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Ecological structure of diversity-dependent diversification in Phanerozoic marine bivalves

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Rigorous analysis of diversity-dependence—the hypothesis that the rate of proliferation of new species is inversely related to standing diversity—requires consideration of the ecology of the organisms in question. Differences between infaunal marine bivalves (living entirely within the sediment) and epifaunal forms (living partially or completely above the sediment–water interface) predict that these major ecological groups should have different diversity dynamics: epifaunal species may compete more intensely for space and be more susceptible to predation and physical disturbance. By comparing detrended standing diversity with rates of diversification, origination, and extinction in this exceptional fossil record, we find that epifaunal bivalves experienced significant, negative diversity-dependence in origination and net diversification, whereas infaunal forms show little appreciable relationship between diversity and evolutionary rates. This macroevolutionary contrast is robust to the time span over which dynamics are analysed, whether mass-extinction rebounds are included in the analysis, the treatment of stratigraphic ranges that are not maximally resolved, and the details of detrending. We also find that diversity-dependence persists over hundreds of millions of years, even though diversity itself rises nearly exponentially, belying the notion that diversity-dependence must imply equilibrium diversity dynamics.

1. Introduction

(a) Diversity-dependent diversification in the history of life

Whether the rate of proliferation of new species depends on standing diversity remains a fundamental, largely unanswered question in ecology, evolutionary biology and palaeontology [1]. The fossil record of marine life often shows rates of diversification to be negatively correlated with diversity [1–7]. Periods of relatively high diversity in the oceans saw suppressed diversification rates compared to times when there were fewer taxa, as in the immediate aftermaths of mass extinctions. Despite abundant palaeontological evidence for diversity-dependence, this crucial issue remains contentious [1,8,9]. Long-term dynamics over tens to hundreds of millions of years are mostly understood from analyses of the global biota and a few major clades, and while the patterns are strong [2,7,10], the broad taxonomic scope of most analyses often encompasses ecologically disparate taxa that are unlikely to interact. Thoroughly testing potential drivers requires an analytical design that explicitly incorporates ecological differences among lineages and larger clades [5], focuses on species that have the potential to interact ecologically, draws data from clades with a robust and temporally well-resolved fossil record, and covers the long spans of time relevant to macroevolutionary dynamics. Marine bivalves satisfy these desiderata. Moreover, compared to analyses of only living taxa, long-term

palaeontological time series can better delimit the roles of speciation and extinction [6,7,11,12].

(b) Potential role for ecology in bivalve diversification

Competition for available space has been widely documented in living marine species [13,14] and has been argued to underpin diversity dynamics at the macroevolutionary scale in certain habitats [4,15–17]. Using the fossil record of marine bivalves, a model system for studying macroevolution through the Phanerozoic [3,18–20], we test for differences in the diversity-dependence of evolutionary rates in two principal life modes: *infaunal* forms, those living enclosed within a substratum, and *epifaunal* forms, operationally defined here to include those living entirely atop, attached to, or partly within the substratum [21–26].

Epifauna experience greater exposure to predation and substratum disturbance than infauna, both from physical processes (wave energy) and churning of sediments by other animals (bioturbation), the latter having substantially increased through the Phanerozoic [27–29]. Predation and bioturbation can limit the relative amounts of habitat available to epifauna, restricting those taxa to spatially limited refugia, hardgrounds or undisturbed soft sediment [27,30]. Thus, we would expect epifauna to show stronger negative diversity-dependence than infauna. Given the wide availability of infaunal habitats across continental shelves through time, we expect weaker diversity-dependence in the evolutionary rates of infauna, although, on ecological scales, certain infaunal bivalves show density-dependent migration or repositioning in response to crowding from other bivalve taxa [31,32]. Finally, we test whether the two ecological groups may conceivably interact as a coupled system; bioturbation by infauna might exclude epifauna from potential habitat [27,28,33], raising the possibility that elevated diversity and abundance of infauna negatively impact the evolutionary rates of the epifauna. At the same time, epifauna could potentially affect infauna by increasing the volume of coarse skeletal material in the sediment, thereby inhibiting infaunal burrowing [34,35].

