

## Substrate affinity and diversity dynamics of Paleozoic marine animals

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**Abstract.**—Short-term fluctuations in the diversification rate of Paleozoic marine animal genera are more strongly correlated with extinction-rate variation than with origination-rate variation. Diversity dynamics are strikingly different in the Mesozoic and Cenozoic, when variation in origination is more important than extinction. Data on the lithologic context of taxonomic occurrences in the Paleobiology Database are used to assess the substrate affinities of Paleozoic genera. The greater role of extinction-rate variation in the Paleozoic is found to characterize genera with an affinity for carbonate substrates but not those that prefer terrigenous clastic substrates. It is therefore plausible that the Paleozoic to post-Paleozoic shift in diversity dynamics is underlain in part by the secular decline in the relative areal extent of carbonate environments, and the concomitant decline in the relative diversity of carbonate- versus clastic-loving taxa.

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### Origination and Extinction Components of Diversification

How is variance in the net rate of taxonomic diversification partitioned into its origination and extinction components? Previous work has shown that short-term fluctuations in marine diversity are more strongly coupled to extinction during the Paleozoic and to origination during the Mesozoic and Cenozoic (Foote 2000a). Because this shift in diversity dynamics is seen within individual higher taxa, it is unlikely to reflect selective removal of intrinsically extinction-dominated clades. Moreover, because an ecologically broad range of groups shifts from extinction- to origination-dominance, the shift does not seem to reflect clade-specific ecology.

The purpose of this paper is to test one hypothesis for the major change in diversity dynamics from the Paleozoic to the post-Paleozoic, namely that it is intimately tied to a temporal trend in the distribution of available substrates. One of the most striking secular changes in paleoenvironments seen in the geologic record is the Phanerozoic decline in the areal extent of marine carbonate environments relative to that of terrigenous clastic sediments (which I will hereinafter generally refer to as *clastics* for short, a term that excludes detrital and other carbonates; see Table

1). Although some analyses suggest rather little trend in the absolute extent of certain carbonate facies (Kiessling et al. 2003) and others show a conspicuous decline (Walker et al. 2002), it seems quite clear that the *relative* extent of carbonates versus terrigenous clastics has declined over the Phanerozoic (Ronov et al. 1980; Ronov 1994; Walker et al. 2002). If this secular trend underlies the Paleozoic to post-Paleozoic change in diversity dynamics, then some predictions follow. Within a given span of geologic time, animal taxa that prefer carbonate environments should be more “Paleozoic-like” in their diversity dynamics. In other words, they should have diversity fluctuations that are more strongly correlated with variance in extinction rate than origination rate. This should be less true of taxa that prefer clastic substrates. Along with these differences, we should expect to see a reduction over the Phanerozoic in the relative diversity of carbonate-loving taxa.

### Data and Methods

**Stratigraphic Ranges and Substrate Affinities.**—Testing the proposed hypothesis requires data of two kinds: stratigraphic ranges and substrate affinities. The former are taken from Sepkoski’s (2002) genus-level compendium. The latter are derived from genus occurrences

TABLE 1. Lithologies assigned to principal lithologic categories.

Category	Lithologies included
Carbonate	Limestone, dolomite, lime mudstone, packstone, grainstone, wackestone, "reef rocks," bafflestone, framestone, bindstone, rudstone, floatstone, "carbonate"
Clastic	Shale, mudstone, claystone, siltstone, sandstone, conglomerate, quartzite, phyllite, schist, slate, "siliciclastic"
Mixed	Marl, "mixed carbonate-siliciclastic"

linked to collections with lithologic information in the Paleobiology Database ([www.paleodb.org](http://www.paleodb.org)). Analyses were limited to the Paleozoic to test for the effects of substrate preference without the overprint of the Phanerozoic-scale secular trend in substrate availability. To avoid edge effects in the calculation of taxonomic rates (Foote 2000b), the Cambrian was excluded from analysis. Results are compatible if the Cambrian is included. Parts of the upper Carboniferous are sparsely represented in the Paleobiology Database, at least relative to the coverage of the Ordovician, Silurian, and Devonian. Results are compatible if analyses are restricted to the Ordovician through Devonian.

TABLE 2. Stratigraphic intervals used for baseline analyses.

Stage	No. of divisions
Tremadocian	2
Arenigian	2
Llanvirnian	1
Llandeilian	1
Caradocian	3
Ashgillian	3
Llandoveryian	3
Wenlockian	1
Ludlovian	1
Pridolian	1
Gedinnian	1
Siegenian	1
Emsian	1
Eifelian	1
Givetian	1
Frasnian	3
Famennian	3
Tournaisian	2
Visean	2
Serpukhovian	2
Bashkirian	2
Moscovian	2
Stephanian	2
Asselian	1
Sakmarian	1
Leonardian	1
Guadalupian	2
Tatarian	2

Following an earlier treatment (Foote 2005), Sepkoski's basic stratigraphic divisions (hereinafter *stages*) were subdivided only if at least 60% of the first and last appearances are resolved to the substage level. This leads to the operational timescale of Table 2. Note that Sepkoski's divisions of the Ordovician and Permian do not follow more recent conventions (e.g., Gradstein et al. 2004), but they are internally consistent. Stratigraphic ranges could have been based on the occurrences in the Paleobiology Database, but, on the whole, these are not as finely resolved stratigraphically as are Sepkoski's ranges.

The Paleobiology Database consists of *collections*, each containing a list of taxa. An *occurrence* is a distinct presence of a taxon in a collection. Genus occurrences were downloaded from the marine invertebrate section of the Paleobiology Database; data were current as of 14 April 2005. The protocol for analysis included the following: (1) Multiple occurrences of a genus within a collection were not combined; i.e., several species of the same genus were treated as distinct occurrences. (2) To be compatible with Sepkoski, subgenera were treated as distinct genera. (3) Occurrences were included even if they are outside the stratigraphic range of the genus according to Sepkoski's compendium. (4) Because the analyses presented here are at the genus level, generically indeterminate occurrences were ignored, but specifically indeterminate occurrences were included if they are assigned to genera. (5) Informal genus names and genus names qualified by "aff." or quotation marks were disregarded. The first three items are somewhat arbitrary; I will show below that results are robust to these choices.

In addition to the genus name, the two data fields that are relevant to the present analysis are the primary lithology and secondary li-

TABLE 3. Assignment of collections and occurrences to lithologic categories (with proportion of total in parentheses). Collections without lithologic information, or with lithologies (e.g., coal) not classified here as carbonate, clastic, or mixed, are excluded.

Primary lithology	Secondary lithology	Assignment	Collections	Occurrences
Carbonate	None	Carbonate	4913 (0.368)	47,002 (0.344)
Carbonate	Carbonate	Carbonate	1072 (0.080)	13,999 (0.103)
Carbonate	Clastic	Mixed	1506 (0.113)	17,923 (0.131)
Carbonate	Mixed	Mixed	124 (0.009)	1690 (0.012)
Clastic	None	Clastic	2963 (0.222)	26,762 (0.196)
Clastic	Carbonate	Mixed	969 (0.073)	12,159 (0.089)
Clastic	Clastic	Clastic	1475 (0.111)	13,692 (0.100)
Clastic	Mixed	Mixed	38 (0.003)	557 (0.004)
Mixed	None	Mixed	88 (0.007)	825 (0.006)
Mixed	Carbonate	Mixed	174 (0.013)	1598 (0.012)
Mixed	Clastic	Mixed	24 (0.002)	307 (0.002)
Mixed	Mixed	Mixed	1 (<0.001)	4 (<0.001)
Total			13,347	136,518

thology. Table 1 shows the values of these fields that were used and the corresponding assignment of each lithology to carbonate, clastic, and mixed categories. These are straightforward with the possible exception of marls, here treated as a mixed lithology. Below I will show that results are not substantially affected by treating marls, which account for only 5% of the collections, as pure carbonates or pure clastics. Assignment of each collection and its respective occurrences to a lithologic category is based on the combination of primary and secondary lithologies, as outlined in Table 3.

The Paleobiology Database includes fields that indicate whether the fossils in a collection are known to occur in the primary lithology, the secondary lithology, or both. This information is not always contained in the original publications, however, and therefore is not consistently entered into the Database. For this reason, occurrences from mixed lithologic settings are categorized as *mixed*, even though they may in fact come only from clastic or carbonate lithologies within the mixed setting. This adds imprecision to the lithologic classification of occurrences, but there is no obvious reason to think that the analyses are biased as a result.

Given a list of genus occurrences and their corresponding lithologies, some protocol is needed for assigning each genus a lithologic preference (a *substrate affinity* sensu Miller and Connolly 2001). The reliability with which this

assignment can be made depends on the number of occurrences of a genus. For example, a genus that occurs but once in the database, in a mudstone, has 100% clastic affinity, but this determination is statistically weak. I have therefore assigned each genus a lithologic preference only if over 50% of its occurrences are from the given lithologic category (carbonate, clastic, or mixed), and if the percentage of occurrences differs significantly from 50% at the 0.1 level of significance (one-tailed). For example, suppose a genus had ten occurrences, six of them in carbonates. The binomial probability of obtaining 6 or more carbonate occurrences, if the true probability for each occurrence is 0.5, is about 0.17, and so the genus would not be assigned to any lithologic category. If this genus instead had 7 of 10 occurrences in carbonates, the corresponding probability would be only 0.055, and the genus would be assigned a carbonate affinity (Table 4). Using 50% rather than 33 $\frac{1}{3}$ %—which would have been a defensible choice given that there are three lithologic categories—is meant as a way to insist on a comparatively strong substrate affinity. As shown below, results for two alternative protocols, one requiring mere plurality rather than majority, and the other requiring a supermajority of 70%, yield consistent results.

An additional condition, which overrides the majority-rule protocol, is that there be at least four occurrences. Thus, a genus with three or fewer occurrences is not used even if

TABLE 4. Minimum number of occurrences in a given lithologic category required for assignment of a genus to that category.

Total occurrences	No. needed to assign to lithologic category
4	3
5	4
6	5
7	5
8	6
9	6
10	7
20	13
30	19
40	24
50	30
100	56

all of its occurrences are from the same lithologic category (which could have made it acceptable by the majority-rule protocol).

Note that Miller and Connolly (2001) needed to characterize the substrate affinities of long-lived and potentially heterogeneous orders and classes; this largely accounts for the differences in method between that study and the present one. In particular, by assigning each genus a single lithologic preference, this study tacitly assumes that such preferences are relatively fixed throughout the life span of a genus.

This assumption is tenable on at least two grounds. First, most genera are sufficiently short lived, relative to the stratigraphic resolution used here, that the capacity for switching lithologic preference is likely to be limited. Of genera that first appear in the Ordovician through Permian, 47% are confined to a single stage, and 62% have ranges of one or two stages.

Second and more important, of those genera that are longer lived, relatively few vary their lithologic preferences substantially. To draw this inference, I identified those genera that have an overall lithologic preference ac-

ording to the protocol described above and that have a separately discernible lithologic preference within more than one stratigraphic system. Each system-specific preference was based only on occurrences within that system, and the same protocol was applied to these occurrences as to the entire set of occurrences. Of 181 genera that meet these criteria, 142 (78.5%) have the same lithologic preference in every system in which it can be determined.

