

Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics

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Abstract.—Changes in genus diversity within higher taxa of marine animals on the temporal scale of a few million years are more strongly correlated with changes in extinction rate than with changes in origination rate during the Paleozoic. After the Paleozoic the relative roles of origination and extinction in diversity dynamics are reversed. Metazoa as well as individual higher taxa shift from one mode of diversity dynamics to the other. The magnitude of taxonomic rates, the relative variance of origination and extinction rates, and the presence or absence of a long-term secular increase in diversity all fail to account for the shift in importance of origination and extinction in diversity changes. Origination and extinction rates both tend to be diversity-dependent, but different modes of diversity-dependence may contribute to the change in diversity dynamics from the Paleozoic to the post-Paleozoic. During the Paleozoic, there is a weak tendency for extinction rates to be more diversity-dependent than origination rates, whereas after the Paleozoic the two rates are about equally diversity-dependent on average.

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Components of Diversity Change during the Phanerozoic

How does variation in diversity during the history of life depend on variation in origination and extinction rates? Any change in taxonomic diversity necessarily implies a difference between origination and extinction rates, but by itself it says nothing about the magnitude of the rates or how they may have changed individually. Although diversity can change if the underlying taxonomic rates are constant, these rates in fact appear to have fluctuated considerably over the scope of the Phanerozoic (Raup and Sepkoski 1982; Van Valen 1984; Raup 1991; Foote 1994; Sepkoski 1998). The central question I will address concerns the relationship between these fluctuations in origination and extinction rate and the corresponding changes in diversity. Does diversity change tend to result more from change in origination rate or change in extinction rate, or is there no systematic pattern? The answer has obvious implications for diversity dynamics (Alroy 1998). For example, one could imagine an extreme case in which extinction rate within a clade is approximately constant, perhaps for intrinsic biological reasons, while origination rate varies as a result

of evolutionary innovations and ecological opportunities (Walker and Valentine 1984; Gilinsky and Bambach 1987). In such a case, most of the variation in diversity within a clade would be attributable to variation in origination rate. Conversely, if variation in diversity is correlated primarily with variation in extinction rate, this might imply a characteristic rate of origination that is offset by external perturbations leading to extinction.

Whether temporal variation in diversity more clearly reflects variation in origination rate or variation in extinction rate is likely to be related to temporal and taxonomic scale. Some analyses of extant clades that are a few million years old have suggested that reconstructed branching patterns are best explained by a model in which there is no extinction (Hey 1992), although simulation studies have shown that it may be difficult to identify past extinction when only living representatives of the clade are studied (Hey et al. 1998; cf. Raup 1983; Nee et al. 1995; Harvey and Rambaut 1998). At the scale of animals as a whole over the Phanerozoic, there has been a net diversity increase since the Paleozoic, implying an increase in the difference between origination and extinction rates, but this increase has been accompanied by a decline in both rates (Raup

and Sepkoski 1982; Van Valen 1984). At the level of classes and orders over hundreds of millions of years, these higher taxa tend to experience a secular decline in family origination rate, but extinction rate may be relatively stationary (Van Valen 1985a; Van Valen and Maiorana 1985; Gilinsky and Bambach 1987). Thus, the long-term diversity history of many groups seems to be attributable to changes in origination rate rather than extinction rate. There is considerable variation in rate superimposed on these secular trends, however. It is this finer-scale variation on which I will focus. Analysis of genera and families within higher taxa suggests that variation in extinction rate was more important than variation in origination rate in determining diversity changes during the Paleozoic and that the relative importance of extinction and origination reversed from the Paleozoic to the Mesozoic.

Note that the question of temporal variation which I address is distinct from that of variation among biologic groups. A few studies have attempted to factor differential diversification of related taxa into origination and extinction components. For example, Cheetham and Jackson (1996) suggested that two coeval genera of cheilostome bryozoans have had similar histories of origination, and that the difference in their respective species richness is therefore due to a difference in extinction rate. Conversely, Van Valen (1973) compared artiodactyl and perissodactyl mammals and found similar extinction rates, suggesting that the greater diversity of artiodactyls is attributable to a higher origination rate. Another related question concerns the relative importance of stages of allopatric speciation in net rates of origination. Allmon (1992) has cogently argued that differences in speciation rate may be better understood mechanistically if one investigates differences in rates of isolate formation, isolate persistence, and isolate divergence.

Data and Methods

I analyzed stratigraphic range data from Sepkoski's unpublished compendium of Phanerozoic marine animal genera (see Sepkoski 1996b, 1997, 1998 for a description of the data). By dividing and combining standard

stratigraphic stages and series, I split the Phanerozoic into 107 intervals in an attempt to minimize the variance in estimated interval length; the mean interval duration is 5.1 m.y., with a standard deviation of 1.7 m.y. I also used an alternative subdivision of the Phanerozoic (see Sepkoski 1996b; Foote and Sepkoski 1999) and found the results to be consistent. The timescale is mainly that of Harland et al. (1990), with some modifications for the lower Paleozoic based on the timescales of Tucker and McKerrow (1995) and Bowring and Erwin (1998). I will argue that inaccuracies in absolute dating are not responsible for the results presented here. All told, I included 25,049 fossil genera whose first and last occurrences could both be fully resolved to one of the 107 intervals. Of these, 13,302 (53.1%) have ranges that span more than one interval and thus could be used for analysis, as explained below. I included extant genera that have a fossil record. I will show that excluding them to remove potential biases resulting from nearly complete knowledge of the living fauna has a relatively small effect on the results. In addition to analyzing the data as a whole, I analyzed subsets corresponding to the more diverse phyla, classes, and orders.

I measured diversity as the number of genera known to cross interval boundaries (Raymond and Metz 1995; Alroy 1996, 1998; Bambach 1999). This provides an estimate of instantaneous standing diversity that does not increase systematically with interval length and that, by ignoring single-interval genera, is not expected to be as sensitive to variation in preservation rate as is the total number of genera known from an interval (Pease 1985; Sepkoski 1990, 1993, 1996b, 1997, 1998; Buzas and Culver 1994, 1998; Raymond and Metz 1995; Harper 1996; Alroy 1996, 1998; Bambach 1999; Foote 2000). Diversity was measured on a logarithmic scale in order to monitor proportional change (Sepkoski 1991), but results are similar if an arithmetic scale is used.

For each interval, I estimated extinction rate (q_i) per lineage-million-years (Lmy) based on the proportion of genera present at the start of an interval that survived at least to the end of the interval. Similarly, I estimated origination rate (p_i) per Lmy based on the proportion of

genera present at the end of an interval that had already originated by the start of the interval. Thus, $\hat{q}_i = -\ln[(N_{bt})/N_b]/\Delta t$ and $\hat{p}_i = -\ln[(N_{bt})/N_t]/\Delta t$, where N_b is the total number of genera that cross the bottom interval boundary, N_t is the total number of genera that cross the top interval boundary, N_{bt} is the number of genera that cross both boundaries, and Δt is the duration of the interval (Foote 1999: Appendix 7; Foote 2000). Although \hat{p}_i and \hat{q}_i are estimates of the true values p_i and q_i , for simplicity I will hereinafter refer to these estimates as p_i and q_i . These rate estimates satisfy the requirements of branching theory that $N_{bt} = N_b e^{-q_i \Delta t}$, $N_{bt} = N_t e^{-p_i \Delta t}$, and $N_t = N_b e^{(p_i - q_i) \Delta t}$ (Kendall 1948; Raup 1985). A temporal sequence of rates therefore fully determines the temporal sequence of diversity. Note that the estimates are for average rates through an interval; the method of estimation does not assume that rates are constant within an interval.

The diversity measure and rate estimates ignore single-interval genera, a procedure that has been advocated by a number of paleontologists as a means of reducing the effects of incomplete and variable preservation (Pease 1985; Sepkoski 1990, 1993, 1996b, 1997, 1998; Alroy 1996, 1998; Harper 1996; Foote and Raup 1996; Foote 1997). The metrics I use are not simply ad hoc corrections, however. They derive from explicit, if simplified, modeling of evolution and preservation, and can be shown to be relatively insensitive to incomplete preservation under a range of conditions (Foote 2000). The rationale behind developing diversity and rate measures that ignore single-interval taxa is not that such taxa must be artifacts; surely some were truly restricted to single intervals. Rather, it is that the relative frequency of single-interval taxa is affected disproportionately by incomplete preservation (Sepkoski 1993; Foote and Raup 1996; Foote 1997, 2000). (Although the term *singleton* has been used to refer to species known from a single specimen [Buzas and Culver 1994, 1998], hereinafter I will use the term to refer to any taxon confined to a single stratigraphic or temporal interval [Alroy 1998].)

One potential result of the observed overabundance of singletons is of special concern

in this study. Rate metrics that include singletons assign these taxa to both the origination and extinction tabulations for a given interval. If the number of singletons fluctuates artificially as a result of varying quality of preservation, then a spurious correlation between origination and extinction rates may result. This can be shown theoretically (Foote 2000); it has also been shown empirically for Cenozoic mammals (Alroy 1996, 1998). Such a spurious correlation could make it difficult to separate diversity changes into their origination and extinction components. Singletons would not present such a problem if origination and extinction rates were equal within a given interval, since estimates of both rates would be affected equally. If the rates differ, however, the lower rate estimate is affected disproportionately. Rate estimates can be artificially correlated even with metrics that ignore singletons (Holland 1995; Holland and Patzkowsky 1999), but the effect is stronger when singletons are included (Foote 2000). Although variable preservation may obscure patterns of correlation between change in diversity and change in origination and extinction rates, it affects both rate metrics, and there is no obvious reason to think that it would act in a biased way to produce the Paleozoic/post-Paleozoic difference documented herein.

Because there are long-term secular trends in diversity and taxonomic rates, it is useful to analyze the short-term variation in the data with first differences. For each interval, the change in diversity ΔD_i was calculated as the logarithm of standing diversity at the end of the interval minus the log of standing diversity at the start of the interval. Intervals in which diversity did not change were excluded, but, because relatively few intervals lack a diversity change, the results are similar if they are included. The change in origination rate Δp_i was calculated as $p_i - p_{i-1}$, provided that p_i and p_{i-1} are both defined. (Rate estimates are undefined in the few cases where no genera of a given group range through the entire interval, usually the first interval of a group's existence or the last interval for an extinct group.) Likewise, Δq_i was calculated as $q_i - q_{i-1}$.

To reduce the effect of outliers and other

problematic aspects of data distribution, I used a nonparametric correlation coefficient, Kendall's τ . There is often a correlation (sometimes positive, sometimes negative) between Δp and Δq in the data analyzed here. It is not clear to what extent this is noise, to what extent it is a biological signal (Webb 1969; Mark and Flessa 1977), and to what extent it could reflect an artifact of variable preservation, errors in absolute dating, or pseudoextinction and pseudo-origination, nuisances that affect both rates similarly. Whatever the cause, it has the potential to affect patterns of correlation. I therefore measured the strength of the association between ΔD and Δp and between ΔD and Δq using partial correlations, $\tau_{(\Delta D, \Delta p) \cdot \Delta q}$ and $\tau_{(\Delta D, \Delta q) \cdot \Delta p}$. In some cases partial correlations reveal structure in the data that may not be evident otherwise (Figs. 1A, 2A). The use of partial correlations is not without its own risks, however. If the two correlations that one is attempting to factor out are nonexistent, so that their estimates represent noise distributed around zero, then it is possible for the correlation of interest to be inflated when the others are partialled out. In this study, however, the results are consistent if raw correlations are used. Moreover, if there were no difference between the Paleozoic and post-Paleozoic, the artificial inflation of apparent correlations should affect both broad intervals of time in the same way.

Relative Importance of Origination and Extinction

Changes in diversity, origination, and extinction are shown in Fig. 1 for all data over the entire Phanerozoic. The partial correlation between ΔD and Δp is positive as one would expect, although it is weak. Larger increases in origination rate tend to be associated with larger increases in diversity, and larger decreases in origination rate with larger decreases in diversity. Similarly, the partial correlation between ΔD and Δq is negative. Larger increases in extinction rate are associated with larger drops in diversity, and larger decreases in extinction rate with larger rises in diversity. The stronger correlation between ΔD and Δq suggests that, for animals as a whole over the Phanerozoic, variation in extinction rate may

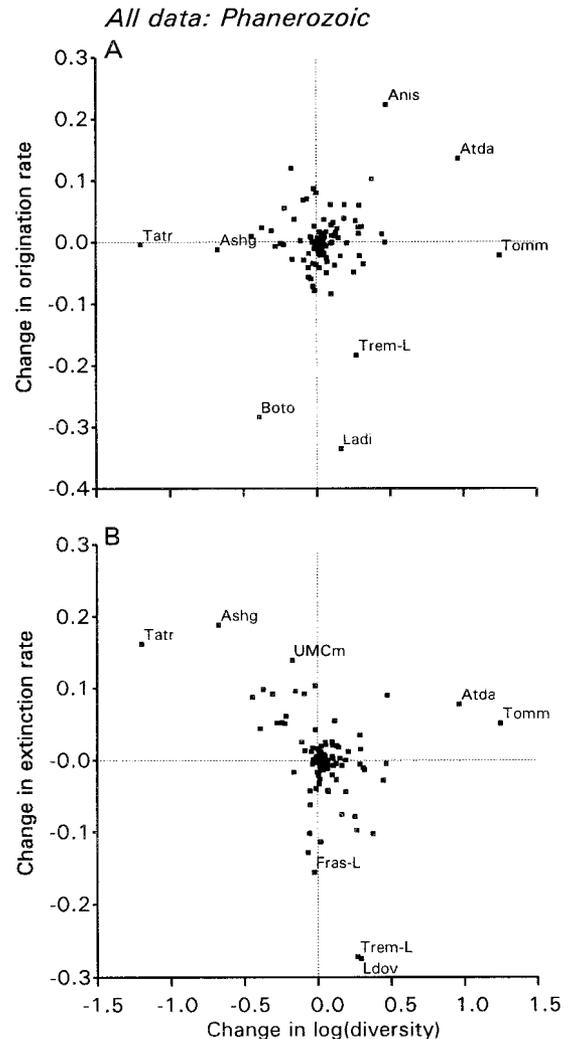


FIGURE 1. Comparison between change in diversity and change in per-capita origination rate (A) and extinction rate (B) for Phanerozoic marine animal genera. Partial correlation between change in diversity and change in origination rate is positive but weak ($\tau_{(\Delta D, \Delta p) \cdot \Delta q} = 0.190$), while the correlation is negative for extinction rate ($\tau_{(\Delta D, \Delta q) \cdot \Delta p} = -0.264$). Overall, the extinction correlation is stronger, suggesting that more of the variation in diversity changes is attributable to variation in extinction rate than origination rate. Intervals labeled in this and the next four figures are those that fall more than two standard deviations from the mean. Abbreviation: UMCm, Upper Middle Cambrian (sensu Sepkoski 1978). Other abbreviations are for standard stages and series.