2. Material and methods

(a) Data

We analyse diversity dynamics using a database of 3365 fossil marine bivalve genera, compiled from a compendium of first and last stratigraphic occurrences [36] that has been heavily vetted and substantially expanded using the primary literature and museum collections over more than 20 years [18–20,23,37–39]. Genera were classified as *infaunal* ($N = 2098$) and *epifaunal* ($N = 1267$) using aspects of their functional morphology and phylogenetic affinity [21,22,24–26] (electronic supplementary material, tables S1, S2).

(b) Analysis of diversity dynamics

Estimates of richness and taxonomic rates of evolution used the standard ‘boundary-crosser’ methods for stratigraphic range data [40]. To minimize edge effects [40,41] and the impact of sparse Cambrian and earliest Ordovician data, we analyse data from the Ordovician Floian Stage through the Miocene Epoch (electronic supplementary material, text; electronic supplementary material, table S1). This approach tacitly assumes that palaeontological completeness is high enough to treat observed

first and last appearances as proxies for times of origination and extinction. Many methods exist for estimating rates with incomplete sampling [7,41,42], but the high fidelity of the bivalve record and the similar preservation potential of the two ecological groups obviate the need for complex approaches. In the spatial and temporal parts of the geological record analysed here, using methods in [43–47], we estimate that over 90% of bivalve genera are sampled at least once during their lifetimes, and, on average, over 90% of their original durations are represented by their preserved stratigraphic ranges (electronic supplementary material, table S3). These exceptionally high completeness estimates, even compared with those from an early version of this database [48], exceed estimates with data from the Paleobiology Database [49] (electronic supplementary material, table S3). High completeness reflects both the intrinsic preservability of bivalve molluscs [50] and the continued growth and vetting of the database, and it gives us confidence in inferring evolutionary dynamics.

Our approach to testing for diversity-dependent diversification follows recent studies [6,7,51] that compare standing diversity at the start of a time interval to rates of origination, extinction, and net diversification (origination minus extinction) in the ensuing part of that interval. To reflect the multiplicative nature of diversification, richness is expressed logarithmically. To avoid the assumption of a constant carrying capacity or a particular model of diversification [2,4,52,53], we detrend all time series, via LOWESS regression with a smoothing span $f = 0.5$, and measure the rank-order correlations between residuals of diversity and taxonomic rates relative to long-term trends (figures 1 and 2, electronic supplementary material, S1, S2; table 1). The hypothesis of diversity-dependence predicts a negative correlation between diversity residuals and diversification-rate residuals. Given the general statistical phenomenon of regression to the mean, diversity and diversification rate tend to be negatively correlated even if rates are independent of diversity [54,55]. We therefore use a randomization procedure [6,7] to determine whether observed correlations are stronger than would be expected for a diversity-independent process.

All analyses were carried out in R version 4.3.0 [56].

3. Results and discussion

(a) Contrasting diversification dynamics

Class Bivalvia has diversified over the past 500 million years in a roughly exponential pattern [3] (figure 1). Both the infauna and epifauna followed this upward diversification trajectory, although infauna outpaced the epifauna starting in the Jurassic, ultimately becoming three times as rich by the Miocene (figure 1*a,b*; electronic supplementary material, table S2). Each group shows high temporal variation in diversification rate, but the average over the Phanerozoic barely exceeds nil in either group (figure 1*c,d*), a nice illustration of the compounding effect of even a slightly positive diversification rate over hundreds of millions of years.

Mass extinctions depleted diversity in both groups, disproportionately affecting infauna at the end-Permian and epifauna at the end-Cretaceous, but both groups re-diversified after these and other events [3] (figure 1*a,b*). Analysing and interpreting each fluctuation in these diversity curves is beside our main objective, but certain patterns observed here align with prior knowledge of bivalve diversification. For example, the relatively high standing diversity of the epifauna in the Late Cretaceous reflects the exceptional diversification of the tropical-platform rudists and the reclining gryphaeids and inoceramids.

