

PROCEEDINGS B

rspb.royalsocietypublishing.org

Research



Cite this article: Foote M, Cooper RA, Crampton JS, Sadler PM. 2018 Diversity-dependent evolutionary rates in early Palaeozoic zooplankton. *Proc. R. Soc. B* **285**: 20180122.
<http://dx.doi.org/10.1098/rspb.2018.0122>

Received: 16 January 2018

Accepted: 8 February 2018

Subject Category:

Palaeobiology

Subject Areas:

palaeontology, evolution

Keywords:

macroevolution, diversity-dependence, diversity dynamics, Graptoloidea, plankton evolution

Author for correspondence:

Michael Foote

e-mail: mfoote@uchicago.edu

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4007638>.

THE ROYAL SOCIETY
PUBLISHING

Diversity-dependent evolutionary rates in early Palaeozoic zooplankton

Michael Foote¹, Roger A. Cooper², James S. Crampton^{2,3} and Peter M. Sadler⁴

¹Department of the Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA

²Department of Paleontology, GNS Science, Lower Hutt 5040, New Zealand

³School of Geography, Environment and Earth Sciences, Victoria University of Wellington, Wellington 6140, New Zealand

⁴Department of Earth Sciences, University of California, Riverside, CA 92521, USA

MF, 0000-0003-3836-5980

The extent to which biological diversity affects rates of diversification is central to understanding macroevolutionary dynamics, yet no consensus has emerged on the importance of diversity-dependence of evolutionary rates. Here, we analyse the species-level fossil record of early Palaeozoic graptoloids, documented with high temporal resolution, to test directly whether rates of diversification were influenced by levels of standing diversity within this major clade of marine zooplankton. To circumvent the statistical regression-to-the-mean artefact, whereby higher- and lower-than-average values of diversity tend to be followed by negative and positive diversification rates, we construct a non-parametric, empirically scaled, diversity-independent null model by randomizing the observed diversification rates with respect to time. Comparing observed correlations between diversity and diversification rate to those expected from this diversity-independent model, we find evidence for negative diversity-dependence, accounting for up to 12% of the variance in diversification rate, with maximal correlation at a temporal lag of approximately 1 Myr. Diversity-dependence persists throughout the Ordovician and Silurian, despite a major increase in the strength and frequency of extinction and speciation pulses in the Silurian. By contrast to some previous work, we find that diversity-dependence affects rates of speciation and extinction nearly equally on average, although subtle differences emerge when we compare the Ordovician and Silurian.

1. Introduction

It is axiomatic and intuitive that the standing level of biodiversity within a clade at any time is a function of the long-term, integrated history of diversification rates preceding that time. Less obvious are the generality and strength of feedbacks whereby diversity itself influences rates of diversification [1–4], despite the fact that over 40 years have passed since palaeontologists first adapted population-biology models to probe the dynamics of diversification on geological time scales [5–7]. The hypothesis of negative diversity-dependence posits that, all else being equal, higher levels of diversity tend to suppress rates of diversification—a phenomenon which in turn is generally thought to reflect competition and other direct and indirect biotic interactions involving ecologically similar species—whereas lower diversity tends to enhance diversification rates because of relaxed competitive pressure and weaker interactions [2,6]. Models of positive diversity-dependence have also been discussed [8] but have received less scrutiny. Empirical tests for negative diversity-dependence have taken three principal forms: (i) evaluation of the branching structure and implied diversity history in phylogenetic trees of living species relative to predictions of alternative diversification models [2,9,10]; (ii) comparison between observed temporal trajectories of diversity from the fossil record and those predicted by diversification models [6,11–14], including models in which carrying capacity is environmentally determined [13]; and (iii) direct comparison between fossil diversity trajectories and

rates of diversification across a wide range of diversity changes, including rebounds from mass extinctions [11,12,15–18]. Here, we analyse the highly resolved, global fossil record of a major group of zooplankton, the graptoloids, and apply this third strategy to document the nature of species-level diversity dynamics in this clade.

It is important to distinguish between diversity-dependence and the existence of fixed or varying hard upper bounds on diversity. [4,8,11,17,19–21]. A negative relationship between diversity and diversification rate, for which we are testing, is evidence for diversity-dependence, but it need not imply that a clade is close to its ecological limits [4], although it is reasonable to suppose that the strength of diversity-dependence may increase as a clade approaches an ecological limit.

2. Material and methods

(a) Data

Data on stratigraphic ranges are sourced from a radioisotopically calibrated, global, temporal ordination of first and last appearances of 2041 expertly vetted species of graptoloid graptolites (including subspecies analysed at species rank) from 493 local stratigraphic sections spanning the entire history of the graptoloid clade, from approximately 491.1 to approximately 411.4 Ma. The ordination and calibration procedures are described in detail elsewhere [22–24]. The average spacing between resolvable temporal levels in this ordination is approximately 0.037 Myr. Considering only the span of time covered by this study (see below), the average spacing is approximately 0.030 Myr overall, approximately 0.034 Myr in the Ordovician, and approximately 0.026 Myr in the Silurian.

(b) Methods

The majority of our analyses rest on a tabulation of standing species diversity, D_t , at specified points in time separated evenly by $\Delta t = 0.25$ Myr. The number of species extant at each time point is the total whose stratigraphic ranges cross the time line, i.e. those with the first appearance before it and last appearance afterwards [25]. Consistent with our previous analyses [23], this tabulation implicitly requires that we omit 247 species whose first and last appearances are at exactly the same temporal level, as they have no measurable stratigraphic range. These species are scattered throughout the time series [22], and results are not sensitive to this protocol (see below). The net diversification rate per lineage-million-years (Lmy) during the interval between successive time points, r_t , is equal to $\ln(D_{t+1}/D_t)/\Delta t$. To avoid edge effects [25] near the ends of the time series, as well as excessive noise when diversity is extremely low, we have confined our analysis to the time period from 481 to 419 Ma, leaving a total of 1724 species surveyed over 248 0.25-Myr time intervals.