be more important than variation in origination rate in producing short-term variation in diversity. This difference is consistent with previous observations that extinction rates are more variable than origination rates (see New-

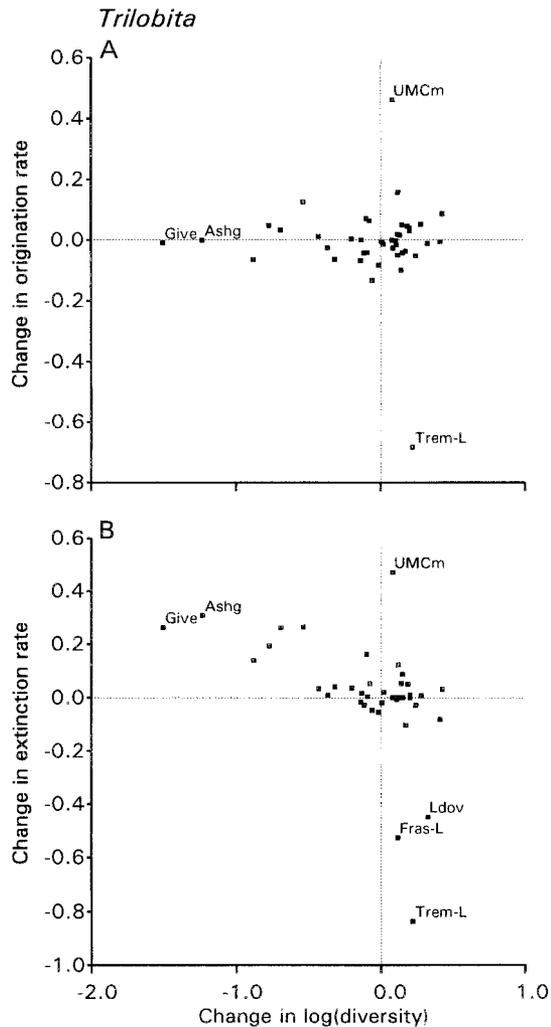


FIGURE 2. Comparison between change in diversity and change in per-capita origination rate (A) and extinction rate (B) for trilobite genera. As for the data as a whole, the extinction correlation is stronger ($\tau_{(\Delta D, \Delta p) - \Delta q} = 0.228$; $\tau_{(\Delta D, \Delta q) - \Delta p} = -0.420$).

ell 1967; Foote 1994; Sepkoski 1998). Nevertheless, differential variability of rates is unlikely to be the sole explanation for such differences (see below).

The comparison between origination and extinction correlations in Figure 1 may not seem very impressive. In fact, this portrayal represents something of a worst possible case for detecting variation in diversity dynamics. This is because the Phanerozoic data are quite heterogeneous. They are composed of taxa with very different characteristic rates (Van Valen 1973, 1985a; Stanley 1979, 1985, 1990;

Van Valen and Maiorana 1985; Sepkoski 1987, 1998), which are averaged together over a long span of time during which rates declined through the Paleozoic, rose again in the early Mesozoic, then declined again through the post-Paleozoic (Raup and Sepkoski 1982; Van Valen 1984; Sepkoski 1998). It is therefore worth exploring the relationships between diversity, origination, and extinction for more homogeneous subsets of data. The difference between origination and extinction correlations will then be assessed statistically by way of consistent patterns exhibited by various subsets of the data.

Trilobites provide an example of a major group that is restricted to the Paleozoic. Like the data as a whole, trilobites show a weak positive correlation between ΔD and Δp and a stronger, negative correlation between ΔD and Δq (Table 1, Fig. 2). The directions of correlation are unsurprising and nearly universal, so they will not be discussed further. Of more interest here is that, as for the Phanerozoic data as a whole, the extinction correlation is stronger than the origination correlation (Table 1). There is nevertheless substantial noise in the data; the effects of outliers and other potential artifacts will therefore be explored below.

An important post-Paleozoic group, the Echinoidea (Table 1, Fig. 3), shows the opposite pattern: the origination correlation is stronger than the extinction correlation. Cephalopods, a group with characteristically high taxonomic rates that spans both the Paleozoic and post-Paleozoic, show higher extinction correlations in the Paleozoic and higher origination correlations in the post-Paleozoic (Table 1, Fig. 4). The same difference is found for gastropods, a group with characteristically low taxonomic rates (Table 1, Fig. 5).

The partial correlations between ΔD and Δp and between ΔD and Δq are succinctly portrayed in the format of Figure 6, which shows the entire space of possible results. We would expect correlations to fall in the lower right quadrant, corresponding to a positive association between ΔD and Δp and a negative association between ΔD and Δq . A few results fall outside this quadrant. These are difficult to interpret, but they may reflect noise in the

TABLE 1. Partial correlations between change in diversity and change in origination rate and extinction rate. N is the number of multiple-interval genera. Difference is that between the absolute values of $\tau_{(\Delta D, \Delta p) \cdot \Delta q}$ and $\tau_{(\Delta D, \Delta q) \cdot \Delta p}$. Negative differences indicate that extinction correlation is stronger, positive differences that origination correlation is stronger. Statistical significance of individual correlations is not tested. For averages of taxa (bottom of table), medians are tested against null hypothesis of zero correlation and zero difference in correlation, with standard errors based on bootstrap resampling. Because there is an expectation of the sign of each correlation, tests for average correlation are one-tailed. Tests for difference in average correlation are two-tailed. †, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Group	Paleozoic				Post-Paleozoic			
	N	$\tau_{(\Delta D, \Delta p) \cdot \Delta q}$	$\tau_{(\Delta D, \Delta q) \cdot \Delta p}$	Difference	N	$\tau_{(\Delta D, \Delta p) \cdot \Delta q}$	$\tau_{(\Delta D, \Delta q) \cdot \Delta p}$	Difference
Arthropoda	1345	0.108	-0.436	-0.328	625	0.381	-0.289	0.092
Trilobita	837	0.228	-0.420	-0.192	—	—	—	—
Phacopida	180	0.412	-0.448	-0.036	—	—	—	—
Proetida	142	0.293	-0.398	-0.105	—	—	—	—
“Ptychopariida”	168	0.272	-0.259	0.013	—	—	—	—
Malacostraca	28	—	—	—	199	0.540	-0.357	0.183
Ostracoda	444	-0.053	-0.374	-0.321	361	0.400	-0.193	0.207
Brachiopoda	1187	0.147	-0.391	-0.243	313	0.360	-0.261	0.100
Articulata	1069	0.178	-0.329	-0.151	309	0.358	-0.216	0.142
Orthida	168	0.252	-0.362	-0.110	—	—	—	—
Rhynchonellida	129	0.244	-0.501	-0.258	99	0.387	-0.333	0.053
Spiriferida	199	0.230	-0.467	-0.237	16	—	—	—
Strophomenida	403	0.321	-0.296	0.025	0	—	—	—
Terebratulida	37	—	—	—	183	0.474	-0.097	0.377
Lingulata	103	0.059	-0.559	-0.501	4	—	—	—
Bryozoa	315	-0.073	-0.303	-0.229	477	0.179	-0.300	-0.120
Gymnolaemata	5	—	—	—	331	0.303	-0.208	0.095
Stenolaemata	310	-0.081	-0.313	-0.232	145	0.170	-0.352	-0.181
Chordata	262	0.167	-0.308	-0.142	811	0.327	-0.264	0.063
Conodonts	168	0.328	-0.336	-0.008	7	—	—	—
Chondrichthyes	21	—	—	—	109	0.303	-0.218	0.085
Osteichthyes	17	—	—	—	549	0.310	-0.245	0.066
Cnidaria	458	0.364	-0.439	-0.075	262	0.333	-0.345	-0.012
Anthozoa	436	0.250	-0.389	-0.139	252	0.367	-0.409	-0.041
Rugosa	313	0.336	-0.419	-0.083	—	—	—	—
Tabulata	121	0.377	-0.544	-0.167	—	—	—	—
Scleractinia	—	—	—	—	236	0.347	-0.409	-0.062
Echinodermata	480	0.275	-0.229	0.047	454	0.320	-0.235	0.085
Crinoidea	314	0.295	-0.455	-0.160	83	0.238	-0.216	0.022
Cladida	145	0.365	-0.361	0.003	—	—	—	—
Echinoidea	3	—	—	—	296	0.548	-0.208	0.340
Regular	3	—	—	—	114	0.493	-0.199	0.294
Irregular	—	—	—	—	179	0.351	-0.266	0.085
Graptolithina	89	0.295	-0.577	-0.282	—	—	—	—
Mollusca	860	0.326	-0.511	-0.185	3417	0.376	-0.325	0.051
Bivalvia	137	0.281	-0.347	-0.066	1138	0.248	-0.344	-0.095
Heterodonta	7	—	—	—	685	0.261	-0.399	-0.138
Pteriomorpha	59	—	—	—	331	0.336	-0.207	0.129
Cephalopoda	405	0.287	-0.481	-0.194	532	0.465	-0.361	0.104
Ammonoidea	157	0.277	-0.607	-0.330	446	0.501	-0.355	0.146
Nautiloidea	246	0.274	-0.443	-0.169	21	—	—	—
Gastropoda	214	0.079	-0.531	-0.452	1705	0.420	-0.209	0.211
Archaeogastropoda	120	0.264	-0.431	-0.167	227	0.475	-0.334	0.141
Neogastropoda	—	—	—	—	663	0.302	-0.321	-0.019
Neotaenioglossa	18	—	—	—	616	0.424	-0.220	0.203
Opisthobranchia	3	—	—	—	180	0.492	-0.289	0.204
Porifera	170	0.361	-0.466	-0.105	126	0.460	-0.205	0.255
Cambrian fauna	1048	0.188	-0.399	-0.212	4	—	—	—
Paleozoic fauna	3087	0.130	-0.322	-0.191	1725	0.311	-0.171	0.140
Modern fauna	783	0.144	-0.388	-0.244	5306	0.348	-0.214	0.133
All data	5750	0.199	-0.362	-0.164	7552	0.292	-0.201	0.091
Median of phyla	—	0.221**	-0.414***	-0.193*	—	0.347***	-0.277***	0.070*
Median of classes	—	0.239***	-0.405***	-0.166*	—	0.358***	-0.218***	0.140*
Median of orders	—	0.277***	-0.431***	-0.154***	—	0.406***	-0.327***	0.079

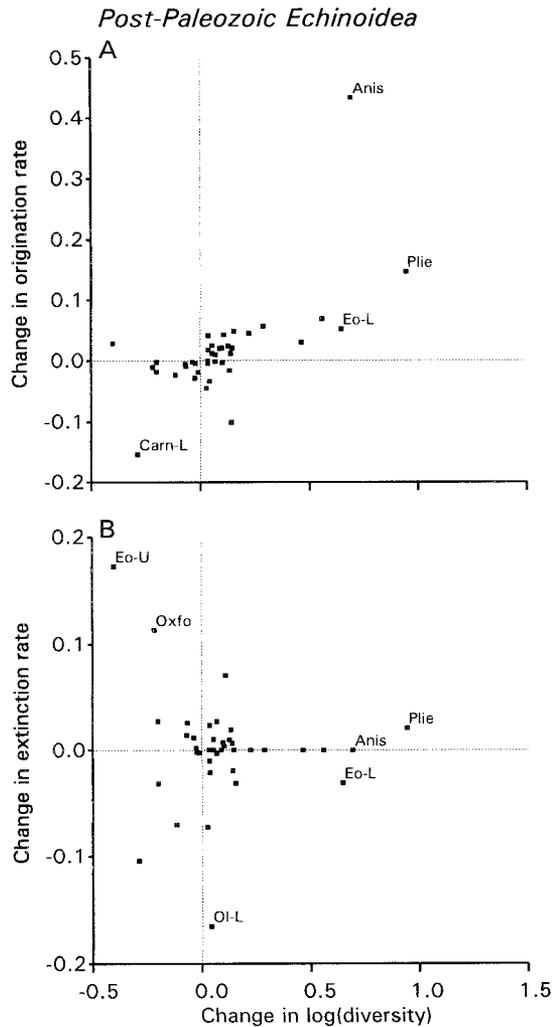


FIGURE 3. Comparison between change in diversity and change in per-capita origination rate (A) and extinction rate (B) for post-Paleozoic echinoids. In contrast to the data as a whole, the origination correlation is stronger ($\tau_{(\Delta D, \Delta p)} = 0.548$; $\tau_{(\Delta D, \Delta e)} = -0.208$).

data. The dotted line of slope -1 is a line of isometry, or equal strength of the two correlations. The Paleozoic falls below this line while the post-Paleozoic is above it. The angle between a pair of correlations and the line of isometry will be used below to measure the deviation from isometry.