In summary, for a genus to be used in this study, it must occur in the Paleobiology Database with a statistically reliable substrate affinity and occur in Sepkoski's compendium with an adequately resolved first and last appearance. All told, 3230 genera meet these conditions for the Ordovician through Permian. As Table 5 shows, there are more than twice as many genera with a carbonate affinity as there are genera with a clastic affinity. Results will be presented for carbonate-loving genera, clastic-loving genera, and all genera combined. The number of genera that prefer mixed lithologies is not sufficient to produce robust results.

*Rates of Origination, Extinction, and Diversification.*—For each stratigraphic interval, the per capita rates of origination ( $p$ ) and extinction ( $q$ ) were computed from Sepkoski's stratigraphic ranges following Foote (2000b). Rates were expressed per interval rather than per million years for two reasons. First, some interval durations are highly uncertain, especially for substages. Second, normalization by interval length tacitly assumes that origination and extinction were spread rather evenly within stages, an assumption that is probably not tenable (Foote 2005; see also Raup and Sepkoski 1984; Van Valen 1984). Although the per capita rate per Myr implicitly assumes continuous turnover, the per capita rate per interval conveys the overall intensity of origination and extinction in the interval even if

TABLE 5. Summary of rate variances and product-moment correlations.

Genera	$n$	$S^2_{\Delta p}$	$S^2_{\Delta q}$	$r_{\Delta p \Delta q}$	$r_{\Delta p \Delta d}$	$r_{\Delta q \Delta d}$
Carbonate affinity	1831	0.016	0.063	0.11	0.37	-0.88
Clastic affinity	848	0.039	0.023	0.37	0.70	-0.41
All	3230*	0.016	0.034	0.081	0.53	-0.80

\* Includes 551 genera showing affinity for mixed lithologies or no clear lithologic affinity.

turnover is episodic. Moreover, relative to other measures of pulsed turnover (Foote 2003, 2005), it has the advantage for this study that it leads to a simple analysis of diversity dynamics (Appendix). The net rate of diversification ( $d$ ) was tabulated as the difference between origination and extinction rates. Rates were analyzed only for intervals with at least five first and/or last appearances. Results are consistent, however, if no such minimum is imposed or if the threshold is raised to ten appearances.

*Assessing Diversity Dynamics.*—For each time interval, the changes in rate relative to the previous interval,  $\Delta p$ ,  $\Delta q$ , and  $\Delta d$ , were tabulated. First differences were used to emphasize short-term rate fluctuations and because the variance in origination rate in the Paleozoic is dominated by a major secular decline (see Fig. 9 below). Figure 1A shows the first differences in rates for genera of all lithologic affinities combined. The short-term changes in rate were compared with each other to assess the strength of the correlation between variation in origination and in diversification and that between variation in extinction and in diversification. In Figure 1A, for example, the product-moment correlation coefficient between changes in origination and diversification rates,  $r_{\Delta p \Delta d}$ , is equal to 0.53, while  $r_{\Delta q \Delta d} = -0.80$  (Table 5). Thus, the directions of correlation are as one might have expected—positive for origination and negative for extinction—and the variation in diversification rate is more strongly coupled to the variation in extinction rate than to origination rate.

Diversity dynamics are analyzed slightly differently here than in an earlier study (Foote 2000a). In that work, I compared the change in origination and extinction from interval  $i$  to  $i + 1$  with the change in log diversity within interval  $i + 1$  (i.e., the net diversification rate for interval  $i + 1$ ) rather than with the change in net diversification rate from interval  $i$  to  $i + 1$ . Nonetheless, the results of both approaches are consistent in demonstrating an unequal contribution of origination and extinction to the diversity variation of Paleozoic marine genera.

The change in protocol allows a simpler algebraic treatment of the relationships between

origination, extinction, and diversity. Because net rate of diversification is by definition the difference between origination and extinction, there can be no unknown sources of variance in diversification rate. If origination and extinction rates were independent and identically distributed, then  $r_{\Delta p \Delta d}$  would be equal to  $1/\sqrt{2}$  and  $r_{\Delta q \Delta d}$  would be equal to  $-1/\sqrt{2}$ ; i.e., the correlations would be equal in magnitude and their sum of squares would be unity (Appendix). This would hold for raw values as well as first differences.

## Results

Empirically, the correlations  $r_{\Delta p \Delta d}$  and  $r_{\Delta q \Delta d}$  do not agree with what we would expect if  $p$  and  $q$  were independent and identically distributed (Table 5, Fig. 1A). The extinction-diversification correlation is stronger and the sum of squared correlations is less than unity. These deviations reflect two factors (Appendix): (1) If origination and extinction rates are not identically distributed, the process with the greater variance will correlate more strongly with diversification rate. (2) If origination and extinction rates are correlated, some of the variance in diversification rate must be explained by the mutual correlation of the two component rates. Thus, the process that is more variable—origination or extinction—will have a stronger correlation with variation in the net rate of diversification, but how much stronger depends not only on the relative variances of the two processes but also on the correlation between them (Appendix).

In the data of Figure 1A, first differences of extinction have about twice the variance as those of origination (0.034 versus 0.016; Table 5), and the correlation between origination and extinction differences is equal to 0.081. The large difference in variances accounts for the substantial difference between  $|r_{\Delta p \Delta d}|$  and  $|r_{\Delta q \Delta d}|$ . Given the slight correlation between  $\Delta p$  and  $\Delta q$ , however,  $r_{\Delta p \Delta d}^2 + r_{\Delta q \Delta d}^2$  is equal to 0.92, only slightly less than the value of 1.0 to be expected if  $p$  and  $q$  were uncorrelated.

The information on correlations just presented can be summarized in the form of a simple plot of  $r_{\Delta p \Delta d}$  versus  $r_{\Delta q \Delta d}$  (Fig. 1B). The dashed diagonal line in Figure 1B denotes equal strength of the two correlations. A po-

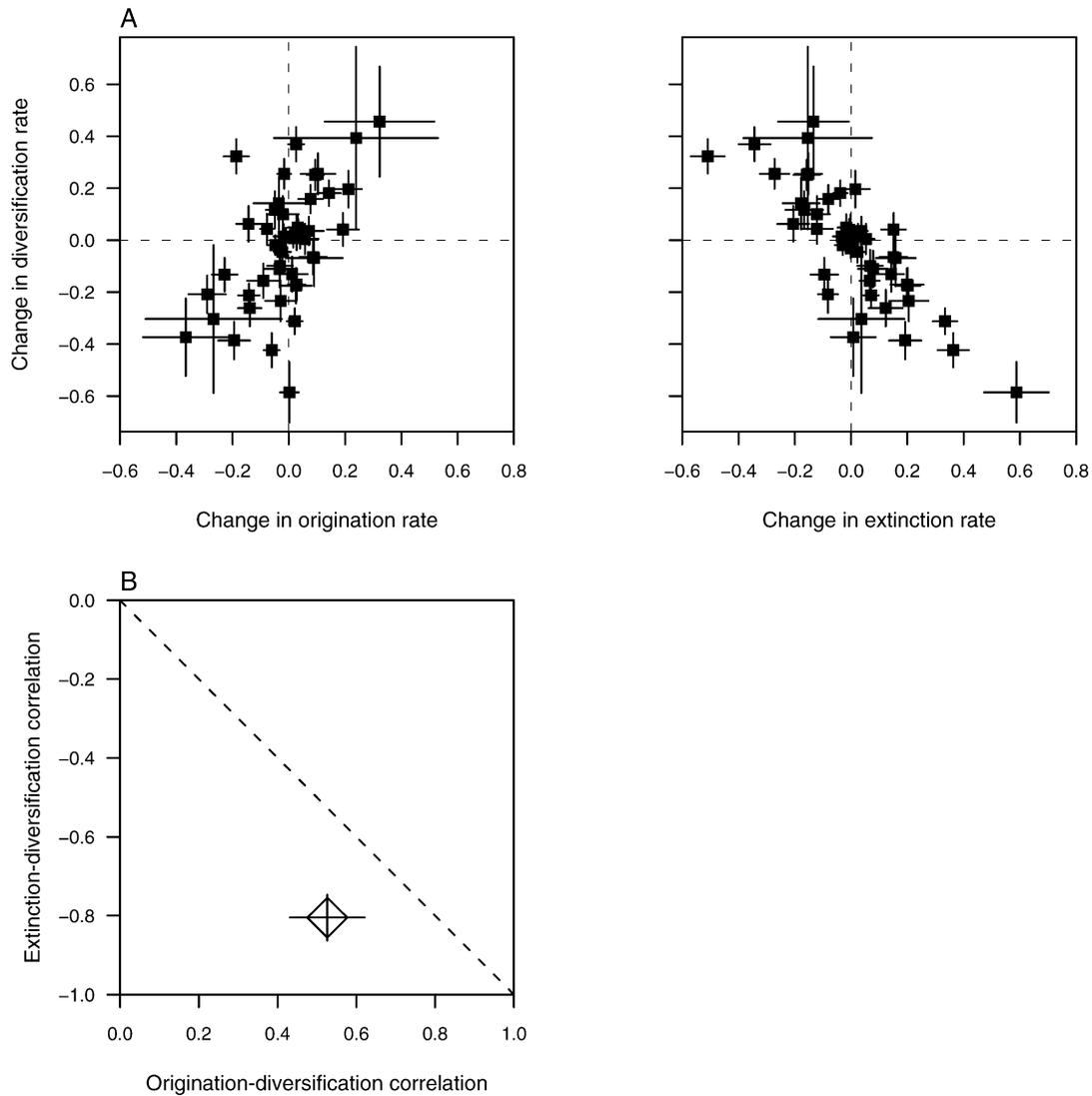


FIGURE 1. Diversity dynamics in Paleozoic marine animal genera. A. First differences in origination rate, extinction rate, and net diversification rate of Ordovician through Permian genera. The correlation between extinction and diversification appears to be tighter than that between origination and diversification. B. Plot of the pair of product-moment correlations corresponding to the two panels of part A. The diagonal line marks equality of the origination-diversification and extinction-diversification correlations; a pair of correlations above or below this line indicates that diversification is more strongly correlated with origination or extinction, respectively. In this case, the variation in the net rate of diversification is more strongly tied to extinction rate. Error bars in this and subsequent figures give plus or minus one standard error, based on bootstrap resampling of genera with 1000 replicates (Efron and Tibshirani 1993; Foote 2005).

sition below this line means that the fluctuations in diversification rate are more strongly attributable to variation in extinction rate. Origination variation is more important if a point falls above the line. Because some distributions contain what appear to be outliers, Spearman rank-order correlation coefficients will be presented in subsequent figures. Em-

pirically this tends to reduce the observed difference between genera with carbonate versus clastic affinities, and therefore is conservative (see next section).

