Diversity-Dependent Diversification in the History of Marine Animals

Michael Foote*

Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois 60637 Submitted May 16, 2022; Accepted November 11, 2022; Electronically published March 20, 2023 Online enhancements: supplemental PDF.

ABSTRACT: By comparing detrended estimates of diversity (taxonomic richness) and rates of origination, extinction, and net diversification, I show that at the global scale over the course of the Phanerozoic eon, rates of diversification and origination are negatively correlated with diversity. By contrast, extinction rates are only weakly correlated with diversity for the most part. These results hold for both genus- and species-level data and for many alternative analytical protocols. The asymmetry between extinction on the one hand and origination and net diversification on the other hand supports a model whereby extinction is largely driven by abiotic perturbations, with subsequent origination filling the void left by depleted diversity. Diversity dependence is somewhat weaker, but still evident, if the initial Ordovician radiation or rebounds from major mass extinctions are omitted from analysis; thus, diversity dependence is influenced, but not dominated, by these special intervals of Earth history. In the transition from Paleozoic to post-Paleozoic time, diversity dependence of origination weakens while that of extinction strengthens; however, diversity dependence of net diversification barely changes in strength. Despite nuances, individual clades largely yield results consistent with those for the aggregate data on all animals. On the whole, diversitydependent diversification appears to be a pervasive factor in the macroevolution of marine animal life.

Keywords: diversity dependence, diversification, macroevolution, speciation, origination, extinction.

Introduction

The extent to which rates of taxonomic diversification within an ecosystem, a biogeographic region, or the entire biosphere—are affected by the level of standing diversity remains an important and contentious question within ecology, evolutionary biology, and paleobiology. Some of the main issues at stake are (1) whether there is a discernible carrying capacity, a maximal number of species that can be accommodated; (2) if so, how and why that capacity varies over time and whether it has actually ever been attained;

* Email: mfoote@uchicago.edu.

ORCIDs: Foote, https://orcid.org/0000-0003-3836-5980.

(3) whether diversity follows a trajectory of logistic growth toward a dynamic equilibrium, an average long-term balance between speciation and extinction; and (4) the relative importance of biotic interactions and environmental change in macroevolution (Sepkoski 1978, 1984, 1996; Van Valen 1985; Stanley 2007; Alroy 2008, 2010*b*; Ezard et al. 2011; Cornell 2013; Harmon and Harrison 2015; Rabosky and Hurlbert 2015; Marshall and Quental 2016; Bush and Payne 2021; Rillo and Etienne 2022). It is important to keep these issues distinct. For example, prevalent biotic interactions need not imply diversity dependence, and diversity dependence need not imply logistic or equilibrial diversity with a fixed carrying capacity.

Discussion has mainly concerned negative diversity dependence, the hypothesis that diversification rate is inversely correlated with richness, generally as a result of variation in the intensity of direct or diffuse competition among ecologically similar species (Rillo and Etienne 2022). Approaches to testing for negative diversity dependence include nonlinear modeling of diversity and rate trajectories of potentially interacting segments of the biota (Sepkoski 1984, 1996; Sepkoski et al. 2000; Ezard et al. 2011; Liow et al. 2015; Ezard and Purvis 2016; Lidgard et al. 2021), reconstructing temporal changes in diversity and rates from phylogenetic trees of living species (Rabosky 2013; Etienne et al. 2016), and direct comparisons between standing diversity and rates of taxonomic origination, extinction, and net diversification (Mac-Arthur and Wilson 1963; Sepkoski 1978; Miller and Sepkoski 1988; Alroy 1996, 2008, 2010b; Foote 2010; Foote et al. 2018). Perhaps the strongest-certainly the most direct-evidence for negative diversity dependence has come from time series of diversity and diversification rates in the fossil record, which often show accelerated diversification in the wake of extinction events (e.g., Miller and Sepkoski 1988), agree with the predictions of multiphase coupled logistic models (e.g., Sepkoski 1984), and sometimes reveal negative correlations between the diversity

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trajectories of ecologically similar clades (e.g., Sepkoski et al. 2000) and between standing diversity and rates of diversification (e.g., Alroy 1996; Foote 2010). Nonetheless, it is safe to say that no general consensus has emerged regarding the importance of negative diversity dependence in the history of life (Harmon and Harrison 2015; Rabosky and Hurlbert 2015; Rillo and Etienne 2022).