We use relatively short, equal-length intervals rather than conventional stratigraphic zones to take maximal advantage of temporal resolution in the data and to avoid well-known artefacts, whereby variable interval length may distort taxonomic rates of evolution [25,26], especially when taxonomic turnover is used to delineate intervals [26], as is the case with biozones. An interval-length variation would be especially problematic in the present case, as graptolite zones vary in length by over an order of magnitude, from approximately 0.1 Myr to nearly 4.0 Myr [27,28].

For analyses involving interval-specific speciation and extinction rates, λ_t and μ_t , respectively, we used the per-taxon rate estimates of [25]: $\lambda_t = \ln(D_{t+1}/D_{t,t+1})/\Delta t$ and $\mu_t = \ln(D_t/D_{t,t+1})/\Delta t$, where $D_{t,t+1}$ is the number of species extant at both successive time points, t and $t + 1$. Note that the two ways of calculating

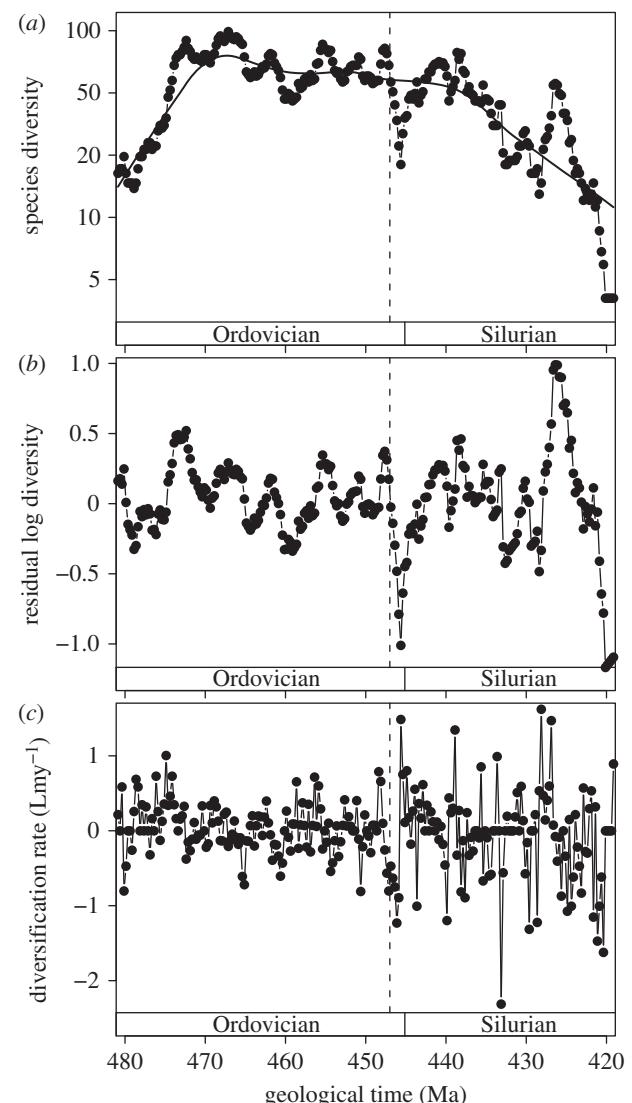


Figure 1. Diversity and diversification history of graptoloids. (a) Diversity at the start of 0.25-Myr intervals. LOWESS smoothing indicated by solid curve. (b) Residual log diversity, ε_t . (c) Net diversification rate. Vertical dashed line shows division of time series, at 447 Ma, into segments operationally referred to as Ordovician and Silurian herein [23].

net diversification rate, $r_t = \ln(D_{t+1}/D_t)/\Delta t$ and $r_t = \hat{\lambda}_t - \hat{\mu}_t$, are algebraically identical.

The long-term expansion and contraction of graptoloid species richness (figure 1a) provide prima facie evidence that, if a carrying capacity or diversity limit existed, it was not constant or was not reached for much of the clade's history. Therefore, fitting a simple logistic or other model [7] with a fixed carrying capacity would seem to make little sense. Recent work has proposed parametrizations of a time-varying carrying capacity [21,29], but the resulting models predict a smooth expansion and contraction in diversity that is evidently belied by the many 5–10-Myr excursions superimposed on the long-term expansion and contraction of graptoloid diversity. Moreover, the models make assumptions about the causes of changing carrying capacity that may not hold. We have therefore adopted a direct, statistical approach in which we ask, time interval by time interval, whether diversification rates are predicted by standing diversity. This approach requires that data be suitably detrended so that, in effect, we are asking about the possible influence of diversity anomalies, i.e. residuals in diversity above or below their long-term smoothed trajectory [17].

Because diversification is a multiplicative process, we expressed diversity as its natural logarithm (figure 1a). Using the

intrinsic lowess () function in R v. 3.3.0 [30], we detrended log diversity using a LOWESS regression with a smoothing span of 0.3, and we retained the residuals of this regression, ε_t , for further analysis (figure 1b). A span of 0.3 qualitatively captures the broad trends in graptoloid diversity (figure 1a), but our conclusions are not sensitive to this parameter choice (see below). Diversity and rates of speciation, extinction, and net diversification are given in the electronic supplementary material, table S1.

