

# Covariation in macrostratigraphic and macroevolutionary patterns in the marine record of North America

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## ABSTRACT

Students of Earth history have long recognized the correlation between the quantity of preserved sedimentary rock and the diversity of life recorded as fossils. But paleontologists have yet to determine whether this pattern reflects a causal relationship or a unidirectional sampling bias in fossil data imposed by preserved rock quantity. Distinguishing between these two alternatives has been complicated by the fact that many of the basic patterns of paleontologic and lithologic covariation have yet to be quantified rigorously. Here we present the first analyses of the covariation between the macrostratigraphic and macroevolutionary histories of North America based on geographically and temporally explicit co-occurrences of rocks and fossils. The analyses use independent quantitative summaries of the stratigraphic and fossil records by integrating the Paleobiology Database (PaleoDB) and Macrostrat, a macrostratigraphy database for North America, which allows a more direct comparison of the stratigraphic and biological histories of the continent than has heretofore been possible. Within the Macrostrat database, the rock record is divided into discrete packages of sediment that are bound by hiatuses resolvable at the stage-level. Using per interval, per package rates of sediment package initiation and truncation, and genus first and last appearances (herein *regional* origination and extinction), we find a substantially stronger positive correlation between sediments and biology for extinction-like parameters than we do for origination-like parameters. Four of the largest coincident pulses of regional extinction and sediment truncation occur during the widely recognized end-Ordovician, late Permian, end-Triassic, and end-Cretaceous

mass extinction intervals. A further comparison of the global ranges of North American genera to North American macrostratigraphy indicates that the regional and global extinction of genera are more likely to occur in the same stage than are global and regional originations. Together, these results suggest that our general understanding of biodiversity dynamics from the fossil record may not be strongly biased by the preservation of sediments and leaves open the possibility that certain large perturbations to the Earth system are responsible for major changes of state in both the sedimentary and biological systems.

## INTRODUCTION

The drivers of macroevolutionary phenomena are a central focus of paleobiological research, but biological signals in the fossil record bear an overprint from taphonomic processes (Kidwell and Flessa, 1995) and the architecture of the stratigraphic record (Holland, 1995, 2000; Kidwell and Holland, 2002; Crampton et al., 2006). Of particular and longstanding interest is the observed covariation between the quantity of rocks preserved of a given age and estimates of taxonomic richness (Raup, 1976; Peters and Foote, 2001; Smith, 2001; Smith and McGowan, 2007; McGowan and Smith, 2008; Wall et al., 2009) and macroevolutionary rates (Patterson and Smith, 1987; Smith, 2001; Peters and Foote, 2002; Peters, 2005, 2008). Knowing the extent and basis of covariation between quantitative estimates of macroevolution and the rock record is important for correctly interpreting the history of life.

Two major hypotheses have been put forward to explain the observed covariation between the rock and fossil records: (1) the dominant signal in the fossil record is the result of a sampling bias imparted by the abundance and preservation of sedimentary outcrops (Raup, 1976; Smith, 2001; Smith et al., 2001; Smith and McGowan,

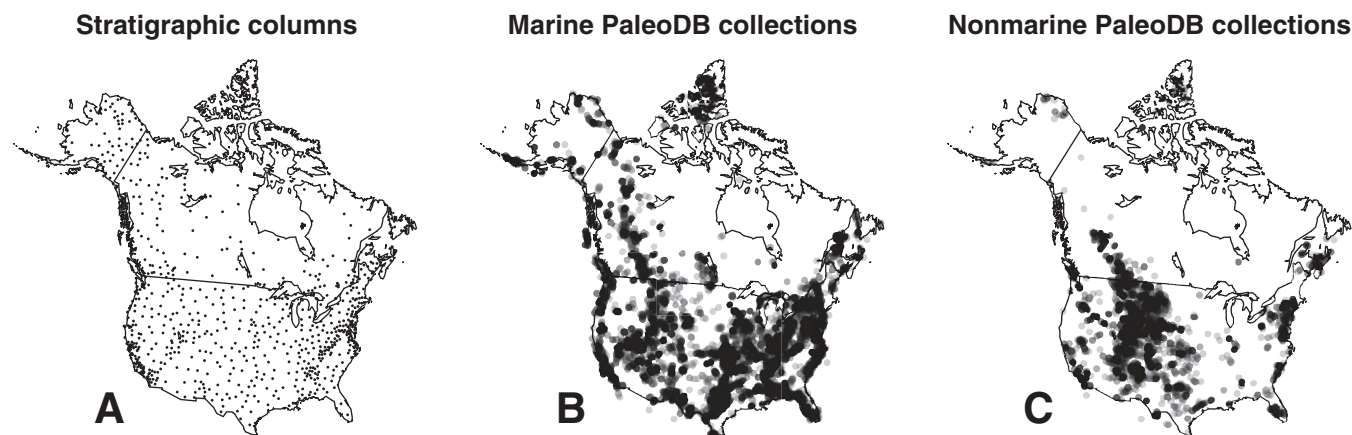
2007, 2008; McGowan and Smith, 2008), and (2) the sedimentary rock and fossil records are both similarly controlled by one or more exogenous factors, such as changes in continental shelf area and covarying environmental factors, such as global climate (Newell, 1952, 1967; Peters, 2006a, 2008). A sound interpretation of the history of life requires a quantitative understanding of the degree of bias existing within the fossil record, and the first step is to rigorously measure the covariation between sedimentary rock and fossil records.

Previous attempts to quantify covariation between the rock and fossil records have been rigorous and insightful but suffered from a mismatch between the spatial scale and/or coverage of geological and paleontological data. For example, the compendium of global marine genera compiled by Sepkoski (2002) has been compared with regional geological data sets for North America (Peters and Foote, 2002; Peters, 2005, 2008) and western Europe (Smith and McGowan, 2007; McGowan and Smith, 2008). However, these studies have compared geographically and temporally precise regional geological data with a compilation of global first and last occurrences. On the other hand, several studies have used global geological data, which tend to be both geographically and temporally imprecise, with global genus ranges compiled from the literature (Raup, 1976) or the PaleoDB (Wall et al., 2009). These, however, suffer from the unavoidable problem of uneven sampling of the paleontologic data relative to that of the geological data. For example, the English-language paleontological literature is dominated by fossil occurrences from North America and western Europe, whereas large tracts of sedimentary basins in northern Africa and Siberia remain comparatively poorly sampled (Kiessling, 2005).

