivalves (Cardenas & Harries 2010; Hannisdal & Peters 2011; Mayhew *et al.* 2012; Melott *et al.* 2012). Briefly, fluctuations in $\delta^{18}0$ reflect global climate change, including temperature and ice volume, while $\delta^{13}C$ holds in part signals of global productivity. $\delta^{34}S$ reflects the burial efficiency of pyrite, while $^{87}Sr/^{86}Sr$ reflects volcanism, tectonic uplift and continental weathering (Hannisdal & Peters 2011).

Data transformation

Origination and extinction estimates from the Pradel model are transition probabilities across temporal boundaries. For example, the first estimate for origination in our time series is the probability of genus origination from the Tremadocian to Floian and the first estimate for sampling probability is for the Tremadocian (485.4 to 477.7 million years ago). For diversification estimates, the temporal boundaries of transitions are the input for subsequent analyses while stage midpoints are the input for sampling estimates.

All estimated probabilities were transformed into rates because geological stages are unequal in duration. Given a constant origination rate over each time interval, a longer time interval will have a higher origination probability than a shorter one. For this transformation, we use a Poisson model where events are assumed to be independent. The probability of no event (i.e. origination, extinction or sampling) within a time interval is $P(\text{no event}) = e^{-\lambda T}$, where λ is the event rate and T is the time interval length. Thus, if origination probability is Q_S, its origination rate will be $\lambda_S = -\log(1 - Q_S)/T$. We then transformed these rates into log-rates, since our analytical tools were built on the assumption of normality, while these rates are strictly positive. Probabilities that are 0 or 1 are not amendable to this log-transformation and associated with very large confidence intervals. Hence, we remove probabilities that are 0 or 1 from subsequent analyses (Table S1). After transformation, the time intervals for origination and extinction rates start from the middle of one stage in the ICS time scale, and end in the middle of the next. For sampling rates, the time interval in question was the start and the end of the stage in question. For example, the first brachiopod survivorship probability from the Tremadocian to the Floian is 0.751 (Table S1). Thus, the extinction probability is 0.249. The genus extinction rate per million years is then $-\log(1 - 0.249)/(477.7 - 470.0) = 0.037$, which after logging is -3.30. This last value, with its uncertainty estimate, is the data used for time series modelling.

We checked our data for this using the Kolmogorov–Smirnoff test. Normality was not rejected for all of the transformed biotic time series and three of the abiotic time series, namely $\delta^{13}C$, $\delta^{34}S$ and sea level. We transformed $\delta^{18}0$ and $^{87}Sr/^{86}Sr$ before applying SDE analyses (see Supporting Information).

Stochastic differential equations as a time series analysis tool

The aim of many paleontological analyses of time series data is to seek causal relationships among biotic variables and/or paleoenvironmental proxies in order to understand evolutionary processes. However, previous tools commonly used in paleontological analyses, such as approaches related to linear regression, infer only correlative relationships and not causal ones. It is next to impossible to attribute causal agents to historical time series in the sense causality is used in laboratory settings. However, we can search for statistical properties that mimic causal mechanisms by attributing change in one time series to the state of another (see next paragraph). In addition, paleontological time series data are often irregularly spaced in time. When standard regression approaches are used for inference, temporal autocorrelation and non-independent noise terms in time series data can cause Type I errors where null hypotheses are falsely rejected and uncertainty in inference is grossly underestimated (Montgomery *et al.* 2012). A common way to partially alleviate temporal autocorrelation in paleontological studies is to study the correlation of first differences among time series of interest. However, this practice requires temporally equally spaced data and forces the discretisation of the temporal processes. Similarly, formalised time series analyses tools, usually based on ARIMA (Autoregressive Integrated Moving Average) models, also tacitly require that data points are regularly spaced in time. If, however, data points are irregularly spaced in time, one would have to impose extra complexity on such models in an *ad hoc* way. One solution to such temporal irregularity of data is to use statistical tools developed for continuous time, such as stochastic differential equations (see Supporting Information for comparisons with regression approaches).

A SDE is a differential equation in which at least one term in the equation is a stochastic process. A basic SDE can be written as

$$dX(t) = -\alpha(X(t) - \mu)dt + \sigma dB(t) \tag{1}$$

where $X(t)$ is the process of interest and where the first part of the right side of eqn (1) is an ordinary differential equation (ODE) and the second part is a stochastic component. The deterministic part of the process (the ODE) is described by α and μ, while the stochastic part is described by σ. In many practical applications, α, μ and σ are assumed to be constant: an Ornstein-Uhlenbeck (OU) process is defined as such. In a well-known evolutionary application of the OU process, α, μ and σ represent the strength of the attracting force towards an evolutionary optimum, the phenotype of the optimum and the intensity of random fluctuations, respectively. If the deterministic part of the equation is zero, the OU process reduces to Brownian Motion (alternatively termed Wiener Process or Random Walk), characterised by only the stochastic part of equation (simulated in Fig. 1a, b).