We want to ask whether higher residual diversity at the start of an interval corresponds with lower diversification rate during that interval or subsequent intervals, i.e. whether ε_t is negatively cross-correlated with r_t , r_{t+1} , etc. [15–17]. Though there is a slight downward trend in diversification rate, a LOWESS regression accounts for less than 4% of the variance in rate, compared with approximately 75% of the variance in diversity. Thus, the correlation between raw diversity and diversity residuals is nearly perfect (product-moment correlation: 0.991), and detrending would have little effect on our analysis. For simplicity, we therefore did not detrend diversification rate, but results are not sensitive to this decision (electronic supplementary material, figure S2C).

For specified temporal lags, we calculated the Spearman rank-order correlation between residual diversity and diversification rate, ε_t and $r_{t+\text{lag}}$, where the lag is expressed in terms of the number of intervals. (Note that the lagged correlation between ε_t and $r_{t+\text{lag}}$ involves only the diversification rate in the single 0.25 Myr interval at $t + \text{lag}$, not the net diversification rate from interval t through to interval $t + \text{lag}$.) We used this measure of correlation to allow detection of a monotonic but potentially nonlinear relationship and to avoid undue influence of outliers. A lag of zero compares residual diversity at the start of an interval with diversification rate within that same interval. A significant negative correlation, exceeding the expectations of an appropriate null model (see below), is taken as evidence for diversity-dependence of diversification rate.

We chose the comparison between observed correlations and a null model, rather than testing for cross-correlation between observed first differences, for two reasons: (i) differences focus on short-term fluctuations in the time series, but we are also interested in the possibility of more persistent features, for example, if several successive time intervals have higher than average diversity and lower than average diversification rate; and (ii) the nature of our time series generally forces first differences to have a strong, negative correlation. Recall that the diversification rate, r_t , is equal to $D_{t+1} - D_t$ with diversity measured on a log scale. In other words, r_t is exactly equal to the first difference of diversity indexed to time interval t , $(\Delta D)_t$. Thus, the correlation between the first differences of diversity and the first differences of diversification rate reduces to the correlation between r_t and $(r_{t+1} - r_t)$, which is of the general form a versus $(b-a)$. The expected product-moment correlation in such a case is approximately equal to -0.71 (i.e. $-\sqrt{0.5}$) if a and b are independent random variables with equal variance ([31], p. 650). In the present case, although r_t and r_{t+1} of course have nearly identical variances, they are not independent (see below), and the expected correlation between $(\Delta D)_t$ and $(\Delta r)_t$ is therefore reduced somewhat. It is nonetheless rather strong at -0.62 .

Discussion of bias in the detection of diversity-dependence has largely focused on difficulties with drawing indirect inferences from evolutionary trees of living species [3,4,9,10]. In the case of direct tests for cross-correlation, a potential bias arises from regression to the mean [15,16,32,33]. In the present context, there will be a tendency for higher-than-average values of diversity to be immediately followed by decreases (i.e. negative diversification rates), and for lower-than-average values to be followed by increases, inducing a correlation between diversity and diversification rate at zero lag. In the absence of true diversity-dependence, the expected, induced correlation is stronger when

successive diversity values are less similar to each other [32], i.e. when diversity is more volatile, as well as for time series of diversity that are shorter and those that end closer to their starting value (electronic supplementary material, figure S10).

To avoid this artefact, we have therefore developed a non-parametric null expectation for the cross-correlation between diversity and diversification rate by generating an ensemble of empirically scaled, synthetic diversity histories in which, by construction, diversification rate is completely unaffected by diversity (electronic supplementary material, R code). Each simulated history results from a randomization of the observed net diversification rates. It begins at the observed, initial diversity level, and each successive diversity level, expressed as its natural logarithm, is equal to the previous diversity level plus a diversification rate chosen randomly without replacement from the observed values. In this way, the sum of diversification rates is conserved, and the beginning and ending diversity levels of the entire time series match those in the observed data. We also constrained each simulation to maintain a diversity of at least one species at all times; simulations that fell below that threshold were discarded. An ensemble of 10 000 successful simulated histories was generated. Each was detrended and analysed exactly as for the observed data, yielding a cross-correlation between residual diversity and diversification rate. For graphical purposes, the resulting distribution of correlations was smoothed with a kernel density estimator using the intrinsic density () function in R [30] with default options. Also indicated in the figures are the tails corresponding to the extreme 5% of the simulated correlations, for one-tailed comparisons against the directional hypothesis of negative diversity dependence.

Net diversification rate can be affected via the speciation rate, the extinction rate, or both. We, therefore, developed a randomization procedure for assessing diversity-dependence in speciation and extinction rates, which shuffles net diversification rates but keeps track of the coupled speciation and extinction components. Because of the large increase in speciation and extinction rates at about 447 Ma [22,23], these rates were investigated separately for the time spans 481–447 Ma and 447–419 Ma, and all steps in the analysis, including the detrending of data and the randomization, were confined to the intervals within these time spans. Speciation and extinction rates are significantly cross-correlated (for 481–447 Ma, $r = 0.37$, $p < 0.001$; for 447–419 Ma, $r = 0.35$, $p < 0.001$). We, therefore, calculated partial rank-order correlations between speciation and residual diversity with extinction held constant, and between extinction and residual diversity with speciation held constant.