It is important to note that most studies of covariation between the rock and fossil records have focused on diversity, an emphasis that is likely due to the great deal of effort that has been devoted to generating a Phanerozoic

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**Figure 1.** Maps of the United States and Canada showing the locations of stratigraphic columns (A), marine Paleobiology Database (PaleoDB) collections (B), and nonmarine PaleoDB collections (C). PaleoDB points are transparent so that dark areas indicate many stacked collections.

diversity curve over the past several decades (e.g., Valentine, 1970; Raup, 1972; Sepkoski, 1981; Sepkoski et al., 1981; Niklas et al., 1983; Benton, 1985; Alroy et al., 2001, 2008). Another reason for the focus on diversity is that the units of diversity typically employed in global studies (i.e., number of families, genera, and species) are the same as those that have traditionally been used to quantify the rock record (e.g., number of formations, and map area); that is, they are raw counts. However, tallies of rock units and taxonomic richness may not be the most appropriate metrics for analyzing large-scale patterns in the geologic record. Counts are particularly sensitive to sample size, and temporal patterns in taxonomic richness at large spatial and temporal scales are strongly influenced by sampling intensity (Alroy et al., 2001, 2008; Bush et al., 2004). Furthermore, taxonomic richness and total rock quantity are at least one step removed from the processes that generate those two records. For example, the number of species alive on the surface of the Earth at any one time is the result of origination and extinction operating over some previous interval of geologic time, and a given change in taxonomic richness could be driven by many different changes in the underlying rates of evolution. Examining rates will, therefore, move analyses one step closer to the processes that actually govern biodiversity and evolution in both the biological and sedimentary systems.

Presented here is the first study of covariation between Phanerozoic-scale patterns of macroevolution and macrostratigraphic patterns in the sedimentary record for a spatially and stratigraphically explicit subset of paleobiological data. Rates of initiation and truncation of hiatus-bound sedimentary rock packages are computed

and compared to rates of regional origination and extinction. The geographic scope of this study is limited to those rocks and fossils that occur in North America. However, analyses are presented based on the global and regional genus ranges of North American taxa. When using North American genus ranges, true global origination and extinction of genera cannot be calculated because many genera have global stratigraphic ranges that are longer than their ranges within North America. Thus, regional origination is used to describe the sum of true originations that take place in North America plus immigrations from other regions, and regional extinction is the sum of true extinctions that take place in North America plus extirpation. Global genus origination and extinction rates are referred to as such. The bulk of the analyses focus on the marine sedimentary and paleontological records of North America, but preliminary results for the nonmarine rock and fossil records are also included.

## DATA AND METHODS

### Geologic Data

The geologic data derive from stratigraphic summary charts published for Canada by the Geological Survey of Canada (Douglas, 1970) and the United States by the American Association of Petroleum Geologists (Childs, 1985; Salvador, 1985). Three additional stratigraphic summary columns have been added to cover gaps in the Salton Trough of California (Susanne Janecke, 2009, personal commun.) and the upper Mississippi Embayment in the states of Missouri (Grohskopf, 1955) and Mississippi (Dockery, 2008). The macrostratigraphic database (Mac-

rostrat) consists of 17,993 sedimentary and volcanoclastic lithostratigraphic units that are partitioned into 5312 hiatus-bound sedimentary packages and distributed among 815 geographic regions in Canada and the United States (Fig. 1; <http://macrostrat.geology.wisc.edu>). The stratigraphic data for each geographic region represent an areal composite for that region, and region size and spacing are based on geologic complexity as determined by the authors of the original correlation charts. Forty stratigraphic columns in the Canadian Shield do not contain any pre-Pleistocene, Phanerozoic-aged sedimentary units and are therefore not relevant to these analyses. Hiatus-bound packages are local stratigraphic intervals that record continuous deposition at a given temporal resolution, in this case stages, and are bound above and below by unconformities (GSA Data Repository Fig. DR1<sup>1</sup>). Because these packages are hiatus-bound, a time of first appearance (first appearance datum [FAD]) and last appearance (last appearance datum [LAD]) can be defined for each. See Peters (2006a) for a full description of the package recognition procedure.

Geological ages for the top and bottom of each rock unit were referenced to a standardized set of time intervals (primarily stages) in the Phanerozoic (Appendix DR1 [see footnote 1]). The numerical ages for these discrete time intervals derive from estimates by the International Commission on Stratigraphy (<http://www.stratigraphy.org/geowhen/geolist.html>) and from the TimeScale Creator (<http://tscreator>

<sup>1</sup>GSA Data Repository item 2010183, five supplemental figures and three data appendices, is available at <http://www.geosociety.org/pubs/ft2010.htm> or by request to [editing@geosociety.org](mailto:editing@geosociety.org).

.org). Analyses were conducted only for the 80 time intervals that span from the Dresbachian (Upper Cambrian) through the Pliocene due to the large number of informal and unnamed Pleistocene alluvial and glacial sedimentary units and to the lack of stage-level subdivisions in the current version of Macrostrat for the Early and Middle Cambrian. See Appendices DR1–DR3 and Figures DR1–DR5 (footnote 1) for a complete listing of the time intervals, numerical ages, and data used in this study.

Paleoenvironments for all 17,993 sedimentary rock units have not yet been fully resolved in Macrostrat, but an initial effort to identify nonmarine units revealed a minimum of 2663. Nonmarine units were identified in several ways. First, the original correlation charts for Canada explicitly identified all nonmarine units, and some nonmarine units are identified as such in the original compilation for the United States. Second, units were identified as nonmarine on the basis of their geographic position and on age (e.g., all Cenozoic units in the continental interior must be nonmarine). Finally, many units could be identified as nonmarine on the basis of data contained in matched PaleoDB fossil collections (see Peters and Heim, 2010). For example, if the number of fossil collections identified as nonmarine is greater than the number of marine collections matched to that same unit, then that unit is considered to be primarily nonmarine. In all analyses presented here, units that are not explicitly identified as nonmarine by one of the above criteria are assumed to be marine. In the cases where a single hiatus-bound sediment package contains both marine and nonmarine units, that package was split into individual marine and nonmarine components based on contiguous series of units with the same environmental designation. The temporal durations of these new packages are based on their constituent units, not the original package duration.

### Paleontologic Data

The paleontologic data derive from the official mirror of the Paleobiology Database (PaleoDB) located at the University of Wisconsin–Madison (<http://paleodb.geology.wisc.edu>). The mirror is synced daily with the primary archive at <http://paleodb.org>, and data for all analyses were accessed on 13 October 2009. The PaleoDB contains 28,405 fossil collections in Canada and the United States (excluding Hawaii) and 249,651 genus occurrences from 11,321 genera. Synonymies and reidentifications were applied to all occurrences based on the taxonomic authority information in the PaleoDB, and only fossil occurrences that can be resolved to the genus level were included. Most genera are identifiable as

marine or nonmarine based on higher level taxonomy and the paleoenvironmental information entered for each PaleoDB fossil collection. For higher taxa that are exclusively marine (e.g., brachiopods) or nonmarine (e.g., conifers), no paleoenvironmental information from PaleoDB collections is needed to determine environmental affinities. For genera that are constituents of higher taxa that occur in both marine and nonmarine environments (e.g., arthropods and vertebrates), the number of marine and nonmarine occurrences was tabulated for each genus in order to identify each as marine or nonmarine. Genera whose number of marine occurrences was greater than or equal to the number of nonmarine occurrences were assigned a marine environment. Less than 10% of the marine genera used were identified by this last criterion, and those were spot checked for accuracy. A small number of genera (1.7%) could not be assigned to either a marine or nonmarine environment and were excluded from the environment-specific analyses.

Genus ranges were determined independently of Macrostrat and lithostratigraphic units by using the collection age information contained within the PaleoDB. In order to maintain consistency between the time scale used for the analyses here and the multiple time scales used in the PaleoDB, correlations were established between 389 time intervals in the PaleoDB and the 80 time intervals used by Macrostrat (Appendix DR1 [see footnote 1]). Genus ranges were then calculated based on all of those occurrences that could be correlated with the Macrostrat time scale.

