

**Electronic supplementary material for:**  
**Ecological structure of diversity-dependent diversification in Phanerozoic marine bivalves**

Michael Foote<sup>1\*</sup>, Stewart M. Edie<sup>2</sup>, David Jablonski<sup>1</sup>

<sup>1</sup>Department of the Geophysical Sciences, University of Chicago, Chicago IL 60637, USA.

<sup>2</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA.

\*Corresponding author. Email: mfoote@uchicago.edu

This electronic supplement includes supplementary text, three supplementary figures, four supplementary tables, seven supplementary references, and R code.

**Supplementary text: materials and methods**

The times of first and last appearance of 3365 marine bivalve genera (2098 infaunal and 1267 epifaunal) were placed within 118 stratigraphic intervals, mainly corresponding to international stages and substages [38–39]. Because of the legacy nature of the data [36], however, some stratigraphic intervals are no longer widely used, particularly in parts of the Ordovician System (table S1). All stratigraphic range endpoints are nonetheless internally consistent. Our operational time scale reflects a compromise between temporal resolution and inclusion of genera; higher resolution means that fewer genera can be used. We also sought to minimize variation in length among time intervals. 406 genera with moderate resolution in their first or last appearance are extended to their maximal reasonable range; for example, a Maastrichtian first appearance is treated as Lower Maastrichtian, and a Tithonian last appearance is treated as Upper Tithonian. Of these, 264 are infaunal and 142 epifaunal.

These data differ from those in the Paleobiology Database (paleobiodb.org) in a key way. The Paleobiology Database consists of fossil collections that may be incorporated haphazardly or systematically based on contributor interest. Thus, a genus will ultimately be sampled multiple times throughout its stratigraphic range—which enables a broad spectrum of important paleontological studies—but there is generally no specific effort to find oldest or youngest occurrences of a given genus. By contrast, an overriding goal in the construction of the data set we use here is to identify these oldest and youngest occurrences, based on published literature, museum collections, and taxonomic and stratigraphic standardization. It is these first and last appearances that are essential in estimating diversity and evolutionary rates using the methodology we lay out below.

Genera were assigned to infaunal and epifaunal categories by reference to published observations on living species and extinct relatives, as well as morphological traits such as the presence or absence of scars on the shell indicating cementation to hard substrate as adults, and embayments in the shell indicating the presence of byssal threads as adults [21–22,24–26]. Ordinal assignments used to assess the distribution of life modes among higher taxa were based mainly

on [20,82–84]. We took a conservative approach, listing ordinal status as uncertain in ambiguous cases.

We use the standard “boundary-crosser” approach to estimating richness and taxonomic rates [40–41] (figures 1, S1). Denoting the number of genera extant at the beginning of an interval as  $N_b$ , the number extant at the end as  $N_t$ , and the number extant at both the beginning and the end as  $N_{bt}$ , we estimate the per-capita origination rate per genus per interval as  $\ln(N_t/N_b)$  and the extinction rate per genus per interval as  $\ln(N_b/N_{bt})$ . The net diversification rate per genus per interval is then  $\ln(N_t/N_b)$ , which is equivalent to the difference between origination rate and extinction rate. Note that  $N_b$  and  $N_t$  are measures of instantaneous standing richness, not richness accumulated over a time interval.

We ask whether richness at the beginning of a time interval ( $N_b$ ) is correlated with rates in the ensuing interval. Use of  $N_b$  allows a temporally more immediate comparison between diversity and rates than would be achieved with accumulated diversity in the preceding time interval, as in [55]. Given the multiplicative nature of diversification, we express diversity as  $D = \ln(N_b)$ . Some previous studies have been based on models with a fixed carrying capacity, whether for one clade [52] or a number of clades in a multi-phase system [2,4]. In general, it is not necessary to assume such a model [7,51,53]. In the case of bivalves, such a model would be especially problematic in light of their roughly exponential diversification history [3] (figure 1). We therefore adopt a previous approach that does not assume a particular diversification model [6–7,51]. We detrend the time series of diversity and taxonomic rates by calculating a LOWESS regression through each time series, using a smoothing span of 0.5, and then analyse the residuals. This approach in effect asks whether times of higher or lower diversity compared to the trend line are correlated with higher or lower taxonomic rates. The hypothesis of diversity dependence predicts a negative correlation between diversity residuals and diversification-rate residuals. To avoid assumptions about linear versus nonlinear relationships between diversity and rates, we use the Spearman rank-order correlation coefficient,  $r_s$  (figures 2, S2).