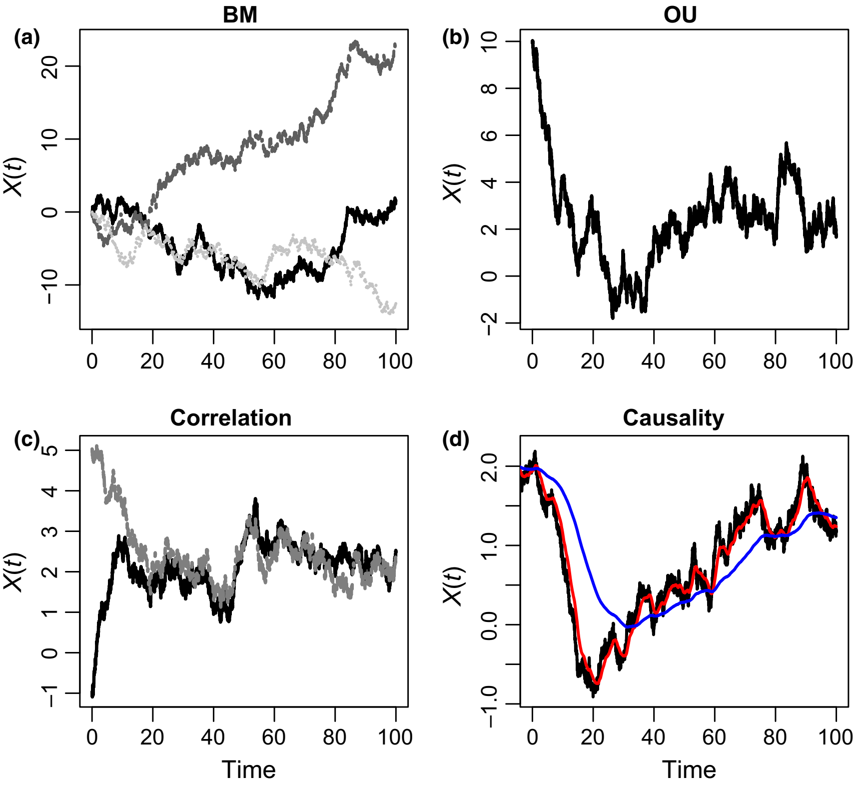

Figure 1 Examples of linear SDEs. (a) Brownian Motion (BM), where all three examples have $\sigma = 1$. (b) An Ornstein-Uhlenbeck (OU) process where $\Delta t_{1/2} = 8$, $\mu = 2$, $s = 2$. (c) Two correlated OU processes where $\Delta t_{1/2,1} = \Delta t_{1/2,2} = 15$, $\mu_1 = \mu_2 = 2$, $s_1 = s_2 = 2$, $\rho = 0.5$. (d) Causally linked processes where an OU X_1 (black) drives X_2 (red, short half-life) and X_3 (blue, long half-life). Here, $\Delta t_{1/2,1} = 30$, $\Delta t_{1/2,2} = 1$, $\Delta t_{1/2,3} = 8$, $\mu_1 = \mu_2 = \mu_3 = 2$, $s_1 = 2$, $s_2 = s_3 = 0$, $\beta_{1,2} = \beta_{1,3} = 1$. X_2 and X_3 are not simply time-lagged versions of X_1, because the processes are integrated over the entire past and does not simply reflect the immediately preceding interval. $\Delta t_{1/2}$ and S are the half-life and the stationary standard deviation of an OU process, respectively (see eqns 5 and 6).

SDEs can also be used for studying the effect of one time series on another, even in situations where one of them is unmeasured: this is how we will be applying SDEs. We briefly summarise below how we use linear SDEs in analyses that follow (see Supporting Information and Reitan *et al.* 2012 for details, simulations and proofs).

Say we have two time-continuous temporal processes, global temperature, $X_1(t)$ and bivalve diversification $X_2(t)$ which may be correlated with each other, or even causally linked. We represent both of these processes by SDEs where,

$$dX_1(t) = -\alpha_1(X_1(t) - \mu_1)dt + \sigma_1 dB_1(t) \qquad (2)$$

$$dX_2(t) = -\alpha_2(X_2(t) - \mu_2)dt + \sigma_2(1 - \rho^2)^{0.5}dB_2(t) + \rho\sigma_2 dB_1(t). \qquad (3)$$

Equations (2) and (3) are linked via $dB_1(t)$ such that ρ represents the strength of the correlation between the two processes. Note that (2) and (3) could have been ‘reversed’ such that the correlation term resides in the global temperature equation instead of the diversification equation and the systems will be equivalent. While the two processes have their own deterministic parameters, their temporal troughs and peaks will be strongly correlated if ρ is high, even though one process ($X_1(t)$) does not influence the other ($X_2(t)$) and vice versa (simulated in Fig. 1c).

We can also express one process as a function of the other such that a change in one process occurs before a change in the other process (simulated in Fig. 1d), i.e. Granger causality occurs (Granger 1969).

$$dX_2(t) = -\alpha_2(X_2(t) - \mu_2 - \beta[X_1(t) - \mu_1])dt + \sigma_2 dB_2(t). \qquad (4)$$

In eqn (4), bivalve diversification is an OU-like process that has an additive term that is driven by temperature. The relationship between temperature and diversification is here summarized by β. We use the term ‘link model’ when referring to models describing correlative or causal relationships.