3. Results

At zero lag (i.e. ε_t versus r_t), there is a negative correlation between residual diversity and diversification rate, but it is well within the null distribution (figure 2). The correlation becomes stronger and deviates further from the null expectation as the lag increases to 1 Myr (i.e. ε_t versus r_{t+4}), then it drops into the background after a lag of about 1.5 Myr. Consistent with the hypothesis of negative diversity-dependence, observed diversification rates are predicted by residual diversity to an extent that is incompatible with a diversity-independent model. A peak correlation at a lag of four time intervals would not be expected from regression to the mean, nor is it likely to be an artefact of incomplete sampling (electronic supplementary material, figures S6–S8). That negative correlations in the null model persist past zero lag is a combination of regression to the mean and the autocorrelation of diversity. For example, D_t and r_t will be correlated by regression

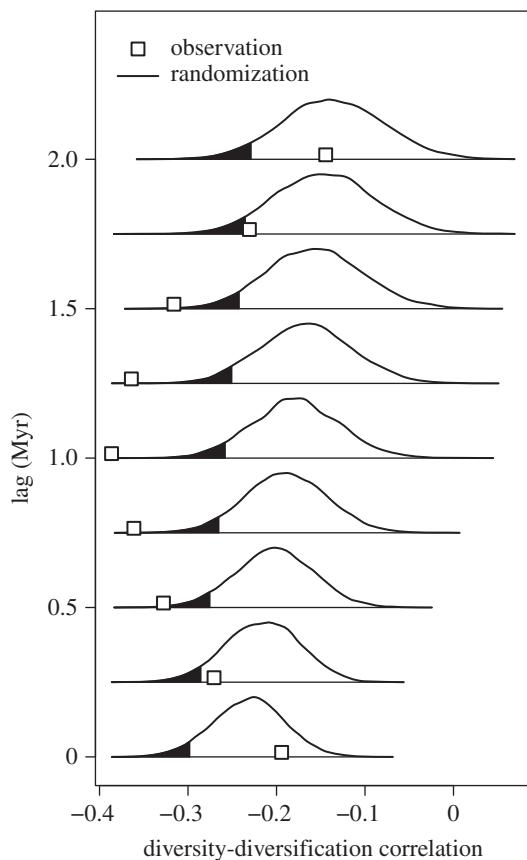


Figure 2. Observed rank-order correlation between diversity and diversification rate compared with a diversity-independent diversification model based on randomizing the observed diversification rates. In this and subsequent figures, probability distribution of synthetic diversity-diversification correlations is based on 10 000 realizations; vertical scale arbitrary. Shaded tails correspond to the extreme 5% of the simulated correlations, for one-tailed comparisons against the directional hypothesis of negative diversity dependence. Observed correlations at 0.5–1.5 Myr fall outside the null distribution with a *p*-value of 0.05 or lower.

to the mean. Because D_{t-1} and D_t are also correlated, D_{t-1} and r_t will be correlated as well, albeit more weakly than D_t and r_t .

At a lag of 1 Myr, some 15% of the rank-order variance in diversification rate is potentially explained by diversity-dependence (figure 3). Given that cross-correlations in the randomized time series have a magnitude of approximately 0.18 on average at this lag, accounting for approximately 3% of the variance, we conservatively estimate that the proportion of variance that can be attributed to diversity-dependence is closer to 12%. Our results are robust to a number of alternative protocols, including, among others: ignoring the magnitude of residual diversity and diversification rate and simply coding them as binary variables, negative versus positive; omitting intervals with zero net diversification; analysing diversity on an arithmetic rather than logarithmic scale; using a looser or tighter LOWESS smoothing to detrend the diversity data; omitting species that may be relatively poorly sampled; and binning data into longer time intervals (electronic supplementary material, figures S1–S4).

Note that the observed cross-correlations between diversity and diversification rate at different lags are not independent of each other, because diversity itself is autocorrelated. If r_t depends only on $D_{t-\text{lag}}$, we may observe a correlation, for example, between r_t and $D_{t-\text{lag}+1}$, reflecting the correlation between $D_{t-\text{lag}}$ and $D_{t-\text{lag}+1}$ (electronic supplementary material, figure S8).

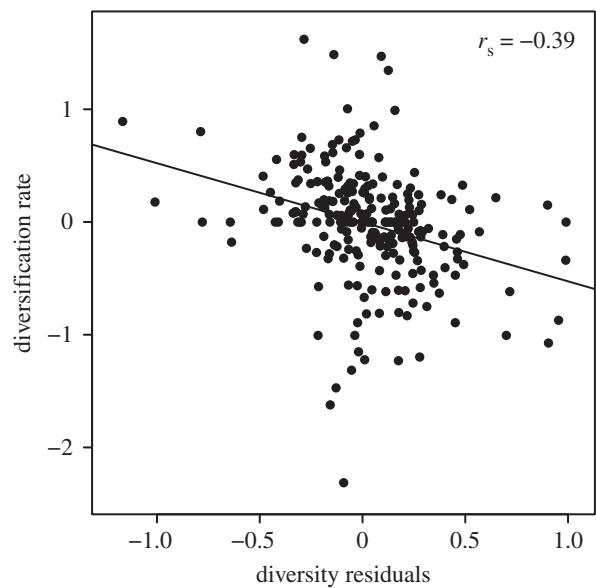


Figure 3. Diversity residuals versus diversification rate at a lag of four time intervals (1.0 Myr). Points depict each of 248 0.25-Myr time intervals.

In light of the late Ordovician change in diversity dynamics, leading to an approximate doubling of speciation and extinction rates [22,23] and more pronounced fluctuations in net diversification rate (figure 1), we tested whether the two broad time spans, 481–447 Ma and 447–419 Ma, are characterized by different strengths of diversity-dependence (figure 4). Diversity-dependence of net diversification is comparably strong between the two time spans, but in the younger interval it is somewhat less persistent, showing a peak at a lag of approximately 0.5 Myr and dropping within the null range after approximately 1 Myr. This difference in persistence may be related to a difference in average species duration, which is about half as long in the Silurian as in the Ordovician [23].

Turning to the component speciation and extinction rates that determine net diversification, we see that extinction is impacted similarly in the Ordovician and Silurian, with peak effect at a lag of 0.25–0.5 Myr. Speciation rate is impacted in the Ordovician (over a lag interval of 0.75 to ≥ 2 Myr) more strongly than in the Silurian. This result suggests that in the Ordovician, when greenhouse climatic conditions dominated [23], the dependence of diversification on diversity may have operated initially through extinction and, with a longer lag interval, also through speciation. But in the Silurian icehouse, where background extinction is repeatedly punctuated by sharp spikes linked to environmental disturbances [22,23], it operated mainly through extinction rate. Thus, external perturbations and internal dynamics are not mutually exclusive processes.