Because the PaleoDB records global fossil occurrences, global ranges for the genera found in North America were used to test for the influence of immigrations and extirpations. Immigrants are those genera whose global FAD is older than their North American FAD by at least one time interval, and extirpated genera are those whose global LAD is younger than their North American LAD by at least one time interval. Endemic genera are those that have no occurrences outside of the United States and Canada. This data set of global ranges contains the same genera as the North American marine data set, and the time-interval correlations were computed as for North American ranges.

For purposes of tabulating genus stratigraphic ranges, it is assumed that genera are present continuously between their FAD and LAD. This assumption is valid for global ranges but potentially invalid for North American ranges because genera could become regionally extinct and then be reestablished by immigration. However, confidently distinguishing true temporary absences from sampling

failures is not possible at the present time. To test the potential influence of stratigraphic gaps in North American genus ranges, analyses were completed using only those genera with no stratigraphic gaps. This subset of genera contains 54% of the total number of marine genera and yielded results comparable to the full genus list (see Results section).

### Macrostratigraphic and Macroevolutionary Rates

Because both sedimentary packages and genera have temporal durations, it is possible to calculate analogous turnover rates for both entities. Rates were calculated following the methodology of Foote (2000), whereby genera and packages present within each time interval are divided into four classes based on the relationships between package and genus FADs and LADs and time-interval boundaries (Appendices DR2 and DR3 [see footnote 1]). Origination-like parameters are designated by  $p$ , and extinction-like parameters are designated by  $q$ . For packages, turnover rates are for sediment initiation and truncation. Each genus in the list of North American genera has a global and a North American range. Rates calculated on the global ranges reflect origination and extinction, while the rates for the North American ranges reflect regional origination, which is origination plus immigration, and regional extinction, which is extinction plus extirpation.

To test the hypothesis that macroevolutionary rates are linked to macrostratigraphic rates, Spearman rank-order correlation coefficients ( $\rho$ ) were computed between first differences in equivalent turnover metrics for packages and genera. Spearman rank-order correlation was used because it is not overly sensitive to outliers and because it does not assume a linear relationship between the variables. First differences were used in all comparisons because they emphasize interval-to-interval changes, which are important for making casual inferences. An alternative comparison between rocks and fossils was made with the number of package and genus FADs and LADs, rather than rates. Measuring turnover in terms of per capita rates emphasizes duration (Foote, 2000) whereby genera and packages that span multiple intervals are counted in each time interval, and those entities that are confined to a single time interval are ignored. The number of FADs and LADs, on the other hand, emphasizes the actual timing of all genus and package first and last occurrences.

To further evaluate the statistical significance of the observed correlations between macrostratigraphic and macroevolutionary patterns, empirical genus durations were sampled



with replacement and randomized in time. New time series of regional extinction and origination rates were then calculated from the randomized data. This process was repeated 1000 times to generate the expected distribution of correlation coefficients between genus and sedimentary package patterns under a null model of stochastically constant rates of regional ge-

nus origination and extinction. The ranges of the temporally randomized genera were determined following the same procedure described above for the original Paleodb data. In addition to providing a general test of significance, this randomization specifically addressed the spurious correlation that could be induced by variability in the interval durations that are common to both the macrostratigraphic and macroevolutionary rates.

## RESULTS

### Geologic Results

As previously noted by Peters (2006a), the total quantity of sedimentary rock in North America (Fig. 2) roughly parallels global estimates of sea level (Vail et al., 1977; Hallam, 1984, 1989; Haq et al., 1987; Miller et al., 2005). Rates of initiation and truncation of sedimentary packages are also similar to those reported previously based on an older version of the macrostratigraphy database that contained only data for the United States (Peters, 2006a). Of particular note is the large peak in package initiation in the Early Triassic and the large peaks in package truncation in the late Permian and end-Cretaceous.

Macrostratigraphic patterns in North America are dominated by the marine record (Fig. 2), particularly in the pre-Cenozoic (Fig. 2 and Table 1). The nonmarine rock record shows an overall increasing trend from the Devonian to the Pliocene. Spearman rank-order correlations between the total, marine, and nonmarine rock records were only tabulated for the Anisian (Middle Triassic) through the Pliocene (Table 1) because of the comparatively few lithostratigraphic units that are environmentally resolved and also nonmarine prior to the Triassic.

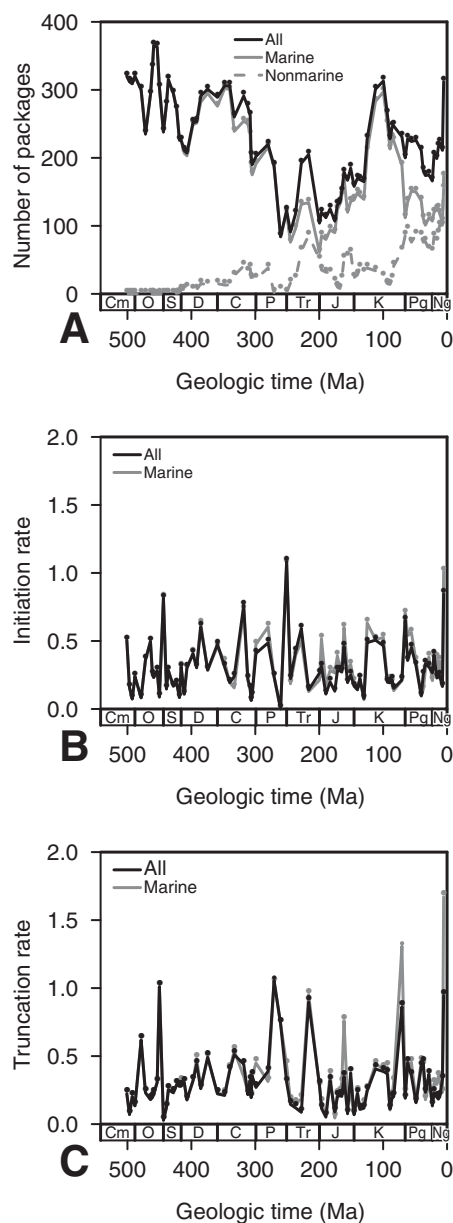
### Paleontologic Results

Genera are assumed to be present in North America during all time intervals between their

first and last North American occurrences. Genus richness was tabulated in two ways: first by counting the number of genera that cross each time-interval boundary and second by counting all genera that range through each time interval. Qualitatively, the two richness data sets are similar and highly correlated (spearman rank-order coefficient is 0.74 for raw data and 0.85 for first differences). Only the data for the total range of genera through richness are presented, keeping in mind that the focus of this study is on turnover rates and not genus richness. The time series of North American genus richness based on the Paleodb genus list is similar to previous tabulations of global marine diversity (Fig. 3; Sepkoski, 1981; Sepkoski et al., 1981; Alroy et al., 2001, 2008). However, there are important differences between the richness time series for North America and previous estimates of global marine genus richness. First, rather than a steady increase from the Early Triassic through the Holocene, North American richness remains low from the Triassic through the Early Cretaceous. Second, the post-Paleozoic increase in total richness peaks in the Late Cretaceous and then remains relatively constant at a level only slightly higher than the Paleozoic richness plateau (e.g., Sepkoski, 1979; Valentine and Walker, 1986). If only marine genera are used, the Cenozoic plateau is similar in magnitude to that of the Paleozoic. Thus, the North American fossil record, at least as recorded in the Paleodb, shows little or no long-term increase in genus richness, even when all genera, including those that are nonmarine, are included (Fig. 3). Like genus richness, patterns of genus origination and extinction are dominated by marine genera.