It is important to note that the null hypothesis in this analysis is not that correlations between  $\Delta p$  and  $\Delta d$  and between  $\Delta q$  and  $\Delta d$  are equal to zero. Because  $d = (p - q)$  by defini-

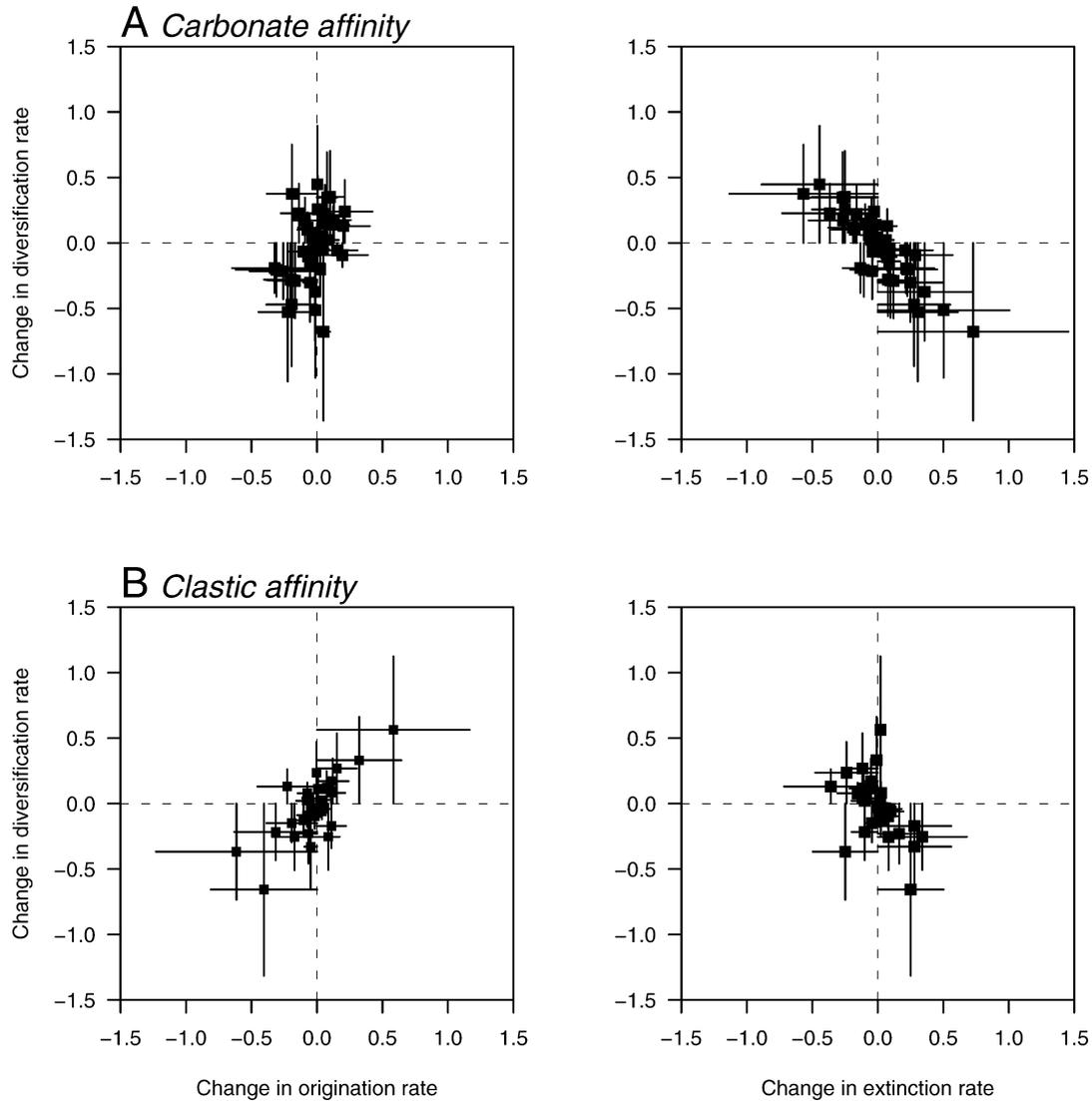


FIGURE 2. First differences in origination rate, extinction rate, and net diversification rate of genera with affinities for carbonate (A) and clastic (B) substrates.

tion, a random time series of origination and extinction rates will on average yield correlations of  $\pm 1/\sqrt{2}$  (Appendix). Instead, the empirical correlations should be compared with the null expectation that  $|r_{\Delta p \Delta d}| = |r_{\Delta q \Delta d}|$ .

*Carbonate versus Clastic Diversity Dynamics.*—Scatterplots of first differences in origination, extinction, and diversification suggest that, for carbonate-loving genera, the correlation with variation in diversification rate is stronger for extinction than for origination (Fig. 2A). For clastic-loving genera, the roles of origination and extinction appear to be about

equal (Fig. 2B). These impressions are supported by the comparison between correlation coefficients (Fig. 3); the pair of correlations for carbonate genera is substantially below the line of isometry, whereas the correlations are essentially the same for clastic genera. The correlations are similar for carbonate genera as for all genera combined; this is to be expected given that there are more than twice as many carbonate-loving as clastic-loving genera (Table 5).

Results differ somewhat if product-moment correlations are used. In particular,  $|r_{\Delta p \Delta d}|$  is

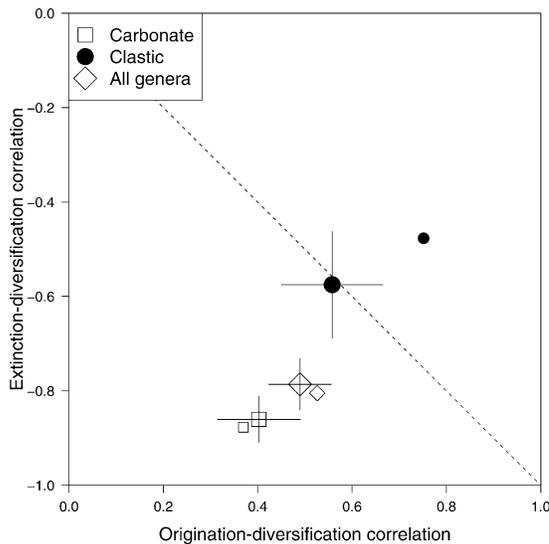


FIGURE 3. Pairs of Spearman rank-order correlations between origination, extinction, and diversification corresponding to the scatterplots of Figures 1A (all genera), 2A (carbonate affinity), and 2B (clastic affinity). Smaller symbols show product-moment correlations for comparison. Extinction evidently contributes more to variation in the diversification rate of carbonate-loving genera but not of clastic-loving genera.

greater than  $|r_{\Delta q \Delta d}|$  for clastic genera (Table 5; small symbols on Figs. 3 and 12), whereas these two correlations are about equal when the Spearman coefficient is used. The high value of  $r_{\Delta p \Delta d}$  reflects a few extreme points, in the lower left and upper right of Figure 2B; the Spearman coefficient therefore is arguably more appropriate. In any event, the fact that the correlations for carbonate and clastic genera are substantially offset from each other—which is the principal result of interest—does not depend on which correlation coefficient is used.

These results show that the greater role of extinction versus origination in determining diversity fluctuations in the Paleozoic can be attributed mainly to the evolutionary behavior of genera with an affinity for carbonate environments. This is consistent with the idea that the secular change in diversity dynamics over the course of the Phanerozoic results from a decline in the relative extent of carbonate versus terrigenous clastic environments. One likely consequence of this decline is depicted in Figure 4, which shows a striking, post-Paleozoic increase in the diversity of clastic-lov-

ing genera but not of carbonate-loving genera. Rules for assigning genera are the same as those used in the foregoing analyses. Given the requirements for a genus to be tabulated, it is likely that the levels of diversity seen in this figure, although based on Sepkoski's data, partly reflect the number of collections in the Paleobiology Database. Thus, without sampling standardization (Alroy et al. 2001), the fine details of the diversity trajectories should not be taken literally. Nonetheless, unless the relative coverage of carbonate versus clastic environments is severely distorted, and distorted in a way that changes systematically over time, the post-Paleozoic proliferation of clastic-loving genera relative to genera with carbonate affinities is likely to be robust.

#### Potential Errors and Biases

Before taking these results too seriously, it is worth considering a number of ways in which the analysis may have gone astray. First, there are various details of the protocol that involve uncertainty but should not obviously bias the results in the direction observed. Second, there is reason to think that the results, in principle, could be inherently biased.

*Sensitivity to Protocol.*—To determine the sensitivity of results to the choices outlined above, several additional analyses were conducted, each of which varied one aspect of the protocol: (1) Marls were treated as carbonates. (2) Marls were treated as clastics. (3) The lithologic assignment of each occurrence was based only on the primary lithology of the corresponding collection. (4) The lithologic assignment of each occurrence was based on a weighted combination of primary and secondary lithologies. To take a few examples: an occurrence from a collection with a clastic primary lithology and a carbonate secondary lithology would be counted as half an occurrence of each lithology; an occurrence with a carbonate primary lithology and a carbonate secondary lithology would be counted as one carbonate occurrence; and an occurrence from a collection with a clastic primary lithology and no secondary lithology would be counted as one clastic occurrence. (5) The analysis was restricted to benthic and presumably nekto-

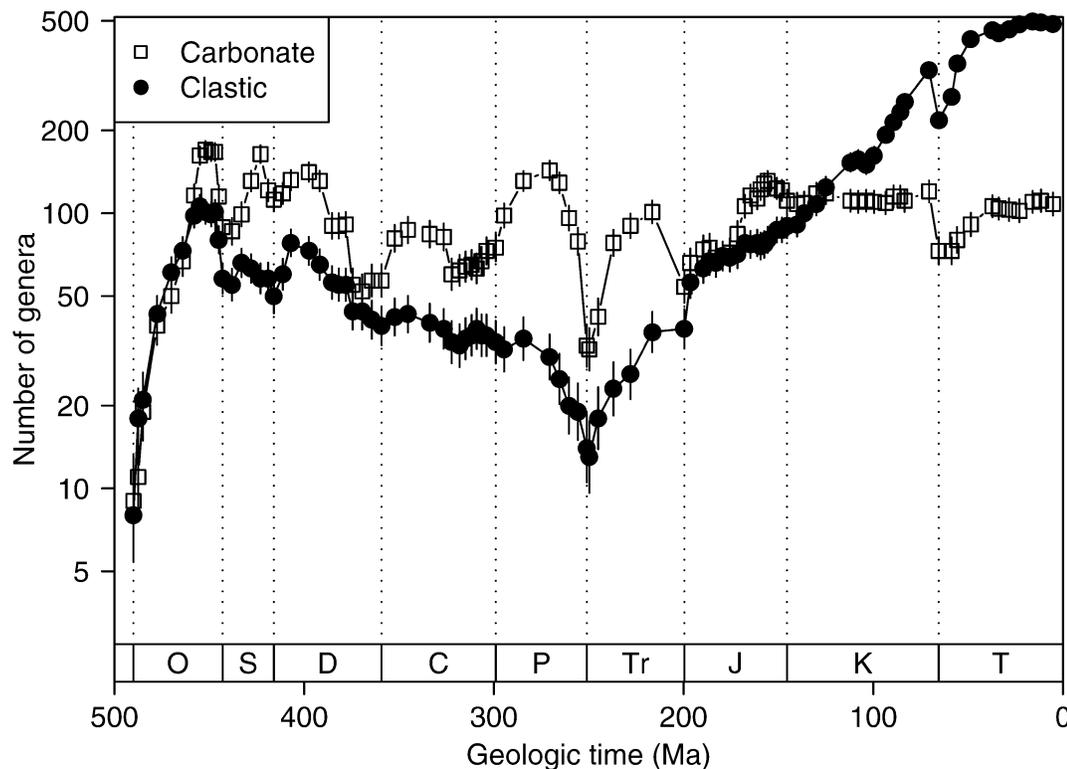


FIGURE 4. Taxonomic diversity of genera with carbonate and clastic affinities, on a logarithmic scale, tabulated as the number of genera extant at the beginning of each stratigraphic interval (Bambach 1999). Clastic-loving genera diversify markedly throughout most of the post-Paleozoic, while carbonate-loving genera hold steady or decrease slightly. Plot spans the Ordovician through Pliocene. The same criterion that was applied to determine whether Paleozoic stages are subdivided is used for the post-Paleozoic as well (see "Data and Methods").