Figures 7–9 and Table 1 show results for phyla, classes, and orders. Since all three levels show the same pattern, they will be presented together in subsequent figures. For separate Paleozoic and post-Paleozoic analyses, each higher taxon was analyzed if it had

at least 100 multiple-interval genera first appearing in the given time span. In addition, I analyzed three groups that fell short of this criterion: Graptolithina, because of its paleontological importance in the Paleozoic, and post-Paleozoic Crinoidea and Rhynchonellida, to enable comparison with the Paleozoic (Table 1). In general, a higher taxon was not broken down into subtaxa if most of the Paleozoic genera belong to a single subtaxon and most of the post-Paleozoic genera belong to a different subtaxon. Thus, for example, Ostracoda was not divided into Paleozoic Palaeocopida and post-Paleozoic Podocopida. A number of higher taxa are confined to either the Paleozoic or the post-Paleozoic (e.g., trilobites in the Paleozoic, scleractinian corals after the Paleozoic) or have sufficient diversity to allow analysis in only one of these two major time intervals (e.g., lingulate brachiopods in the Paleozoic, gymnolaemate bryozoans after the Paleozoic). Those taxa that are diverse throughout much of the Phanerozoic, however, tend to shift toward greater strength of correlation between changes in diversity and changes in origination rate (Table 1).

The pattern can be compared against the null hypothesis that time (Paleozoic vs. post-Paleozoic) does not predict the side of the line of isometry to which a higher taxon falls. The results are generally inconsistent with this null hypothesis, based on a two-tailed Fisher exact test: for phyla $p = 0.041$; for classes $p = 0.00011$; and for orders $p = 0.079$. (It should be noted that, with only 16 phylum-level observations contributing to this first test [8 Paleozoic and 8 post-Paleozoic], the probability distribution is rather discontinuous. The only probabilities that could have been obtained in the immediate neighborhood of $p = 0.041$ are $p = 0.13$, $p = 0.12$, $p = 0.077$, $p = 0.041$, $p = 0.026$, $p = 0.010$, and $p = 0.0070$. It is therefore possible that the shift of a small number of points from one side of the line to the other could substantially affect our perception of the significance of this result.)

Although the relative roles of origination and extinction are opposite in the Paleozoic and post-Paleozoic, the post-Paleozoic is not a simple reflection of the Paleozoic. The predominance of Paleozoic extinction correla-

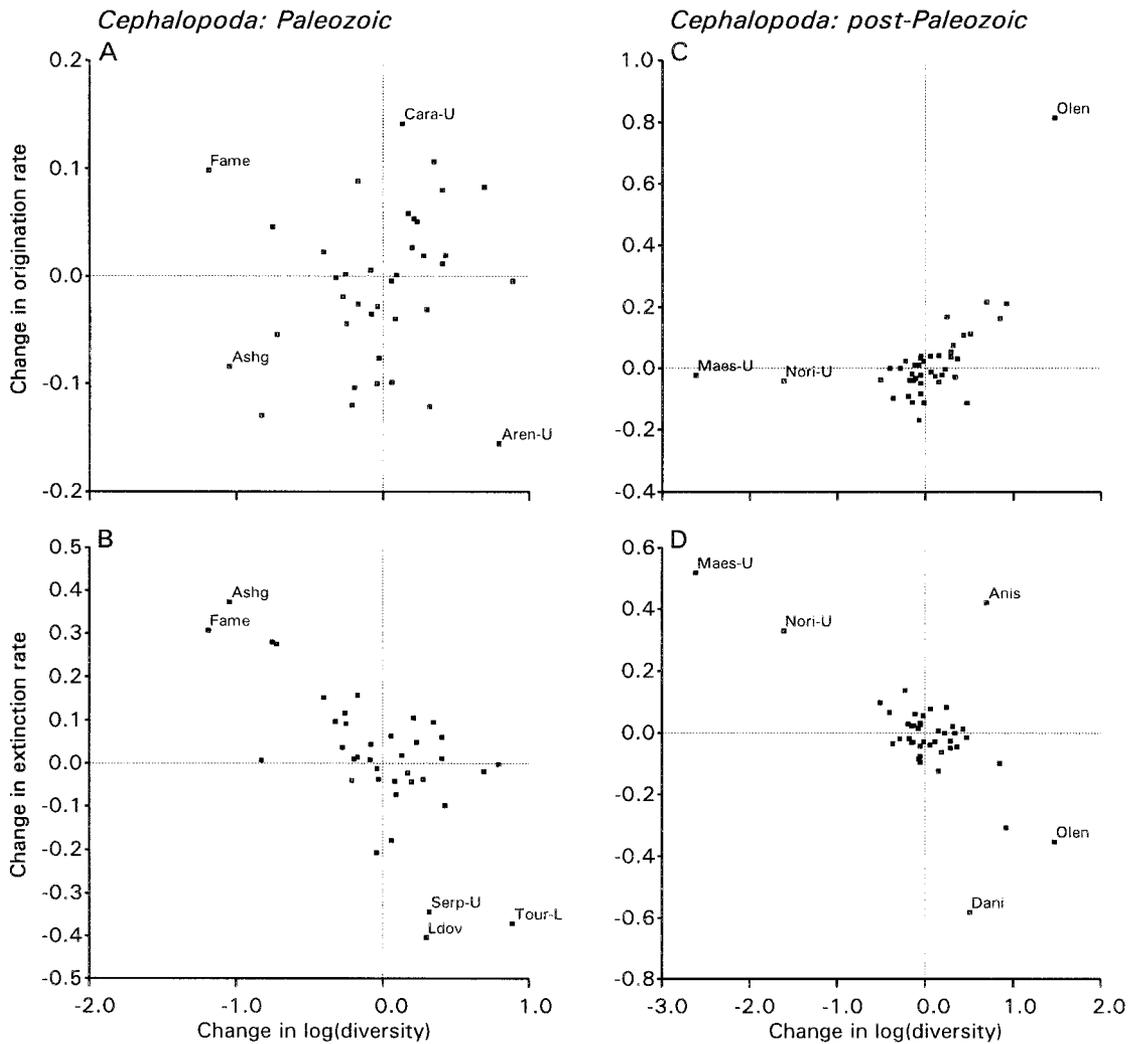


FIGURE 4. Comparison between change in diversity and change in per-capita origination rate and extinction rate for Paleozoic (A and B) and post-Paleozoic (C and D) cephalopods. In the Paleozoic, the extinction correlation is stronger ($\tau_{(\Delta D, \Delta p) \cdot \Delta q} = 0.287$; $\tau_{(\Delta D, \Delta q) \cdot \Delta p} = -0.481$), while the origination correlation is stronger in the post-Paleozoic ($\tau_{(\Delta D, \Delta p) \cdot \Delta q} = 0.465$; $\tau_{(\Delta D, \Delta q) \cdot \Delta p} = -0.361$).

tions over origination correlations is greater than the subsequent predominance of origination correlations over extinction correlations. This can be seen in the differences between $\tau_{(\Delta D, \Delta p) \cdot \Delta q}$ and $\tau_{(\Delta D, \Delta q) \cdot \Delta p}$ (Table 1) and in the angular deviation from the line of isometry (Figs. 7–9). Moreover, Paleozoic extinction correlations tend to be greater than post-Paleozoic origination correlations, and post-Paleozoic extinction correlations tend to be greater than Paleozoic origination correlations (Table 1). This suggests that the overall tendency for animals during the Phanerozoic is

toward greater importance of extinction. This of course is the same pattern shown in Figure 1.

We see the same shift from extinction- to origination-dominance if the data are decomposed into sets of higher taxa constituting the three “evolutionary faunas” (Sepkoski 1981, 1984). Since each fauna represents a number of taxa showing similar diversity histories, and since the faunas are distinct in their diversity patterns and evolutionary rates, one might expect that they would show characteristically different correlations between diversity change and change in taxonomic rates. In-

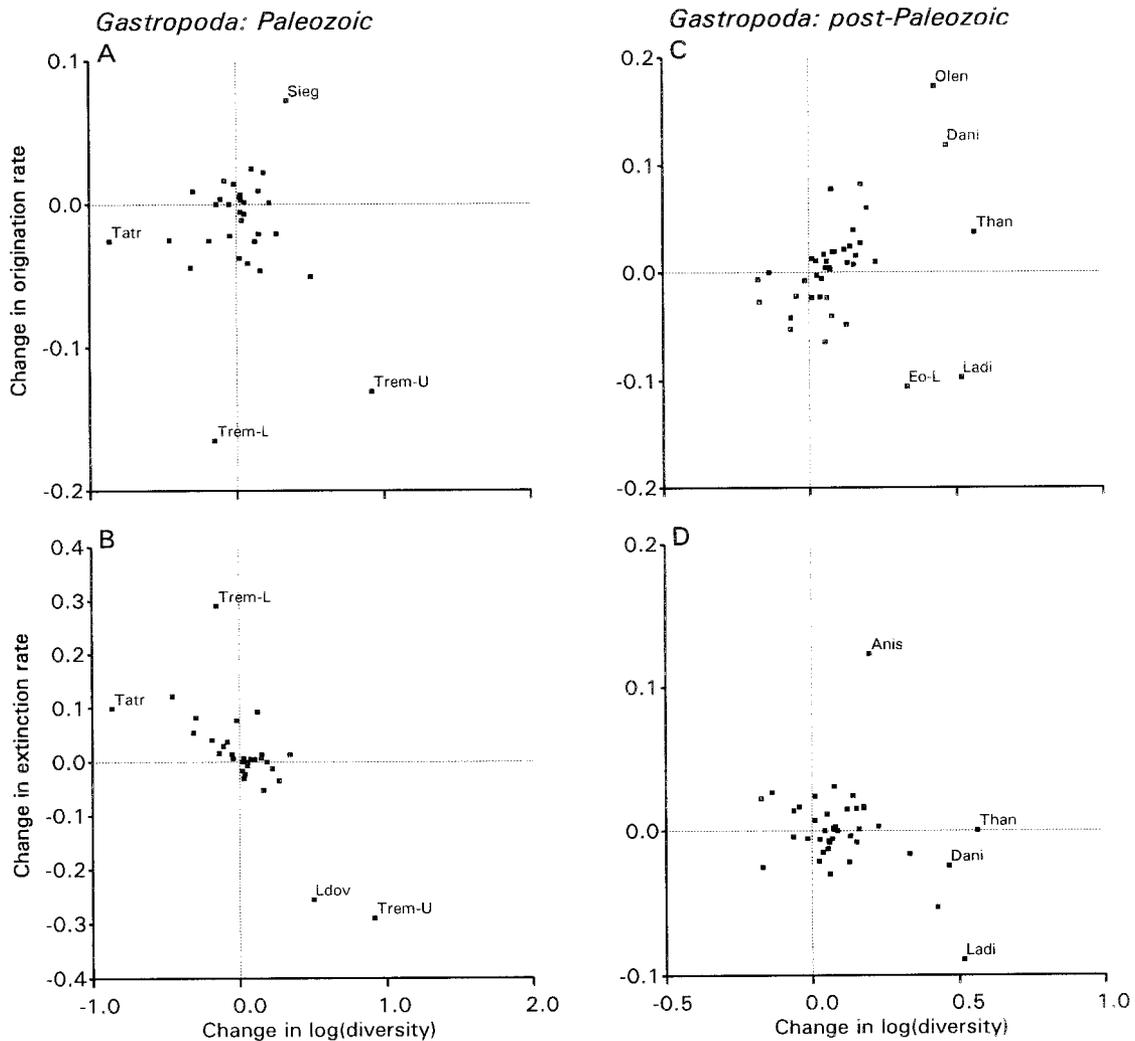


FIGURE 5. Comparison between change in diversity and change in per-capita origination rate and extinction rate for Paleozoic (A and B) and post-Paleozoic (C and D) gastropods. In the Paleozoic, the extinction correlation is stronger ($\tau_{(\Delta D, \Delta p), \Delta q} = 0.079$; $\tau_{(\Delta D, \Delta q), \Delta p} = -0.531$), while the origination correlation is stronger in the post-Paleozoic ($\tau_{(\Delta D, \Delta p), \Delta q} = 0.420$; $\tau_{(\Delta D, \Delta q), \Delta p} = -0.209$).

stead, the evolutionary faunas behave like Metazoa and like individual higher taxa (Table 1, Fig. 10).

These results suggest a striking directionality in the history of animal life. Changes in diversity are more strongly determined by changes in extinction rate than by changes in origination rate during the Paleozoic. After the Paleozoic the relative importance of origination and extinction is reversed. There are a number of biological explanations that could plausibly contribute to this transition. Before

they are explored, however, some potential biases need to be considered.