Positive diversity dependence has also been hypothesized-diversity begetting more diversity as species create ecological opportunities for other species (Benton and Emerson 2007; Erwin 2007; Jablonski 2008). This positive feedback has been tested less explicitly than that of negative feedback, but it is consistent with many observations from the fossil record, including long-term increases in alpha richness within local communities (Bambach 1977; Bush and Bambach 2004), ecospace utilization and the number of major ways of making a living (Bambach 1985; Bush et al. 2007; Novack-Gotshall 2007; Bush and Bambach 2011), and evenness of abundance distributions within communities (Powell and Kowalewski 2002; Wagner et al. 2006). It is also consistent with present-day evidence for diversification of one clade depending on resources provided by another clade (e.g., insects and angiosperms; Mitter et al. 1988; Farrell 1998; Lewinsohn and Roslin 2008). These lines of evidence generally concern richness as a response variable, whereas the postulated causal factors are aspects of diversity and ecology other than richness per se. Here I focus on negative diversity dependence, but it is worth bearing in mind that both aspects of diversity dependence can in principle operate simultaneously if positive feedbacks promote diversification on very long timescales while shorter-term variation reflects negative feedbacks (Rabosky 2013; Marshall and Quental 2016).

Rather than addressing the immense issue of the general role of biotic interactions in macroevolution, I focus specifically on whether taxonomic rates are diversity dependent, which is one key aspect of the broader question. Using detailed occurrence data on marine animals over the course of the Phanerozoic eon, I ask whether, all else being equal, times of higher-than-average richness are followed by lowerthan-average origination and diversification rates and higher-than-average extinction rates (and conversely for lower-than-average richness). I do not assume any particular diversification model (e.g., logistic), nor do I assume a constant carrying capacity or equilibrial diversity. I show that, in general, origination and diversification exhibit negative diversity dependence. By contrast, in aggregate over the course of the Phanerozoic eon, extinction generally shows little response to the level of diversity in the world's oceans, although some subsets of data reveal diversity-dependent extinction. It is plausible that diversification can respond to diversity on timescales shorter than the time intervals used here, which would suggest a bias against detecting diversity dependence. That we can detect its effects over millions of years is therefore likely to be a conservative result.

Data

Occurrences of Phanerozoic marine animals were downloaded from the Paleobiology Database (https://paleobiodb .org) on August 16, 2019. (In this context, an occurrence consists of the presence of a taxon in a fossil collection.) Occurrences with uncertain genus identifications were excluded, as were occurrences flagged as form taxa or trace fossils. Inevitably, some nonmarine taxa and environments find their way into the download. Such occurrences were vetted by searching for specific taxa (e.g., pulmonate gastropods) and environments (e.g., deltas, which may be either freshwater or marine), inspected in conjunction with ancillary collection data. Occurrences with unspecified environments were also downloaded; these were inspected and included in the data if ancillary collection information or the presence of clearly marine taxa indicated a marine setting. Although the database's scripts update taxonomic names if relevant opinions have been entered, a few homonyms persist. These were updated with reference to the primary systematic literature. Occurrences were assigned to one of 79 stratigraphic intervals, mainly international stages, based on interval assignments in the database as well as associated stratigraphic information, especially that for biozones and formations, cross-referenced to several standard sources on regional or global correlation (Gradstein et al. 2004, 2012; Ogg et al. 2016; Rasmussen et al. 2019) and more specific stratigraphic references (Henningsmoen 1958; Berg-Madsen 1987; Dean 1989; Terfelt et al. 2008; Adrain et al. 2009; Candela 2015). Occurrences that could not be assigned uniquely to one of these intervals were omitted. All told, 742,230 occurrences of 30,764 genera were retained for analysis. For species-level analysis, occurrences assigned to a genus but not to a species were omitted. This left 562,736 occurrences of 132,623 species. Analyses were focused on genera because of their relatively robust properties of sampling and nomenclature, but species-level analysis yields consistent results (see the supplemental PDF).

Methods

Estimating Taxonomic Rates and Diversity

Species and genera in the Paleobiology Database are conventional Linnean taxa, morphologically defined for the most part (as are the vast majority of described living species). An inferred cladogenetic event (i.e., a taxonomic origination event) is taken to be the oldest occurrence of a taxon in the fossil record (suitably adjusted for incomplete sampling—see below; Raup 1985). Likewise, a lineage termination (i.e., extinction) is marked by the youngest occurrence of a taxon. This approach stands in contrast to the estimation of taxonomic rates from divergence times in phylogenies of living species and corresponding branch lengths (Nee et al. 1994; Nee 2006; Morlon 2014; Louca and Pennell 2020). One salient contrast between paleontological and many neontological approaches is that paleontology generally treats cladogenesis as giving rise to a new lineage, with its ancestor persisting, rather than giving rise to two new lineages, with the ancestor terminating (Raup 1985; Wagner and Erwin 1995; Foote 1996). An active area of research today lies in the melding of paleontological and neontological approaches to the estimation and analysis of taxonomic rates of evolution (Silvestro et al. 2018; Stadler et al. 2018; Warnock et al. 2020; Crouch et al. 2021). There is no reason at this time to think that the paleontological approach is biased toward or against the detection of diversity dependence.

What we ideally mean by the per capita rate of origination within a time interval is the number of lineages that originated in that time interval divided by the sum of all lineage durations within that interval (Raup 1985). The concept for extinction rate is analogous. Because of limited temporal resolution within time intervals, we cannot generally tabulate the sum of lineage durations against which the numbers of individual origination and extinction events are scaled—hence the need for the variety of rate estimation methods that have been developed for the analysis of occurrence data aggregated by temporal interval (see below).