In our analyses of individual time series, we compared models with and without time trends in a Bayesian framework. We also incorporated information on both process covariance and measurement uncertainty (the varying confidence intervals presented in Figs 2 and 3 and uncertainty inherent in the paleoenvironmental proxy time series) (see Supporting Information for details). We then used the best model for each individual time series (Table 1), to examine relationships among time series. If two time series are truly correlated but one does not drive the other, we will observe, amidst noise from process and measurement errors, that many peaks and troughs ‘line up’ in the two time series. In contrast, if one time series truly drove the other, whether we detect the causal link depends on the strength of the causal relationship (β), how noisy the data are and the resolution of the observations with respect to their half-lives. A causal link may be inferred as correlative if response times are rapid relative to the temporal resolution of the observations. If data are too noisy or if the strength of the causal relationship is too weak, then no relationship will be detected. We add that the driven time series in a causal link model might

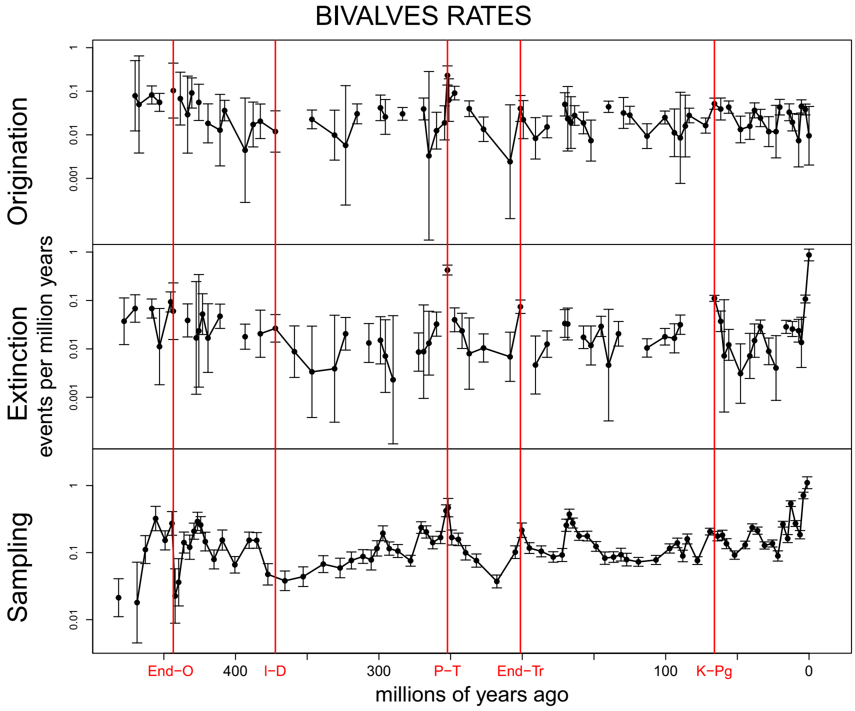

Figure 2 Bivalve diversification and sampling estimates. These are per Myr rates of origination, extinction and sampling for bivalves through the Phanerozoic, plotted on log axes (transformed from probabilities, see main text). In the first two panels, each point is the estimated average transition rate across the stage boundary, whereas for the lowest panel, each point is the average sampling rate in the stage. Vertical lines are 95% confidence intervals. Missing points do not contribute to SDE inferences (see Table S1). The x-axis is in millions of years (Myr) and red lines mark mass extinctions abbreviated as End–O (End Ordovician, crossing the Hirnantian upper boundary), l-D (Late Devonian, crossing the Frasnian and Famennian boundary), P-T (the Permian-Triassic extinction), End-Tr (the End Triassic extinction) and the K-Pg (the end Cretaceous extinction).

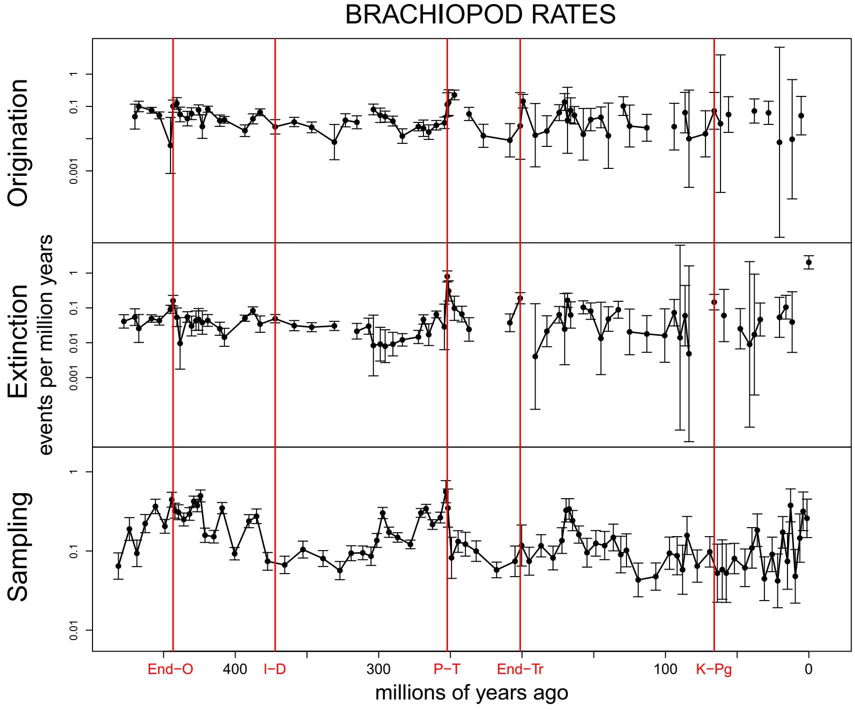

Figure 3 Brachiopod diversification and sampling estimates. Conventions used follow Fig. 2.