Some previous work has assumed [34] or detected different strengths of diversity-dependence in the origination and extinction components of net diversification. In Cenozoic mammals, rates of speciation were found to be diversity-dependent, but not so for rates of extinction [12]. Using somewhat different methods, two analyses of Phanerozoic marine animals at the genus level found support for stronger diversity-dependence of extinction in one case [15] and origination in the other [17]. In contrast to these studies (the last two of which were carried out at coarser temporal resolution than the mammal analysis or the present one), our results suggest that speciation and extinction in graptoloids responded to diversity with comparable strength, on average,

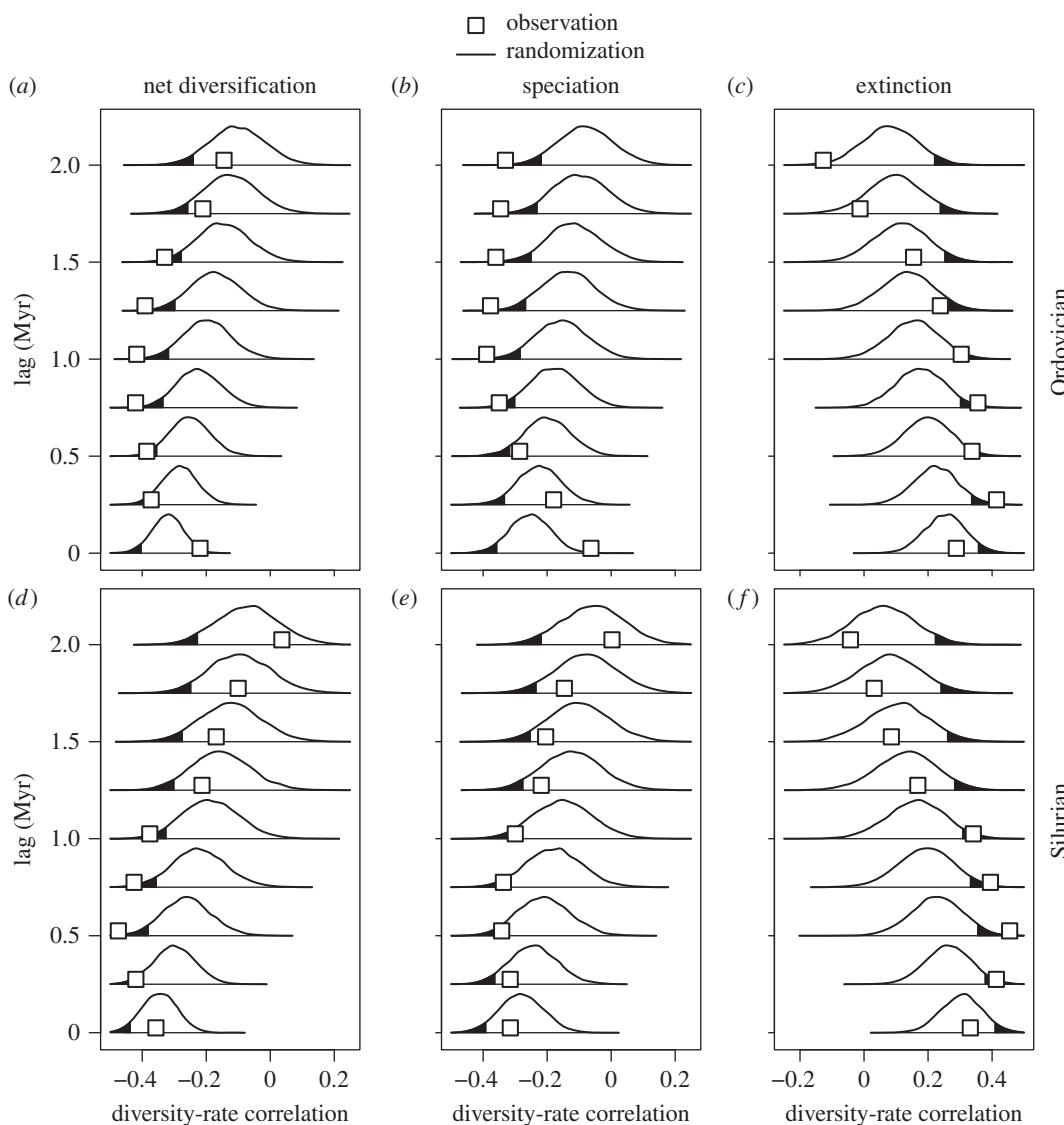


Figure 4. Test for diversity-dependence of diversification, speciation, and extinction rates for segments of graptoloid history corresponding to lower and higher average rates. Lower and higher rates pertain to 481–447 Ma and 447–419 Ma, respectively. Format as in figure 2. (a) Net diversification, 481–447 Ma; (b) speciation, 481–447 Ma; (c) extinction, 481–447 Ma; (d) net diversification, 447–419 Ma; (e) speciation, 447–419 Ma; (f) extinction 447–419 Ma. Peak correlation in net diversification occurs at shorter lags in the Silurian.

although, as already noted, we detect a somewhat weaker effect on speciation than on extinction during the Silurian.