### Relationships between Geologic and Paleontologic Data

A comparison of the macrostratigraphic and macroevolutionary time series reveals much similarity (Figs. 4 and 5; Table 2). Spearman rank-order correlation coefficients are positive



**Figure 2.** Time series of the number of packages and macrostratigraphic rates. (A) The total number of marine and nonmarine hiatus-bound packages. Per capita, per interval sediment initiation (B) and truncation (C) rates based on a model of continuous initiation and truncation. Points are plotted at time-interval bases.

TABLE 1. SPEARMAN RANK-ORDER CORRELATION COEFFICIENTS ( $\rho$ ) BETWEEN MARINE, NONMARINE, AND TOTAL RATES FOR GENERA AND PACKAGES

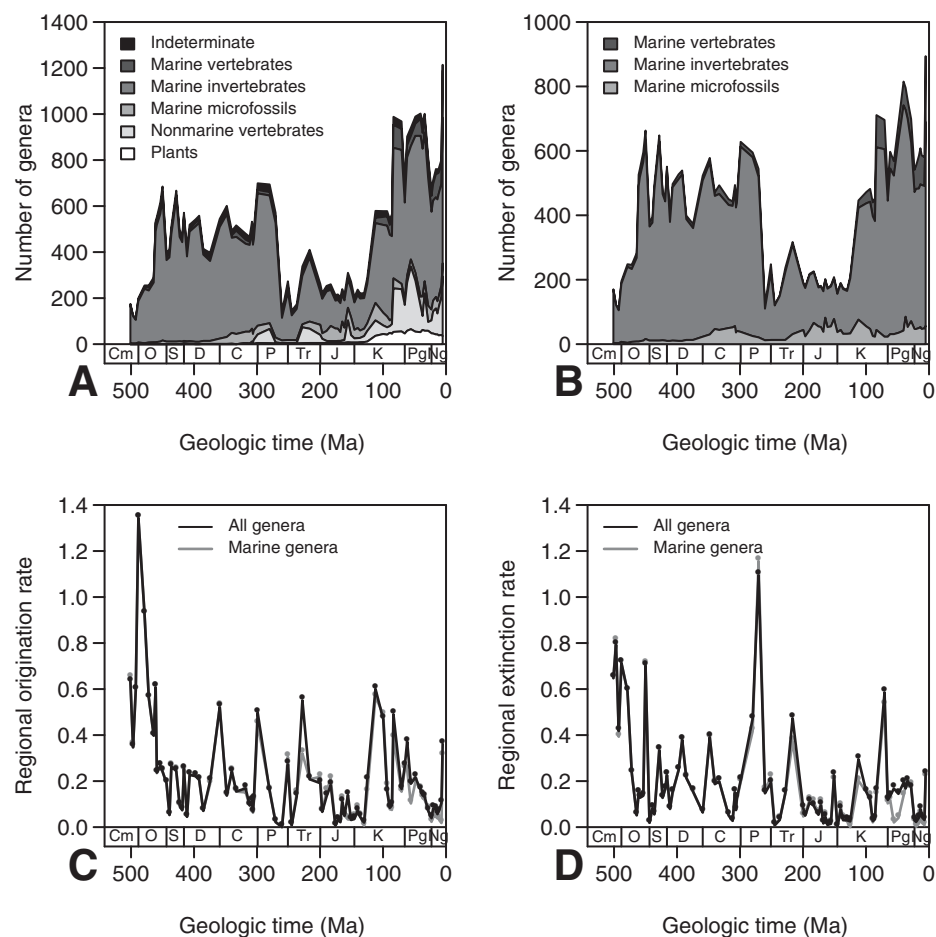
	$\rho_p$ (p-value)	$\rho_q$ (p-value)
All packages-marine packages	0.876 ( $<10^{-4}$ )	0.900 ( $<10^{-4}$ )
All packages-nonmarine packages	0.506 ( $8.58 \times 10^{-4}$ )	0.625 ( $<10^{-4}$ )
Marine packages-nonmarine packages	0.263 (0.096)	0.493 (0.001)
All genera-marine genera	0.902 ( $<10^{-4}$ )	0.894 ( $<10^{-4}$ )
All genera-nonmarine genera	0.719 ( $<10^{-4}$ )	0.751 ( $<10^{-4}$ )
Marine genera-nonmarine genera	0.447 (0.003)	0.490 (0.001)

Note: The origination-like parameters of package initiation and regional origination are designated by the subscript "p," and extinction-like parameters of package truncation and regional extinction are designated by the subscript "q." All correlations are performed on first differences and p-values are given in parentheses. Because of the scarcity of Paleozoic nonmarine packages and taxa, the correlations are performed only for the Anisian through the Pliocene.

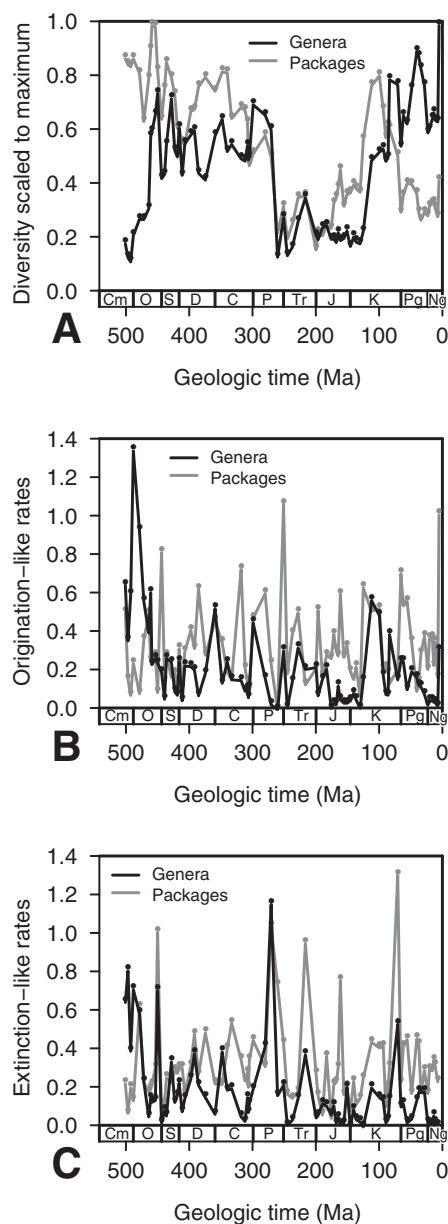
and significant for both  $p$  and  $q$ , but the correlation between regional extinction and package truncation is substantially stronger than that for regional origination and package initiation. In addition to the general similarity, several coupled macroevolutionary and macrostratigraphic pulses are apparent. The interval-to-interval differences in regional extinction and package truncation (Fig. 5B) show coincident pulses during four of the “big five” mass extinctions (Raupe and Sepkoski, 1982): the end-Ordovician (combined Richmondian and Hirnantian), Late Permian (Guadalupian), end-Triassic (combined Norian and Rhaetian), and end-Cretaceous (Maastrichtian). There is no qualitative difference between the comparisons of rocks and fossils using rates (Figs. 4 and 5; Table 2) and those using the numbers of FADs and LADs (Fig. DR2 [see footnote 1]; Table 2).