Although occurrences in the Paleobiology Database have associated age estimates in millions of years before present (Ma), fossils are rarely dated directly; these numerical age estimates instead reflect the lower and upper boundaries of discrete stratigraphic intervals from which the material comes and which are defined mainly on the basis of paleontological markers rather than numerical age estimates. It is therefore sensible to use methods that recognize the discrete nature of time intervals in which fossil occurrences are found. It is also important to take incomplete sampling into account.

On this last point, we have a number of approaches available to estimate fossil richness on the one hand (Alroy et al. 2001, 2008; Alroy 2010a, 2010b; Close et al. 2018; Alroy 2020) and rates of origination and extinction on the other hand (Alroy 2008, 2010a, 2014; Liow and Nichols 2010). In general, these richness estimates integrate over an entire time interval and are not related to rate estimates in a straightforward way. The approach of this article is to attain a straightforward relationship through the correspondence between the history of taxonomic rates and that of standing richness (i.e., the number of taxa extant at a moment in time). A time series of estimated taxonomic rates is first obtained, and these are then used to yield a time series of richness estimates (fig. 1). This approach to estimating diversity has been used before (Foote 2003) but appears not to be widespread.

Consider a time series of per capita, per-interval origination (cladogenesis) and extinction (lineage termination) rates, λ_i and μ_i , where *i* denotes the interval number, from oldest to youngest, and the net diversification rate is equal to $\lambda_i - \mu_i$. If richness at the start of interval 1 is given by D_0 , then richness at the end of interval *n* must be equal to

$$D_n = D_0 \exp \left[\sum_{i=1}^n (\lambda_i - \mu_i) \right]$$

Time intervals



- 1. Estimate origination and extinction rates for intervals 1, 2, ..., *i* 1.
- 2. From these, calculate net diversification rates.
- 3. These rates are used to compute log richness at start of interval *i* (as the sum of all preceding diversification rates).
- 4. Test whether richness at start of interval *i* is correlated with rates in intervals *i*, *i* + 1, *i* + 2, ..., *n*.

Figure 1: Method for reconstructing diversity history. Per capita origination and extinction rates can be estimated by a variety of methods. Rates for intervals 1 through i - 1 fully determine richness at the start of interval *i* (indicated by the arrow); this richness value is logically independent of all subsequent rates.

or, more conveniently,

$$\ln(D_n) = \ln(D_0) + \sum_{i=1}^n (\lambda_i - \mu_i)$$

(Kendall 1948). Unless otherwise specified, by "diversity" I hereinafter mean the natural logarithm of taxonomic richness.

The relationship between rates and richness is an algebraic necessity and involves no assumptions other than the accuracy of the rate estimates. The rates preceding a given time interval fully determine standing diversity at the start of that interval (fig. 1), but this diversity level is logically independent of any subsequent rates. This independence is important because the empirical test for diversity dependence, described below, hinges on the empirical relationship between diversity at a point in time and taxonomic rates after that time.

The principal analyses in this study are based on a maximum likelihood method of rate estimation that can be thought of as a variant of Alroy's (2008) three-timer method, following a logic similar to that of capture-mark-recapture methods (Pradel 1996; Liow and Nichols 2010). Consider three successive time intervals, *i*, *j*, and *k*, oldest to youngest, and focus on all taxa present in interval i (table 1). Then, with 1 denoting the presence of a taxon in a time interval and 0 denoting its absence, we can determine the probabilities of all possible patterns of occurrence, 100, 101, 110, and 111, in terms of the probabilities of extinction (Q) and sampling (R) in each interval. Consider the pattern 100. This can come about in three ways: (1) a taxon can become extinct in the first interval, with probability Q_i ; (2) it can survive the first interval, become extinct in the second interval, and fail to be sampled in the second interval, with probability $(1 - Q_i)Q_i(1 - R_i)$; and (3) it can survive both the first interval and the second interval and fail to be sampled in the second and third intervals, with probability $(1-Q_i)(1-Q_i)(1-R_i)(1-R_k)$. Similar reasoning holds for the other occurrence patterns. Thus, for any three-interval window, the probability distribution

Table 1: Probability of pattern of occurrence in three successive time intervals, conditioned on occurrence in interval i

Pattern ^a	$Probability^{b}$
100	$Q_i + (1 - Q_i)Q_j(1 - R_j) + (1 - Q_i)(1 - Q_j)(1 - Q_$
	$R_j(1 - R_k)$
101	$(1 - Q_i)(1 - Q_j)(1 - R_j)R_k$
110	$(1 - Q_i)Q_iR_j + (1 - Q_i)(1 - Q_j)R_j(1 - R_k)$
111	$(1 - Q_i)(1 - Q_j)R_jR_k$

^a 1 denotes presence; 0 denotes absence.