benthic macroinvertebrates; thus, conodonts and graptoloid graptolites were excluded as pelagic, and foraminifera and radiolarians were excluded as unicellular. (6) Multiple occurrences of a genus within a collection were lumped to constitute a single occurrence. (7) Subgenera were not treated as distinct genera. (8) The assignment of lithologic preferences to genera was based on a plurality rather than a majority of occurrences, with the condition that the genus must be represented by at least ten occurrences. This is a less stringent standard than the baseline protocol. (9) The assignment of lithologic preferences was based on a supermajority—at least 70% of the occurrences must be assigned to the same lithologic category for the genus to be assigned to that category, and the genus must have at least five occurrences to be counted. This is a more stringent standard than the baseline protocol. (10) Occurrences were excluded if they are

outside the stratigraphic range of the genus according to Sepkoski's compendium. (11) The requirement that a time interval have at least five first and/or last occurrences was relaxed. (12) This same requirement was increased to a minimum of ten first and/or last occurrences.

The results of these alternative analyses are shown in Figure 5. Bold type indicates the clastic-loving subset of genera, and oblique type indicates the carbonate-loving subset. In every case, the genera with carbonate affinity show a more pronounced tendency for variation in diversification rate to be correlated with extinction. Of particular interest is the difference between the baseline analysis and analyses 8 and 9. The more stringent standard for assigning genera to a lithologic affinity yields a greater separation between carbonate- and clastic-loving genera, whereas the opposite is true for the less stringent standard. This

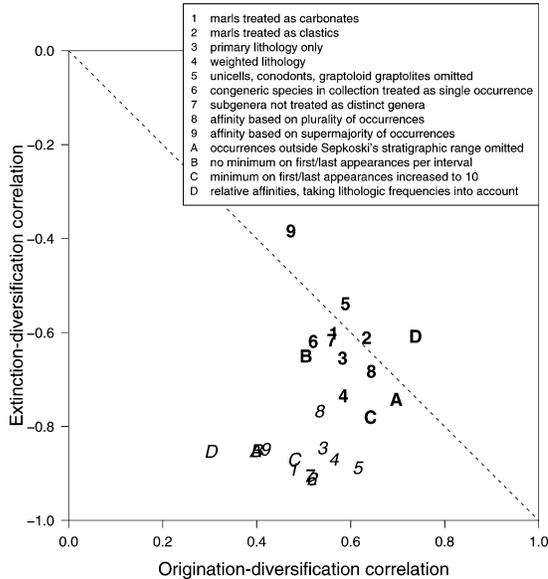


FIGURE 5. Rank-order correlations for data treated according to different protocols. Bold and oblique fonts denote clastic- and carbonate-loving genera, respectively. In all cases, carbonate genera are more extinction-dominated. This is especially the case when more stringent criteria are used to assign lithologic affinities to genera (analyses 9 and D). Please see text for further discussion of protocols.

suggests that there is a true difference between carbonate and clastic genera, which is blurred when there is more uncertainty in the assignment of genera to their appropriate lithologic affinities.

One further aspect of the protocol that deserves to be singled out is that, in contrast to Miller and Connolly's (2001) evaluation of substrate affinities of higher taxa, it does not scale lithologic preferences to the relative frequency of the various lithologies. If, for example, 80% of all occurrences were in carbonates, then a genus with 40% terrigenous clastic occurrences would actually show a strong *relative* affinity for clastics, and a genus with 60% carbonate occurrences would show a weak relative affinity for carbonates. Because there are more carbonate collections and occurrences (Tables 3, 5), relative preferences have real potential to differ from absolute preferences.

To explore this possibility, relative substrate affinities were assessed as follows. The occurrences of each genus were divided into lithologic categories and stratigraphic systems:  $N_{ijk}$  is the number of occurrences of genus  $i$  in sys-

tem  $j$  and lithology  $k$  (where  $k = 1, 2,$  and  $3$  arbitrarily denote carbonate, clastic, and mixed lithologies). Within system  $j$ ,  $E_{ijk}$  is defined as the number of occurrences expected if these were distributed in proportion to the marginal totals for the given genus and the given lithology in that system. Following the usual contingency-table approach,  $E_{ijk} = \sum_i N_{ijk} \times \sum_k N_{ijk} \div \sum_i \sum_k N_{ijk}$ . The expected values are calculated separately for each system  $j$  to take into account the fact that the relative proportions of the three lithologies are not constant over time. Results are similar, however, if expected values are calculated over the entire array of occurrences as  $E_{ijk} = \sum_i N_{ijk} \times \sum_j N_{ijk} \times \sum_k N_{ijk} \div (\sum_i \sum_j \sum_k N_{ijk})^2$ . The deviation between observed and expected occurrences was calculated as  $D_{ijk} = N_{ijk} - E_{ijk}$ . Negative and positive deviations imply fewer and more occurrences than expected. Note that sum of  $D_{ijk}$  over any genus, system, or lithology is equal to zero. The overall affinity of genus  $i$  for lithology  $k$  is given by  $A_{ik} = \sum_j D_{ijk}$ .

Because  $\sum_k A_{ik} = 0$  for each genus, it is necessary that  $A_{ik}$  be non-negative for at least one lithology and non-positive for at least one lithology. Relative substrate affinities were assessed with a stringent approach whereby a genus is assigned to a lithologic category only if its affinity is positive for that lithology and negative for the other two lithologies.

Assigning genera on the basis of relative affinities yields a clearer distinction between carbonate and clastic diversity dynamics than seen in the baseline analysis (Fig. 5). This result stands to reason, because a genus must display an even stronger preference for a given lithology than under the baseline protocol. It also provides further evidence, along with analyses 8 and 9 of Figure 5, that imprecise assignment of lithologic preferences blurs a true evolutionary signal, which stands out more clearly when the assignment is more reliably made. The baseline protocol, while arguably flawed in its failure to take the overall lithologic distribution of occurrences into account, is actually somewhat conservative with respect to the conclusions of this study.

*Effect of Sample Size.*—If there is a real asymmetry in the role of origination versus extinction, this may be obscured by noise in the

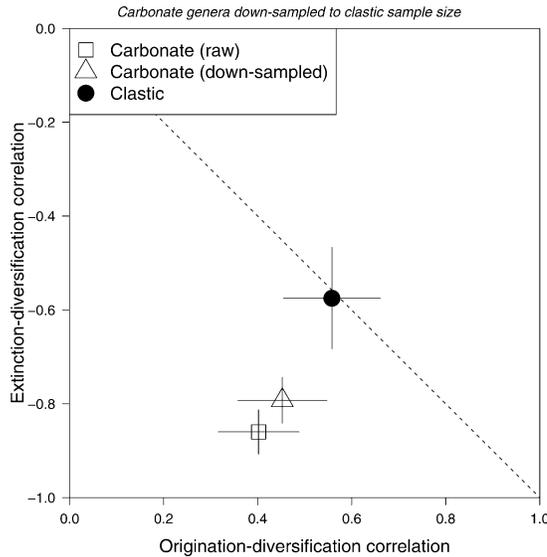


FIGURE 6. Rank-order correlations resulting when the number of carbonate-loving genera is reduced to be equal to the number of clastic-loving genera. The open triangle shows the mean pair of correlations for 1000 replicates in which carbonate genera were down-sampled. Down-sampling moves the correlations toward the line of isometry, but not enough to obscure the difference between carbonate and clastic genera.

data. It is therefore conceivable that the equality of  $|r_{\Delta p \Delta d}|$  and  $|r_{\Delta q \Delta d}|$  for the clastic genera is partly an artifact of the relatively small number of clastic-loving genera in the data. Of course we cannot say how the analysis would have turned out if there had been more clastic genera, but we can ask what would have happened if there had been fewer carbonate genera. There are 848 clastic-loving genera (Table 5); this number of carbonate genera was therefore randomly chosen without replacement, the correlations were calculated, and this procedure was repeated 1000 times. The mean

and standard error are compared in Figure 6 with the clastic correlations and with the carbonate correlations without down-sampling. Down-sampling has moved the carbonate point closer to the line of isometry, but this point is nonetheless distinctly below it. This implies that the difference between carbonate and clastic genera reflects more than simply the number of genera that prefer each substrate.

*Geographic Scope of Sampling.*—It is well known that sampling of the fossil record is biased toward certain regions such as North America and western Europe. Table 6 lists selected tectonic plates and the corresponding number of marine invertebrate collections in the Paleobiology Database. The geographic assignments, kindly carried out by David B. Rowley, were based on the present-day latitude and longitude of the collections as reported in the Paleobiology Database. The plates listed in Table 6 are those that are inferred to have existed in the late Paleozoic (Lottes and Rowley 1990). Several of these are likely to have consisted of smaller plates earlier in the Paleozoic (Scotese and McKerrow 1990).

Over 60% of all collections come from the North American and Eurasian plates. This may complicate the present study in two ways. First, it is possible that the evolutionary patterns documented here are regional rather than global. This would make them of no less interest, but could require a different interpretation. Second, much of North America and Eurasia occupied tropical latitudes for large parts of the Paleozoic but also showed pronounced latitudinal shifts (Scotese and

TABLE 6. Tabulation of Ordovician–Permian collections by tectonic plate (with proportion of total in parentheses).