Table 1 Stand-alone time series summary: single-layered process inference

	Average temporal resolution (Myr)	Best (minimum) temporal resolution (Myr)	Half-life (Myr)	μ	S	σ	Status
δ^{18}O (Low Latitude, Normalised)	0.3	0.001	5.3 (3.2–11)	0.06 (−0.16, 0.31)	0.58 (0.48, 0.80)	NA	OU-like (linear trend, $\eta = 0.0053$ Myr^{-1})
δ^{13}C (Low Latitude)	0.3	0.001	7.7 (4.7–17)	1.9 (1.2, 2.6)	1.5 (1.2, 2.1)	NA	OU
^{87}Sr/^{86}Sr (Normalised)	0.17	1.60E-06	NA	NA	NA	0.16 (0.14, 0.18)	BM
δ^{34}S	1.5	0.007	NA	NA	NA	0.89 (0.68, 1.1)	BM
Sea level	5.0	2.8	NA	NA	NA	3.3 (2.9, 3.8)	BM
Bivalve sampling rate (log per Myr)	5.7	1.3	4.7 (2.2–11)	−2.1 (−2.4, −1.9)	0.7 (0.5, 0.9)	NA	OU
Brachiopod sampling rate (log per Myr)	5.7	1.3	6.4 (3.1–16)	−2.1 (−2.4, −1.8)	0.6 (0.5, 0.9)	NA	OU
Bivalve extinction rate (log per Myr)	5.8	1.0	2.9 (0.04–9.5)	−3.8 (−4.2, −3.4)	1.0 (0.8, 1.3)	NA	OU
Brachiopod extinction rate (log per Myr)	6.5	1.0	5.9 (0.6–130)	−3.1 (−3.5, −0.8)	1.0 (0.8, 3.1)	NA	OU
Bivalve origination rate (log per Myr)	6.1	1.8	0.2 (0.001–4.4)	−3.6 (−3.8, −3.4)	0.6 (0.4, 0.7)	NA	OU
Brachiopod origination rate (log per Myr)	6.2	1.0	1.6 (0.007–6.3)	−3.2 (−3.4, −2.9)	0.6 (0.5, 0.8)	NA	OU

Summaries of five paleoenvironmental time series and six biotic time series are presented. The first two columns show average and minimum temporal resolution of the given time series and the next four columns show parameter estimates and 95% credibility intervals for each time series from stand-alone analyses using SDE. μ and S have the same units as the time series themselves. σ has a unit of the variable in question, divided by the square root of time in Myr. The last column states the best model in a Bayesian model comparison among a simple OU model, an OU-like model with a linear trend and a Brownian Motion (BM) model, i.e. an OU with a half-life exceeding the time period of the data. We assume all models have equal prior probability.

not have an easily visually matched time lag relative to the driver time series.

While a single-layered SDE could describe a given time series, it may be causally affected by an underlying unmeasured time series which in turn could be driven by yet another time series. Unmeasured underlying processes can be described by a multi-layered linear SDE model (Reitan *et al.* 2012). In a two time series single-layered SDE system like that we described in eqns (3) and (4), X_1 could be erroneously inferred to have driven X_2, even though X_1 and X_2 are not causally linked. One way this error could happen is if X_1 is tracking a third unmeasured variable X_3 so fast that it mimics X_3, and X_3 in addition drives X_2. Such an explanation for our observation entails added complexity and assumptions, and is thus unparsimonious. Where our analyses of stand-alone time series indicated multiple layers, we did explore multi-layered models in addition to single-layered models when testing pairwise relationships, allowing us to detect more complex models. Increasing the complexity of our models caused only small qualitative changes to our results and hence multi-layered models are not further discussed (see Supporting Information Tables).

Parameter estimates from SDEs

The extinction, origination and sampling rates and paleoenvironmental proxies are associated with temporal point estimates that do not necessarily match in time, even though each time series spans most of the Phanerozoic. However, because the process models we fit are time-continuous we circumvent the problem of non-matching times when inferring relationships among the various time series. The parameter estimates describing these time-continuous SDEs in addition to those already described (ρ and β) are as follows.