^b j = i + 1; k = i + 2; Q = extinction probability; R = sampling probability.

of occurrence patterns depends on two extinction probabilities (Q_i and Q_j) and two sampling probabilities (R_j and R_k). (The three-interval occurrence patterns starting with interval *i* provide no constraints on R_i or Q_k , but these are constrained by neighboring three-interval windows.) Because this estimation method explicitly allows for temporal variability in sampling, the procedure was not preceded by a round of subsampling (compare Foote 2010 with Alroy 2014), a step that would unnecessarily reduce the amount of data used.

For each time interval, the number of taxa with each occurrence pattern is tabulated, and the entire time series of Q and R is found that maximizes the likelihood over all time intervals. As is the case with most methods of rate estimation, this approach tacitly assumes that all taxa are characterized by the same average extinction and sampling probabilities within a time interval. To convert Q to a per capita rate, we note that $Q = [1 - \exp(-\mu)]$, so that $\mu = -\ln(1 - Q)$. This conversion between extinction probabilities and per capita rates relies on the simplifying assumption that taxonomic turnover is concentrated at interval boundaries. In effect it treats time intervals as having unit length, a necessary element of the randomization procedure used to test for diversity dependence (see below). This turnover model has been supported by previous analyses (Foote 1994, 2005, 2007; but see Alroy 2008).

Analytically, origination is akin to extinction with the direction of time reversed (Pradel 1996). To estimate origination rates, we focus on three-interval windows, youngest to oldest, so that the pattern 100, for example, means present in the youngest interval and absent from the two older intervals. In other words, we simply reverse the order of columns in a taxon-by-interval presence/absence matrix and proceed as if we were estimating extinction rates. Because of the need to consider three successive intervals, extinction rates cannot be estimated for the last two time intervals, and origination rates cannot be estimated for the first two time intervals. Note that the sampling probabilities for the forward and backward analyses are not constrained to be the same. In fact, however, for the data analyzed here, they are strongly correlated at r = 0.99. The main motivation for separate forward and backward fits is computational efficiency; for the length of the time series analyzed herein, it takes about two-thirds as much CPU time to perform two separate fits compared with a single, simultaneous fit of origination, extinction, and sampling. The parameters estimated with separate versus simultaneous fits are nearly identical: r > 0.999 for origination, extinction, and diversification and r > 0.997 for sampling. Finally, alternative rate estimates were developed, using four successive intervals (table S1) as well as the entire time series of stratigraphic intervals (Pradel 1996). These variants and additional

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estimation methods yield results consistent with the three-interval approach (table S2, lines 13–17).

In light of prior evidence for abundant variation in taxonomic rates (e.g., Raup and Sepkoski 1982; Van Valen 1984; Van Valen and Maiorana 1985; Alroy 2014), all rate estimates were based on a model in which rates are estimated independently for each time interval rather than one that takes minimal rate variation as a starting point and attempts to fit a parametric model relating time to rate shifts (e.g., PyRate [Silvestro et al. 2014]; for an evaluation of the PyRate method, see Černý et al. 2021). Standard errors of rate estimates (fig. 2), developed via bootstrap resampling of genera, allow one to test whether rates in successive intervals are "significantly" different if that question is of interest. Another rationale for the approach used herein is that it in effect allows a nonparametric test for diversity dependence rather than fitting a particular diversification model (e.g., Sepkoski 1984; Maurer 1989; Lehtonen et al. 2017).

Because we are interested in the shape of the diversity curve rather than its absolute magnitude, we begin with an arbitrary value of $\ln(D_0) = 0$ (i.e., $D_0 = 1$) at the start



Figure 2: Diversity and taxonomic rates for Phanerozoic marine animal genera. Diversity corresponds to standing richness at the start of each time interval, and rates are estimated over the span of the interval itself. All values plotted at the start of an interval. Error bars indicate 1 standard error, based on bootstrap resampling of genus occurrence histories. Intervals immediately following five widely recognized mass extinction events are indicated by solid squares. Thick lines show LOWESS regression, using the lowess() function in R with default parameters except for the smoothing span, which is set to 0.5. O = Ordovician; S = Silurian; D = Devonian; C = Carboniferous; P = Permian; Tr = Triassic; J = Jurassic; K = Cretaceous; Pg = Paleogene.

of interval 1 and compute subsequent values of $\ln(D)$ as the cumulative sum of net diversification rates (i.e., the cumulative sum of the differences between origination and extinction rates). This arbitrary starting value has no bearing on any subsequent analyses. Provided that rate estimates are accurate, the resulting diversity estimates provide accurate relative values, albeit not the true numbers of genera that lived at any time in the past.

Rate and diversity estimation and all subsequent analyses in this article were carried out in R version 3.3.0 (R Core Team 2016). Data and code are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.02v6wwq6d; Foote 2022).