Plates	No. of collections
North American plate	5953 (0.408)
Other areas in present-day North America	1765 (0.121)
South American plate	425 (0.029)
Other areas in present-day South America	145 (0.010)
Eurasia	2901 (0.199)
Other areas in present-day Europe (including Svalbard, Iberia, Alps, Carpathians, etc.)	384 (0.026)
Yangtze Platform (South China)	1081 (0.074)
Australia	667 (0.046)
Present-day Africa (including Madagascar)	449 (0.031)
Other areas	738 (0.051)
Total	14,608

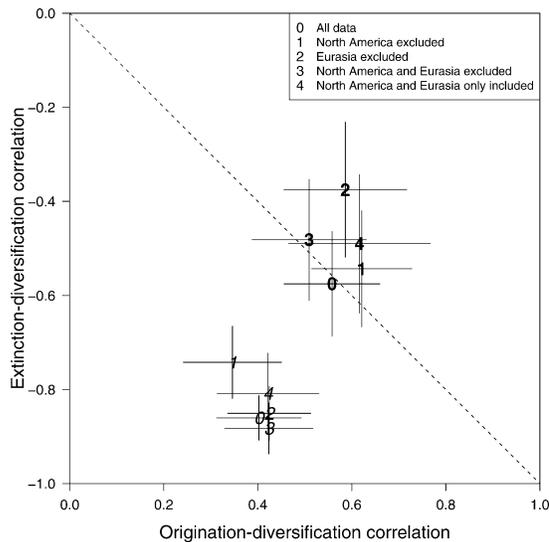


FIGURE 7. Rank-order correlations for genera assigned to lithologic affinities based on geographic subsets of collections (see Table 6). See Figure 5 for graphing conventions. The difference between carbonate and clastic genera does not result simply from the dominance of Eurasia and North America in paleontological collections.

McKerrow 1990). Thus, geographic and secular variation may be conflated.

One way to determine whether these problems are important is to reanalyze the data without the collections that come from North America and/or Eurasia. Figure 7 compares the baseline results with results obtained by (1) excluding North America, (2) excluding Eurasia, (3) excluding both North America and Eurasia, and (4) including only North America and Eurasia. In all of these alternative treatments, there is still a striking difference between carbonate- and clastic-loving genera. This difference therefore seems unlikely to result from geographic bias in sampling and is reasonably seen as global in scope.

*Taxonomic Scope of Results.*—Just as it was possible in principle that the carbonate-clastic difference could have reflected a regional rather than a global pattern, it could be that this difference is attributable to just a small number of higher taxa with specific environmental preferences. Perhaps the carbonate pattern is really a coral pattern, or the clastic pattern one of bivalve molluscs, for example. As with the question of geographic scope, such an out-

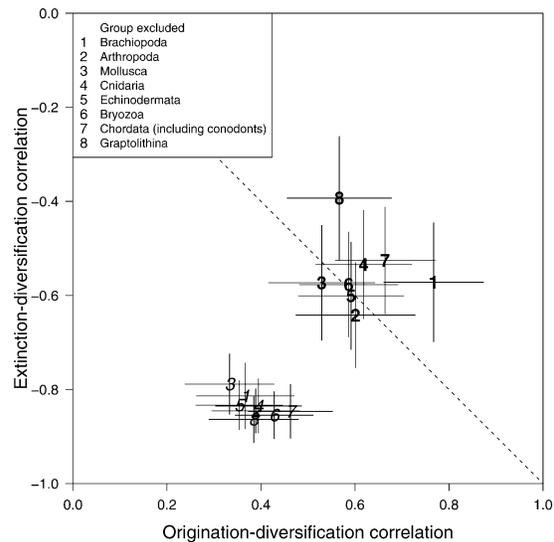


FIGURE 8. Rank-order correlations resulting when the major higher taxa are omitted in turn. See Figure 5 for graphing conventions. The difference between carbonate and clastic genera holds for all analyses, and thus does not simply reflect the idiosyncratic diversity dynamics of a particular higher taxon.

come would be no less interesting than one that is taxonomically broad, but it could entail a different interpretation. Data are still too sparse to conduct separate analyses of carbonate- versus clastic-loving genera within each higher taxon. Any of the major higher taxa can be omitted altogether, however, to assess its influence upon the overall results.

Figure 8 shows the correlations with each of the following groups omitted in turn while retaining all other taxa: (1) Brachiopoda, (2) Arthropoda, (3) Mollusca, (4) Cnidaria, (5) Echinodermata, (6) Bryozoa, (7) Chordata, and (8) Graptolithina. With any group omitted, there is still a consistent difference between carbonate and clastic genera. Clearly, therefore, the carbonate-clastic difference in diversity dynamics cannot be attributed to any single group. Until data are available to assess each of the major higher taxa separately, it is reasonable to regard this difference in diversity dynamics as a fairly general biotic feature.

*Temporal Pattern in Rates.*—Having established that extinction plays a greater role than origination in the diversity fluctuations of carbonate-loving genera but not of clastic-loving genera, it is worth relating this fairly distilled summary of taxonomic rates to the rates them-

selves. To this end, Figure 9 portrays the time series of origination and extinction rates separately for carbonate and clastic genera. Rates for intervals that do not meet the minimum data threshold are shown by smaller symbols.

The carbonate and clastic rates differ in two ways: First, carbonate rates are somewhat higher on average. This is not relevant to the results presented herein, which depend on the temporal variance and covariance of rates rather than on their magnitude. Second, carbonate rates, especially extinction rates, seem to be more volatile. There are several stretches of time with comparatively little variation in extinction rate of clastic genera and an excursion in the carbonate extinction rate—for example the middle and upper Ashgillian, the Wenlockian through Pridolian, the Emsian through Givetian, and the Famennian. The greater volatility of carbonate rates is in accord with the pattern of temporal variation in diversity shown earlier (Fig. 4).

It is natural to ask whether the statistical difference between carbonate and clastic diversity dynamics can be attributed to just a few time intervals. The carbonate extinction excursions that appear most striking are those in the middle Ashgillian, the Ludlovian, the Givetian, the late Frasnian, and the late Famennian. These intervals were therefore omitted. (Two Permian intervals that also contain conspicuous extinction of carbonate-loving genera do not need to be excluded, as they do not meet the minimum data threshold and so were not included in the first place.) Because the analysis considers first differences, leaving out an interval eliminates two points. Figure 10 shows that the carbonate correlations move closer to the line of isometry when the selected intervals are omitted, yet they remain below this line. Thus, the carbonate-clastic difference in diversity dynamics does not appear to hinge on a small number of extinction events.

#### Temporal Scaling

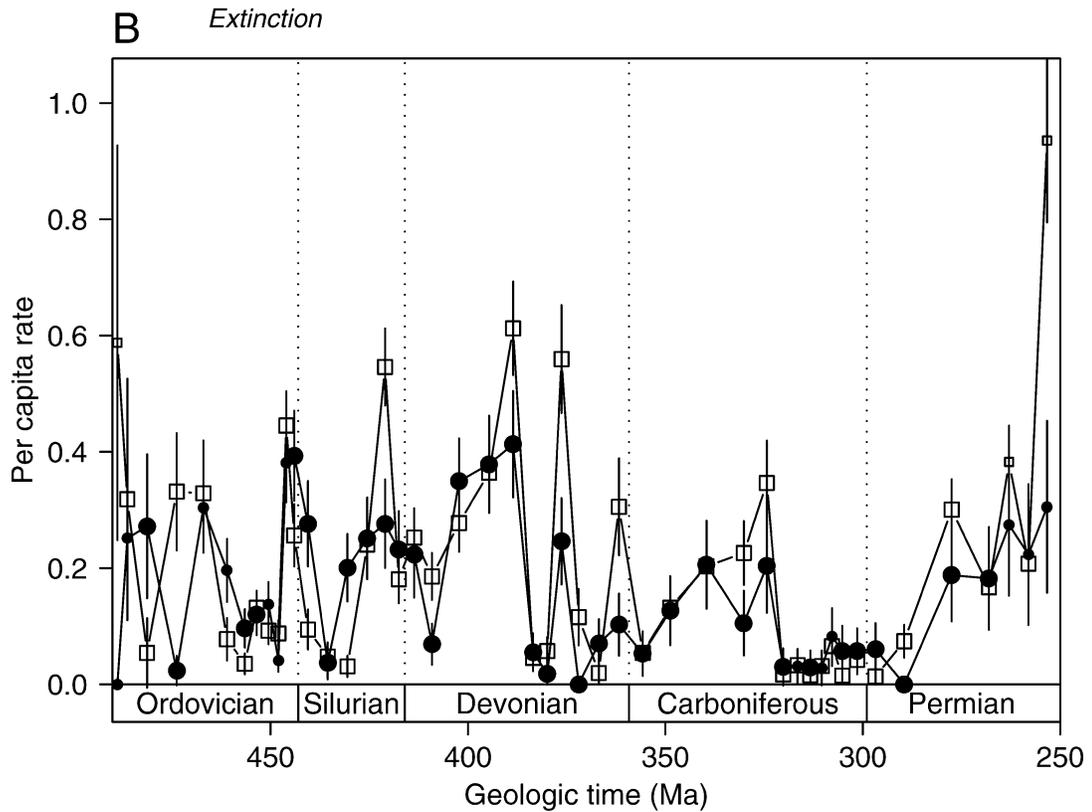
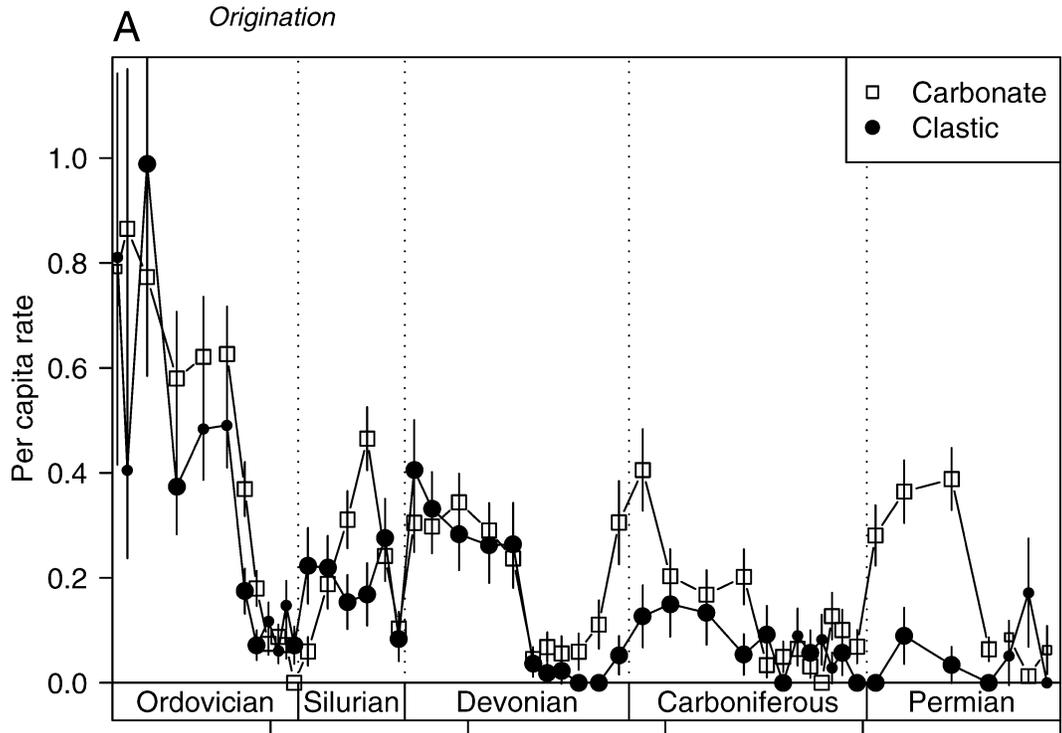
Although the results are not completely dominated by a few particular intervals of time, Figure 9 conveys the impression that the carbonate-clastic differences in rate variance have a short characteristic time scale. To determine whether these differences persist at a

lower degree of temporal acuity, analyses were repeated without dividing stages into substages. The stage-level rates (Fig. 11) suggest less discrepancy between genera of carbonate and clastic affinity. This is borne out by the comparison of correlations (Fig. 12), which shows that neither carbonate- nor clastic-loving genera deviate appreciably from isometry. This does not contradict previous work that documented asymmetries between origination and extinction (Foote 2000a), for that study involved stratigraphic subdivisions similar to the substages used for most of the analyses here.