If an OU process is the best model, a time series can be characterised by its half-life

$$\Delta t_{1/2} = log(2)/\alpha, \tag{5}$$

which is the time it takes for the given temporal process to approach half the distance to the expected value μ. We also report σ rescaled as the stationary standard deviation

$$S = \sigma/(2\alpha)^{0.5}. \tag{6}$$

If a Brownian Motion process (BM) is the best model, we report σ. To represent an OU-like model that tracks a linear trend, we add a linear term to eqn (1) where μ_0 is the value of the linear trend at $t = 0$, and report the linear term η if such a process is the best model, such that $dX(t) = -\alpha(X(t) - [\mu_0 + \eta t])\mathrm{d}t + \sigma \mathrm{d}B(t)$

Correction for multiple testing

We are interested in the possible relationships among five abiotic time series (low latitude $\delta^{18}0$, low latitude δ^{13}C, δ^{34}S, ^{87}Sr/^{86}Sr and eustatic sea level) and six biotic time series. The latter consist of brachiopod and bivalve origination, extinction and sampling, where sampling estimates encompass a variety of biological signals including shell durability, body size, rarity, in addition to physical processes such as sedimentation and erosion rates, as well as sampling effort. In each case, the null model of no relationship among time series is given an *a priori* probability of 50% with all the remaining models sharing 50%. Whether there is evidence for a relationship can then be established by how much the probability of the null model deviates from 50%. Because we studied combinations of time series in pairs, we correct for multiple testing. We used a Bonferroni-like correction where relationships are deemed significant if the probability for the null hypothesis drops below $50\%/\sqrt{k}$, where k is the number of comparisons made (Westfall *et al.* 1997).

RESULTS

Diversification dynamics of brachiopods and bivalves

Brachiopod and bivalve origination, extinction and sampling rates are presented in Figs 2 and 3. Mass extinction events have in general higher extinction rates than their flanking time intervals, with the exception of the Late Devonian extinction. Several unconstrained extinction and origination estimates scattered over the Phanerozoic were removed from subsequent analyses (Table S1). There are also some poorly constrained diversification estimates notably for brachiopods in the Cenozoic (66–0 million years ago); these are due to brachiopod diversity and abundance being low during the Cenozoic and because Cenozoic brachiopods are poorly documented in the PaleoDB. We note that because we include the uncertainty estimates in our subsequent time series analyses, poorly constrained estimates are down weighted in our inferences.

Temporal characteristics of diversification, sampling and paleoenvironmental proxies

The paleoenvironmental proxies exhibit long half-lives with respect to the resolution of the data (Table 1), indicating that there is strong temporal autocorrelation and that ordinary regression and related approaches should not be used when examining their relationship with other time series. The half-lives of brachiopod origination and extinction rates are longer than those for bivalves, meaning that brachiopod diversification rates change more slowly than bivalve rates. However, the origination and extinction rates of brachiopods are higher than for bivalves, with little or no overlap in the estimated μ's (Table 1).

Relationships among brachiopod and bivalve time series and paleoenvironmental proxies

There are no detectable effects of any of the five paleoenvironmental proxies on any of the origination, extinction or fossil sampling time series if multiple testing is accounted for (Table S3 and S4). We also examined relationships among the five paleoenvironmental time series but discuss these briefly only in the Supporting Information (see Table S5 and S6) given their general lack of relationship with the biotic time series of interest.

Relationships among brachiopod and bivalve time series

Since we have not found statistically detectable relationships between any of the five available paleoenvironmental time series and the six biotic time series, no corrections for contributions from these time series were necessary when analysing the relationships among the biotic time series. For fifteen combinations among the six biotic time series, the target posterior probability for a link model is $50\%/\sqrt{15} = 12.9\%$. Looking first at the causal relationships among diversification rates, there is strong evidence that high bivalve extinction rates are followed by high brachiopod origination rates (Table 2, $\beta = 1.0$ (0.53, 0.99)). A β of 1.0 means that if bivalve extinction rate changes by one order of magnitude, then brachiopod origination rate also changes by an order of magnitude in time, as specified by the half-life of brachiopod origination (1.6 Myr, Table 1). There is weaker evidence that high brachiopod extinction rates are followed by high brachiopod origination rates. There is strong evidence that bivalve and brachiopod extinction rates ($\rho = 0.89$, 95% CI = (0.73, 0.98)) and their origination rates are positively correlated ($\rho = 0.83$, 95% CI = (0.53, 0.99)). While no direction of causation can be established between bivalve extinction and origination, they are positively correlated. Note that this may be because there is truly no causal relationship between bivalve extinction and origination or because we cannot detect such a relationship as the half-life of bivalve origination is somewhat shorter than the temporal resolution of the bivalve origination estimates. There is no detectable relationship between brachiopod extinction and bivalve origination (Table 2A). Because these diversification estimates are not confounded by uneven sampling across time intervals, our results can be interpreted directly.

Brachiopod and bivalve sampling rates are highly correlated over the Phanerozoic (Table 2B). Brachiopod sampling rates are positively linked to both bivalve origination and extinction but the type of link model is uncertain in both cases. Bivalve sampling rates are positively correlated with brachiopod and bivalve extinction rates, but not their origination rates (Table 2B). Note that sampling as estimated here is a heterogeneous signal composed of true abundance, spatial occupancy, various geological and chemical processes, as well as research effort and taxonomic practices.