The remainder of the discussion will focus on the rate results.

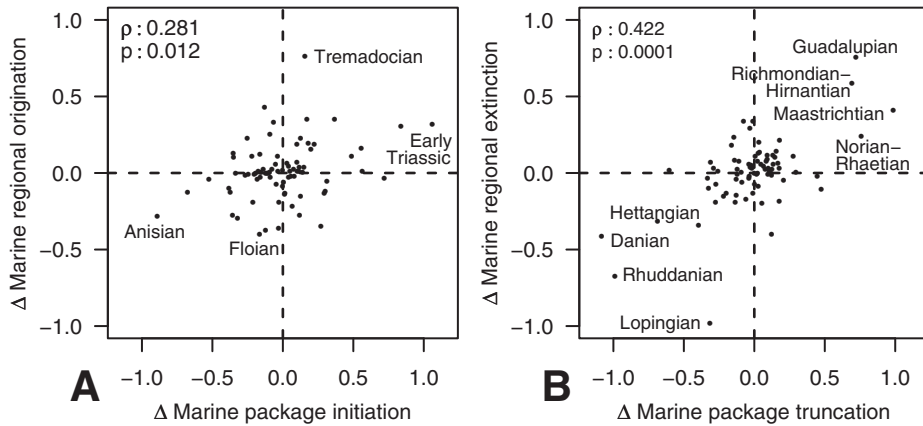
It is worth noting that globally, the Permian mass extinction occurs in the latest Permian Lopingian stage (e.g., Jin et al., 2000; Bambach et al., 2004; Foote, 2007; Miller and Foote, 2009), but extinction is concentrated in the Guadalupian in this data set. Elevated extinction rates in the Guadalupian have long been recognized globally and ascribed to either a prolonged period of late Permian extinction (Raupe and Sepkoski, 1982) or two distinct extinction pulses (Stanley and Yang, 1994). However, the unusually low rates of regional extinction in North America during the subsequent Lopingian stage are likely due to a combination of high Guadalupian extinction and poor Lopingian sediment preservation. The North American minimum in preserved Phanerozoic sediment



**Figure 3.** Time series of the number of genera and macroevolutionary rates. (A) The number of genera belonging to various marine and nonmarine taxonomic groupings. (B) The total number of marine genera, partitioned into invertebrates, vertebrates, and microfossils. (C) Per capita, per interval regional origination rates. (D) Per capita, per interval regional extinction rates. Rates are based on a model of continuous origination and extinction; rates for all genera are plotted with a dark line, and marine genera are plotted with a light line. Points are plotted at time-interval bases.



**Figure 4.** Time series of marine genus richness (dark lines) and the number of packages (light lines) and macrostratigraphy and macroevolution rates. (A) Marine packages and genera. Each time series is scaled to the maximum number for easy comparison. (B) Per capita, per interval marine package initiation and regional origination rates. (C) Per capita, per interval marine package truncation and regional extinction rates. All rates, counts, and plotting conventions are the same as for Figures 2 and 3.



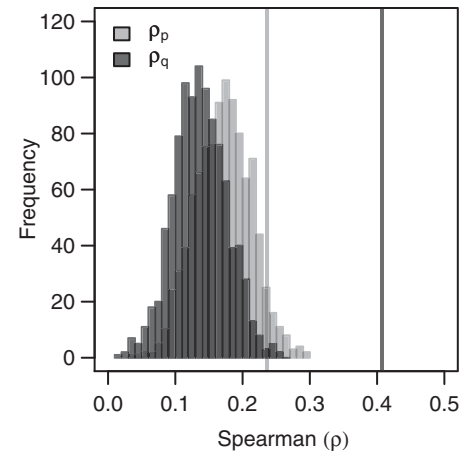
**Figure 5.** Scatter plots of macrostratigraphy versus macroevolutionary parameters. (A) First differences in marine package initiation rate versus marine regional origination rate. (B) First differences in marine package truncation rate versus marine regional extinction rate. Some time intervals with large changes in rate are labeled. Spearman rank-order correlation coefficients are given for each plot ( $\rho$ ). Note that  $p$ -values are for the significance of the correlation between genus and package rates, which is in part due to autocorrelation induced by sharing a common time scale. See text and Figure 7 for correlations in which time scale-induced autocorrelation has been corrected.

cover is in the Lopingian (Fig. 2), and of those packages that are preserved, only ~10% of them have fossil collections recorded in the Paleodb (Peters and Heim, 2010). The poor preservation of Lopingian sediments and fossils potentially accentuates the magnitude of Guadalupian extinction and depresses that of the Lopingian.

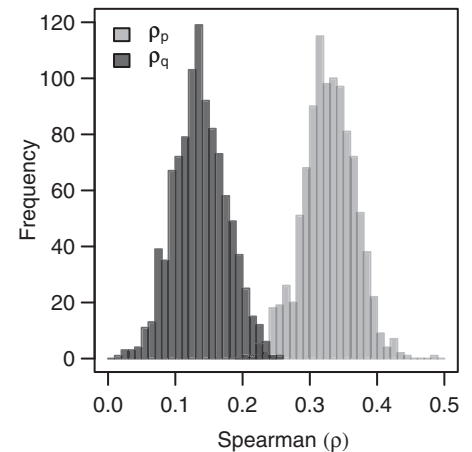
The expected distribution of correlation coefficients under the null model of no statistical relationship was generated by randomly distributing genus ranges, with replacement, in time (Fig. 6). The null distributions for  $\rho_p$  and  $\rho_q$  have means of ~0.20 and 0.15, respectively. The distributions are not zero-centered because both the macrostratigraphic and genus data share a time scale that has variable interval durations. Nevertheless, the observed correlation between package truncation and regional extinction is far outside

the range of the null distribution of correlation coefficients, indicating a highly statistically significant relationship between package truncation and regional extinction rates ( $p < 0.001$ ). The observed correlation between regional origination and initiation, however, falls within the right tail of the null distribution and fails a significance test ( $p$ -value = 0.06).

Important differences between rates of regional extinction and rates of regional origination for North American genera are not limited to the strength of their correlations with macrostratigraphic data. Observed rates of regional origination are significantly more similar to the randomized rates of regional origination than the observed rates of regional extinction are to the randomized regional extinction rates (Fig. 7). This difference indicates that, at least in North



**Figure 6.** Null distributions of correlations between marine macrostratigraphy and macroevolution. Distributions are based on randomizing genus ranges in time and recalculating the Spearman rank-order correlation coefficients on first differences. The randomization was performed 1000 times. Vertical lines mark the observed correlations between marine package initiation and regional origination (light gray) and marine package truncation and regional extinction (dark gray).