Potential Biases

Choice of Rate Metric.—The extinction and origination metrics I have used incorporate interval length in an attempt to estimate per-capita rates, and they ignore singletons in an attempt to correct for incomplete preservation. Although the rate metric chosen can be justified theoretically, we can also explore the sensitivity of the results empirically. For example,

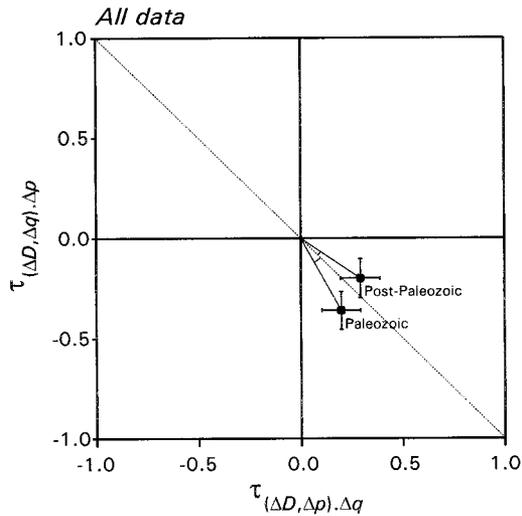


FIGURE 6. Correlation between diversity change and origination change (abscissa) versus correlation between diversity change and extinction change (ordinate) for all Paleozoic genera and all post-Paleozoic genera. Error bars show ± 1 standard error, based on the normal approximation (Siegel and Castellan 1988). The lower right quadrant is where correlations are generally expected to lie (positive for origination and negative for extinction). The dotted line with slope -1 shows the expected relationship if origination correlations and extinction correlations are equally strong. Below this line, extinction correlations are stronger; above the line, origination correlations are stronger. Direction and magnitude of deviation from equal strength (isometry) can be measured by the angle between the line of isometry and the vector to the pair of correlations.

tabulating percent origination and extinction (number of origination and extinction events normalized by total diversity) is quite different from the approach used here, as it does not normalize for interval length and it includes singletons. The results are nevertheless consistent even if this very different metric is used (Fig. 11). Results (not presented) are also consistent for a number of other metrics, including percent origination and extinction normalized by interval length, number of events normalized by interval length and by estimated average standing diversity (Van Valen 1984), and a variation on this last metric (Harper 1996) in which singletons are omitted. Thus, the major Paleozoic/post-Paleozoic asymmetry is unlikely to be an artifact of the rate metric chosen.

Edge Effects, Mass Extinctions, and Other Outliers in the Data.—The distributions of ΔD , Δp , and Δq (Figs. 1–5) suggest the possibility that the results could be unduly influenced by extreme rates at the start or end of the time series (Van Valen 1984, 1985a; Van Valen and Maiorana 1985; Gilinsky and Bambach 1987; Foote 1999: Appendix 7; Foote 2000), by a few large origination or extinction episodes, or by a few anomalous points that result from error in absolute dating. There are a number of reasons

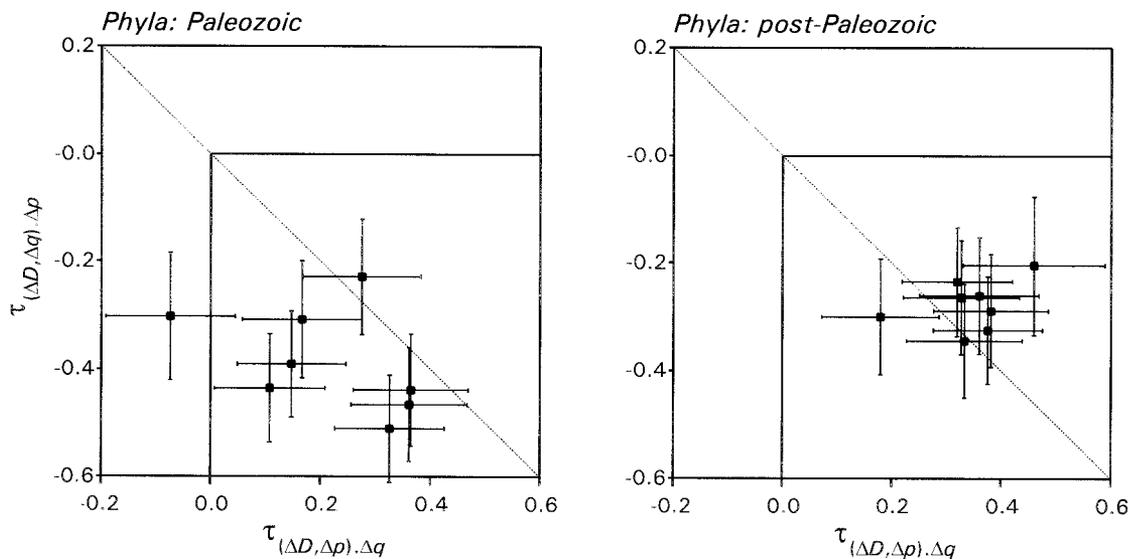


FIGURE 7. Extinction and origination correlations for phyla in the Paleozoic and post-Paleozoic. Scale is different from that of Figure 6; lower right quadrant is outlined by a bold line. Extinction correlations tend to be stronger in the Paleozoic, while origination correlations tend to be stronger in the post-Paleozoic. See Table 1 for list of phyla.

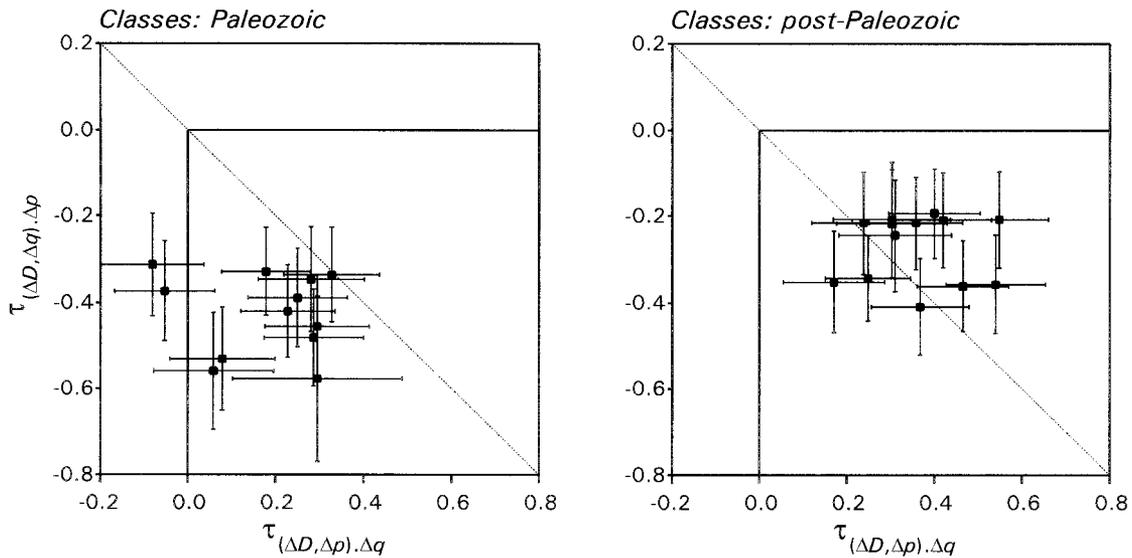


FIGURE 8. Extinction and origination correlations for classes in the Paleozoic and post-Paleozoic. As for phyla, extinction correlations tend to be stronger in the Paleozoic, and origination correlations tend to be stronger in the post-Paleozoic. See Table 1 for list of classes.

to think that the Paleozoic/post-Paleozoic asymmetry is not an artifact, however:

1. The correlations between change in diversity and change in rate are measured with a rank-order statistic. Thus, for example, the end-Ordovician and late-Permian increases in extinction rate, which sit well above the bulk of the data in Figure 1B, have the same influ-

ence on the correlation coefficients that they would have if they were just slightly above the rest of the data.

2. Analyses were repeated with the first and last four intervals of each time series omitted. The results (Fig. 12) are largely consistent with those in which all intervals are included.

3. Extremes in the origination and extinc-

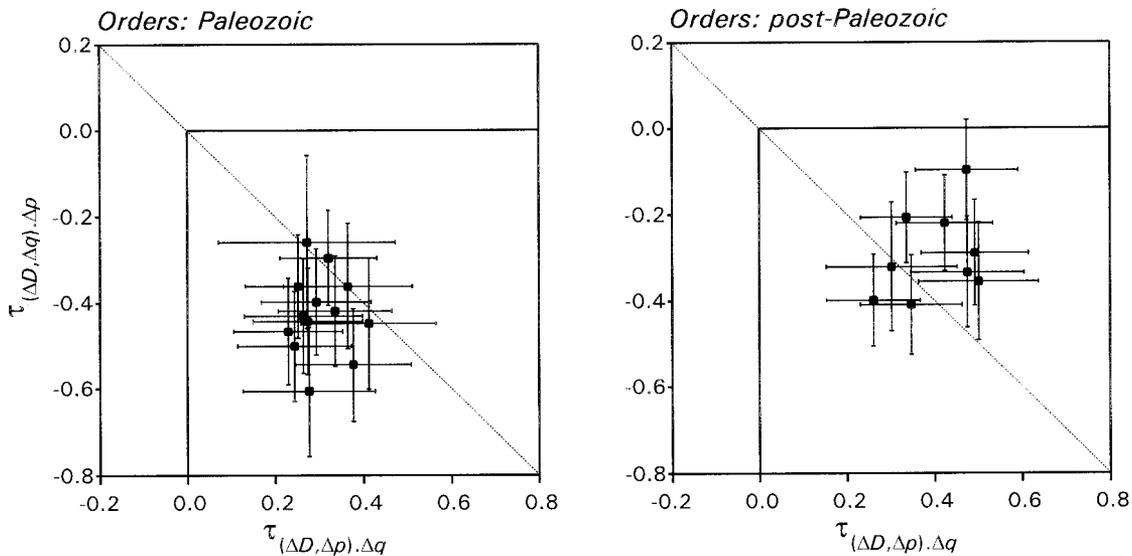


FIGURE 9. Extinction and origination correlations for orders in the Paleozoic and post-Paleozoic. Orders show the same pattern as phyla and classes. See Table 1 for list of orders.

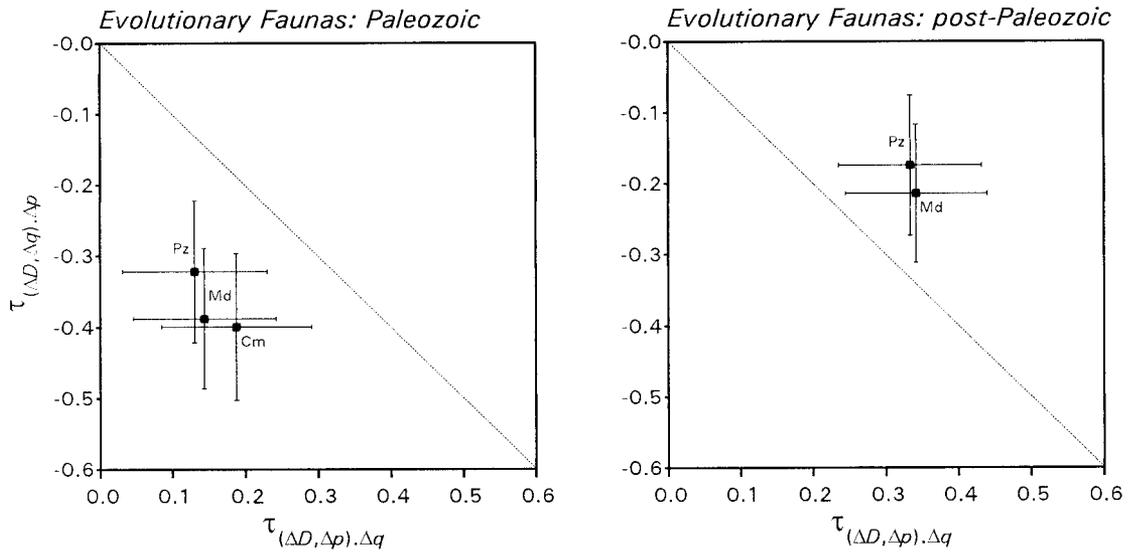


FIGURE 10. Extinction and origination correlations for the Paleozoic and post-Paleozoic, with genera sorted into the three Evolutionary Faunas: Cambrian (Cm), Paleozoic (Pz), and Modern (Md). Classes were assigned to the faunas according to Sepkoski (1984); classes not assigned by Sepkoski to any of the faunas were omitted. Extinction correlations are stronger during the Paleozoic, and origination correlations are stronger after the Paleozoic. Cambrian fauna is omitted from the post-Paleozoic analysis since it has very low diversity (Table 1).

tion data were identified in two ways and removed. In one approach, extremes were identified as those intervals in each time series with the highest ratios of origination or extinction rate to the average rate of the two adjacent intervals. In the other approach, ex-

tremes were identified as those intervals with the largest absolute increase in rate relative to the previous interval. The second approach is relevant to the "outliers" labeled on Figures 1–5. The number of extremes culled was varied; up to five origination peaks and five ex-

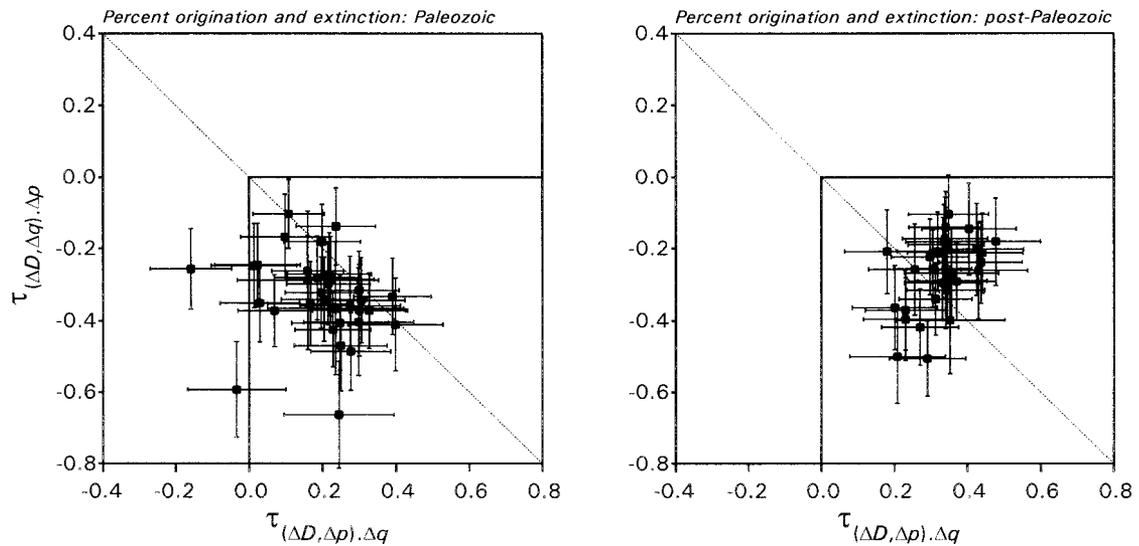


FIGURE 11. Extinction and origination correlations for phyla, classes, and orders in the Paleozoic and post-Paleozoic, using percent origination and extinction (number of events normalized by total diversity) rather than per-capita rates. The pattern of stronger extinction correlations in the Paleozoic and stronger origination correlations in the post-Paleozoic persists. Similar results are found for other origination and extinction metrics as well.