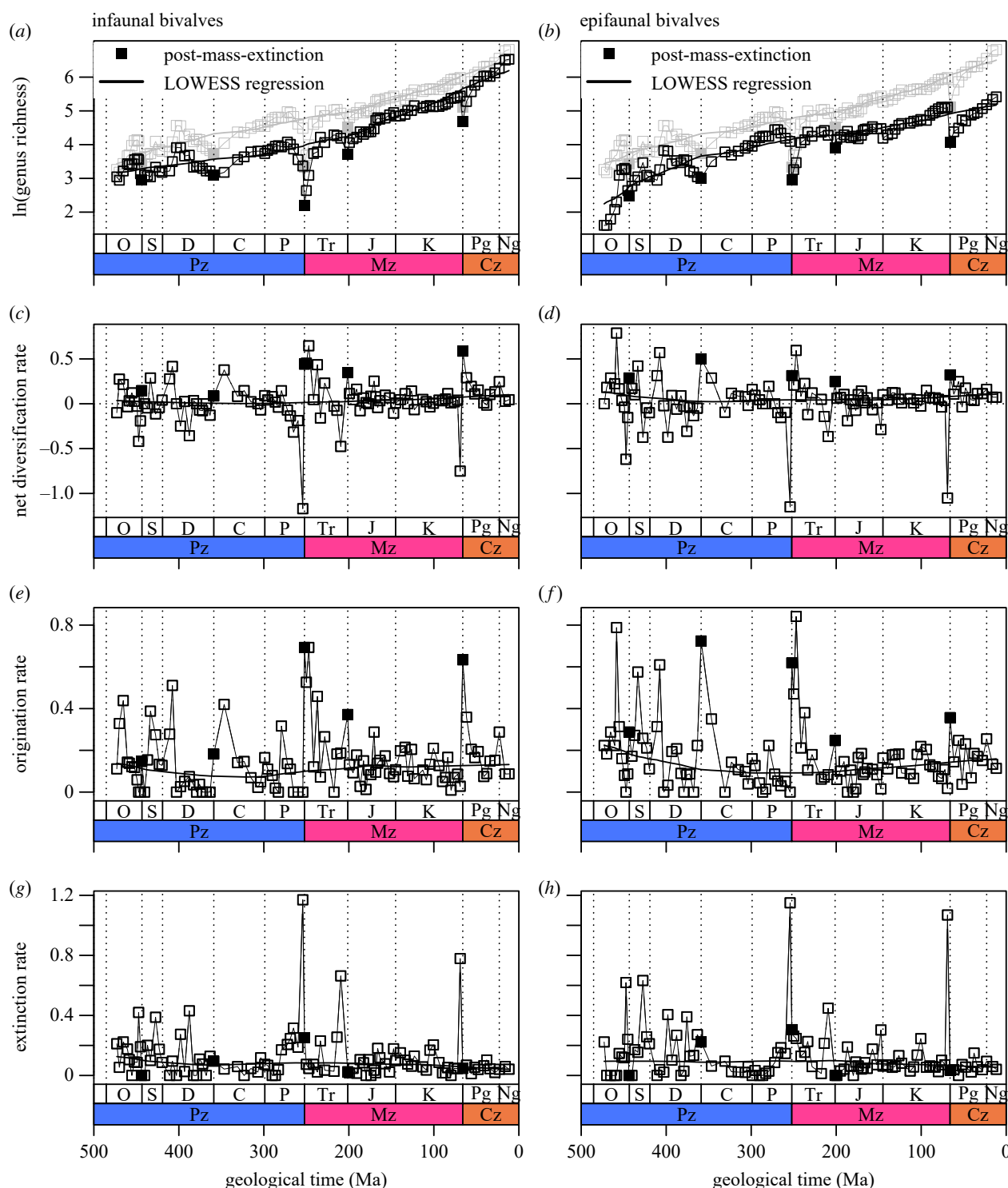


Figure 1. History of diversity and evolutionary rates. Grey: combined infauna + epifauna. Pz, Palaeozoic Era; Mz, Mesozoic Era; Cz, Cenozoic Era; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; Ng, Neogene; Ma, million years before present. Post-mass-extinction intervals: Lower Llandovery, Tournaisian, Induan, Hettangian, Danian.