Observed diversification rate is significantly and positively autocorrelated ($r = 0.218, p < 0.001$) at a lag of one interval, i.e. 0.25 Myr, but not at a lag of two intervals ($r = 0.110, p = 0.09$). It is reasonable to ask whether this aspect of the temporal structure of diversification rate, which need not reflect diversity-dependence, could influence the perception of diversity-dependence. We therefore constructed an alternative null model that also constrains diversification rates to be independent of diversity, but additionally incorporates empirically scaled autocorrelation in the diversification rate. Fitting an AR1 model, $r_t = b_0 + b_1 r_{t-1}$, to the observed diversification rates yields the following: $b_0 = -0.0163$ and $b_1 = 0.219$ ($p < 0.001$), with residual variance, s_e^2 , equal to 0.241. The simulation begins at the observed starting diversity and picks an initial diversification rate at random from the observed distribution. Each subsequent diversification rate is equal to b_1 times the previous one, plus the intercept b_0 , plus a zero-centred normal deviate with variance equal to s_e^2 . Again, diversity histories dropping below one species were rejected, an ensemble of 10 000 simulations was produced, and detrending and analysis

were carried out for each simulation just as for the observed data. Taking the autocorrelation of diversification rate into account in developing the null expectation affects the details of the null distribution. But the principal result, a peak in observed diversity-dependence at approximately 1 Myr, both in absolute terms and relative to the null expectation, persists (electronic supplementary material, figure S5).

4. Discussion and conclusion

We have tested for diversity-dependence in the graptoloids by analysing the correlation between evolutionary rates and diversity anomalies relative to a long-term trajectory. Whether or not this trajectory tracks, at least in part, a history of carrying capacity, an obvious and unanswered question remains: why does it take on the particular shape it has? An initial expansion and final decline are generally to be expected in an extinct clade that is diversifying stochastically [5,18,35], a fact that is explicitly taken into account in our null model. Beyond that, the additional factors potentially responsible, which are outside the scope of this paper, include obvious candidates such as

productivity and nutrient flux; extent of habitable space and suitable environmental conditions; and interaction with other clades [6,11,18,36–39].

Though we have presented evidence for significant diversity-dependence of evolutionary rates, these dynamics account for a minority of rate variation. Oceanographic and climatic change have also strongly influenced speciation and extinction rates in graptoloids [22,23]. In this way, our findings are similar to those for Cenozoic planktonic foraminifera, in which climatic variation contributes substantially to diversity history [14], although the effect of environmental change on graptoloid history appears to be concentrated in discrete events rather than reflecting a smooth continuum [22,23].

A prominent recent essay [4] argues against strict bounds on diversity but nonetheless acknowledges the evidence for diversity-dependence. By concluding that diversification in graptoloids was diversity-dependent, we do not claim that the clade ever reached or even approached its maximal, theoretically possible species richness. As we stated at the outset, it is important to distinguish between diversity-dependence of evolutionary rates and the existence of fixed ecological limits. Consider the history of bivalve molluscs over the past 500 Myr. Diversity steadily increased over this time period, but setbacks at two major mass extinctions were followed by accelerated diversification, putting the clade back on the same upward trajectory it had been following [11]—whether that trajectory reflects unfettered diversification or an expanding carrying capacity. Several other studies have also supported diversity-dependence without demonstrating a clear upper bound on diversity [13–17].

Although graptoloids are ecologically differentiated [40,41,42], they share sufficient ecological similarity that we should not be surprised to detect some degree of diversity-dependence. The mechanisms for diversity-dependence, however, remain an open question. We are certainly not suggesting direct zooid-to-zooid combat—nature red in stipe and nema. Beyond direct biotic interactions, increasing the number of species in an ecosystem can indirectly suppress speciation and/or enhance extinction by reducing population sizes and geographical ranges and enhancing incumbency effects [6]. Although we can separate the speciation and extinction signals (figure 4), we may in fact be seeing two manifestations of the same process. The potential effects of diversity on speciation and extinction are linked by the fact that a reduction in the rate of successful speciation may be the expression of an increase in the extinction rate of incipient species [6,43].

Our results provide important constraints on the characteristic response times inherent in the dynamics of diversification. When we consider net diversification rate over the entire time series, the effects of diversity are detectable on several time scales, peaking at a lag of approximately 1 Myr. One possible reason for this temporal lag is that speciation and extinction are not instantaneous processes. The lag of approximately 1 Myr, for example, roughly agrees with some estimates of the time needed for speciation to be completed through the establishment of secondary sympatry in the face of barriers to dispersal [44]. However, this reason seems unlikely in an oceanic pelagic environment, where barriers have been thought to play a minor role [45] (but cf. [46] and references therein). Perhaps a more likely mechanism is that species' first and last appearances are diachronous, i.e. species take time to spread throughout their geographical range, at least partly reflecting habitat availability [47], and to contract from their

maximal range [48–50]. Bearing in mind that our data record global first and last appearances, the global first appearance of a species does not coincide with its first opportunity to interact with other species at local and regional scales, and its global extinction follows a period of local and regional extirpation. To consider a simple scenario, an increase in species diversity can impact local populations only after expansion and dispersal of the new species. Similarly, the ultimate extinction of existing species can occur considerably after they initially experience local competition with new species, if the older species are gradually 'pushed into a corner'.

Because we are working with a calibrated, global event sequence and the timing of local events is not as well calibrated, we cannot test directly and rigorously for diachroneity. Diachroneity, if it were ultimately shown to be extensive in graptoloids, could reflect stratigraphic as well as biological causes. In particular, if species did in fact instantly spread throughout their full geographical range but stratigraphic sections in different places covered only part of each species' true duration, species would falsely appear to expand gradually throughout their geographical ranges. However, we would not expect such a source of diachroneity to yield a lag in diversity-dependence, because, under this scenario, species would interact with each other throughout their entire time of coexistence, i.e. the time scale of diversity-dependence would be set by the global first and last appearances.