Regression to the mean may induce a negative correlation between diversity and diversification rates even if diversification is truly independent of diversity [54–55]. We therefore adopt a previously developed randomization procedure to test whether an observed correlation exceeds the expectation of regression to the mean [6–7]. Coupled origination and extinction rates are randomized with respect to time, producing a synthetic diversity history that by its very nature is diversity-independent. The natural logarithm of richness at the start of each interval is simply the sum of all preceding diversification rates (scaled to an arbitrary starting richness, which has no bearing on the test for diversity dependence). The resulting time series are detrended just as the observed ones, and the correlations between residuals are calculated. This randomization is repeated 10,000 times to produce a frequency distribution of correlations expected without diversity dependence. The observed correlations are then compared to this distribution to assess the probability that they could have resulted from a diversity-independent process (figures 2, S2; table 1).

As stated in the main text, our rate and diversity estimates assume that observed first and last appearances are good proxies for true times of origination and extinction. To assess completeness, we modify a prior approach [43–44] to model the expected frequency distribution

of stratigraphic ranges resulting from a distribution of true durations and a per-genus, per-interval sampling probability.

Let  $\lambda$  and  $\mu$  be the per-interval *species-level* rates of origination and extinction. Then the probability that a genus will have become extinct at or before the passing of  $T$  time intervals is given by

$$P_{0,T} = \frac{\lambda T}{1+\lambda T} \text{ if } \lambda = \mu,$$

and

$$P_{0,T} = \frac{\mu(e^{(\lambda-\mu)T}-1)}{\lambda e^{(\lambda-\mu)T}-\mu} \text{ if } \lambda \neq \mu$$

([45]: Eqs. A11, A13).

This last expression can also be stated as

$$P_{0,T} = 1 - \frac{1-a}{1-ae^{-bT}},$$

where  $a = \mu/\lambda$  and  $b = \lambda - \mu$  ([46]: Eq. 2). The latter formulation proves convenient for numerical optimization, because it easily allows realistic constraints on parameter combinations. To convert from  $(a,b)$  to  $(\lambda,\mu)$ ,  $\lambda = \frac{-b}{a-1}$  and  $\mu = \frac{-b}{1-1/a}$ . Analyses of generic survivorship often yield estimates of  $\lambda$  that are less than  $\mu$  [47,85–87]. This result reflects the fact that  $\lambda$  gives the rate of speciation within a genus; speciation events giving rise to new genera are (implicitly) excluded [45,47].

The probability of a true duration  $T$  is given by

$$P_{D,T} = P_{0,T} - P_{0,T-1}.$$

Let  $R$  be the per-genus, per-interval sampling probability. Then the probability that a genus with true duration  $T$  will have an observed stratigraphic range  $t$ , denoted  $P_{t|T}$  is equal to

$$(1 - R)^T \text{ if } t = 0,$$

$$RT(1 - R)^{T-1} \text{ if } t = 1,$$

and

$$R^2(T - t + 1)(1 - R)^{T-t} \text{ if } t > 1 \text{ and } t \leq T$$

[43].

The proportion of genera preserved is therefore equal to

$$P_{\text{pres}} = \sum_{T=1}^{\infty} P_{D,T} [1 - (1 - R)^T] .$$

The overall probability that a stratigraphic range will equal  $t$ , given all possible values of  $T$ , is given by

$$P_t = \sum_{T=t}^{\infty} P_{D,T} P_{t|T}$$

The probability of a stratigraphic range  $t$ , conditioned on the genus being preserved, is then given by  $P^*_t = P_t / P_{\text{pres}}$ .

Given a set of  $N$  observed stratigraphic ranges,  $t_1, \dots, t_N$ , the log-likelihood (support) of a parameter set  $(\lambda, \mu, R)$  is equal to

$$S = \sum_{i=1}^N \ln (P^*_{t_i}),$$

where  $P^*_{t_i}$  is the expected probability of a range equal to  $t_i$ , given  $(\lambda, \mu, R)$ .

This log-likelihood is maximized numerically to find the best-fitting parameter values, which are then used to calculate  $P_{\text{pres}}$ . To avoid truncation effects (i.e., one does not know the ultimate stratigraphic range of a genus that is still extant), we include only extinct genera in this analysis.

In addition to the overall probability that a genus is sampled, we would like to know what proportion of its original duration is represented by its preserved stratigraphic range. The expected (mean) value of this proportion is given by

$$E(t/T) = \sum_{t=1}^{\infty} \sum_{T=t}^{\infty} (t/T) (P_{D,T} P_{t|T}) / P_{\text{pres}} .$$

In addition to the foregoing estimate of the per-interval sampling probability,  $R$ , we report an alternative estimate, the *FreqRat* [43], which is equal to  $n_2^2 / (n_1 n_3)$ , where  $n_t$  is the observed number of genera with a range of  $t$  intervals.