Across the study interval, infaunal and epifaunal genera, and bivalves as a whole, show that extinction rates do not increase with diversity (figure 2*i-l*; table 1), consistent with previous analyses [7,57,58]. These distinct ecological groups, however, show different dynamics in their rates of origination and net diversification. Infaunal genera have experienced relatively weak, and statistically insignificant, diversity-dependence in origination rate and net diversification rate (figure 2*a,b,e,f*; table 1). Epifauna, by contrast, show stronger and statistically significant diversity-dependence in both their origination and net diversification rates (figure 2*c,d,g,h*; table 1). Rather than rebounding only from major mass

extinctions, origination and net diversification of the epifauna were both enhanced when diversity was reduced and suppressed when diversity increased.

Patterns of diversity-dependence in origination and net diversification rates for both life modes are largely insensitive to variations in analytical protocol (electronic supplementary material, table S4). Starting the study interval after the initial major pulse of diversification in the Early Ordovician, or, even more extreme, after the entire Ordovician radiation, did not impact the observed diversity-dependence in evolutionary rates. Likewise, results persist, albeit somewhat muted, if the immediate aftermaths of major mass extinctions

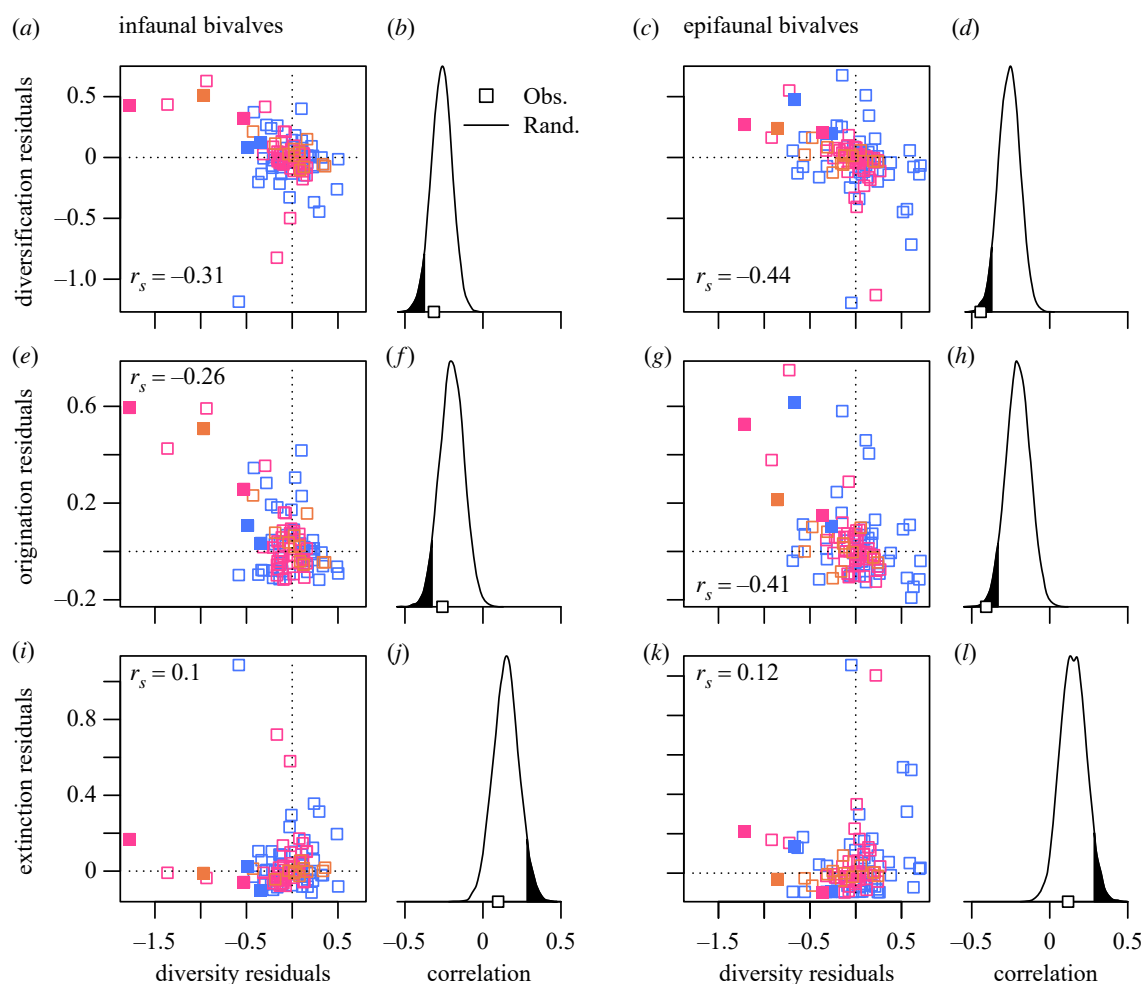


Figure 2. Correlations between diversity residuals and rate residuals. (a,c,e,g,i,k) Scatterplots of residuals, with rank-order correlations indicated. Colour coding of points corresponds to era-level designations of figure 1. (b,d,f,h,j,l) Comparison of observed correlations (open squares) between diversity residuals and rate residuals with correlations resulting from a randomization protocol (solid lines). Shaded area: one-sided 5% of randomized distribution.

are excluded. Results were also robust to details of detrending diversity and evolutionary rates, and to the exclusion of genera lacking finely resolved (mainly substage) first and last appearances (e.g. last appearance as 'Maastrichtian' instead of 'Upper Maastrichtian') (electronic supplementary material, tables S1, S2). Simulations that randomly assign genera to two groups show that the difference in diversity-dependence between these randomized groups rarely exceeds the observed infaunal–epifaunal difference (3% of randomizations for origination; 1% for net diversification) (electronic supplementary material, figure S3). Thus, stronger diversity-dependence in epifauna versus infauna is a robust feature that is unlikely to have arisen by chance, and we therefore conclude that the difference in their diversity dynamics is meaningful and potentially interpretable biologically.