Many demonstrations of diversity-dependence in palaeontological data have worked at the genus level [11,15–17]. Although the foregoing discussion implicitly treats nominal species as 'good' biological species, our test for diversity-dependence does not assume any particular taxonomic level. Even if what we call graptoloid species would in fact be ranked as genera were they alive for study today, what is important is that the rate of change in the number of these units of accounting depended on how many coexisted. Moreover, the potential contribution of diachroneity to the lag in diversity-dependence would still apply, as genera tend to expand and contract over their lifetimes just as species do [35,49]. It is also possible that graptoloid species are oversplit temporally, in light of their use in biostratigraphy. Yet our main results hold if we concatenate successive congeners into longer-lived evolutionary lineages (electronic supplementary material, figure S2).

In summary, by circumventing an important methodological bias and using data documented with exceptionally high temporal resolution, we have shown that evolutionary rates in this major clade of early Palaeozoic zooplankton depend significantly on standing diversity, thus supporting the hypothesis of negative diversity-dependence, and, in turn, a role for biotic interactions in graptoloid evolution [23].

Data accessibility. The data and code supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. R.A.C. and P.M.S. developed the stratigraphic-range data. R.A.C., J.S.C. and M.F. conceived the study. M.F. designed and carried out the analyses. All authors contributed to the interpretation and writing and gave final approval for publication.

Competing interests. We have no competing interests.

Funding. This work was supported by the University of Chicago, GNS Science and Victoria University of Wellington.

Acknowledgements. We thank P. Boehnke, T. H. G. Ezard, G. Hunt, D. Jablonski, F. A. Macdonald, T. D. Price, G. J. Slater, and P. D. Smits for advice and discussion; S. M. Holland, D. Jablonski, and S. E. Peters for comments on the manuscript; D. W. Bapst and two anonymous referees for thoughtful reviews; and J. J. Sepkoski Jr for inspiration.