We used two alternative approaches to assigning stratigraphic ranges to genera whose first or last appearances are not resolved to one of our operational time intervals. Maximum range was based on placing first appearances at their oldest possible level and last appearances at their youngest possible level, as described above. An alternative is to assign a minimum range by placing first appearances at their youngest possible level and last appearances at their oldest possible level. In cases where this results in a negative range, the range is assigned a value of one interval. We also analysed range data including only those genera whose minimum and maximum assigned ranges are identical, i.e., for which the chosen protocol has no bearing on the range. The high level of completeness in the data (table S3) suggests that it is reasonable to take observed stratigraphic ranges at face value.

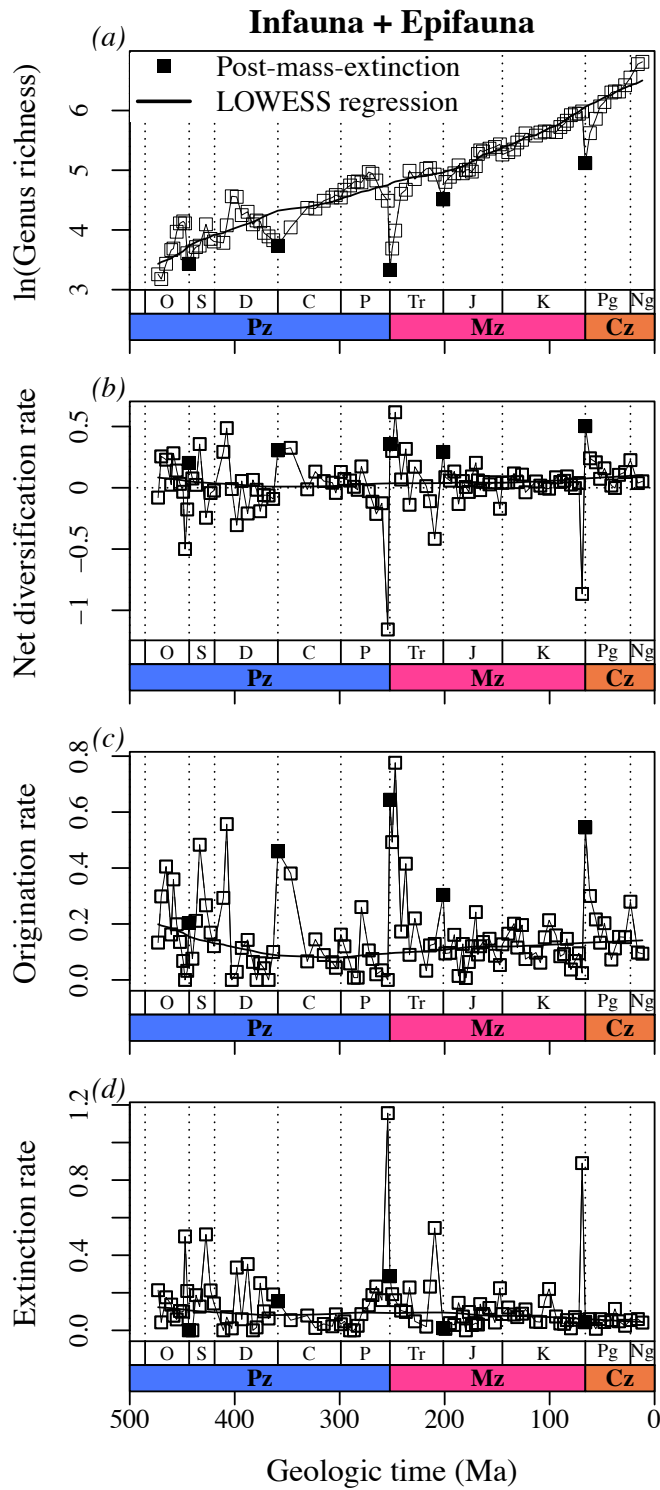


Figure S1. History of diversity and evolutionary rates of combined infaunal and epifaunal bivalve genera. See figure 1 for explanation of plotting conventions.