Evolutionary rates of the two groups within the same time interval are strongly and positively correlated (table 2), consistent with their similar, roughly exponential, diversification histories (figure 1a–d). The correlation is not perfect, however, and the residual variation must account for the observed difference in diversity dynamics between the two groups. Comparing rates with a temporal lag, diversification rate in either group fails to predict the rate in the other group in the following time interval, contrary to what we would expect if one group were suppressing diversification in the other. This limited analysis suggests that there is no prima

facie evidence for negative interaction between the two groups at this temporal scale.

(b) Diversification despite diversity-dependence

Negative diversity-dependence in bivalve evolution despite their steady Phanerozoic diversification suggests that feedbacks have operated throughout their history, without setting a ceiling on their total diversity. This result supports the view that diversity-dependence can operate in a macroevolutionary system even when the overall trajectory of that system is positive rather than asymptotic [3,7,53]. It also stands in contrast to most modelling of macroevolutionary systems, whether based on palaeobiological data or evolutionary trees of living species, that assumes systems are near a fixed carrying capacity for much of their history [2,11,52,59]. One long-standing hypothesis is that background and mass extinction intervene before a theoretical accommodation limit is reached [60,61]; in addition, increased nutrient inputs through the Phanerozoic may have raised diversity limits on the long term [62,63].

The overall bivalve pattern in diversity-dependence is primarily driven by one life mode, the epifauna, as predicted. By contrast, the short-term ecological interactions among infaunal bivalves [31,32] do not manifest at macroevolutionary scales. As observed in other systems [7,60,61,64–67], negative diversity-dependence operates via origination, not extinction.

Table 1. Spearman rank-order correlations (r_s) between diversity residuals and rate residuals.

ecological group	diversification		origination		extinction	
	r_s	p^a	r_s	p^a	r_s	p^a
infauna + epifauna	−0.379	0.043	−0.348	0.031	0.016	0.926
infauna	−0.314	0.227	−0.260	0.218	0.097	0.734
epifauna	−0.443	0.004	−0.407	0.004	0.117	0.662

^aNominal one-tailed p -value is the proportion of randomizations that yield a correlation more extreme than the observed value.