References

1. Stanley SM. 2007 An analysis of the history of marine animal diversity. *Paleobiology* **33**(Suppl. 1), 1–55. (doi:10.1666/06020.1)
2. Rabosky DL. 2013 Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **44**, 481–502. (doi:10.1146/annurev-ecolsys-110512-135800)
3. Rabosky DL, Hurlbert AH. 2015 Species richness at continental scales is dominated by ecological limits. *Am. Nat.* **185**, 572–583. (doi:10.1086/680850)
4. Harmon LJ, Harrison S. 2015 Species diversity is dynamic and unbounded at local and continental scales. *Am. Nat.* **185**, 584–593. (doi:10.1086/680859)
5. Raup DM, Gould SJ, Schopf TJM, Simberloff DS. 1973 Stochastic models of phylogeny and the evolution of diversity. *J. Geol.* **81**, 525–542. (doi:10.1086/627905)
6. Sepkoski Jr JJ. 1978 A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology* **4**, 223–251. (doi:10.1017/S0094837300005972)
7. Sepkoski Jr JJ. 1984 A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* **10**, 246–267. (doi:10.1017/S0094837300008186)
8. Erwin DH. 2007 Increasing returns, ecological feedback and the Early Triassic recovery. *Palaeoworld* **16**, 9–15. (doi:10.1016/j.palwor.2007.05.013)
9. Etienne RS, Pigot AL, Phillippe AB. 2016 How reliably can we infer diversity-dependent diversification from phylogenies? *Methods Ecol. Evol.* **7**, 1092–1099. (doi:10.1111/2041-210X.12565)
10. Quental TB, Marshall CR. 2009 Extinction during evolutionary radiations: reconciling the fossil record with molecular phylogenies. *Evolution* **63**, 3158–3167. (doi:10.1111/j.1558-5646.2009.00794.x)
11. Miller AI, Sepkoski Jr JJ. 1988 Modeling bivalve diversification: the effect of interaction on a macroevolutionary system. *Paleobiology* **14**, 364–369. (doi:10.1017/S0094837300012100)
12. Alroy J. 1996 Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **127**, 285–311. (doi:10.1016/S0031-0182(96)00100-9)
13. Ezard THG, Purvis A. 2016 Environmental changes define ecological limits to species richness and reveal the mode of macroevolutionary competition. *Ecol. Lett.* **19**, 899–906. (doi:10.1111/ele.12626)
14. Ezard THG, Aze T, Pearson PN, Purvis A. 2011 Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* **332**, 349–351. (doi:10.1126/science.1203060)
15. Alroy J. 2008 Dynamics of origination and extinction in the marine fossil record. *Proc. Natl. Acad. Sci. USA* **105**(Suppl. 1), 11 536–11 542. (doi:10.1073/pnas.0802597105)
16. Alroy J. 2010 Geographical, environmental, and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* **53**, 1211–1235. (doi:10.1111/j.1475-4983.2010.01011.x)
17. Foote M. 2010 The geological history of biodiversity. In *Evolution since Darwin: the first 150 years* (eds MA Bell, DJ Futuyma, WF Eanes, JS Levinton), pp. 479–510. Sunderland, MA: Sinauer Associates.
18. Quental TB, Marshall CR. 2013 How the Red Queen drives terrestrial mammals to extinction. *Science* **341**, 290–292. (doi:10.1126/science.1239431)
19. Kitchell JA, Carr TJ. 1985 Nonequilibrium model of diversification: faunal turnover dynamics. In *Phanerozoic diversity patterns: profiles in macroevolution* (ed. JW Valentine), pp. 277–309. Princeton, NJ: Princeton University Press.
20. Cornell HV. 2013 Is regional species diversity bounded or unbounded? *Biol. Rev.* **88**, 140–165. (doi:10.1111/j.1469-185X.2012.00245.x)
21. Marshall CR, Quental TB. 2016 The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities. *Phil. Trans. R. Soc. B* **371**, 20150217. (doi:10.1098/rstb.2015.0217)
22. Cooper RA, Sadler PM, Munnecke A, Crampton JS. 2014 Graptoloid evolutionary rates track Ordovician–Silurian global climate change. *Geol. Mag.* **151**, 349–364. (doi:10.1017/S0016756813000198)
23. Crampton JS, Cooper RA, Sadler PM, Foote M. 2016 Greenhouse–icehouse transition in the Late Ordovician marks a step change in extinction regime in the marine plankton. *Proc. Natl. Acad. Sci. USA* **113**, 1498–1502. (doi:10.1073/pnas.1519092113)
24. Sadler PM, Cooper RA, Melchin M. 2009 High-resolution, early Paleozoic (Ordovician–Silurian) time scales. *Geol. Soc. Am. Bull.* **121**, 887–906. (doi:10.1130/B26357.1)
25. Foote M. 2000 Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* **26**(Suppl. 1), 74–102. (doi:10.1666/0094-8373(2000)26[74:OECOT]2.0:CO;2)
26. Foote M. 1994 Temporal variation in extinction risk and temporal scaling of extinction metrics. *Paleobiology* **20**, 424–444. (doi:10.1017/S0094837300012914)
27. Cooper RA, Sadler PM, Hammer O, Gradstein FM. 2012 The Ordovician period. In *A geologic time scale 2012* (eds FM Gradstein, JG Ogg, MD Schmitz, GM Ogg), pp. 489–523. Amsterdam, The Netherlands: Elsevier.
28. Melchin MJ, Sadler PM, Cramer BD, Cooper RA, Gradstein FM, Hammer O. 2012 The Silurian period. In *A geologic time scale 2012* (eds FM Gradstein, JG Ogg, MD Schmitz, GM Ogg), pp. 525–558. Amsterdam, The Netherlands: Elsevier.
29. Lim JY, Marshall CR. 2017 The true tempo of evolutionary radiation and decline revealed on the Hawaiian archipelago. *Nature* **543**, 710–713. (doi:10.1038/nature21675)
30. R Core Team. 2016 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
31. Sokal RR, Rohlf FJ. 1981 *Biometry*, 2nd edn. New York, NY: Freeman.
32. Kelly C, Price TD. 2005 Correcting for regression to the mean in behavior and ecology. *Am. Nat.* **166**, 700–707. (doi:10.1086/497402)
33. Freckleton RP, Watkinson AR, Green RE, Sutherland WJ. 2006 Census error and the detection of density dependence. *J. Anim. Ecol.* **75**, 837–851. (doi:10.1111/j.1365-2656.2006.01121.x)
34. Walker TD, Valentine JW. 1984 Equilibrium models of evolutionary species diversity and the number of empty niches. *Am. Nat.* **124**, 887–899. (doi:10.1086/284322)
35. Foote M. 2007 Symmetric waxing and waning of marine invertebrate genera. *Paleobiology* **33**, 517–529. (doi:10.1666/06084.1)
36. Sepkoski Jr JJ. 1976 Species diversity in the Phanerozoic: species-area effects. *Paleobiology* **2**, 298–303. (doi:10.1017/S0094837300004930)
37. Bambach RK. 1993 Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* **19**, 372–397. (doi:10.1017/S009483730000336)
38. Vermeij GJ. 1995 Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* **21**, 125–152. (doi:10.1017/S0094837300013178)
39. Hannisdal B, Peters SE. 2011 Phanerozoic Earth system evolution and marine biodiversity. *Science* **334**, 1121–1124. (doi:10.1126/science.1210695)
40. Cooper RA, Fortey RA, Lindholm K. 1991 Latitudinal and depth zonation of early Ordovician graptolites. *Lethaia* **24**, 199–218. (doi:10.1111/j.1502-3931.1991.tb01468.x)
41. Underwood CJ. 1993 The position of graptolites within Lower Palaeozoic planktic ecosystems. *Lethaia* **26**, 189–202. (doi:10.1111/j.1502-3931.1993.tb01517.x)
42. Sheets HD, Mitchell CE, Melchin MJ, Loxton J, Štöck J, Carlucci KL, Hawkins AD. 2016 Graptolite community responses to global climate change and the late Ordovician mass extinction. *Proc. Natl. Acad. Sci. USA* **113**, 8380–8385.
43. Allmon WD. 1992 A causal analysis of stages in allopatric speciation. *Oxford Surv. Evol. Biol.* **8**, 219–257.
44. Weir JT, Price TD. 2011 Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *Am. Nat.* **177**, 462–469. (doi:10.1086/658910)
45. Norris RD. 2000 Pelagic species diversity, biogeography, and evolution. *Paleobiology*

- 26(Suppl. 1), 236–258. (doi:10.1666/0094-8373(2000)26[236:PSDBAE]2.0.CO;2)
46. Mousing EA, Richardson K, Bendtsen J, Cetinić I, Perry MJ. 2016 Evidence of small-scale spatial structuring of phytoplankton alpha- and beta-diversity in the open ocean. *J. Ecol.* **104**, 1682–1695. (doi:10.1111/1365-2745.12634)
47. Foote M. 2014 Environmental controls on geographic range size in marine animal genera. *Paleobiology* **40**, 440–458. (doi:10.1666/13056)
48. Liow LH, Stenseth NC. 2007 The rise and fall of species: implications for macroevolutionary and macroecological studies. *Proc. R. Soc. B* **274**, 2745–2752. (doi:10.1098/rspb.2007.1006)
49. Foote M, Crampton JS, Beu AG, Marshall BA, Cooper RA, Maxwell PA, Matcham I. 2007 Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science* **318**, 1131–1134. (doi:10.1126/science.1146303)
50. Žliobaitė I, Fortelius M, Stenseth NC. 2017 Reconciling taxon senescence with the Red Queen's hypothesis. *Nature* **552**, 92–95. (doi:10.1038/nature24656)