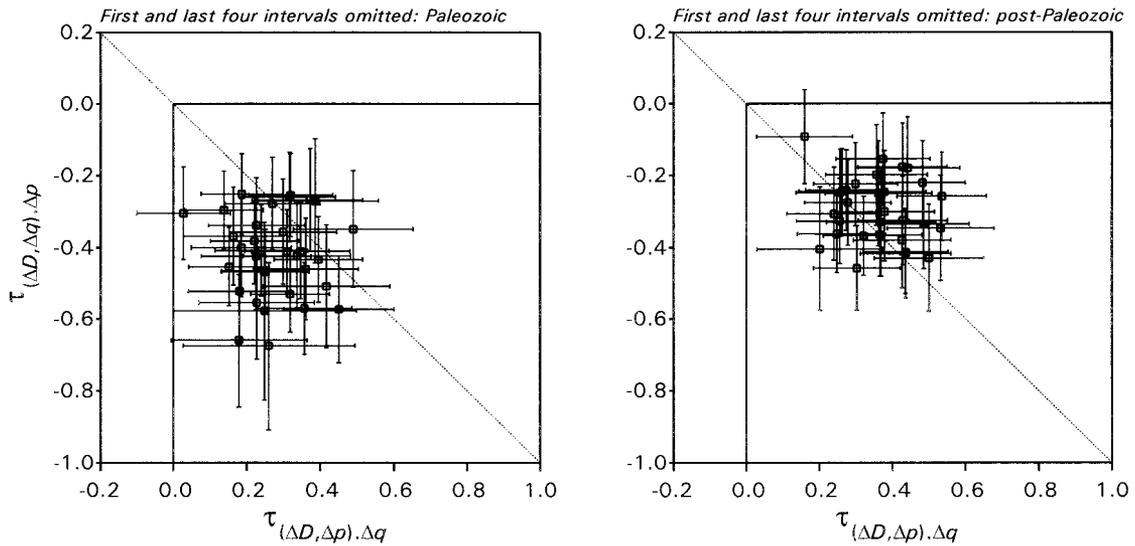


FIGURE 12. Extinction and origination correlations for all taxonomic levels, with first and last four intervals omitted from the time series for each taxon. There is still a tendency for stronger extinction correlations in the Paleozoic and stronger origination correlations in the post-Paleozoic, suggesting that this pattern is not an artifact of edge effects.

tion peaks were removed. When an interval was removed, the change from the preceding interval and the change to the succeeding interval were both ignored. Thus, up to ten changes (or about 20% of each time series) were removed. Figure 13 shows the results of

an extreme culling procedure. The correlations clearly tend to fall closer to the line of isometry than they do in the analysis of raw data, showing that extremes have an influence. The Paleozoic points are nevertheless concentrated below this line and the post-Paleozoic

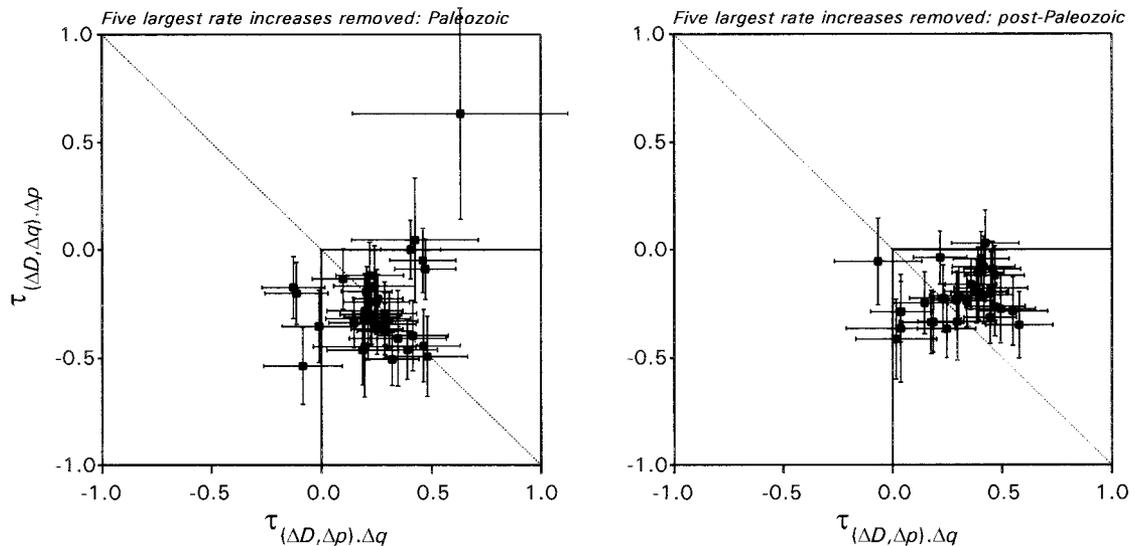


FIGURE 13. Extinction and origination correlations for all taxonomic levels, omitting intervals in which the five largest increases in origination rate and extinction rate occur. There is still a tendency for stronger extinction correlations in the Paleozoic and stronger origination correlations in the post-Paleozoic, suggesting that this pattern is not determined by extreme events only.

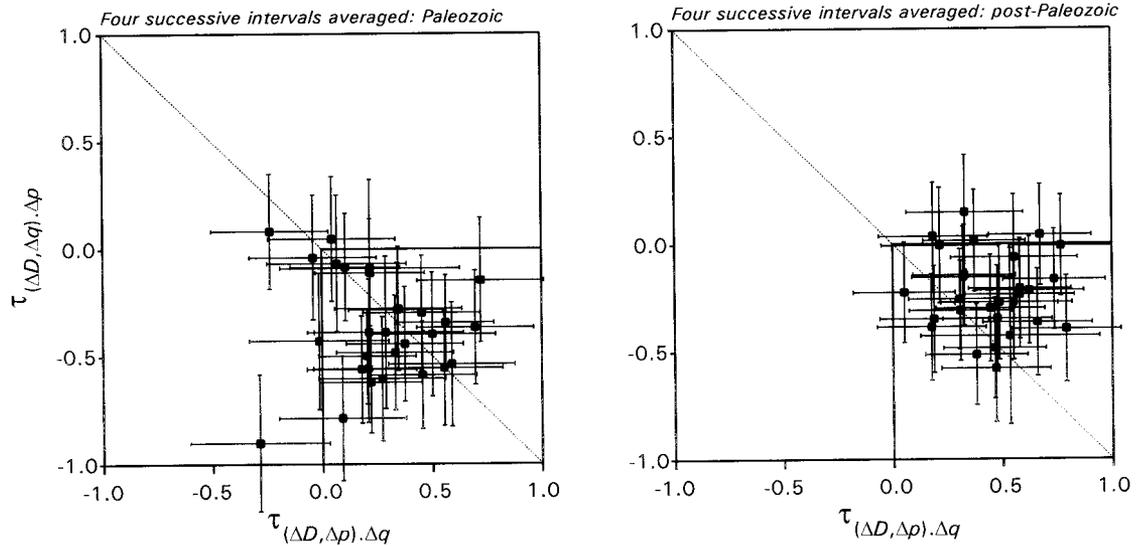


FIGURE 14. Extinction and origination correlations for all taxonomic levels, with diversity changes and average rates tabulated across four successive intervals. Sets of four intervals are nonoverlapping. There is still a tendency for stronger extinction correlations in the Paleozoic and stronger origination correlations in the post-Paleozoic, but this tendency is damped. See text for discussion.

points above it. Results of less extreme culling procedures are consistent with these.

4. To reduce the influence of absolute dating error, which affects estimates of origination and extinction rate similarly, the rates for nonoverlapping sets of n successive intervals were averaged as

$$\bar{p} = \frac{\sum_{i=1}^n p_i \Delta t_i}{\sum_{i=1}^n \Delta t_i},$$

and similarly for \bar{q} , where Δt_i is the estimated interval duration and n is varied up to 4. Note that these are not moving averages. With this method of averaging, only the errors in the base of the first interval and the top of the last interval are relevant (Foote 1999: Appendix 7). For each set of intervals, ΔD was calculated as the log of diversity at the end of the last interval minus the log of diversity at the start of the first interval, and Δp and Δq were calculated as the average rate for the set of intervals minus the average rate for the previous set of intervals. If four successive intervals are averaged together, the results are much noisier since fewer changes contribute to each estimated correlation (Fig. 14). Nevertheless, there is still a tendency for Paleozoic data to

be concentrated below the line of isometry and post-Paleozoic data above this line.

While the foregoing procedure represents an attempt to compensate for dating error, it also results in an analysis of diversity changes at a coarser temporal scale. Thus, the difference between these analyses and analyses of raw data does not simply reflect dating error. In fact, the results based on percent origination and extinction (Fig. 11), to which dating error does not contribute, are substantially in agreement with the analyses of raw data. Moreover, dating error affects origination and extinction rates similarly, so it should tend to blur rather than create distinctions between them. Thus, error in absolute dating does not seem to have a major influence on the observed Paleozoic/post-Paleozoic asymmetry.

Taxonomic Level.—Although many large-scale patterns of diversity, origination, and extinction are similar across taxonomic levels (Sepkoski et al. 1981; Bambach and Sepkoski 1992; Sepkoski 1997), there are often conspicuous differences. For example, the average trajectory of diversity over the Phanerozoic is similar at the genus and family levels, but there is much more variation around this average at the genus level (Sepkoski 1997). One

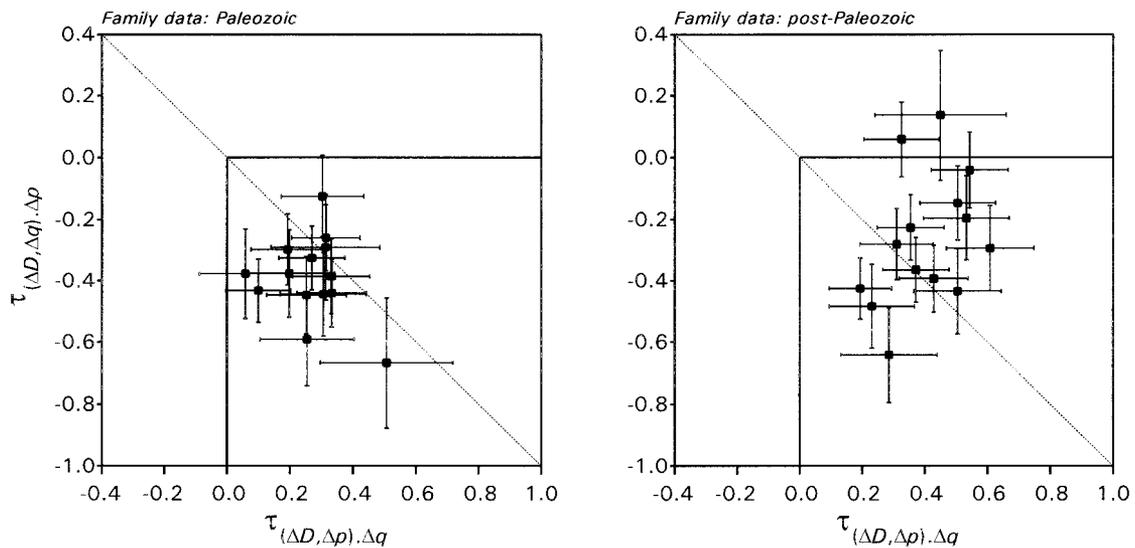


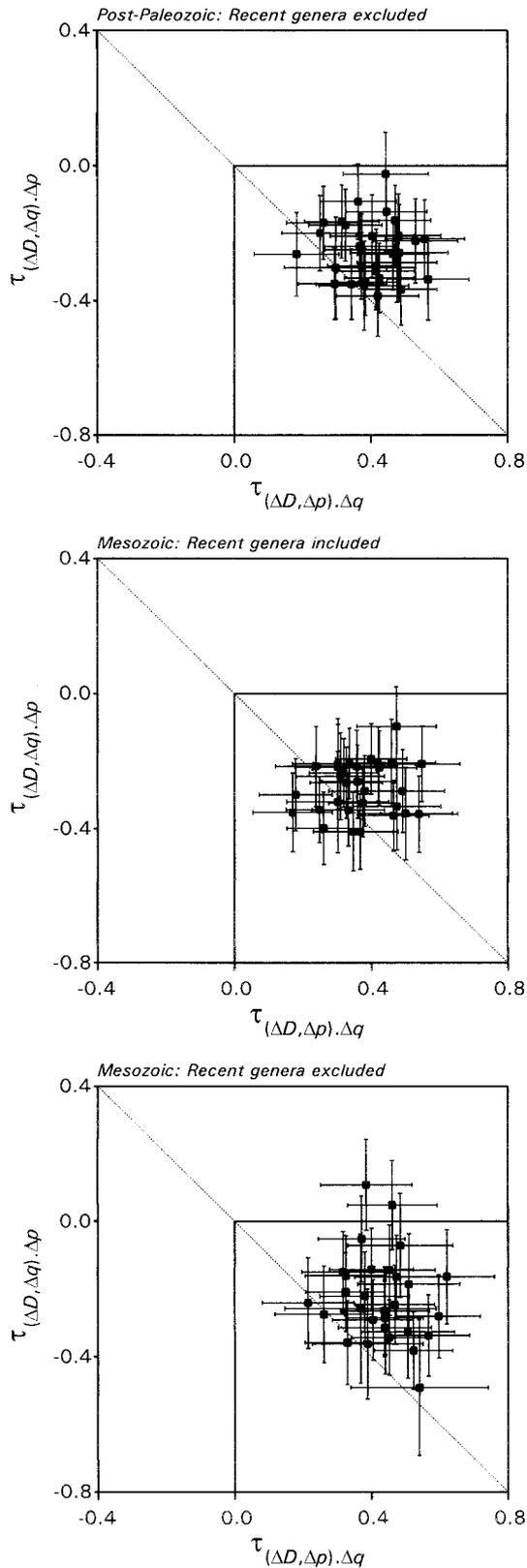
FIGURE 15. Extinction and origination correlations for phyla and classes, based on families within higher taxa. Data are from Sepkoski (1992) with updates (J. J. Sepkoski Jr. personal communication 1998). Higher taxa analyzed are: Arthropoda, Trilobita, Ostracoda, Brachiopoda, Articulata, Bryozoa, Chordata, Cnidaria, Anthozoa, Echinodermata, Crinoidea, Echinoidea, Mollusca, Bivalvia, Cephalopoda, Gastropoda, and Porifera. Orders generally have too few families to permit analysis. Families show the same tendency as genera toward stronger extinction correlations in the Paleozoic and stronger origination correlations in the post-Paleozoic.

might expect this difference in volatility to influence the dynamics of diversification (Gilinsky 1994, 1998). We find, however, that the Paleozoic/post-Paleozoic asymmetry is also present when diversity, origination, and extinction are measured at the level of families within higher taxa (Fig. 15).