DISCUSSION

Both paleobiologists (Jablonski 2008) and neontologists (Rabosky 2013) have attempted to elucidate the roles of ecological interactions in diversity dynamics. Such dynamics can be studied using morphospace occupation, where one might expect competition to lead to character displacement (Kimura *et al.* 2014). A complementary approach is to study diversification dynamics using molecular phylogenies or the fossil record and to fit models that involve ecological interactions to these data (Condamine *et al.* 2013). Although recent methodological developments have facilitated the modelling of diversification dynamics using molecular phylogenies (Morlon 2014), extinction dynamics are still challenging to estimate from such phylogenies. The more direct approach of using the occurrences of fossils to infer diversification dynamics has a long history (Simpson 1944; Stanley 1979), aided now by the recent availability of big data and the development of methods that begin to overcome sampling biases inherent to fossil records.

Table 2 Relationships among biotic time series of bivalves and brachiopods

Table 2A	Brachiopod extinction rate (logged)	Brachiopod origination rate (logged)	Bivalve extinction rate (logged)
Brachiopod origination rate (logged)	1.5% * ↑ $\beta = +1.1$ (0.49, 2.3)		
Bivalve extinction rate (logged)	3.0E-7%*** **corr** $\rho = +0.89$ (0.73–0.98)	0.13%** ← $\beta = +1.0$ (0.53, 0.99)	
Bivalve origination rate (logged)	45%	0.05%*** corr $\rho = +0.83$ (0.53, 0.99)	1.2%** **corr** $\rho = +0.74$ (0.37, 0.97)

Table 2B	Brachiopod extinction rate (logged)	Brachiopod origination rate (logged)	Bivalve extinction rate (logged)	Bivalve origination rate (logged)	Brachiopod sampling rate (logged)
Brachiopod sampling rate (logged)	61%	76%	11.3% * corr $\rho = +0.56$ (0.17, 0.81)	8.1% * ← $\beta = +0.59$ (0.29, 0.90)	
Bivalve sampling rate (logged)	0.06% *** **corr** $\rho = +0.73$ (0.47, 0.92)	72%	0.46% ** corr $\rho = +0.70$ (0.37, 0.90)	45%	5E-11%*** **corr** $\rho = +0.90$ (0.78, 0.96)

The first line in each cell is the Bayesian posterior probability for the null hypothesis (no relationship). *means the posterior probability is lower than the multiple testing limit of 12.9%; **<1.29% and ***<0.13%. The second line in a cell denotes the most probable link model if the null hypothesis was rejected. The link model can be correlative ('corr'), or causative (arrows point towards the causal driver). Black link models are where the probability of the best link model is more than twice that of the next best link model and uncertain links are in grey. ρ characterises the correlation (eqn 3) while β characterises the strength of the causal relationship (eqn 4). The last line gives the 95% credibility interval for the ρ or β. See Table 1 for models used for each time series.

Using what we feel are currently the best available statistical approaches (see Supporting Information for simulations), we found strong evidence that brachiopod origination rates increase following elevated bivalve extinction rates. This suggests that the ecological expansion of bivalves led to the suppressed diversification of brachiopods over the Phanerozoic, with the caveat that we have little information on brachiopod diversification rates during the Cenozoic (Fig 3). One interpretation is that the filling of ecological niches by bivalves is more rapid and pervasive than that of brachiopods. There is no evidence, however, that higher origination rates in bivalves negatively influenced brachiopod origination. Rather, over the broad time intervals studied, brachiopod originations and bivalve originations are positively correlated, suggesting that biotic and/or abiotic conditions that were favourable for bivalve evolution were also generally favourable for brachiopod evolution (Table 2). This does not rule out the possibility that at a more local level, bivalve populations may outcompete brachiopod populations (Thayer 1985; Tomašových 2008). In contrast, brachiopod extinctions had no detectable effects on bivalve originations, consistent with the hypothesis that brachiopods were the weaker competitor of the two marine clades. The extinction rates of brachiopods and bivalves are strongly correlated (Table 2) suggesting that these might be driven by common biotic forces, such as competitors (e.g. sponges), disease agents, predators, and/or unmeasured environmental drivers.

Bivalve sampling rates are strongly positively linked to brachiopod and bivalve extinction rates and brachiopod sampling rates (Table 2 and Table S7). That sampling rates drive diversification time series may seem counterintuitive since our approach produces diversification estimates that are intended to be unbiased by variable sampling through time. However, sampling reflects a complex suite of factors including biological traits (e.g. body size, shell chemistry, local abundance and geographic spread) of organisms that could potentially be fossilised, as well as the geological and geochemical conditions affecting their likelihood of fossilisation and hence discovery potential. One possible interpretation is that there is a greater interest in extinction time intervals, hence the better sampling. However, assessing this and other plausible hypotheses requires additional work, not least to estimate sampling and preservation separately.