It is not immediately evident why diversity dynamics depend on temporal resolution. Whatever factors give rise to the difference in diversity dynamics between carbonate- and clastic-lovers, they appear to act on a relatively short time scale. One can speculate that the cause lies in geologically brief environmental perturbations that preferentially affect carbonate environments, but this possibility needs to be independently tested.

#### Discussion

This study adds to the existing evidence that substrate affinity is an important factor in macroevolution when the availability of substrates changes on geologic time scales. To cite just two examples of previous work: (1) During the Ordovician, articulated brachiopods diversified globally at a higher rate than trilobites, and this was arguably because they shifted their preference toward terrigenous clastic environments, which were increasing in extent, while trilobites increased in their relative affinity for carbonates (Miller and Connolly 2001). (2) Although the global diversity trajectories of bivalve and gastropod molluscs were quite similar during the Ordovician, bivalves were more diverse in clastic settings and gastropods in carbonate settings. Thus, the similar history of these two groups at the global scale must have depended in part on the precise mixture of environmental settings and how it changed through the Ordovician (Novack-Gottshall and Miller 2003). And of course many other studies could be mentioned in this context (Bretsky 1968; Sheehan 1985; Miller 1988; Guensburg and Sprin-



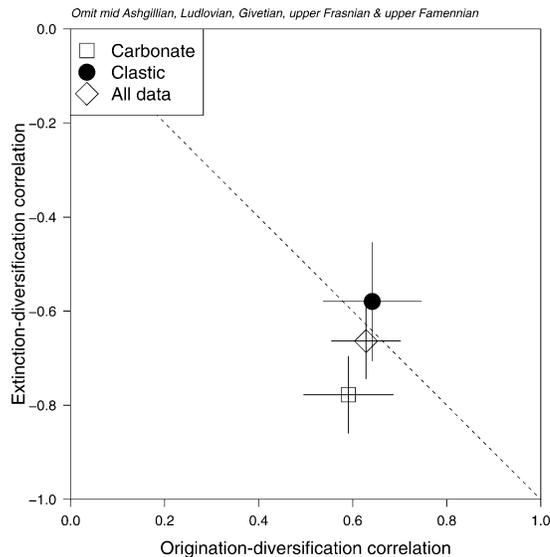


FIGURE 10. Rank-order correlations resulting when the intervals with the most conspicuous extinction-rate excursions are omitted. The difference between carbonate and clastic genera persists but is less pronounced.

kle 1992; Miller and Mao 1995; Cope and Babin 1999; Waisfeld et al. 2003). Much of this work deals with the broad question of what determines secular trends in standing diversity. Here I have focused on a particular part of this question, namely how fluctuations in origination and extinction rate contribute to variance in diversity.

The principal result of this study is that short-term variation in the net rate of diversification is more strongly coupled to extinction than to origination for carbonate-loving genera. In one sense, this reduces to little more than the fact that extinction rate fluctuates with more volatility than origination rate. This equivalence is not trivial, however, for the magnitude of the difference between origination-diversification and extinction-diversification correlations depends also on the weak, positive correlation between origination and extinction—something that is by no means a foregone conclusion.

Diversity variation within clastic lovers is

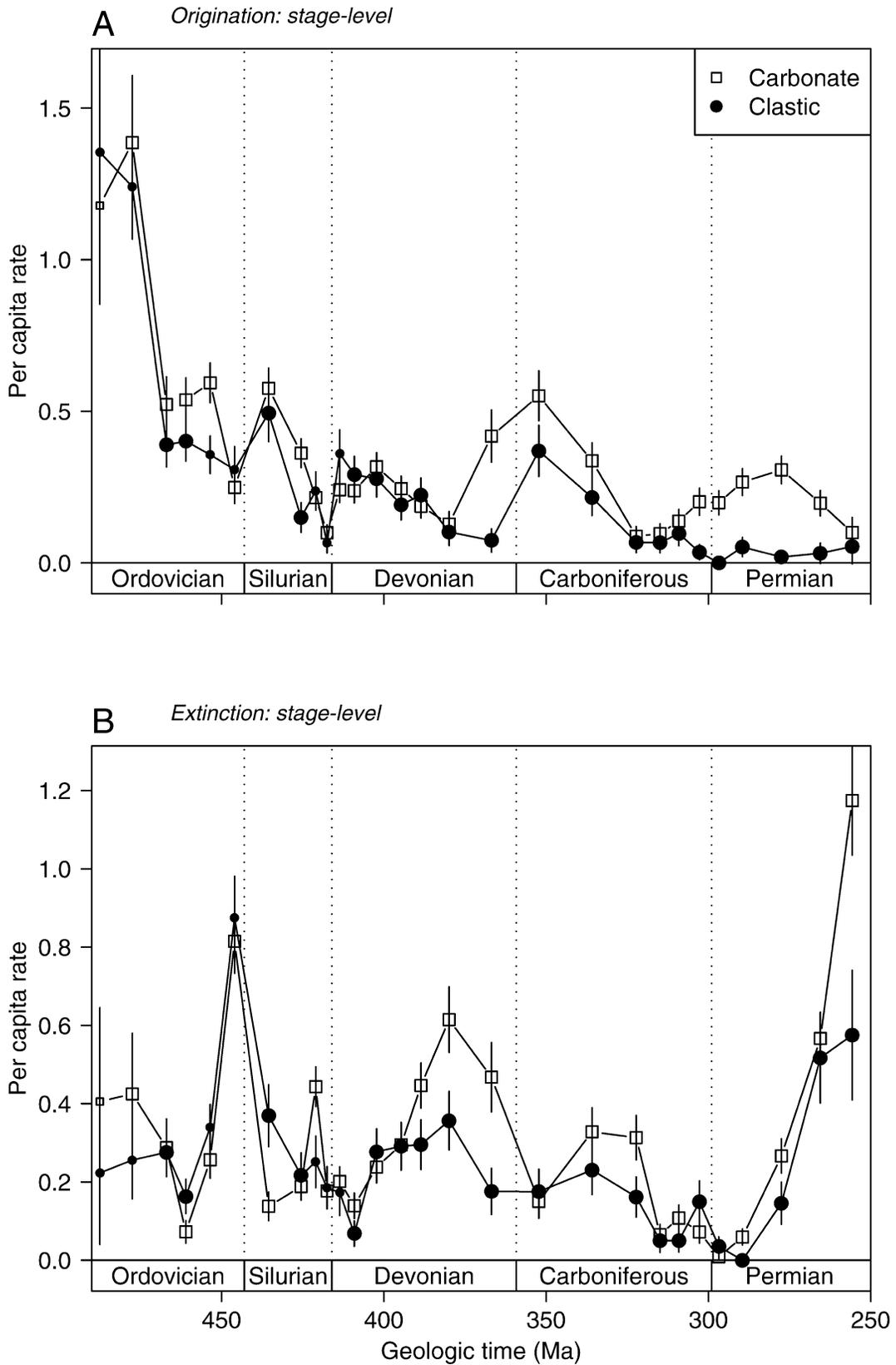
not dominated by extinction-rate variation; nor is it unambiguously dominated by origination-rate variation, however. Thus, it is not entirely clear that the evolutionary behavior of clastic lovers is a good proxy for that of post-Paleozoic animals, whose diversity dynamics are origination-dominated (Foote 2000a). Given the great similarity between carbonate and Paleozoic diversity dynamics, however, it is quite plausible that the secular decline in carbonate environments contributes to the shift in diversity dynamics from the Paleozoic to the post-Paleozoic, even if other factors also play a role.

This paper so far has bypassed the important question of whether it is carbonate substrate per se or some correlate that is important. The vast majority of genera in this study are benthic. The analyses of Figures 5 and 9 show that omitting taxa that are not tied to the substrate, notably conodonts and graptoloid graptolites, has little effect on the results. This does not mean that the evolutionary behavior of non-benthic taxa is the same as that of benthic taxa, however, a result which would suggest that it is not substrate per se but some correlate of substrate that is important. At present the data are too sparse to analyze non-benthic taxa separately; we can only conclude that their diversity dynamics are not sufficiently different to obscure the signal of the benthic taxa.

Widespread carbonates tend largely to be tropical to subtropical and of relatively shallow-water origin (James 1984; Kiessling et al. 2003), which is not to deny the existence of cool-water carbonates (James and Clarke 1997), and they often develop in lower-nutrient settings (Hallock and Schlager 1986). Thus the carbonate-clastic differences documented here could in fact reflect latitudinal, bathymetric, or oceanographic variation in diversity dynamics. Indeed, the secular decline in carbonates is roughly correlated with the movement of several continents away from the

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FIGURE 9. Time series of origination and extinction rates used in analyses of Figures 2 and 3. Small symbols depict intervals that did not meet the minimum data threshold; these were excluded from further analysis. Genera of carbonate affinity have more volatile rates and show a number of short-lived excursions, especially in extinction, that are not reflected in the rates of clastic-loving genera.



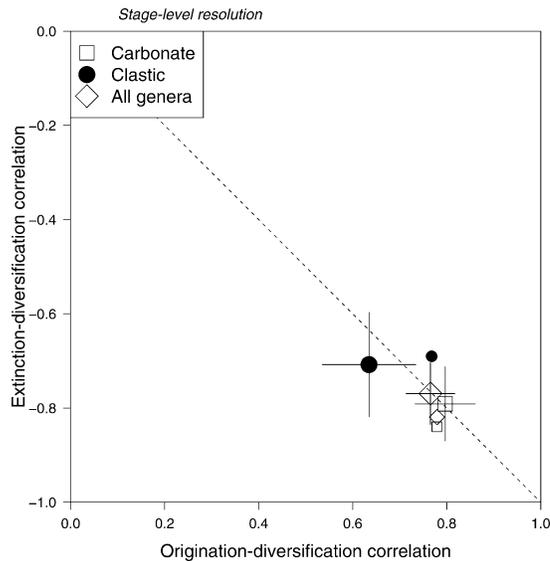


FIGURE 12. Rank-order correlations for rates with undivided time intervals (Fig. 11). See Figure 3 for graphing conventions. Correlations are higher for carbonate genera than for clastic genera, but neither group shows an asymmetry between the origination and extinction contributions to diversification rate.

equator (Allison and Briggs 1993) and with reduced cratonic flooding (Ronov 1994). Ideally, one would partition data in such a way that the relevant factors could be independently examined. At the coarsest scale, considering just a few likely factors, there would be at least eight combinations of substrate (carbonate versus clastic), depth (shallow versus deep), and geography (tropical versus extratropical), and of course many important factors—western versus eastern coastlines for example—would be neglected by such a basic approach.