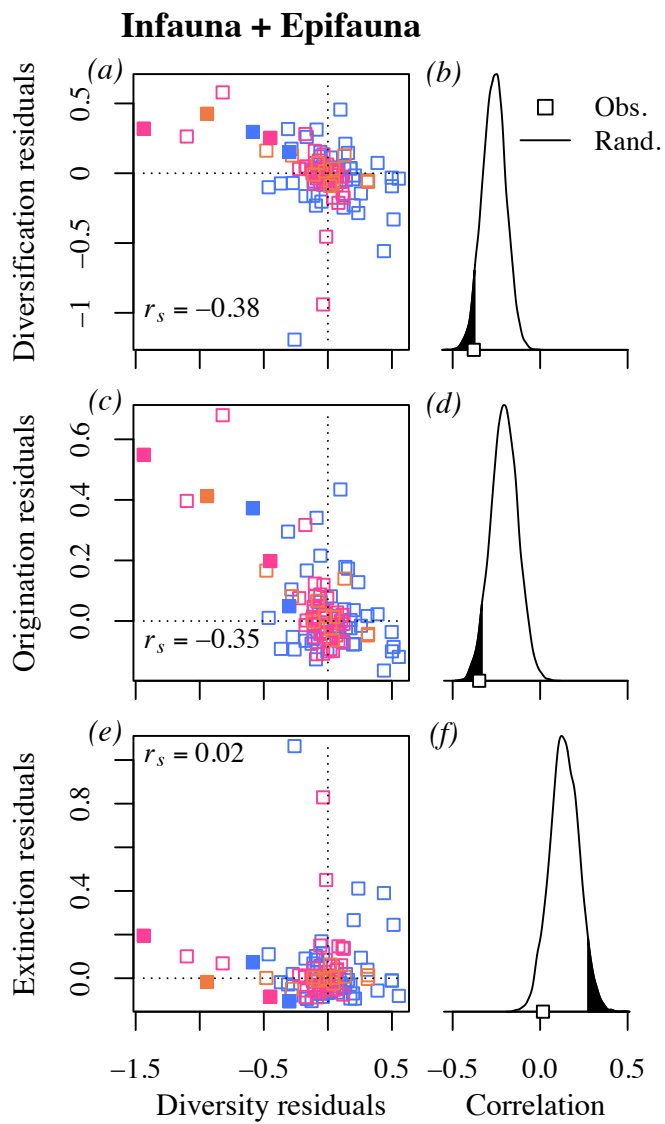


Figure S2. Correlations between diversity residuals and rate residuals for combined infaunal and epifaunal bivalve genera. See figure 2 for explanation of plotting conventions.

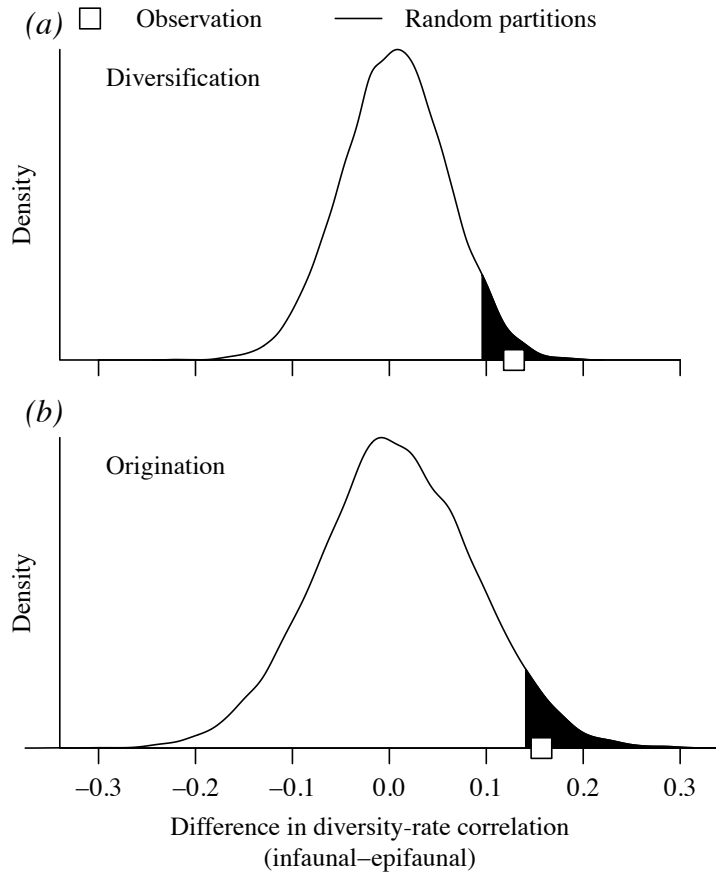


Figure S3. Difference in infaunal versus epifaunal residual diversity-rate correlations, compared with random partitioning into two groups. Distribution based on 10,000 random partitions into two groups with 2098 and 1267 genera, corresponding to the observed numbers for infauna and epifauna, respectively. For diversification rate (a), only 1% of random partitions yield a difference as great as that observed (0.13). For origination rate (b), only 3% of random partitions yield a difference as great as that observed (0.16).