Testing for Diversity Dependence of Taxonomic Rates

The hypothesis of diversity dependence predicts a negative correlation between diversity and rates of origination and net diversification and a positive correlation between diversity and rates of extinction (MacArthur and Wilson 1963; Sepkoski 1978; Alroy 1996). Diversity dependence need not imply a constant equilibrium or carrying capacity (Sepkoski 1978, 1984, 1996; Foote 2010; Ezard et al. 2011; Rabosky and Hurlbert 2015; Marshall and Quental 2016; Foote et al. 2018), and of course diversity has varied substantially over the course of the Phanerozoic (Sepkoski 1984; Stanley 2007; Alroy 2008, 2010b; Alroy et al. 2008; Bush and Payne 2021). Many studies have also detected secular trends in rates of origination and extinction (e.g., Raup and Sepkoski 1982; Van Valen 1984; Van Valen and Maiorana 1985; Gilinsky and Bambach 1987; Sepkoski 1998; Stanley 2007). Therefore, the general approach taken herein is first to detrend rates and diversity by calculating residuals from a LOWESS (locally weighted scatterplot smoothing) regression and then to compute the correlation between diversity residuals and rate residuals (Foote 2010; Foote et al. 2018). I opted against detrending via a moving average because with a relatively short time series, averaging enough points to yield a smooth trajectory leads to the loss of too many data points at the beginning and end of the time series. Differencing is also not advised for the data at hand. The first differences in log richness are nothing more than the diversification rates themselves. Thus, differences in diversity and differences is diversification rate tend to be strongly correlated even in the absence of diversity dependence. The relationship between richness (arithmetic) and rates can be modeled as linear (Sepkoski 1978) or nonlinear (MacArthur and Wilson 1963; Maurer 1989; Brayard et al. 2009). We can bypass this question by focusing on rank-order diversity rate correlations.

Regression to the mean presents a conundrum in comparing diversity and taxonomic rates (Lande et al. 2002; Kelly and Price 2005; Freckleton et al. 2006; Alroy 2008, 2010b; Foote et al. 2018). Even in the absence of diversity dependence, a diversity level that is higher than average is likely to be followed by a decrease in diversity (i.e., a negative diversification rate), and conversely for lower-than-average diversity. The resulting negative relationship between diversity and diversification rate could be misinterpreted as evidence for diversity dependence. To address this problem, I used the approach of Foote et al. (2018). The observed taxonomic rates are randomized with respect to time, keeping origination and extinction rates coupled, and a synthetic diversity curve is constructed from these shuffled rates. Diversity and rates are detrended in the same way as the empirical data, and the correlations between residuals are calculated. The procedure is repeated many times (in this case, 10,000) to develop a probability distribution of correlations to be expected from a random but empirically scaled time series of rates-a time series of rates that is by construction diversity independent. If the correlations in the observed data are stronger than all or most of those resulting from the randomization, this result is interpreted as evidence for diversity dependence.

Although rates and diversity are estimated for the entire Phanerozoic, the analysis of diversity dependence is restricted to the Ordovician through Paleogene periods— 69 time intervals spanning just over 460 million years. The purpose is to avoid edge effects on certain rate estimation methods (Alroy 2014) and limits to stratigraphic correlation in the Cambrian (Foote and Miller 2013; Sundberg and Webster 2021). Taxa can contribute to rate estimation if some of their occurrences fall outside this window of time. Once rates are estimated, however, the randomization procedure involves only the time intervals within this restricted window.

The baseline analysis herein is at zero lag, meaning diversity at the start of an interval is compared with rates within that interval. Sepkoski (1998) noted that whereas extinction events tend to reduce diversity abruptly, rebounds from extinctions are often more drawn out, consistent with a previous suggestion (Stanley 1990) that recoveries from extinction events could be delayed because of suboptimal environmental conditions, among other factors. It is therefore of interest to study the correlations between diversity and taxonomic rates at a lag. Here I explore lags of up to three time intervals.

Diversity dynamics are known to vary with geographic, geologic, and environmental setting (e.g., Miller 1997; Jablonski 1998; Foote 2006; Jablonski et al. 2006; Kiessling and Aberhan 2007; Hull et al. 2011; Close et al. 2020; Benson et al. 2021). The data analyzed herein are at the global scale, which means that the test for diversity dependence may be asymmetric in the following sense: if taxonomic rates are diversity dependent at local or regional scales, such a signal could conceivably be blurred when data are aggregated into a global composite (Rabosky and

Hurlbert 2015; Benson et al. 2021). Therefore, failure to detect diversity dependence should not be taken as strong evidence that it does not exist. But the ability to detect it despite limitations in the data gives real confidence that it exists. In other words, it is hard to think of any way in which a global aggregation of data will lead to the spurious appearance of diversity dependence if, say, regional dynamics are not diversity dependent. (It is also difficult to imagine how data aggregation would affect origination and extinction very differently, although this question deserves more attention.) As a preliminary check on this intuition, I analyzed data divided into two distinct subsets: tropical (less than 30 degrees paleolatitude), consisting of 385,195 occurrences of 20,805 genera; and extratropical, consisting of 333,679 occurrences of 19,458 genera.