At this time, the Paleobiology Database does not have sufficient collections representing all the combinations of factors even in this simplest of schemes. Table 7 presents the number of collections by lithology and inferred paleolatitude, based on Christopher Scotese's paleogeographic transformation as implemented on the Database website. Some caution is called for here, as the paleogeographic interpretations are based not only on paleomag-

netism but also on biogeographic and lithologic data (Scotese et al. 1979; Scotese 2005). There is thus the chance of some circularity, but I will accept these reconstructions for the sake of discussion. The data show the expected tendency for carbonates to increase relative to clastics toward lower latitudes. If collections are divided into two subsets—arbitrarily at 30° or lower versus greater than 30°—then we find that many time intervals fail to meet the minimum data threshold. Of 48 intervals in the Ordovician through Permian, only 29 meet the threshold for clastic-loving genera when collections are restricted to the low latitudes, and only 24 and 33 meet the threshold for carbonate- and clastic-loving genera, respectively, when collections are restricted to the higher latitudes. The limitations in data presumably reflect both the current state of sampling in the Paleobiology Database and the preserved sediments that are available to be sampled.

In a preliminary attempt to explore the effects of substrate with latitude factored out, I assigned relative affinities, using a variant on the procedure described earlier (see "Potential Errors and Biases"). The analysis here is the same, except that latitudinal bins take the place of time intervals. Thus,  $N_{ijk}$  is the number of occurrences of genus  $i$  in latitudinal bin  $j$  and lithology  $k$ , where  $j = 1, 2, \dots$  refer to paleolatitudes between 0° and 10°, between 10° and 20°, and so on, and  $k = 1, 2, \text{ and } 3$  denotes carbonate, clastic, and mixed lithologies.

As it turns out, the correlation between lithology and latitude is so strong that very few genera have a lithologic preference that cannot be seen as a latitudinal preference as well. Using the previous criterion for assessing relative affinities, namely that a genus be assigned to a lithologic category only if its relative affinity is positive for that lithology and negative for the other two lithologies, only 115 genera prefer carbonates more than expected on the basis of the marginal totals for genera and

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FIGURE 11. Time series of origination and extinction rates with intervals not subdivided (see Table 2). See Figure 9 for graphing conventions. The carbonate and clastic curves are evidently much more concordant than they are with subdivided intervals.

TABLE 7. Collections by lithology and absolute paleolatitude. Numbers in parentheses are the proportion of collections for the given latitudinal bin that have the given lithology. Collections without lithologic information, or with lithologies not classified here as carbonate, clastic, or mixed, are excluded.

Latitudinal range (absolute degrees)	No. of collections			
	Carbonate	Clastic	Mixed	Total
0–10	2276 (0.540)	1226 (0.291)	709 (0.168)	4211
10–20	1390 (0.558)	482 (0.193)	619 (0.248)	2491
20–30	1405 (0.425)	861 (0.260)	1043 (0.315)	3309
30–40	599 (0.346)	888 (0.512)	246 (0.142)	1733
40–50	225 (0.277)	395 (0.486)	192 (0.236)	812
50–60	21 (0.118)	109 (0.612)	48 (0.270)	178
60–70	49 (0.145)	253 (0.749)	36 (0.107)	338
70–80	17 (0.093)	143 (0.786)	22 (0.121)	182
80–90	3 (0.032)	81 (0.871)	9 (0.097)	93
Total	5985	4438	2924	13,347

for lithologic and paleolatitudinal bins. For terrigenous clastics the number is 40 genera. This approach to assessing relative affinities is arguably too draconian. It is nonetheless evident that a clear separation between lithologic and latitudinal patterns of occurrence is a complicated matter that remains to be resolved.

Even with the incomplete data now available, it is clear that carbonate-loving and clastic-loving genera are characterized by distinct styles of diversity dynamics, with extinction variation more important for carbonate lovers and origination and extinction about equally important for clastic lovers. This does not, however, explain *why* these groups of genera behave differently. In a proximal sense, the difference reflects short-term excursions in the extinction rate of carbonate genera that are not seen in clastic genera. This is consistent with geologically brief perturbations of carbonate environments, which could be exacerbated by the predominance of epicontinental seas in the Paleozoic (Johnson 1974; Ronov 1994). Comprehensive, global data needed to test this possibility are not yet readily available at a sufficiently fine scale of temporal resolution. Ongoing work (Peters 2005) suggests that such data may soon exist.

There are many sources of error that could affect the results presented here, and a number of them were explicitly tested above. One that is more difficult to assess is incomplete sampling. Any process that yields different temporal variances in *apparent* origination and extinction rates will produce different corre-

lations between origination and diversification on the one hand and extinction and diversification on the other (Appendix). If the true variances of origination and extinction are equal, then random temporal variation in the quality of sampling may induce a spurious correlation between origination and extinction rates but it will not affect origination and extinction differently (Foote 2000b). If, however, the quality of sampling varies in a way that is correlated with true taxonomic rates, there is the potential for origination and extinction to be affected differently.

Suppose, for example, that peaks of extinction tend to be followed by comparable peaks of origination and that sampling tends to be better during intervals of extinction than during the subsequent recovery intervals. In such a situation, there will be more forward smearing of origination than backward smearing of extinction. Thus, the origination variance will be artificially dampened more than that of extinction, with the result that  $|r_{\Delta q \Delta d}|$  will be greater than  $|r_{\Delta p \Delta d}|$ . Although this scenario sounds ad hoc, it is in fact empirically supported by a comparison of sampling rates with origination and extinction rates that themselves were estimated with incomplete sampling taken into account (Foote 2003).

We thus have a plausible mechanism by which extinction-diversification and origination-diversification correlations could be affected differently by incomplete sampling. To dismiss the results presented here and elsewhere (Foote 2000a), however, would leave two questions unanswered. Why is origina-

tion more important in post-Paleozoic diversity fluctuations? And why are carbonate-and clastic-loving genera affected differently? A possible answer to the second question is that extinction peaks and sampling peaks tend to coincide for carbonate genera but not for clastic genera. This suggestion is testable in principle.

### Summary

1. Fluctuations in the diversification rate of Paleozoic marine animal genera are more strongly correlated with variance in extinction rate than in origination rate. Previous work shows that origination is the more important component in the post-Paleozoic.
2. The greater importance of extinction in the Paleozoic holds for genera that have an affinity for carbonate environments but not for genera with a clastic affinity. It is therefore plausible that the shift in diversity dynamics from the Paleozoic to the post-Paleozoic results at least in part from the secular decline in the relative extent of carbonate environments and the concomitant decrease in the relative diversity of carbonate-loving genera.
3. The difference between carbonate and clastic diversity dynamics reflects the greater volatility of extinction in carbonate-loving genera. Several intervals of time are marked by brief excursions in the extinction rate of carbonate genera but not of clastic genera. The carbonate-clastic difference largely disappears if data are analyzed at a coarser level of temporal resolution, as does the origination-extinction asymmetry more generally. Thus, the factors that distinguish carbonate from clastic genera seem to act on relatively short (<5 Myr) time scales.

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Appendix

Expected Correlations between Origination, Extinction, and Net Diversification

Let  $p_i$ ,  $q_i$ , and  $d_i$  be the per capita rate of origination, extinction, and net diversification in time interval  $i$ , where  $d_i = p_i - q_i$ . Let  $\Delta p_i = p_i - p_{i-1}$ ,  $\Delta q_i = q_i - q_{i-1}$ , and  $\Delta d_i = d_i - d_{i-1}$  be the first differences in these rates. Note that  $\Delta d_i = \Delta p_i - \Delta q_i$ .

Let  $s_{pr}^2$ ,  $s_{qd}^2$ , and  $s_d^2$  be the variances in  $p$ ,  $q$ , and  $d$  taken over the series of time intervals, and let  $s_{pq}$ ,  $s_{pd}$ , and  $s_{qd}$  be the covariances between the subscripted variables. The variance of a random variable  $X$  is given by

$$s_x^2 = E(X^2) - \mu_x^2 \tag{1a}$$

where  $E(X^2)$  denotes the expectation of  $X^2$  and  $\mu_x$  is the mean of  $X$  (Feller 1968: p. 227). Rearranging yields

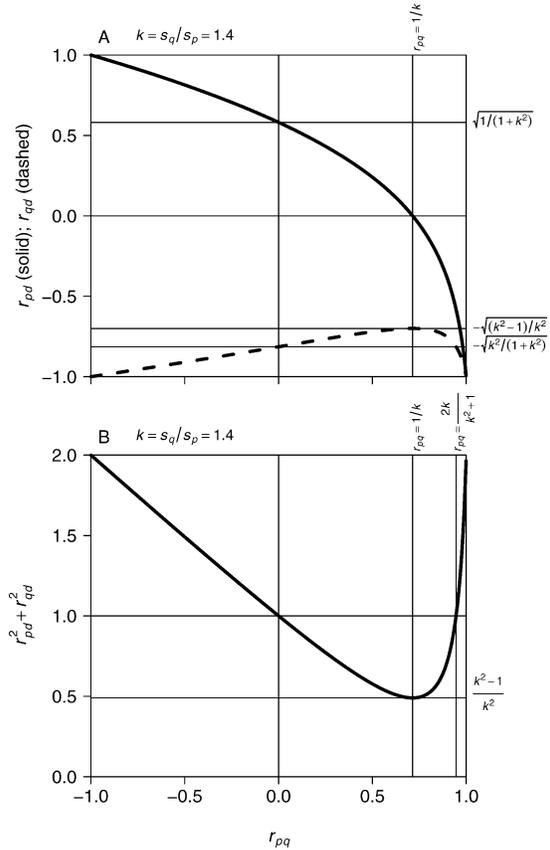


FIGURE 13. Expected relationships among  $r_{pd}$ ,  $r_{qd}$ , and  $r_{pq}$  when extinction rate is more variable than origination rate. For this figure, the ratio  $k$  of  $s_q$  to  $s_p$  is equal to 1.4. A,  $r_{pd}$  (solid) and  $r_{qd}$  (dashed) as a function of  $r_{pq}$ . When extinction rate varies more than origination rate,  $|r_{qd}| > |r_{pd}|$  for all values of  $r_{pq}$  and  $r_{pd} > 0$  only if  $r_{pq} < 1/k$ . B,  $r_{pd}^2 + r_{qd}^2$  as a function of  $r_{pq}$ . Lines marked by values in the margins are cases discussed in the text.