Pull of the Recent.—There are a number of reasons to suspect that the Pull of the Recent (Raup 1972, 1979) and related factors could influence the results documented here. Average taxonomic rates decline toward the Recent (Raup and Sepkoski 1982; Van Valen 1984), and quality of preservation may have increased (Raup 1976b, 1979). Both factors tend to reduce the number of singletons, which are excluded from analysis, as we approach the Recent. Inclusion of singletons, however, did not affect the results of this study materially (Fig. 11). An additional problem relates to our essentially complete knowledge of the living fauna. Because of this, (1) the nearly monotonic increase in diversity through the Cenozoic may be partly an artifact (Sepkoski 1997; Foote 2000). Moreover, (2) a genus that is known only from its first fossil appearance and the Recent will be a singleton as far as the

fossil record is concerned, but it will not be excluded from analysis. It will therefore contribute positively to the origination rate for its interval of first fossil appearance. The number of these fossil singletons that artificially contribute to the origination rate should increase toward the Recent. These two factors suggest the potential for a spurious correlation between increases in diversity and increases in origination rate.

The nature of the origination and extinction metrics used here suggests that the post-Paleozoic pattern is not an artifact of complete knowledge of the living fauna. Mathematical modeling of cladogenesis and incomplete preservation suggests that the estimate of origination rate should be unaffected while the estimate of extinction rate should decline artificially (Foote 2000). It is nevertheless worth exploring this potential bias empirically. Sepkoski's genus data systematically include only first and last appearances. As a means of compensating for the Pull of the Recent, Sepkoski (personal communication 1998; see Sepkoski 1993, 1997) had begun to note which of the extant genera in his compendium have Plio-Pleistocene fossil occurrences. To



the best of my knowledge, this task was not completed. I have therefore taken two other approaches (Raup 1991; Foote and Sepkoski 1999): (1) to exclude extant genera from analysis of the post-Paleozoic, and (2) to exclude the Cenozoic altogether. (There are very few Paleozoic genera still extant. Although Paleozoic data were reanalyzed without extant genera, the results barely differ from those in which extant genera are included and are therefore not presented here.) Both approaches yield results largely in agreement with those based on the raw data (Fig. 16).

Potential Biological Explanations

Having ruled out plausible artifacts that may contribute to the apparent Paleozoic/post-Paleozoic difference in diversity dynamics, we can consider some likely biological explanations. It is possible to rule out some candidates, but I have been unable to produce results that would conclusively point to one explanation.

Stationary versus Increasing Diversity.—One of the most conspicuous differences between the Paleozoic and post-Paleozoic is that there is little trend in diversity from the Silurian through the Permian, while there is a sustained increase in diversity through much of the post-Paleozoic (Sepkoski 1997). It seems obvious to suppose that this increase in diversity, marked by the exploitation of new adaptive zones (Bambach 1985), might underlie the difference in diversity-rate correlations. There are, however, at least three reasons to believe that whether changes in diversity are more strongly extinction- or origination-dominated is not simply a function of whether diversity is stable or increasing. (1) Several Paleozoic taxa show a stronger extinction correlation even though they increase in diversity after the early Paleozoic (e.g., bivalves, crinoids), while a number of post-Paleozoic taxa

←

FIGURE 16. Extinction and origination correlations for post-Paleozoic data at all taxonomic levels. Compare with Figures 7–9. Results are similar whether extant genera are included or excluded and whether the Cenozoic is included or excluded. Stronger origination correlations in the post-Paleozoic are therefore not likely to be artifacts of the Pull of the Recent.

show a stronger origination correlation even though they do not diversify steadily through the post-Paleozoic (e.g., ammonoids, brachiopods). (2) If increasing diversity itself were the explanation for the stronger origination correlations seen in the post-Paleozoic, we would expect the Cambro-Ordovician data to show this pattern. A comparison between the Cambro-Ordovician, a time of general diversity increase and ecological expansion, and the Silurian-Permian, a time of relatively stationary diversity for animals as a whole, nevertheless shows that extinction correlations tend to be stronger than origination correlations for both segments of the Paleozoic (Fig. 17). (3) Simulation of an idealized diversification process (Raup et al. 1973) in which origination rate and extinction rate are stationary and equally variable, and in which origination rate exceeds extinction rate, yields diversity histories that, on average, have equal correlation between ΔD and Δp and between ΔD and Δq (results not presented).

Average Rates, Volatility, and the Loss of Extinction-Dominated Taxa.—The Phanerozoic decline in average taxonomic rates within marine animals partly reflects the loss of taxa with higher characteristic rates (Van Valen and Boyajian 1987; Van Valen 1994). It is conceivable that the greater volatility of high-rate groups (Gilinsky 1994, 1998), many of which were filtered at the Permian/Triassic boundary, caused Paleozoic diversity to be more strongly regulated by extinction pulses than was post-Paleozoic diversity. There are at least two reasons to suspect that this is not the case, however. (1) Whether a group has stronger correlations between diversity and extinction or origination appears not to be an intrinsic property of that group. Taxa that persist through the Permian/Triassic bottleneck shift from stronger extinction correlations to stronger origination correlations (Table 1, Figs. 7–9). Of course, it is still possible that the relevant filtering is at the level of subtaxa within orders, but the number of genera within suborders and families is generally not adequate to test this. (2) Average rates of origination and extinction are not very good predictors of how far and in what direction a taxon deviates from the null expectation that changes in di-

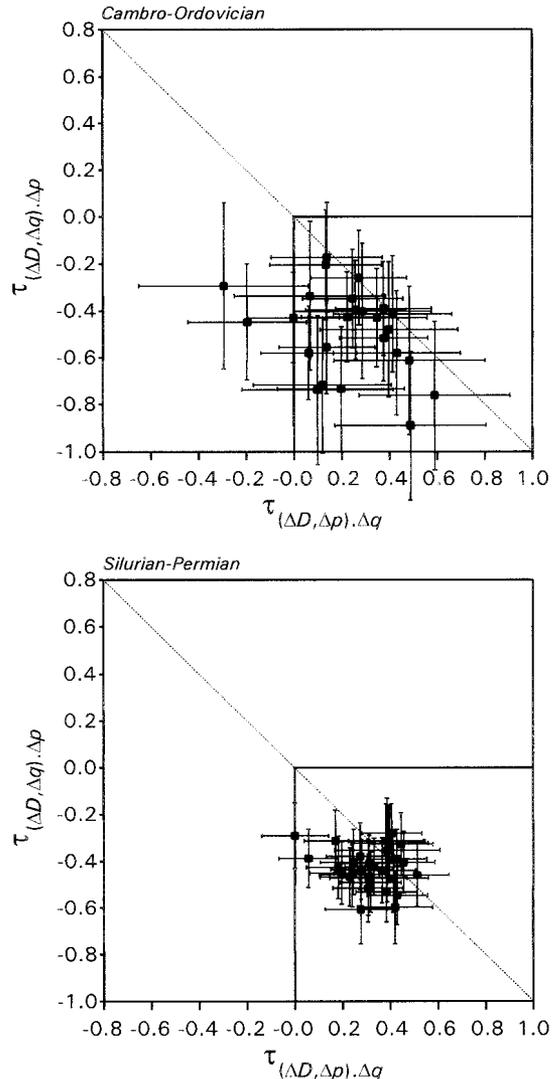


FIGURE 17. Extinction and origination correlations for Paleozoic data at all taxonomic levels. Compare with Figures 7–9. Extinction correlations tend to be stronger during the Cambro-Ordovician radiation as well as during the rest of the Paleozoic. Thus, stronger origination correlations, such as those seen in the post-Paleozoic, are not a necessary consequence of increasing diversity.

versity should be equally influenced by changes in origination rate and changes in extinction rate (Fig. 18).

Temporal Variation in Origination and Extinction Rates.—Imagine constructing a diversity history by drawing origination and extinction rates independently and randomly from two distributions differing only in their variance. In this case, changes in diversity would correlate more strongly with changes in which-

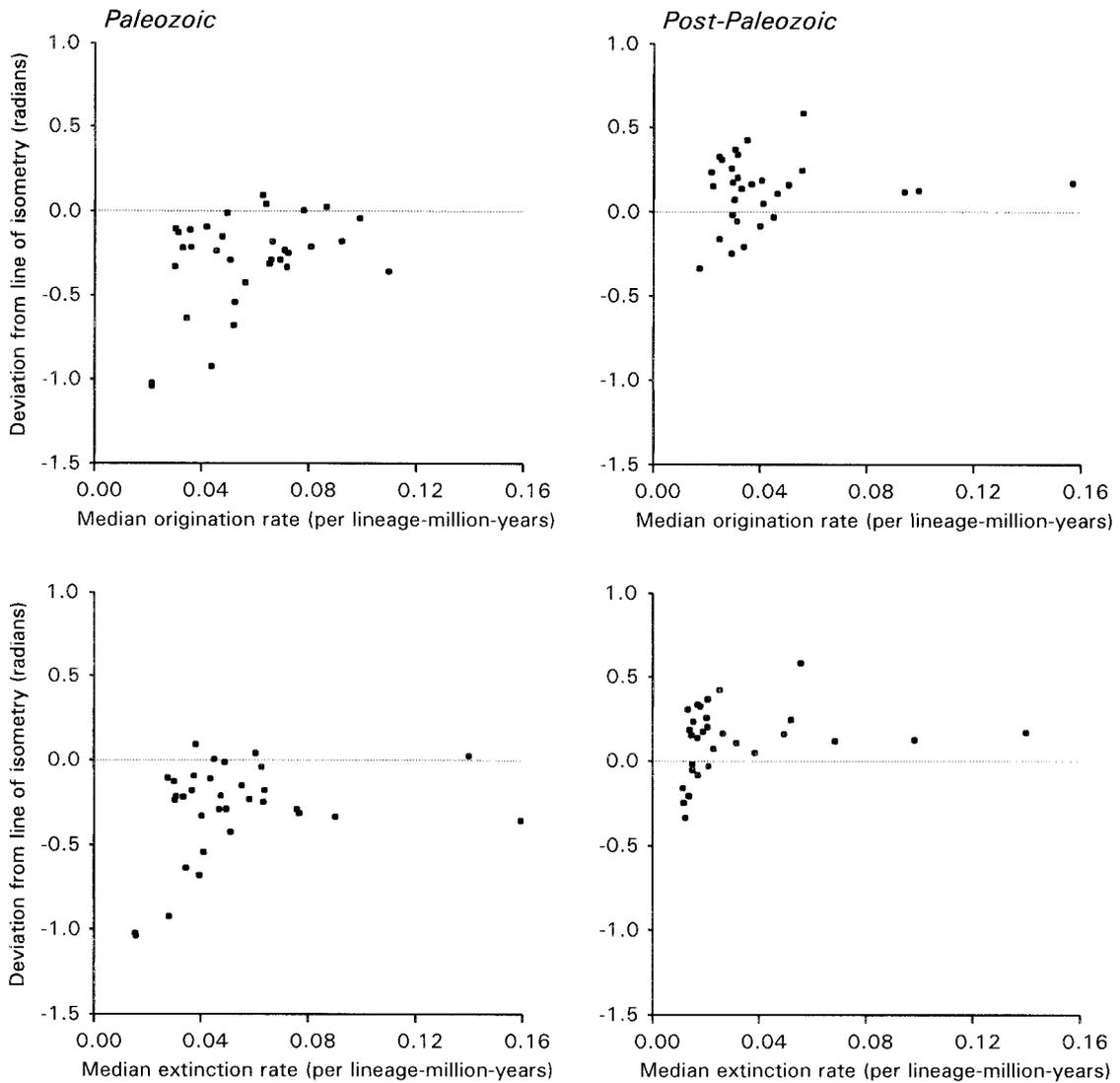


FIGURE 18. Median taxonomic rates versus deviation of origination and extinction correlations from equal magnitude. Deviation is measured as the angle between the line of -1 slope and the vector from the origin to the pair of correlations (see Fig. 6). Deviation is negative in the clockwise direction from isometry and positive in the counterclockwise direction; negative values indicate stronger extinction correlations. For post-Paleozoic taxa, there is some indication of a positive correlation between origination rate and deviation from isometry at lower rates, but, in general, the magnitude of a taxon's deviation from isometry is not well predicted by the magnitude of its origination and extinction rates.