Several studies have pointed to differences in diversity dynamics between the Paleozoic and post-Paleozoic (e.g., Valentine 1969; Sepkoski 1984; Stanley 1990, 2007; Bambach 1999; Miller and Foote 2003; Foote 2000b, 2006). Foote (2000b) found a tendency for changes in diversity within the Paleozoic to be better predicted by extinction rates rather than origination rates, and vice versa for the post-Paleozoic, but those analyses concerned rates leading up to changes in diversity rather than those potentially responding to diversity. With respect to diversity dependence, I have no particular a priori hypothesis to offer, but it is hard to resist the temptation to explore temporal differences in this aspect of dynamics. To do so, the Paleozoic and post-Paleozoic rates were randomized separately, then concatenated into full-length time series of rates and diversification, which in turn were detrended, with residuals subsequently calculated. Diversity rate correlations for the observed and randomized time series were then computed for the Paleozoic and post-Paleozoic segments separately (33 and 36 intervals long, respectively).

Results

Diversity and Taxonomic Rates

As in numerous previous studies, genus richness and taxonomic rates of evolution vary substantially over the Phanerozoic (fig. 2). Many features of the diversity curve reconstructed from taxonomic rates are consistent with diversity estimated by standardized sampling of occurrence data (Alroy 2010*b*)—for example, diversification through the Ordovician, decline through much of the Devonian, setbacks at major extinction events, and a sustained but irregular increase after the Triassic.

Testing for Diversity Dependence

Origination rate and net diversification rate are negatively associated with diversity (fig. 3), consistent with diversity de-



Figure 3: Scatterplots of residuals from LOWESS regression, with Spearman rank-order correlation coefficients indicated. Solid squares correspond to those of figure 2. Net diversification rate and origination rate show a substantial negative correlation with diversity, but extinction rate is nearly independent of diversity.

pendence. The correlation with extinction rate is barely perceptible. Although the correlation coefficients reported in figure 3 accurately depict the strength of association between diversity residuals and rate residuals, interpreting them is complicated because the null expectation is not a zero correlation. To appreciate that point, consider three examples of the randomization procedure described above (namely, the first three produced; fig. 4); for simplicity, only net diversification rate is depicted. Each randomization shown yields a negative correlation between diversity residuals and diversification residuals, which, because the randomized time series are necessarily diversity independent, can be interpreted to reflect regression to the mean.

Considering the entire ensemble of 10,000 randomization, the observed diversity-extinction correlation is well within the null distribution (fig. 5; table 2, line 1), giving no evidence for diversity dependence. However, origination and net diversification are in the tails of the distributions ($P \sim .0001$ and P < .01, respectively), suggesting negative diversity dependence of these rates well beyond what is expected from regression to the mean.

Because of regression to the mean, the observed diversity rate correlations exaggerate the effect size that may be attributable to diversity dependence. A rough idea of the actual effect size can be obtained by subtracting the median squared rank-order correlation coefficient for randomizations from the squared coefficient in the observed data. For net diversification this yields $0.517^2 - 0.333^2 = 0.16$; for origination the figures are $0.528^2 - 0.222^2 = 0.23$. So approximately 16% of the rank-order variance in diversification rate residuals is potentially attributable to diversity dependence, and for origination rate residuals the share is 23%. The asymmetry between extinction and origination is consistent with previous analyses of similar data that used different protocols for estimating diversity and rates and that failed to account for regression to the mean (Foote 2010).

Substantial diversity-diversification and diversityorigination correlations persist at a lag of one time interval, but they are rather weak at a lag of two intervals and effectively absent at a lag of three intervals (table 2, lines 2–4). To the extent that these correlations reflect diversity dependence, we can infer that lower-than-average diversity enhances origination and diversification for several million



Figure 4: Examples of randomization procedure for assessing the strength of diversity rate dependence attributable to the regression to the mean effect. Origination and extinction rate pairs are shuffled to produce a time series of these rates, which imply a synthetic diversity history according to the logic of figure 1. For simplicity, only net diversification rate is depicted. Dashed lines show LOWESS regression. By its very construction, the history of rates is perforce diversity independent. Therefore, any observed correlation between diversity residuals and rate residuals cannot be attributed to diversity dependence. Note that because log diversity is simply the sum of diversification rates, all synthetic diversity histories start and end at the same values as the observed history. Axes in *A* and *B* are as in figure 2*B* and 2*A*; axes in *C* are as in figure 3*A*.



Figure 5: Frequency distributions of correlations between diversity residuals and rate residuals for 10,000 diversity-independent randomizations like those of figure 4. Curves depict the probability distribution of results, based on the R density() function with default parameters. Shaded tails correspond to 5% of the randomized values; observed correlations (open squares) falling within these tails have a nominal one-tailed statistical significance of P < .05 (see table 2). The observed correlations for net diversification rate and origination rate fall outside the expectations of regression to the mean and are therefore interpreted to indicate diversity dependence of these rates. The same is not true for extinction rate.

years. This result is consistent with Alroy's (2010b, fig. 11) finding that total diversity in a time interval is negatively correlated with net diversification rate two intervals later.