Table 2. Cross-correlations of net diversification rate.

analysis	product–moment correlation	p -value
infaunal versus epifaunal, lag 0	0.84	< 0.001
infaunal leading epifaunal, lag 1	0.014	0.89
epifaunal leading infaunal, lag 1	−0.016	0.88

However, diversity-dependent control of diversification by damping or promoting origination has been difficult to explain [10,57]. The most frequent hypothesis involves variations in the survival of incipient species [57,68–70]. Such incipient species typically have small population sizes and narrow geographical ranges, so that temporal variation in biotic and abiotic pressures can alter the probability of establishment as discrete taxa detectable in the fossil record [70,71]. This effect may be strongest among epifauna given their more limited habitat space and greater exposure to physical and biotic disturbances, pressures that would be intensified or relaxed under times of positive or negative diversity excursions, respectively. Although predation intensity has increased over the past 500 million years [30], this trend does not dominate our results; rather, negative diversity-dependence is evident throughout the Phanerozoic (figure 2, electronic supplementary material, figure S2).

The ecological difference we find in diversity-dependence is unlikely simply to reflect clade-specific differences, because infaunal versus epifaunal life mode transcends clade membership (electronic supplementary material, table S2). The primitive life mode for Cambrian bivalves remains uncertain [72], but no matter how that controversy is resolved, the two modes of life are polyphyletic within and among taxonomic orders; nine of the 25 bivalve orders contain both infaunal and epifaunal taxa, signifying at least nine transitions. Thus, epifaunality is likely a deterministic factor in diversity dynamics, given its multiple, independent derivations across distantly related clades and their broad variety of life histories and basic body plans.

Throughout their evolutionary history, bivalve diversification has entailed both functional novelty and continued subdivision of those functions [73,74]. However, epifauna have attained less functional variety than have the infauna [23], which may help to explain both the lower standing

diversity of the group today and the stronger diversity-dependence in its origination rate throughout the Phanerozoic. Thus, for epifauna, short-term runs above the long-term diversity trend might reflect the rare acquisition of new functions and their subdivision, briefly allowing relatively unimpeded diversification that is later damped by negative feedbacks. The infauna may show a steadier establishment of new functions and minor differentiation within them, thereby reducing the kind of interference that would impose significant diversity dependence. Alternatively, enhanced origination owing to abiotic factors such as continental flooding and greater provinciality [75–77], might promote the evolution of new functions, which themselves persist when the promoting conditions fade. Testing these scenarios would require determining whether excursions above the long-term diversity trend were mostly initiated by the evolution of entirely new functions; whether taxonomic diversification, by sheer numbers, itself promoted the evolution of new functions; or whether diversification reflected a proliferation of lineages by finer subdivision of existing functions [78]. Considering the enormous population sizes of many bivalve species, it seems unlikely that such subdivision of niches has reached the theoretical limit set by the smallest sustainable biomass within each species [79]. High-dimensional functional groups of genera (i.e. combinations of motility, tiering, attachment, and feeding) have not been comprehensively assigned to all genera at sufficient temporal resolution [23,73,74]; thus, we cannot yet fully analyse the evolutionary sequence of niche subdivision and the effects of niche packing on diversity dynamics [80].

(c) Coda

Diversity-dependence on macroevolutionary scales remains a difficult but engaging problem, and the stakes are high for determining proximate and ultimate causes given the environmental and climatic turmoil now challenging today's biodiversity [81]. Fossil data have long shown that diversification dynamics in response to episodes of major environmental and climatic change can yield accelerated rebounds in biodiversity following catastrophic losses during mass extinctions. Although these rebounds eventually slow down [3,67], diversity continues to rise, posing the fundamental question of how geologically short-term diversity-dependence within a biological group can be reconciled with its long-term diversity accumulation. This phenomenon is not fully understood, but it is now clearer that a complete theory must involve enhanced diversification at times of reduced diversity; suppressed diversification at times of

higher diversity; the asymmetry between origination and extinction; the ability of diversity to 'overshoot' the long-term trend; and the reasons for the long-term trend itself. Partitioning a major clade into two ecologically defined groups of potentially interacting lineages, we find diversity-dependence in just one, identifying a new set of testable hypotheses for the factors underlying the striking result that diversity-dependence can operate even as the clade and its two ecological groups continue to diversify.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data and code are uploaded as electronic supplementary material [82].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.F.: conceptualization, formal analysis, writing—original draft, writing—review and editing; S.M.E.: conceptualization, data curation, writing—original draft, writing—review and editing; D.J.: conceptualization, data curation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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