ever rate had the higher variance. Could such a simple mechanism as differences in rate variance underlie the results documented here? Although this may be a contributing factor, it does not appear sufficient. Most Paleozoic taxa show higher variance in extinction rate than in origination rate, but post-Paleozoic higher taxa are about equally divided between those in which extinction is more variable and

those in which origination is more variable (Fig. 19). Moreover, in neither the Paleozoic nor the post-Paleozoic is the ratio of variances a good predictor of how much a higher taxon deviates from the null expectation of equal extinction- and origination-correlation of diversity changes (Fig. 19). In fact, the trend in the Paleozoic data is opposite to that expected if the relative variability of rates were the expla-

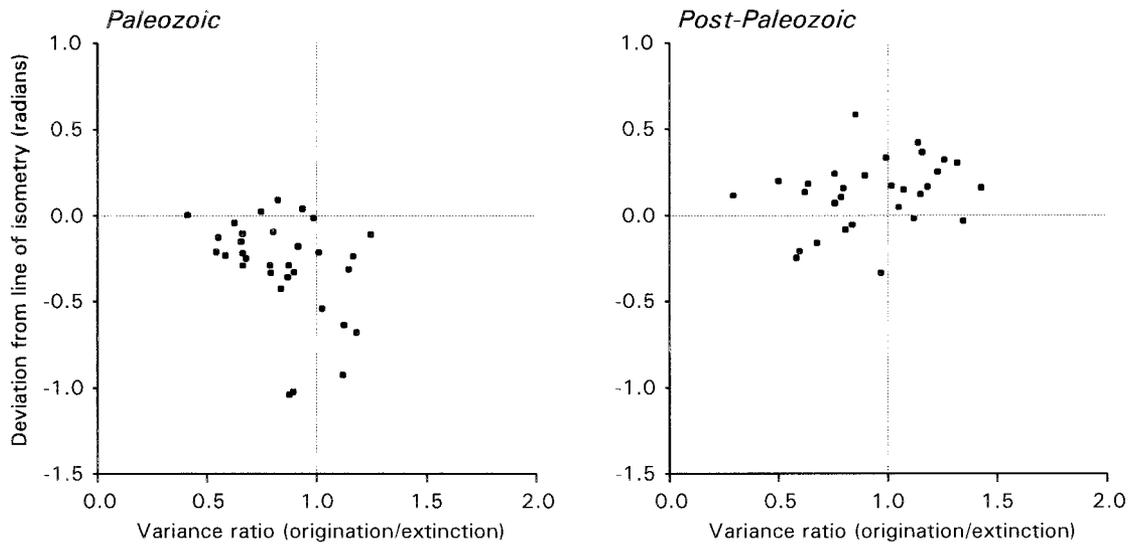


FIGURE 19. Relative variance of origination and extinction rates versus deviation of origination and extinction correlations from equal magnitude. The direction and magnitude of deviations from isometry are not predicted well by the ratio of variances.

nation for asymmetric origination and extinction correlations.

Diversity-Dependence of Rates.—Neither average rate nor variance in rate seems adequate to account for the Paleozoic/post-Paleozoic asymmetry. It seems probable that an important component of the relationship between changes in diversity and changes in taxonomic rates may involve nonrandom structure in the temporal sequence of rates. In a different context, Kirchner and Weil (2000) have shown that there is a statistical lag between the extinction and origination curves for Phanerozoic marine animals, a specific case of which is the well-known delay between mass extinctions and recoveries (Hallam 1991; Erwin 1996, 1998; Sepkoski 1998). A potential mechanism with clear relevance in the present case is diversity-dependence of rates, which has been offered as an explanation for the lack of trend in diversity through much of the Paleozoic (Sepkoski 1979; Jablonski and Sepkoski 1996) and for the apparent fit of a number of diversity curves to logistic growth models (Sepkoski 1978, 1979, 1984; Miller and Sepkoski 1988). The difference between the Paleozoic “plateau” in diversity and the post-Paleozoic rise suggests that there may have been

different patterns of diversity-dependence in effect.

Testing for diversity-dependence is complicated by secular trends in diversity and taxonomic rates. During the post-Paleozoic, for example, origination rate and extinction rate declined while diversity increased. Calculating simple correlations between diversity and taxonomic rate, while appropriate when diversity and rates are stationary (Alroy 1998), could in this case falsely make it appear as though both rates were negatively correlated with diversity. One solution to this problem is to calculate partial correlations in order to remove the effects of time. The variables of interest, however, have different secular patterns, making it difficult to factor out time. In the post-Paleozoic data as a whole, for example, there is a rather steady rise in diversity, whereas the rates drop off quickly up to about the Middle Jurassic and then fluctuate with relatively little trend (Sepkoski 1998).

To test for diversity-dependence of rates with time factored out, I calculated correlations between diversity at the start of each interval and the change in rate relative to the previous interval. In this way, the detrending of rates is accomplished by differencing; the

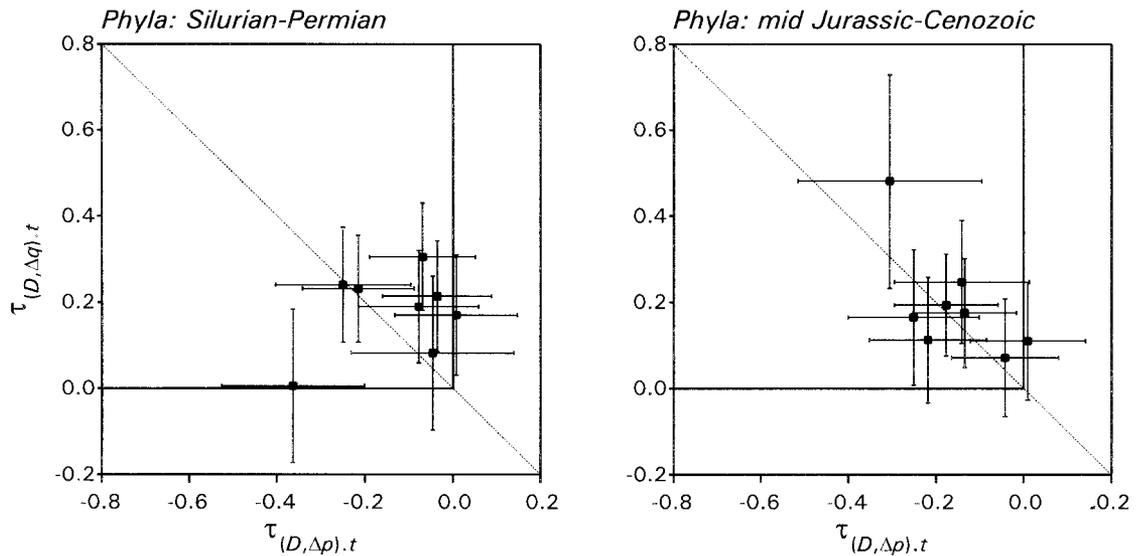


FIGURE 20. Estimated diversity-dependence of origination and extinction rates within phyla. Diversity-dependence is measured as the partial correlation between diversity at the start of an interval and the change in rate relative to the previous interval, with time held constant. Solid line outlines the upper left quadrant, where data are expected to lie if both rates are diversity-dependent. Dotted line is the line of isometry or equal strength of the two correlations. In the Paleozoic, extinction rate tends to be slightly more diversity-dependent than origination rate. In the post-Paleozoic, origination and extinction rates tend to have similar magnitudes of diversity-dependence. See Table 2.

resulting correlations between rate differences and time are rather weak. It is therefore primarily long-term trends in diversity that need to be factored out. This is accomplished by using correlations with time, t , partialled out: $\tau_{(D,\Delta p),t}$ and $\tau_{(D,\Delta q),t}$. In some cases, diversity within a higher taxon is constant and there is no observed origination or extinction for a number of successive intervals. This happens almost exclusively when taxa are at low diversity. Including such intervals could bias tests for diversity-dependence of rates, as low diversity and low rates would necessarily be correlated. I have therefore excluded intervals in which estimated taxonomic rates are zero. To reduce the effect of the steep, initial decline in taxonomic rates, I have omitted the Cambrian and Ordovician and the Triassic through early Jurassic (see Alroy 1998, which used a similar convention for Cenozoic mammals). Results are similar, however, if the early radiations are retained.

If per-capita origination rate depends on diversity, then one should expect negative correlations between D and Δp ; lower levels of diversity lead to an increase in origination rate

while higher diversity leads to a decrease in origination rate (MacArthur and Wilson 1967; Sepkoski 1978, 1979, 1991; Carr and Kitchell 1980; Walker and Valentine 1984). Conversely, one should expect correlations between D and Δq to be positive. This test is more direct than that based on correlations between origination and extinction rates (Webb 1969; Mark and Flessa 1977). There is substantial noise in the data and many of the correlations are not statistically significant, but the majority of phyla show the direction expected under the hypothesis of diversity-dependence (Fig. 20). This is true even for post-Paleozoic phyla, most of which increase in diversity. These results support logistic rather than exponential modeling of biological diversification (Sepkoski 1978, 1979, 1984, 1996a; Alroy 1996, 1998; Miller 1998; Miller and Sepkoski 1988; cf. Benton 1995, 1997).

Although there are a number of exceptions, Figure 20 and Table 2 show a hint of a possible asymmetry in diversity-dependence between the Paleozoic and post-Paleozoic. During the Paleozoic, it appears as though extinction rates depend on diversity more strongly than

TABLE 2. Estimated diversity-dependence of taxonomic rates, measured as partial correlation between diversity and change in origination rate and extinction rate. See Table 1 for description of statistical tests.

Group	Silurian through Permian						Mid-Jurassic through Cenozoic											
	All intervals			Low-diversity intervals omitted			High-diversity intervals omitted			All intervals			Low-diversity intervals omitted			High-diversity intervals omitted		
	$\tau_{(D,\Delta p)H}$	$\tau_{(D,\Delta q)H}$	Difference	$\tau_{(D,\Delta p)H}$	$\tau_{(D,\Delta q)H}$	Difference	$\tau_{(D,\Delta p)H}$	$\tau_{(D,\Delta q)H}$	Difference	$\tau_{(D,\Delta p)H}$	$\tau_{(D,\Delta q)H}$	Difference	$\tau_{(D,\Delta p)H}$	$\tau_{(D,\Delta q)H}$	Difference	$\tau_{(D,\Delta p)H}$	$\tau_{(D,\Delta q)H}$	Difference
Arthropoda	-0.078	0.190†	-0.112	-0.031	0.279*	-0.249	-0.121	0.104	0.017	-0.135	0.175†	-0.041	-0.135	0.175†	-0.041	-0.135	0.175†	-0.041
Brachiopoda	-0.069	0.305**	-0.236	-0.028	0.284*	-0.256	0.001	0.265*	-0.264	-0.141	0.247*	-0.106	-0.141	0.247*	-0.106	-0.141	0.247*	-0.106
Bryozoa	-0.364*	0.005	0.359	-0.227	0.039	0.188	-0.305†	-0.021	0.284	0.010	0.110	-0.101	0.010	0.110	-0.101	0.010	0.110	-0.101
Chordata	0.007	0.170	-0.162	0.100	0.147	-0.047	0.043	0.140	-0.097	-0.218†	0.112	0.106	-0.218†	0.112	0.106	-0.218†	0.112	0.106
Cnidaria	-0.215*	0.231*	-0.016	0.088	0.273*	-0.185	-0.234†	0.167	0.066	-0.251*	0.165	0.086	-0.251*	0.165	0.086	-0.251*	0.165	0.086
Echinodermata	-0.250†	0.240*	0.010	-0.453**	-0.000	0.453*	-0.096	0.367*	-0.270	-0.042	0.071	-0.029	-0.042	0.071	-0.029	-0.042	0.071	-0.029
Mollusca	-0.036	0.214*	-0.177	-0.100	0.200†	-0.100	0.052	0.092	-0.041	-0.177†	0.194†	-0.017	-0.177†	0.194†	-0.017	-0.177†	0.194†	-0.017
Porifera	-0.046	0.082	-0.036	-0.005	0.116	-0.111	0.155	0.236	-0.081	-0.306†	0.481*	-0.175	-0.306†	0.481*	-0.175	-0.306†	0.481*	-0.175
All data	0.054	0.249*	-0.196	0.018	0.180†	-0.162	0.144	0.175	-0.031	-0.170†	0.026	0.143	-0.170†	0.026	0.143	-0.170†	0.026	0.143
Phylum median	-0.074	0.202***	-0.128†	-0.066	0.174**	-0.108	-0.048	0.154**	-0.106	-0.159***	0.170***	-0.011	-0.159***	0.170***	-0.011	-0.159***	0.170***	-0.011

do origination rates; Paleozoic phyla tend weakly to fall above the line of isometry in Figure 20. In the post-Paleozoic, however, the two dependencies are closer to the same magnitude on average. For classes, there is not such a clear difference between the Paleozoic and post-Paleozoic (Fig. 21), although most correlations still show the direction expected under diversity-dependence. These results are not a simple restatement of the earlier analyses regarding change in diversity and change in taxonomic rates. Rather, to the extent that the correlations reflect causation, they indicate a different causal direction. The first set of analyses tested how the change in rates relative to the preceding interval contributes statistically to the change in diversity within the interval in question. The analysis of diversity-dependence tests how the absolute level of diversity at the start of an interval contributes statistically to a suppression or enhancement of rates relative to the preceding interval.