Diversity-diversification correlations are nearly equally strong during the Paleozoic and post-Paleozoic (table 2, lines 5, 6). However, there appears to be a shift in dynamics, with the diversity-origination correlation stronger in the Paleozoic than afterward and the diversity-extinction correlation increasing from the Paleozoic to the post-Paleozoic.

Higher taxa with sufficient data to analyze separately mostly show diversity dynamics largely consistent with the aggregate data (table 2, lines 7–9). Bivalve mollusks are an exception. They show diversity dependence of net diversification comparable in strength to that seen in the aggregate data, but the origination effect is weaker and the extinction effect stronger than in the taxonomic aggregate (table 2, line 10). Further dissecting the bivalves into Paleozoic and post-Paleozoic time spans reveals that diversity dependence in the Paleozoic, like the data as a whole, is concentrated in origination (table 2, line 11). However, post-Paleozoic bivalves, unlike the aggregate, show conspicuous diversity dependence of extinction (table 2, line 12).

Results are robust to alternative analytical protocols, including choice of rate and richness estimators; use of species-level data; details of LOWESS smoothing; whether we focus on lower- or higher-latitude faunas; and whether the initial Ordovician radiation and rebounds from major mass extinctions are included in the analysis (see the supplemental PDF).

Discussion and Conclusions

The principal result of the foregoing analyses is that rates of origination and net diversification generally depend on diversity, whereas most analyses show little dependence of extinction rates on diversity. That is not to say that diversity has no impact on extinction rates, simply that the effects, if any, are more muted than those on origination.

Whether rates of origination, extinction, and net diversification are diversity dependent is a separate, albeit not unrelated, question from whether diversity is at an equilibrium or whether there is a theoretical upper limit to the number of species in the world (Sepkoski 1978, 1984, 1996; Benton and Emerson 2007; Alroy 2008, 2010*b*; Harmon and Harrison 2015; Rabosky and Hurlbert 2015). A basic premise of the present work is that the number of species the world can accommodate may vary over time—because of changes in how finely niches are partitioned (Valentine 1969), biogeographic differentiation (Valentine and Moores 1972; Valentine 1973; Valentine et al. 1978; Zaffos et al. 2017; Holland 2018), and latitudinal gradients in climate (Valentine et al. 1978; Valentine and Jablonski 2010), among other factors—but that superimposed on

	Diversification		Origination		Extinction	
Analysis	r _s	P^{a}	r _s	P^{a}	r _s	P^{a}
1. Baseline ^b	517	.0088	528	.0001	.066	.913
2. Lag 1	473	.0139	453	.0043	.215	.3194
3. Lag 2	296	.2491	295	.096	.085	.6816
4. Lag 3	051	.8982	091	.6245	.026	.7822
5. Paleozoic	552	.04	658	.0002	054	.951
6. Post-Paleozoic	512	.0582	357	.1968	.303	.2922
7. Brachiopoda ^c	470	.0325	542	.0002	.063	.9544
8. Gastropoda ^d	474	.0471	373	.0741	.314	.3305
9. Cephalopoda ^e	381	.2711	360	.0556	.043	.7961
10. Bivalvia ^f	543	.0048	390	.0766	.406	.0554
11. Bivalvia, Paleozoic	524	.1033	617	.0069	.328	.3495
12. Bivalvia, post-Paleozoic	547	.0397	174	.6743	.499	.031

Table 2: Spearman rank-order correlations (r_s) between diversity residuals and rate residuals

^a Nominal one-tailed *P* value is the proportion of randomizations that yield a correlation more extreme than the observed value (fig. 5).

^b Baseline analysis refers to all marine animal genera, a time span from the Ordovician through the Paleogene, a LOWESS smoothing span (f) equal to 0.5, and zero lag.

^c Classes include Chileata, Craniata, Kutorginata, Lingulata, Obolellata, Paterinata, Rhynchonellata, and Strophomenata. ^d Because of the paucity of Cambrian and earliest Ordovician material, analysis of Gastropoda begins in the Floian (second) stage of the Ordovician.

^e Because of the paucity of Cambrian, earliest Ordovician, and Cenozoic material, analysis of Cephalopoda is restricted to the Floian through Cretaceous.

^f Because of the paucity of Cambrian and Early Ordovician material, analysis of Bivalvia begins in the Dapingian (third) stage of the Ordovician.

such long-term temporal changes, rates of diversification may nevertheless vary on shorter timescales in response to diversity fluctuations. Hence the rationale for detrending diversity and rates to study residual variation around secular trends.