**Figure 7.** Null distributions of the correlations between observed marine macroevolutionary rates and macroevolutionary rates of genera randomly distributed in time. These distributions are based on the same randomizations as in Figure 6. Regional origination is in light gray, and regional extinction is in dark gray.

**TABLE 2.** SPEARMAN RANK-ORDER CORRELATION COEFFICIENTS ( $\rho$ ) AND  $p$ -VALUES BETWEEN MACROSTRATIGRAPHY AND MACROEVOLUTION PARAMETERS

	$\rho$	$p$ -value
regional origination–package initiation	0.281	0.012
regional extinction–package truncation	0.422	$1.22 \times 10^{-4}$
global origination–package initiation	0.210	0.064
global extinction–package truncation	0.438	$<10^{-4}$
endemic origination–package initiation	0.333	0.003
endemic extinction–package truncation	0.391	$3.66 \times 10^{-4}$
immigration–package initiation	0.104	0.359
extirpation–package truncation	0.375	$7.29 \times 10^{-4}$

*Note:* The regional origination and extinction values are rates based on North American genus ranges calculated from the Paleodb. Global origination and extinction values are based on rates calculated from the global ranges of North American genera in the Paleodb. Endemic taxa are the subset of North American genera who have no occurrences in the Paleodb outside of the U.S.A. and Canada. Immigrants are those genera whose global FAD is at least one time interval older than their North American FAD, and extirpated genera are those whose global LAD is at least one time interval younger than their North American LAD. All correlations are based on first differences.

America, observed rates of regional origination are more similar to a model of continuous random origination and immigration of genera than are rates of regional extinction. This result implies that there are important differences in the underlying factors that govern the appearance and disappearance of genera in North America.

Because the PaleoDB represents an ongoing, community-based effort to document published fossil occurrences from around the globe, macroevolutionary patterns in the PaleoDB are continually evolving in a manner that reflects the diverse interests of its (presently some 200) contributing members. It is, therefore, expected that many genus ranges based on the data in the PaleoDB are incomplete (Foote and Raup, 1996; Foote, 1997). To evaluate the influence of sampling in the PaleoDB and estimate the extent to which these results are stable, Spearman rank-order correlations were computed between Macrostrat and the cumulative North American genus data for each year from 1998 to 2009 (Fig. DR3 [see footnote 1]). The PaleoDB went online in 1998, and 4627 collections had been entered for Canada and the United States by the end of that year. An average of 2972 collections were entered annually between 1999 and 2008. As the PaleoDB has grown in the number of collections and genera, so too have the correlations between macroevolution and macrostratigraphy tended to increase in strength. A linear regression of year versus Spearman rank-order coefficient indicates that the strength of the correlation between regional extinction and package truncation is increasing at a rate that is a factor of 2.4 greater than that between regional origination and package initiation (Fig. DR3 [see footnote 1]).

Finally, a comparison between macrostratigraphy rates and macroevolution rates for those genera with no stratigraphic gaps shows the same pattern of stronger correlation between extinction-like parameters and nonsignificant correlation between origination and package initiation ( $\rho_p = 0.22$ ,  $p$ -value = 0.083;  $\rho_q = 0.35$ ,  $p$ -value = 0.005). This result lends support to the assumption that gaps in genus ranges do not systematically bias rate estimates.

### Global Genus Ranges and Macrostratigraphy

Using global PaleoDB occurrences, the global ranges for North American marine genera were tabulated, and rates of global origination and extinction were calculated (Fig. DR4 [see footnote 1]). Approximately 53% of the North American marine genera have equal global and North American total ranges at the stage-level of temporal resolution. Considering first and

last occurrences separately, 69% of genera have global and North American FADs in the same time interval, and 71% of genera have global and North American LADs in the same time interval. Nearly 87% of genera have at least one global and regional range end-point in the same time interval.

Extending the stratigraphic ranges of North American genera to include all global occurrences necessarily has the effect of increasing total genus richness in each time interval even though the total number of sampled genera remains constant. The difference between the time series of global richness of North American genera and the time series of genus richness in North America is a measure of the number of North American genera that are not present on the continent at a particular point in time. The number of these absentee genera shows a generally increasing trend through the Phanerozoic that largely mirrors total genus richness (Fig. DR4A [see footnote 1]).

Macroevolutionary rates were calculated for global ranges as they were for North American genus ranges. The differences in the results between global genus ranges and North American genus ranges reflect the degree to which immigration and extirpation are responsive to patterns of sedimentation in North America. Global genus ranges show the same pattern of covariation with North American macrostratigraphy as do the North American genus ranges (Fig. DR5 [see footnote 1]; Table 2). The correlations based on global ranges are slightly weaker for both origination and extinction than for those based on North American ranges. The correlation between origination and initiation is not statistically significant ( $p = 0.07$ ), whereas extinction shows a strong positive correlation with package truncation (Fig. DR5 [see footnote 1]; Table 2). Additional analyses of immigrants, extirpated taxa, and endemic taxa reveal that the origination of endemic taxa is strongly correlated with the initiation of sedimentation, and that the poor correlation between sediment initiation and regional origination is depressed by immigrants (Table 2). True origination, true extinction, and regional extirpation exhibit strong covariation with the aerial extent of sediment cover while the immigration of genera to the continent does not.

### DISCUSSION

The relationship between macrostratigraphy and macroevolution patterns in the North American fossil record documented here exhibits several interesting features. As previously noted (Peters, 2005, 2008), there is a significant correlation between macroevolutionary and mac-

rostratigraphic rates. Of particular note is that regional extinction exhibits a strong, positive relationship with sediment truncation, whereas the correlation between sediment initiation and regional origination is insignificant (Fig. 6). The difference in the strength of  $\rho_p$  and  $\rho_q$  raises the question: what processes control biological evolution and the evolution of sedimentary environments during the Phanerozoic? Although the data presented here do not provide a conclusive answer to this question, they do enhance our understanding of the range of processes that are likely to be involved. Specifically, the relative strengths of the correlations between PaleoDB marine genera and marine macrostratigraphy (Figs. 4 and 5; Table 2) suggest that the processes that control our perception of regional extinction and package truncation are tightly coupled, whereas those that control regional origination and package initiation in North America may be largely decoupled.

The correlation between regional origination and sediment initiation over the course of the Phanerozoic is weak (Fig. 5A and Table 2) and not significantly different from the null expectation that genera are randomly distributed in time (Fig. 6). Further support for the notion that North American regional origination rates are decoupled from package initiation is provided by the relatively strong correlation between observed and randomized regional origination rates (Fig. 7). Observed regional origination rates appear to be more random with respect to genus placement in time than is regional extinction. These results suggest that the environmental factors that have resulted in the initiation of sedimentary packages in North America have exerted relatively little control on the first appearances of genera in North America. However, further insight into regional origination dynamics is gained through the different dynamics of immigrants and endemic genera. The origination of endemic genera is strongly correlated with the initiation of sedimentation (Table 2); the in situ evolution of new genera takes place at a faster rate during intervals of rapid marine sedimentary environment expansion. In contrast to endemic taxa, similar expansions in sedimentary environments do not necessarily promote the immigration of older genera into North America.