Given the prevailing view in the paleontological literature that macroevolution is strongly driven by abiotic perturbations (Benton 2009) and the results of previous studies involving (but not limited to) brachiopods and bivalves (Cardenas & Harries 2010; Mayhew *et al.* 2012) it is striking that none of the five paleoenvironmental time series exhibit any statistical relationships with brachiopod and bivalve diversification rates. Bivalve and brachiopod sampling rates are highly correlated (Table 2B) which may reflect temporal variation in the global extent of marine sedimentary rocks – with enhanced sampling opportunities during intervals with more extensive sedimentary records – and some similarities in the taphonomic filters affecting preservation in these groups. The lack of relationship between the five paleoenvironmental time series and the two sampling time series is notable in light of the common-cause hypothesis (Hannisdal & Peters 2011), which states that global environmental change (e.g. sea-level variation) may have led to temporally coordinated changes in biodiversity and the availability of fossil outcrops.

Differences between our inferences and those previously made are expected for several reasons. The model we used for estimating sampling, origination and extinction probabilities is different in its details from other such models (Harnik & Lockwood 2011), such that discrepancies are expected. In addition, we accounted for autocorrelation, unequally spaced and non-matching time points across different time series and utilise uncertainty in our estimates in our SDE-based time series analyses.

To understand possible controls on macroevolutionary dynamics, both ecological interactions and environmental drivers need to be studied within the same analytical framework (Ezard *et al.* 2011; Condamine *et al.* 2013; Voje *et al.* 2015). Using such an approach here, we have shown that brachiopod and bivalve dynamics are causally linked and that paleoenvironmental changes over the Phanerozoic did not affect the evolutionary dynamics of brachiopod and bivalve genera nor systematically affect their sampling rates through geologic time. Although we have identified statistical causal relationships among the diversification dynamics of bivalves and brachiopods in the fossil record, we emphasise that further work is needed to elucidate the underlying mechanisms through which they are linked. Analysis of ecological proxies, including taxonomic diversity, abundance and spatial distributions may offer insight into mechanisms underlying global bivalve and brachiopod diversification dynamics. Using state-space modelling, stochastic differential equation modelling and fossil occurrence databases, understanding how ecological interactions change evolutionary outcomes under varying environmental backdrops over geological time scales is a goal that is now attainable.

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AUTHORSHIP

LHL & TR designed the analyses, LHL did the CMR analyses and TR did the SDE analyses, LHL and TR wrote the first draft of the manuscript, LHL, TR, PGH discussed analyses, inferences and contributed substantially to revisions.

REFERENCES

Aberhan, M., Kiessling, W. & Fursich, F.T. (2006). Testing the role of biological interactions in the evolution of mid-Mesozoic marine benthic ecosystems. *Paleobiology*, 32, 259–277.

Alroy, J. (2008). Dynamics of origination and extinction in the marine fossil record. *Proc. Natl Acad. Sci. USA*, 105, 11536–11542.

Alroy, J. (2010). The shifting balance of diversity among major marine animal groups. *Science*, 329, 1191–1194.

Alroy, J., Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fursich, F.T. *et al.* (2001). Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proc. Natl Acad. Sci. USA*, 98, 6261–6266.

Benton, M.J. (2009). The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science*, 323, 728–732.

Cardenas, A.L. & Harries, P.J. (2010). Effect of nutrient availability on marine origination rates throughout the Phanerozoic eon. *Nat. Geosci.*, 3, 430–434.

Chave, J. (2013). The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecol. Lett.*, 16, 4–16.

Clapham, M.E. & Bottjer, D.J. (2007). Prolonged permian triassic ecological crisis recorded by molluscan dominance in Late Permian offshore assemblages. *Proc. Natl Acad. Sci.*, 104, 12971–12975.

Clark, J.S. & Bjørnstad, O.N. (2004). Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology*, 85, 3140–3150.

Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. (2013). The ICS international chrongostratigraphic chart. *Episodes*, 36, 199–204.

Condamine, F.L., Rolland, J. & Morlon, H. (2013). Macroevolutionary perspectives to environmental change. *Ecol. Lett.*, 16, 72–85.

Ezard, T.H.G., Aze, T., Pearson, P.N. & Purvis, A. (2011). Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, 332, 349–351.

Foote, M. (2001). Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. *Paleobiology*, 27, 602–630.

Foote, M. (2003). Origination and extinction through the Phanerozoic: a new approach. *J. Geol.*, 111, 125–148.

Gould, S.J. & Calloway, C.B. (1980). Clams and brachiopods - ships that pass in the night. *Paleobiology*, 6, 383–396.

Granger, C.W.J. (1969). Investigating causal relations by econometric models and cross-spectral methods. *Econometrica*, 37, 424–438.

Hannisdal, B. & Peters, S.E. (2011). Phanerozoic earth system evolution and marine biodiversity. *Science*, 334, 1121–1124.

Harnik, P.G. & Lockwood, R. (2011). *Extinction in the marine Bivalvia. Treatise on Invertebrate Paleontology Online*, 29, 1–24.

Jablonski, D. (2008). Biotic interactions and macroevolution extensions and mismatches across scales and levels. *Evolution*, 62, 715–739.

Jablonski, D. & Finarelli, J.A. (2009). Congruence of morphologically-defined genera with molecular phylogenies. *Proc. Natl Acad. Sci.*, 106, 8262–8266.