The lack of consistent evidence for diversity-dependent extinction and the asymmetry between origination and extinction are consistent with several previous proposals. For example, Sepkoski (1978, figs. 5, 7) pictured extinction as having a weaker response to diversity. Stanley (2007) suggested that the apparent lack of trend in diversity during much of the Paleozoic era reflected setbacks at extinction events rather than diversity dependence. One interpretation of the asymmetry between origination and extinction is that extinctions largely reflect environmental perturbations independent of standing diversity, with the opportunities created by extinction leading to enhanced origination. As Walker and Valentine (1984, p. 896) put it, "a sound theory of evolutionary diversity regulation should incorporate the assumption that species turnover is not 'pushed,' but is rather 'pulled' by stochastically constant extinction and the persistent creation of speciation opportunities." (Another way to express this perspective is that species for the most part do not drive each other to extinction.) This view is echoed by Raup and Boyajian's (1988) interpretation of the fact that functionally and ecologically disparate

higher taxa show similar extinction histories. However, the observed asymmetry is not simply a matter of lower-thanaverage diversity leading to higher-than-average origination and diversification. We also see that higher diversity correlates with lower origination and diversification (see the lower right quadrants of fig. 3*A*, 3*B*).

The Walker-Valentine/Raup-Boyajian view could help account for the Paleozoic/post-Paleozoic change in diversity dynamics if environmental perturbations had become less frequent and/or intense with time. Under this scenario, extinction would be freer to respond to diversity. It is not clear, however, that significant perturbations have in fact decreased over the span of the Phanerozoic. The post-Paleozoic is no stranger to extraterrestrial impacts (Rampino 2020), massive volcanism (Bond and Grasby 2017), oceanic anoxic events, and other variations in ocean chemistry (Arthur and Sageman 1994; Meyer and Kump 2008), sea level change (Hallam and Wignall 1999), and global warming (McInerney and Wing 2011; Willis and MacDonald 2011). In any event, such a decrease, if it had occurred, would not in itself explain the weakening of the origination-diversity correlation while the diversitydiversification correlation persists. Whatever mechanism is ultimately hypothesized to account for the shift in dynamics, it needs to apply to bivalves in particular. The mixed signals in bivalves agree with recent analyses that show

ambiguous patterns of diversity dependence of origination and extinction in this clade (Rineau et al. 2022, table 1), the reasons for which remain unclear.

Diversity can fluctuate because of variation in origination, extinction, or both (Kendall 1948; Bambach et al. 2004). Therefore, cross-correlations between origination and extinction, while highly relevant to overall diversity dynamics, are not the most direct way to test whether either rate depends on diversity per se, nor are measures of faunal similarity between successive time intervals (cf. Cuthill et al. 2020). The asymmetry between origination and extinction is nonetheless evident in these cross-correlations. At a lag of zero, the two rates are nearly uncorrelated (r = 0.12). The same is true at a lag of one time interval, with origination leading extinction (r = 0.12). However, a stronger correlation emerges with extinction leading origination at a lag of one interval (r = 0.39). These results are consistent with the notion that extinction opens opportunities for new taxa to originate but that origination does not push taxa to extinction. Alroy found much the same in a previous analysis of similar data (Alroy 2008, p. 11539), as have previous analyses of a different database on Phanerozoic marine diversity (Kirchner and Weil 2000; Kirchner 2002). Liow et al. (2015) found a complementary result, in which high extinction rates of bivalves tend to be followed by high origination rates of brachiopods.

Previous analyses of data like those used herein have led to mixed conclusions on diversity dependence of taxonomic rates (Alroy 2008, 2010b; Foote 2010; Rineau et al. 2022). Using information transfer modeling, Rineau et al. (2022) concluded that for a variety of metazoan and microfossil groups, origination is more clearly diversity dependent than extinction, although net diversification was not explored. A conspicuous difference between the present results and those of some prior research arises in a comparison with Alroy (2008), who found that estimated total richness within a time interval, based on standardized subsampling, is uncorrelated with origination and positively correlated with extinction in the subsequent interval-exactly the opposite of the results found here. The difference is unlikely to reflect the use of total interval diversity versus diversity at the end of that interval (i.e., at the beginning of the next interval-the currency used herein) because the two quantities are generally well correlated. Instead, it seems plausible that the difference reflects Alroy's (2008) use of a subsampling method that is known to flatten out true variation in diversity (Alroy 2010a, 2010b; Close et al. 2018). Indeed, richness estimators that do not have this dampening tendency yield results in agreement with those presented here (table S2, lines 25–27). Thus, the inference of diversity dependence does not depend crucially on estimating diversity as the cumulative sum of net diversification rates.

Despite previous doubts to the contrary, it is difficult to escape the conclusion that rates of taxonomic diversification over the history of marine animal life have responded significantly—and negatively—to the level of taxonomic richness. Analyses like those presented here should enable us to determine whether the same holds true for the terrestrial realm and for other clades.

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Data and Code Availability

Data and code are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.02v6wwq6d; Foote 2022).

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