Regional extinction during the Phanerozoic of North America stands in stark contrast to regional origination. The observed  $\rho_q$  is well outside the null distribution, and the correlation between observed regional extinction rates and rates from randomized genus ranges produces a distribution (Fig. 6) that is nearly identical (two-sample K-S test:  $D = 0.022$ ,  $p$ -value = 0.969) to the correlation between package truncation



and the regional extinction rates of randomized genus ranges (Fig. 7). These observations demonstrate that the overall structure of regional extinction is highly temporally structured; genus last appearances tend to be more pulsed than genus first appearances (Foote, 2005), and last appearances also tend to co-occur with package truncations. Additionally, the rapid overall rate of increase in  $p_q$  as the PaleoDB has grown (Fig. DR3B [see footnote 1]) suggests that the observed correlations based on PaleoDB genus ranges are an underestimate. Furthermore, package truncation rates appear to affect the extinction of endemic taxa and the extirpation of cosmopolitan taxa equally.

The covariation between regional extinction and package truncation has potential explanatory power with regard to mass extinctions. The four largest pulses in package truncations, i.e., the fastest contractions in sedimentary cover, coincide with long-recognized mass extinction intervals (Newell, 1967; Raup and Sepkoski, 1982), and these all show coincident pulses in regional extinction. This coincidence suggests that the relatively rapid contraction of the areal extent of net sediment accumulation is linked to rates of genus extinction and extirpation. The question is whether these intervals of reduced sediment preservation are simply biasing the perception of the fossil record or if a common exogenous process is driving both truncation and regional extinction. The sum of evidence seems to be mounting against the bias hypothesis, but identifying a specific set of common causal mechanisms is far from trivial. By modeling expected richness given the observed area of sediments for geologic stages, Smith and McGowan (2007) found that the drops in marine richness during mass extinction intervals are larger than expected, if the first-order control on genus richness was exposed rock area. Similarly, Foote (2003) found that intervals with high extinction rates also tend to have high rates of sediment preservation.

The empirical results presented here suggest that there is not a strong bias in the macroevolutionary history of North America. The bias hypothesis can be stated as an extension of the species-area relationship that is ubiquitous in modern biological systems (Rosenzweig, 1995). The species-area relationship is an empirical pattern of increasing species richness with increased sampling area. The bias hypothesis predicts more generic richness with increasing areal extent of rock preservation. Furthermore, the bias hypothesis assumes that taxonomic originations and extinctions are distributed randomly in time, and variations in turnover rates are due entirely to variations in sediment preservation. Thus, the bias hypothesis

predicts that as the rate of sediment preservation (initiation) increases, the rate of preservation of genus FADs (origination) will also increase and that as the rate of sediment nonpreservation (truncation) increases, the rate of preservation of genus LADs (extinction) will also increase. The bias hypothesis has previously been formalized from a sequence stratigraphic perspective whereby genus FADs are expected to artificially accumulate at the base of hiatus-bound packages, and LADs are expected to accumulate at package tops (Holland, 1995). In relation to the macrostratigraphy of North America, Holland's model of the stratigraphic distribution of fossils would predict that stratigraphic bias must produce strong positive values of both  $p_p$  and  $p_q$ . The asymmetry in the North America data suggest that this unconformity bias is minor and that regional origination and extinction are governed by fundamentally different processes.

Interestingly, removing the four mass extinction intervals (Richmondian-Hirnantian, Guadalupian, Norian-Rhaetian, and Maastrichtian; Fig. 5B) from the time series for package truncation and genus extinction significantly reduces the covariation between these two parameters ( $p_q = 0.18$ ,  $p$ -value = 0.110). This result demonstrates that package truncation and regional extinction rates do not systematically covary over short durations of geologic time in North America, except during intervals of mass extinction. These data argue that the fossil record of North America is not biased by stratigraphic preservation to the point that biological signals are obscured. This, of course, does not mean that there is no bias in the fossil record. Indeed, the total number of package truncations predicts the total number of regional genus extinctions, even when the four largest mass extinction intervals are removed ( $p_q = 0.39$ ,  $p$ -value = 0.0005). This covariation likely persists when tabulating raw numbers of package and genus LADs because the gaps that define packages are the result of both nondeposition and erosion of previously deposited sediments. When package gaps represent intervals of erosion, it is expected that genus ranges will also be truncated and artificially cause the coincidence of genus and package LADs (e.g., Holland, 1995). It is not possible to determine ratio of erosion to deposition for gaps, which would allow for more refined tests of the bias imparted on the fossil record by package truncations. Despite the presence of bias in the fossil record, it is not so great that important macroevolutionary trends are obscured.

Mass extinctions are an important aspect of biological evolution and hold the attention of many paleobiologists and the general public alike. Since the positive correlation between re-

gional genus extinction and package truncation rates seems to be driven by a few mass extinction events, are mass extinctions simply biases of the extent of sediment preservation? This is likely not the case. The end-Permian and end-Cretaceous mass extinctions mark the boundaries of the Mesozoic era, and by definition, mark major transitions in the biological composition of Earth's biota. Furthermore, the end-Ordovician and end-Cretaceous extinction intervals mark times of relatively high total sediment preservation (Fig. 2A) and high completeness in the fossil record (Peters and Heim, 2010); these extinction events are not driven by failure of sediment preservation or fossil recovery, nor are the gaps that follow them longer than the gaps that follow many other truncations in the rock record (Peters, 2006b). The high fidelity of Phanerozoic mass extinction intervals has also been confirmed by Foote (2003), who used genus occurrences in the PaleoDB to model preservation rates, and Smith and McGowan (2007), who modeled expected extinction rates given observed rock quantity. Given both the results of this and other recent studies, the macroevolutionary history of North America is not severely distorted by the preservation patterns in the sedimentary record over short intervals of geologic time. Although mass extinctions appear to be linked to major changes in the sedimentary regime, a preservation bias is not the proximal cause for the perception of mass extinctions.

Although stratigraphic bias is not the primary driver behind empirical genus turnover rates in North America, it may play a role during certain intervals. The timing of the Permian mass extinction in North America provides an example of how careful regional analysis of the sedimentary and fossil records allows distinctions to be made between bias and true coincidences in macrostratigraphy and macroevolution. Globally, extinction is concentrated at the end of the Permian (Jin et al., 2000; Bambach et al., 2004; Foote, 2007; Miller and Foote, 2009), but the peak is shifted to the end of the Middle Permian (Guadalupian) in North America. This temporal shift is likely due to a combination of truly high extinction rates in carbonate settings of epicontinental seas during the Guadalupian (Miller and Foote, 2009) and poor preservation of sediments (Fig. 2) and fossils (Peters and Heim, 2010) during the Late Permian (Lopingian). Thus, globally the extinction event that occurred at the end of the Permian was a nonevent in marine realm of North America because sea level was at one of the Paleozoic minima (Haq and Schutter, 2008), and marine environments were not readily preserved. As a result, many genera that went globally extinct during the Lopingian appear to go extinct in North America during



the Guadalupian. This hypothesis is supported by extirpation rates (extinction in North America and persistence elsewhere); the Phanerozoic maximum in extirpation rate is during the Guadalupian. This result, however, does not trivialize the magnitude of the Permian extinction in North America; the extinction rate of endemic genera is at a Phanerozoic high during the Guadalupian. Importantly, this result on the North American perspective of the Permian extinction highlights the importance of dissecting global events in Earth history into regional components (e.g., Miller, 1997; Clapham et al., 2009).