There are at least three possible explanations for the discrepancy between the results for phyla and those for classes: (1) The discrepancy reflects greater sampling error at the class level. (2) There is a meaningful, hierarchical effect of taxonomic level. It has been noted, for example, that orders tend not to show diversity equilibria to the same extent as larger composites (Jablonski and Sepkoski 1996). A hierarchical distinction between phyla and classes cannot be ruled out, but, if it were the case, one might also expect a difference between phyla and classes in correlations involving ΔD , Δp , and Δq . No such difference is evident (Table 1, Figs. 7–9). (3) There is in fact no asymmetry in diversity-dependence of origination versus extinction rates in the Paleozoic, and the apparent pattern for phyla is spurious. This is certainly the most conservative conclusion, but one fact suggests that it may be worth retaining this asymmetry as a viable hypothesis: the combined Paleozoic data show diversity-rate correlations consistent with the hypothesis (Table 2).

To the extent that extinction is more diversity-dependent than origination in the Paleozoic, this asymmetry may help to explain why Paleozoic changes in diversity are dominated by changes in extinction rate rather than origination rates.

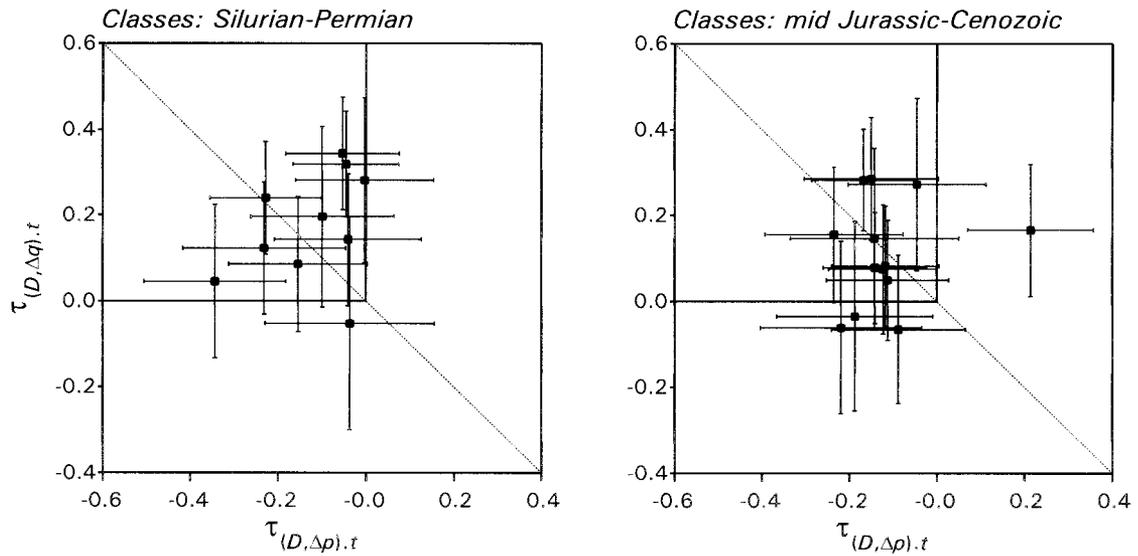


FIGURE 21. Estimated diversity-dependence of origination and extinction rates within classes. Compare with Figure 20. Although most rates still show the direction of correlation expected under diversity-dependence, the distinction between the Paleozoic and post-Paleozoic is not evident. See text for discussion.

ination rate. Lower diversity may lead to a reduction in extinction rate that is more pronounced than the corresponding increase in origination rate, while higher diversity may promote extinction more than it inhibits origination. In the post-Paleozoic, however, it would appear that diversity-dependence, being rather symmetrical, is simply superimposed on whatever causes contribute to the dominance of diversity changes by variation in origination rate. The nature of these causes remains uncertain.

Discussion and Conclusions

This study initially sought to test whether variation in taxonomic diversity is controlled predominantly by origination or by extinction. In fact, no consistent pattern exists throughout the Phanerozoic. Rather, a pronounced shift in the dynamics of animal diversification accompanies the biotic transition from the Paleozoic to the Mesozoic. The magnitude of changes in diversity at the scale of several million years is determined during the Paleozoic more by the magnitude of change in extinction rate, but after the Paleozoic more by the magnitude of change in origination rate. Although the difference between the Paleozoic and post-Paleozoic is statistically significant, the size of the

effect is a different matter. The magnitude of the correlations (Table 1) shows that the shift from extinction- to origination-dominated changes in diversity must not be the single, dominant factor in Phanerozoic diversity dynamics. All plausible sources of artifact can be ruled out, however; thus, the effect is real, and the pattern demands explanation.

It is reasonable to suggest that an ecological decomposition of data might be more meaningful than a taxonomic one. Although it would be desirable to divide all genera into a small number of ecological categories that transcend taxonomic lines, such a large task is beyond the scope of this work. The analyses presented here nevertheless fail to show any obvious effects of the major aspects of autecology (Table 1). For example, primarily benthic groups do not show results consistently different from those of primarily pelagic groups. The predominantly infaunal irregular echinoids are similar to the predominantly epifaunal regulars. And many higher taxa change in diversity dynamics from the Paleozoic to the post-Paleozoic despite maintaining essentially the same general way of life.

The extent to which changes in diversity are origination- or extinction-dominated does not appear to be a simple consequence of the mag-

nititude of taxonomic rates or of the relative variability of origination and extinction rates. Origination- or extinction-dominance is not an intrinsic property of higher taxa. The observed shift in diversity dynamics tends to occur within individual higher taxa, suggesting that the world itself changed in a fundamental way. It is still possible that the Paleozoic contained a mixture of extinction-dominated and origination-dominated taxa, with the latter surviving preferentially. For such a culling process to explain the Paleozoic/post-Paleozoic shift, it would have to have taken place below the level of taxonomic resolution of this study. In other words, the Paleozoic would have to have been marked by a mixture of relatively few origination-dominated families and many more extinction-dominated families, and the former would have to have survived preferentially into the Mesozoic. In the absence of adequate data to test this hypothesis, it seems reasonable to take the shift of most phyla and classes, as well as the few orders for which data are adequate in both the Paleozoic and post-Paleozoic, as *prima facie* evidence that the evolutionary milieu in which taxa find themselves changed substantially.

One of the most salient differences between the Paleozoic and post-Paleozoic marine fossil records is that the majority of the known Paleozoic record is tropical in origin, while extratropical environments are represented to a greater extent after the Paleozoic (Raup 1976a; Allison and Briggs 1993; Hallam 1994; Taylor and Allison 1998). This partly reflects concentration of sampling in Europe and North America (Raup 1976a), but it also reflects the true past positions of continents (Scotese and McKerrow 1990; Hallam 1994) and the extent to which different continents were inundated (Ronov 1994).

A number of empirical observations suggest striking evolutionary differences between the tropical and extratropical realms that are relevant to diversity dynamics. Extinction events are often thought to affect tropical species more than temperate species (Stanley 1984, 1988a,b; Jablonski 1991; Raup and Jablonski 1993; Copper 1994; Smith and Jeffery 1998), although it is possible that geographic patterns of selectivity are sometimes driven by extinc-

tion in a taxonomically limited subset of species (e.g., Late Cretaceous rudist bivalves rather than bivalves as a whole [Jablonski 1991; Raup and Jablonski 1993]). Major morphological innovations (operationally defined as those that characterize new orders) have been found to originate preferentially in the Tropics (Jablonski 1993). One possible explanation for this pattern is that innovations occur as responses to opportunities in the wake of extinction events that preferentially affect the Tropics (Jablonski 1993). There is some evidence that taxonomic rates of evolution may be higher in the Tropics than elsewhere (Stehli and Wells 1971; Flessa and Jablonski 1996; but see Van Valen 1969). There is also a tendency for diversity to be higher in the Tropics than elsewhere (Rosenzweig 1992, 1995; Roy et al. 1998), although this pattern is not without exception (Crame 1997; Rutherford et al. 1999).

Despite these differences between the Tropics and higher latitudes, it is not obvious that tropical versus extratropical setting explains the Paleozoic/post-Paleozoic difference in diversity dynamics. One difficulty is that other environmental factors, which are also known empirically to influence evolutionary patterns, covary with latitude and with each other. Most conspicuously, there is a well-known general tendency for carbonate production to be concentrated in environments that are shallow and tropical (Wilson 1975; Wilkinson 1979; James 1981; Ziegler et al. 1984), although of course this tendency is not without important exceptions (Wilson 1975; James 1981, 1997; James and Clarke 1997; Taylor and Allison 1998). This environmental correlation is important because cratons were evidently flooded to a greater extent during the Paleozoic (Ronov 1994), and because evolutionary patterns are also known to vary with bathymetry and with carbonate versus terrigenous setting. For example, genus origination and extinction rates are higher in shallower (nearshore) environments (Sepkoski 1987), and higher taxa, major morphological novelties, and characteristic associations of higher taxa tend to appear first in nearshore settings (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Bottjer and Jablonski 1988; Jablonski and Bottjer 1990a,b, 1991). It has also been found that, at

least during the Ordovician, diversity tends to be higher in predominantly terrigenous settings (foreland basins and transition zones) than on carbonate platforms (Miller and Mao 1995; see Boucot 1999). Moreover, Smith and Jeffery (1998) suggested selective extinction of certain Late Cretaceous and early Tertiary echinoids that prefer carbonate (chalk) environments. The hypothesis that geographic and environmental setting play a role in the style of diversity dynamics is potentially testable with extensive data on genus occurrences that include lithologic and paleogeographic information (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Bottjer and Jablonski 1988; Jablonski and Bottjer 1990a,b, 1991; Miller and Mao 1995, 1998; Miller 1997a,b).

Taxonomic rates tend to be diversity-dependent, and there is some evidence, albeit weak, that the nature of this dependence changes from the Paleozoic to the post-Paleozoic. During the Paleozoic, specifically the long interval of approximately stationary diversity from the Silurian through the Permian, diversity appears to influence extinction rate somewhat more than origination rate. This pattern is not overwhelming, however, and should be accepted only tentatively. After the Paleozoic, the diversity-dependence of both rates is closer to the same magnitude.

Whether or not the apparent asymmetry in diversity-dependence within the Paleozoic is robust, i.e., whether extinction rates are more diversity-dependent than origination rates or equally dependent, the results of this study differ from previous suggestions that most of the diversity-dependence of taxonomic rates lies in the origination component. This conclusion has been based mainly on two lines of evidence: (1) Within higher taxa, origination rates tend to decline over time while extinction rates are relatively stationary (Van Valen 1985a,b; Van Valen and Maiorana 1985; Gilinsky and Bambach 1987; Jablonski and Sepkoski 1996). This pattern is at a very coarse temporal scale, and so it may not be relevant to processes of diversity-dependence that presumably act on shorter temporal scales. (2) More to the point, origination rates have been shown to fit a diversity-dependent model better than do extinction rates. Sepkoski (1978,

1979) found this for Phanerozoic orders and families (although, for the Cambrian alone, family-level extinction rates show a better fit), as did Alroy (1998) for genera and species of Cenozoic mammals. (The results of Eble [1999] are not obviously pertinent to this issue. Although he inferred diversity-dependence of genus origination rates for two of three higher taxa of marine animals studied, he did not test for diversity-dependence of extinction rates.)

It is unclear why the present results differ from those of Sepkoski and Alroy. The explanation for the discrepancy does not lie in my comparing diversity with first differences in rate where previous authors have compared diversity with the rates themselves. I also estimated diversity-dependence in a more conventional way, using the partial correlation, with time held constant, between diversity at the start of an interval and the taxonomic rate for that same interval (rather than the change in rate from the previous interval). Such an analysis does not yield systematically stronger origination correlations such as those found by Sepkoski and Alroy. Although Stanley (1999) suggested that high rates of extinction were largely responsible for the failure of Paleozoic animals to show a long-term increase in diversity after the Ordovician, his argument that diversity-dependence of rates was not strong during the Paleozoic seems to have been based on analysis of rates of diversification, i.e., the difference between origination and extinction rates, rather than the component rates individually.

To the extent that the Paleozoic asymmetry in diversity-dependence is robust, it could imply at least two constituent patterns: (1) Low diversity levels following extinction pulses are accompanied by a lowering of extinction rate more than an increase in origination rate. (2) The lack of long-term increase in diversity during the mid-late Paleozoic is attributable more to increases in extinction rate than to decreases in origination rate when diversity is high. That the pattern reflects regulation of taxonomic rates at both high and low diversities is suggested by a simple analysis of subsets of Paleozoic data (Table 2). When the 25% of the intervals with the lowest or highest di-

versity are omitted, the pattern of diversity-rate correlations is largely similar to that for the data as a whole. The most conspicuous exception is the echinoderms, for which I can offer no reasonable explanation. The results regarding diversity-dependence of rates are noisy. Regulation of rates by diversity is therefore unlikely to be the principal explanation for the results of this study. It may nevertheless prove to play a role.

It has been suggested that extinction pulses and diversity change in general are often triggered by physical perturbations (Newell 1967; Bretsky and Lorenz 1970; Bretsky 1973; Raup and Boyajian 1988; Stanley 1988a,b; Raup 1991, 1992; Brett and Baird 1995, 1997; Hallam and Wignall 1997; Brett 1998; Miller 1998; Patzkowsky and Holland 1999). This is consistent with the general tendency over the Phanerozoic for variation in extinction rate to have a stronger influence on diversity than does variation in origination rate. More to the point, it would seem that these perturbations extended further in their impact during the Paleozoic than afterwards. Assuming that physical perturbations did not sharply decrease in magnitude or frequency from the Paleozoic to the Mesozoic, the observed difference in diversity dynamics seems to suggest a change in the way ecosystem structure allowed shocks to percolate through the biota. Large-scale, ecosystem-level changes are thought to include increasing niche specialization and greater energy flow (Valentine 1969, 1973; Bambach 1985, 1993, 1999). How these and other aspects of ecosystem evolution have contributed to the evolution of diversity dynamics is yet to be determined.

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