Kimura, Y., Jacobs, L.L. & Flynn, J.J. (2014). Lineage-specific responses of tooth shape in murine rodents (Murinae, Rodentia) to Late Miocene dietary change in the Siwaliks of Pakistan. *PLoS ONE*, 8, e76070.

King, R. (2014). Statistical Ecology. In *Annual Review of Statistics and Its Application*,, 1, 401–426.

Laake, J.L. (2013). *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK.* AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Liow, L.H. & Finarelli, J.A. (2014). A dynamic global equilibrium in carnivoran diversification over 20 million years. *Proc. R. Soc. B. Biol. Sci.*, 281, 20132312.

Liow, L.H. & Nichols, J.D. (2010). Estimating rates and probabilities of origination and extinction using taxonomic occurrence data: Capture-recapture approaches. In *Short Courses in Paleontology: Quantitative Paleobiology*. (eds Hunt, G., Alroy, J.). Paleontological Society, Boulder, Colorado, pp. 81–94.

Lu, P.J., Yogo, M. & Marshall, C.R. (2006). Phanerozoic marine biodiversity dynamics in light of the incompleteness of the fossil record. *Proc. Natl Acad. Sci. USA*, 103, 2736–2739.

Mayhew, P.J., Bell, M.A., Benton, T.G. & McGowan, A.J. (2012). Biodiversity tracks temperature over time. *Proc. Natl Acad. Sci.*, 109, 15141–15145.

Melott, A.L., Bambach, R.K., Petersen, K.D. & McArthur, J.M. (2012). An similar to 60-million-year periodicity is common to marine Sr-87/Sr-86, fossil biodiversity, and large-scale sedimentation: what does the periodicity reflect? *J. Geol.*, 120, 217–226.

Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C. *et al.* (2011). Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, 334, 521–524.

Miller, A.I. & Sepkoski, J.J. (1988). Modeling bivalve diversification: the effect of interaction on a macroevolutionary system. *Paleobiology*, 14, 364–369.

Montgomery, D.C., Peck, E.A. & Vining, P.G.G. (2012). *Introduction to Linear Regression Analysis*, 5th edn. Published by John Wiley & Sons, Inc., Hoboken, New Jersey.

Morlon, H. (2014). Phylogenetic approaches for studying diversification. *Ecol. Lett.*, 17, 508–525.

Payne, J.L., Heim, N.A., Knope, M.L. & McClain, C.R. (2014). Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years. *Proc. R. Soc. B Biol. Sci.*, 281, 20133122.

Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, 52, 703–709.

Prokoph, A., Shields, G.A. & Veizer, J. (2008). Compilation and time-series analysis of a marine carbonate delta O-18, delta C-13, Sr-87/Sr-86 and delta S-34 database through Earth history. *Earth Sci. Rev.*, 87, 113–133.

Rabosky, D.L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annu. Rev. Ecol. Evol. Syst.*, 44, 481–502.

Raup, D.M. (1986). Biological extinction in earth history. *Science*, 231, 1528–1533.

Reitan, T., Schweder, T. & Henderiks, J. (2012). Phenotypic evolution studied by layered stochastic differential equations. *Ann. Appl. Stat.*, 6, 1531–1551.

Sepkoski, J.J. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, 7, 36–53.

Sepkoski, J.J., McKinney, F.K. & Lidgard, S. (2000). Competitive displacement among post-Paleozoic cyclostome and cheilostome bryozoans. *Paleobiology*, 26, 7–18.

Simpson, G.G. (1944). *Tempo and Mode in Evolution*. Columbia University Press, New York.

Stanley, S.M. (1979). *Macroevolution: Pattern and Process*. The John Hopkins University Press, Baltimore, London.

Stanley, S.M. (2008). Predation defeats competition on the seafloor. *Paleobiology*, 34, 1–21.

Thayer, C.W. (1985). Brachiopods versus mussels: competition, predation, and palatability. *Science*, 228, 1527–1528.

Thompson, J.N. (2005). *The Geographic Mozaic of Coevolution*. The University of Chicago Press, Chicago and London.

Tomašových, A. (2008). Substrate exploitation and resistance to biotic disturbance in the brachiopod *Terebratalia transversa* and the bivalve *Pododesmus macrochisma*. *Marine Ecology Progress Series*, 363, 157–170.

Van Valen, L.M. (1973). A new evolutionary law. *Evol. Theory*, 1, 1–30.

Van Valen, L. & Sloan, R.E. (1966). The extinction of the Multituberculates. *Syst. Biol.*, 15, 261–278.

Voje, K.L., Holen, Ø.H., Liow, L.H. & Stenseth, N.C. (2015). The role of biotic forces in driving macroevolution: Beyond the Red Queen. *Proc. R. Soc. B Biol. Sci.*, 282, 20150186.

Wagner, P.J., Aberhan, M., Hendy, A. & Kiessling, W. (2007). The effects of taxonomic standardization on sampling-standardized estimates of historical diversity. *Proc. R. Soc. B Biol. Sci.*, 274, 439–444.

Westfall, P.H., Johnson, W.O. & Utts, J.M. (1997). A Bayesian perspective on the Bonferroni adjustment. *Biometrika*, 84, 419–427.

White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46, 120–139.

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