Finally, one of the more intriguing results of this study is the role of immigration in producing an asymmetry between regional origination and regional extinction. When endemic and immigrant genera are analyzed separately (Table 2), the asymmetry between origination and extinction disappears for endemics. The dynamics of origination, extinction, immigration, and extirpation highlight some fundamental properties of these processes. Firstly, the correlation between North American package truncation and the extinction-like parameters of genera,  $q$ , does not change regardless of the subset of genera used. This suggests that extinction of endemic taxa and regional extirpation of widespread taxa are fundamentally the same. As marine sedimentary environments shrink, populations are driven to extinction locally through a variety of processes such as reduced habitat area, changing environmental conditions, and increased competition for increasingly rare resources. Ultimately, global extinction is a function of geographic range; those taxa that persist outside of the area of the most intense environmental change will persist, while endemic taxa will perish (e.g., Jablonski and Raup, 1995; Jablonski and Hunt, 2006). Secondly, and this is obvious, the evolution of new taxa in situ and the immigration of taxa from outside the region are fundamentally different processes. The strong positive correlation between the origination of endemic genera and package initiation coupled with the noncorrelation of immigration and package initiation suggests that the expansion of sedimentary environments promotes speciation as habit area increases but does not necessarily promote invasion. Further analyses are needed to understand why the expansion of environments promotes originations but not immigrations, but a full analysis of immigration and extirpation patterns is beyond the scope of this study.

The pattern of equal covariation between macrostratigraphy and macroevolution parameters for endemic genera might be argued as support for the bias hypothesis. However, the strong symmetry between  $p_p$  and  $p_q$  is equivocal with regard to the common cause and bias hy-

potheses. At this initial stage, though, it seems that a crucial test may lie in immigration patterns. If immigrations are assumed to be randomly distributed in time, the bias hypothesis predicts that immigration and initiation will be correlated. If immigrations are controlled by sea level such that more immigration takes place during highstands when there are more connections between shallow shelf areas and a greater total habitat area, then the common cause hypothesis will also predict strong symmetry between  $p_p$  and  $p_q$ . The data on North American immigrations and extirpations do not support either of these hypotheses. Extirpation is strongly linked to sediment truncations, but there is apparently no relationship between immigration and sediment initiation. Although this does not necessarily confirm the common cause hypothesis, it does not support the bias hypothesis. If more rocks are preserved, there should be more regional genus FADs preserved, regardless of whether or not they are endemic originations or immigrations. This is apparently not the case in the data analyzed here, but further tests are needed.

Integrating the Paleobiology Database with the macrostratigraphy of North America has allowed for the first time the simultaneous analysis of the stratigraphic and evolutionary histories of a broad region with geographically precise information for both sedimentary rocks and fossils. The focus here is on the macroevolutionary parameters of genus origination and extinction and their macrostratigraphic equivalents, but this database and approach open the possibility of new and innovative research in biogeography, morphological evolution, and stratigraphic paleobiology. The key innovations here are the spatially explicit framework and the quantitative “common currency” with which to compare various aspects of the fossil and sedimentary records. As the paleoenvironmental information in the macrostratigraphy database and the quantity of PaleoDB collections continue to improve, it will become possible, for example, to compare rates of morphological evolution to the rates of expansion and contraction of particular environments over time.

The focus of this study is on the marine record, primarily due to incomplete identification of nonmarine lithostratigraphic units. But the preliminary time series of the quantity of nonmarine sediments (Fig. 2) is also intriguing. In particular, is the trend of increasing nonmarine sediments from the Devonian to the Holocene a sediment supply-dominated trend where the area of nonmarine deposition has been increasing through time; or is it a destruction-dominated trend whereby older nonmarine units are more susceptible to removal from the rock

record than their marine cohorts? The supply-dominated hypothesis seems unlikely because of the vast areas that have been subaerially exposed on present-day North America since the Devonian (Scotese, 2001); these areas still harbor a substantial volume of Paleozoic marine strata. The alternative hypothesis—that the nonmarine record is attrition-dominated—seems more likely. Nonmarine environments are located in regions of net erosion and are less likely to reach the same thickness and geographic extent as marine sediments (of the 2442 units in the macrostratigraphy database that have thicknesses, the nonmarine units have a mean thickness of 106 m [ $n = 1796$ ], and the marine units have a mean thickness of 189 m [ $n = 646$ ]). This, however, does not suggest that all marine sediments have a higher probability of preservation than nonmarine sediments. As the macrostratigraphy database continues to incorporate more paleoenvironmental, paleotectonic, and paleogeographic information, it will become possible to test more nuanced hypotheses about Phanerozoic-scale sedimentary dynamics. Specifically, the hypotheses that the sedimentary record is dominated by marine sediments deposited from epicontinental seas and marine continental margin and nonmarine sediments are removed from the rock record at a faster rate than those from epicontinental seas can be tested. Rigorous tests of these hypotheses will have profound implications for our understanding of the fossil record and its application to our understanding current and future evolution. Furthermore, the data quality in the macrostratigraphy database is rapidly improving, and testing these hypotheses should soon be tractable.

## CONCLUSIONS

(1) Analyses of short-term differences in macrostratigraphic and macroevolutionary rates in North America indicate that the regional origination of genera is largely decoupled from the initiation of sedimentation and that regional extinction and sediment truncation are closely linked. Because there is a strong difference between the correlation of origination-like parameters and extinction-like parameters, stratigraphic bias cannot fully explain the covariation in macrostratigraphy and macroevolution. Interval-to-interval differences in genus extinction and sediment truncation rates indicate that, at least from the perspective of North America, the end-Ordovician, end-Triassic, and end-Cretaceous mass extinction events were in part linked to increased rates of sediment truncation, possibly by a common cause. Within North America, the Permian extinction event was experienced during the Middle Permian

(Guadalupian) rather than the Late Permian (Lopingian). The North American shift in timing relative to the global event is likely due to a combination of high Guadalupian extinction rate and lack of preservation of marine sediments during the Lopingian.

(2) Dissecting North American genera into immigrants, extirpated genera, and endemics reveals the influence of immigration on regional origination rate. The asymmetry between  $\rho_p$  and  $\rho_q$  falls away when endemic genera are analyzed separately, and the asymmetry persists for immigrants ( $\rho_p$ ) and extirpated genera ( $\rho_q$ ). This result suggests that extirpation, extinction, and true origination are linked to the dynamics of sedimentary environments, but that immigration is not. The expansion of marine environments during sea-level rise does not promote genus invasions. Although this result does not explicitly support the common cause hypothesis, it is very difficult to accommodate the bias hypothesis.

(3) An analysis of the global ranges of North American genera suggests that peaks in regional extinction and global extinction (i.e., mass extinctions) tend to occur within the same stage-level time interval and are responses to fundamental changes in the structure of the sedimentary rock record. As the Macrostrat database grows to include more continents, more robust tests of the common cause hypothesis will become possible.

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