$$E(X^2) = s_x^2 + \mu_x^2 \tag{1b}$$

Similarly, the covariance between two random variables  $X$  and  $Y$  is given (Feller 1968: p. 230) by

$$s_{xy} = E(XY) - \mu_x\mu_y \tag{2a}$$

which implies that

$$E(XY) = s_{xy} + \mu_x\mu_y \tag{2b}$$

Because  $d = p - q$ , we also need the general expression for the variance of a difference between two random variables (Feller 1968: p. 230):

$$s_{x(x-y)}^2 = s_x^2 + s_y^2 - 2s_{xy} \tag{3}$$

and for the covariance between this difference and either of the random variables:

$$s_{x(x-y)} = E(X^2) - E(XY) - \mu_x^2 + \mu_x\mu_y \tag{4a}$$

$$s_{y(x-y)} = -E(Y^2) + E(XY) + \mu_y^2 - \mu_x\mu_y \tag{4b}$$

Note that the product-moment correlation is given (Sokal and Rohlf 1995: p. 560) by

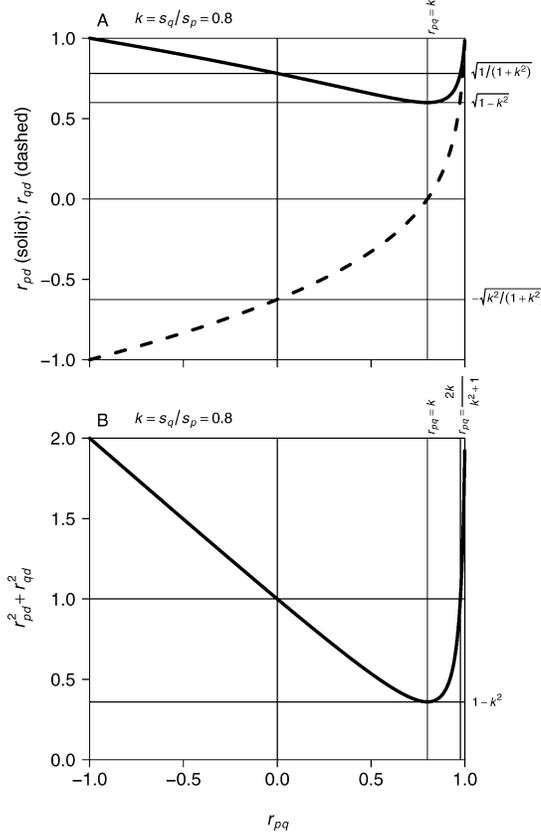


FIGURE 14. Expected relationships among  $r_{pd}$ ,  $r_{qd}$ , and  $r_{pq}$  when origination rate is more variable than extinction rate. For this figure, the ratio  $k$  of  $s_q$  to  $s_p$  is equal to 0.8. See Figure 13 for explanation. When origination rate varies more than extinction rate,  $|r_{pd}| > |r_{qd}|$  for all values of  $r_{pq}$  and  $r_{qd} < 0$  only if  $r_{pq} < k$ .

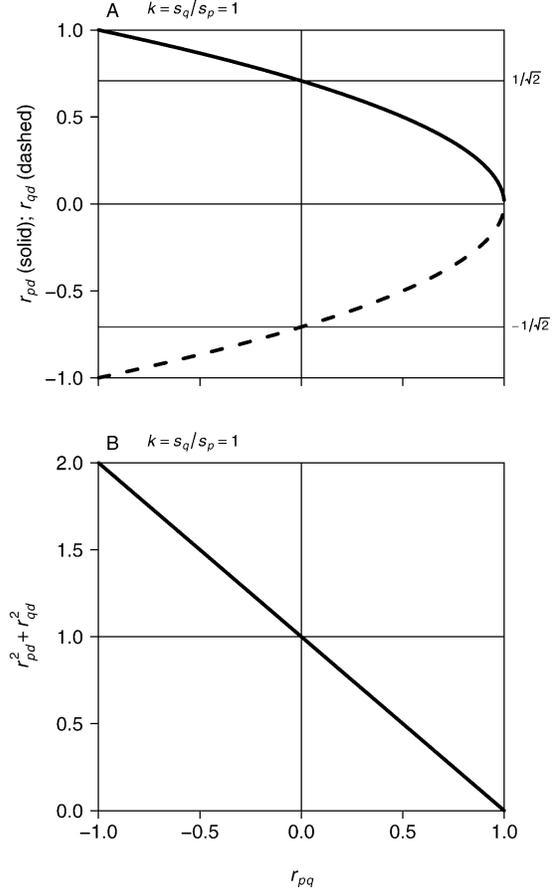


FIGURE 15. Expected relationships among  $r_{pd}$ ,  $r_{qd}$ ,  $r_{pq}$  when origination and extinction are equally variable. See Figure 13 for explanation.

$$r_{xy} = \frac{s_{xy}}{\sqrt{s_x^2 s_y^2}}. \quad (5)$$

Suppose we are given  $s_p^2$ ,  $s_q^2$ , and  $r_{pq}$  and are to determine  $r_{pd}$  and  $r_{qd}$  from these quantities. Starting with  $r_{pd}$  and substituting  $p$  and  $d$  in equation (5),  $p$  and  $q$  in equation (4a),  $p$  and  $q$  in equation (3),  $p^2$  in equation (1b), and  $p$  and  $q$  in equation (2b), we have

$$\begin{aligned} r_{pd} &= \frac{s_{pd}}{\sqrt{s_p^2 s_d^2}} = \frac{\mathbf{E}(p^2) - \mathbf{E}(pq) - \mu_p^2 + \mu_p \mu_q}{\sqrt{s_p^2 (s_p^2 + s_q^2 - 2s_{pq})}} \\ &= \frac{(s_p^2 + \mu_p^2) - (s_{pq} + \mu_p \mu_q) - \mu_p^2 + \mu_p \mu_q}{\sqrt{s_p^2 (s_p^2 + s_q^2 - 2r_{pq} s_p s_q)}} \\ &= \frac{s_p^2 - r_{pq} s_p s_q}{\sqrt{s_p^2 (s_p^2 + s_q^2 - 2r_{pq} s_p s_q)}}. \end{aligned} \quad (6)$$

Similarly, starting with  $r_{qd}$  and substituting  $q$  and  $d$  in equation (5),  $p$  and  $q$  in equation (4a),  $p$  and  $q$  in equation (3),  $q^2$  in equation (1b), and  $p$  and  $q$  in equation (2b), we have

$$r_{qd} = \frac{r_{pq} s_p s_q - s_q^2}{\sqrt{s_q^2 (s_p^2 + s_q^2 - 2r_{pq} s_p s_q)}}. \quad (7)$$

Let  $s_q$  be some multiple of  $s_p$ , so that  $s_q = k s_p$ ,  $s_p s_q = k s_p^2$ , and  $s_q^2 = k^2 s_p^2$ . Substituting into equations (6) and (7), we have:

$$r_{pd} = \frac{s_p^2 (1 - r_{pq} k)}{\sqrt{s_p^2 (s_p^2 + k^2 s_p^2 - 2r_{pq} k s_p^2)}} = \frac{1 - r_{pq} k}{\sqrt{k^2 - 2r_{pq} k + 1}} \quad \text{and} \quad (8)$$

$$r_{qd} = \frac{r_{pq} k s_p^2 - k^2 s_p^2}{\sqrt{k^2 s_p^2 (s_p^2 + k^2 s_p^2 - 2r_{pq} k s_p^2)}} = \frac{r_{pq} - k}{\sqrt{k^2 - 2r_{pq} k + 1}}. \quad (9)$$

Figures 13–15 show how  $r_{pd}$ ,  $r_{qd}$ , and  $r_{pd}^2 + r_{qd}^2$  vary as a function of  $r_{pq}$ . The figures depict three situations:  $k > 1$ ,  $k = 1$ , and  $k < 1$ , i.e.,  $s_p < s_q$ ,  $s_p = s_q$ , and  $s_p > s_q$ . When  $s_p < s_q$ ,  $r_{pd}$  (solid line in Fig. 13A) decreases monotonically as  $r_{pq}$  increases, while  $|r_{qd}|$  (dashed line in Fig. 13A) reaches a minimum value at  $r_{pq} = 1/k$ , i.e., at  $r_{pq} = s_p/s_q$ , and this minimum is equal to  $\sqrt{(k^2 - 1)/k^2}$ . The minimum of  $|r_{qd}|$  coincides with  $r_{pd} = 0$ . Therefore the minimum of  $|r_{qd}|$  also corresponds to a minimum of  $r_{pd}^2 + r_{qd}^2$ , which is equal to  $(k^2 - 1)/k^2$  (Fig. 13B).

When  $k < 1$ , the behavior of  $r_{pd}$  and  $r_{qd}$  is reversed compared with the case where  $k > 1$  (Fig. 14). Here, the minimum of  $r_{pd}$  is equal to  $\sqrt{1 - k^2}$  and occurs when  $r_{pq} = k$ ; this corresponds to  $r_{qd} = 0$  and also to the minimum of  $r_{pd}^2 + r_{qd}^2 = 1 - k^2$ .

Figures 13 and 14 show that positive correlations between extinction and diversification and negative correlations between

origination and diversification are theoretically possible. They are empirically uncommon, however (Foote 2000a; this study).

When  $k = 1$ ,  $r_{pd}$  and  $r_{qd}$  are equal in magnitude and opposite in sign for any value of  $r_{pq}$  decreasing in magnitude monotonically as  $r_{pq}$  increases (Fig. 15A). As a result,  $r_{pd}^2 + r_{qd}^2$  also decreases monotonically as  $r_{pq}$  increases (Fig. 15B).

Regardless of the value of  $k$ ,  $r_{pd}^2 + r_{qd}^2 = 1$  at two points: when  $r_{pq} = 0$  and when  $r_{pq} = 2k/(k^2 + 1)$ .  $r_{pd}^2 + r_{qd}^2$  is less than unity if  $r_{pq}$  is between 0 and  $2k/(k^2 + 1)$ .

A few special cases are worth noting:

1. If  $k = 1$ , then  $r_{pd} = \sqrt{(1-r_{pq})/2}$ ,  $r_{qd} = -\sqrt{(1-r_{pq})/2}$ , and  $r_{pd}^2 + r_{qd}^2 = 1 - r_{pq}$  (Fig. 15).
2. If  $r_{pq} = 0$ , then  $r_{pd} = 1/\sqrt{k^2 + 1}$ ,  $r_{qd} = -k/\sqrt{k^2 + 1}$ , and  $r_{pd}^2 + r_{qd}^2 = 1$  (Figs. 13–15).
3. If  $k = 1$  and  $r_{pq} = 0$ , then  $r_{pd} = 1/\sqrt{2}$ ,  $r_{qd} = -1/\sqrt{2}$ , and  $r_{pd}^2 + r_{qd}^2 = 1$  (Fig. 15).

If, as in this study, we work with first differences, then, because  $\Delta d = \Delta p - \Delta q$ , we simply substitute  $\Delta p$ ,  $\Delta q$ , and  $\Delta d$  for  $p$ ,  $q$ , and  $d$  in all the foregoing expressions.