Table S3: Completeness estimates, based on stratigraphic ranges of extinct genera (table S2).

Data treatment	$P_{\text{pres}}^*$	$E(t/T)^\dagger$	$R_{\ddagger}^\ddagger$	$\text{FreqRat}^\S$	Goodness of fit $^\P$
Maximum range	0.98	0.97	0.92	0.97	0.93
Minimum range	0.94	0.91	0.78	0.85	0.89
Genera with maximum and minimum ranges equivalent $^\#$	0.95	0.92	0.81	0.82	0.91
Paleobiology Database $^{**}$	0.77	0.73	0.44	0.40	0.92

\*Estimated proportion of genera sampled at least once.

$^\dagger$ Estimated mean ratio of stratigraphic range to true duration.

$^\ddagger$ Estimated per-interval sampling probability, based on maximum-likelihood fit to range-frequency distribution.

$^\S$ Alternative estimate of per-interval sampling probability, based on [43].

$^\P$ Squared product-moment correlation between the logarithms of observed and expected stratigraphic-range frequencies.

$^\#$ For these genera, the convention for assigning ranges is irrelevant to the analysis.

$^{**}$ Based on 2723 extinct genera in [49], which uses 79 operational stratigraphic intervals and includes only fossil collections uniquely assignable to one of these intervals.



Table S4: Spearman rank-order correlations ( $r_s$ ) between diversity residuals and rate residuals for alternative analyses.

Analysis	<u>Diversification</u>		<u>Origination</u>		<u>Extinction</u>	
	$r_s$	$p^*$	$r_s$	$p^*$	$r_s$	$p^*$
Begin analysis in mid Ordovician (Caradoc)						
Infauna	-0.312	0.254	-0.242	0.293	0.096	0.751
Epifauna	-0.452	0.004	-0.462	0.0005	0.062	0.854
Begin analysis in Silurian (Llandovery)						
Infauna	-0.337	0.186	-0.204	0.489	0.148	0.488
Epifauna	-0.458	0.005	-0.425	0.004	0.041	0.873
Omit rebounds from mass extinctions						
Infauna	-0.225	0.721	-0.167	0.659	0.098	0.727
Epifauna	-0.374	0.053	-0.331	0.052	0.128	0.609
Linear detrending						
Infauna	-0.231	0.282	-0.169	0.379	0.096	0.541
Epifauna	-0.488	<0.0001	-0.546	<0.0001	0.060	0.700
Wider smoothing span ( $f=0.7$ )						
Infauna	-0.311	0.125	-0.239	0.211	0.131	0.501
Epifauna	-0.454	0.0013	-0.449	0.0001	0.091	0.702
Tighter smoothing span ( $f=0.3$ )						
Infauna	-0.349	0.355	-0.281	0.318	0.085	0.892
Epifauna	-0.405	0.093	-0.374	0.049	0.090	0.885
Exclude genera lacking finely resolved stratigraphic ranges						
Infauna	-0.227	0.651	-0.12	0.771	0.036	0.830
Epifauna	-0.397	0.022	-0.371	0.015	0.066	0.818

\*Nominal one-tailed  $p$ -value is the proportion of randomizations that yield a correlation more extreme than the observed value.

## Supplementary references

82. Bieler R, Carter JG, Coan EV. 2010 Classification of bivalve families. *Malacologia* **52**, 113–133.
83. Carter JG *et al.* 2011 A synoptical classification of the Bivalvia (Mollusca). *Univ. Kans. Paleontol. Contrib.* **4**, 1–47.
84. Lemer S, Bieler R, Giribet G. 2019 Resolving the relationships of clams and cockles: dense transcriptome sampling drastically improves the bivalve tree of life. *Proc. R. Soc. B* **286**, 20182684.
85. Horowitz AS, Blakely RF, Macurda DB Jr. 1985 Taxonomic survivorship within the Blastoidea (Echinodermata). *J. Paleontol.* **59**, 543–550.
86. Foote M. 1988 Survivorship analysis of Cambrian and Ordovician trilobites. *Paleobiology* **14**, 258–271.
87. Baumiller TK. 1993 Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. *Paleobiology* **19**, 304–321.
88. Johnston PA. 1991 Systematics and ontogeny of a new bivalve, *Umburra cinefacta*, from the Silurian of Australia: implications for pteriomorphian evolution. *Alcheringa* **15**, 293–319.