

# MACROSTRATIGRAPHY AND ITS PROMISE FOR PALEOBIOLOGY

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**Abstract**—Macrostratigraphy is the study and statistical analysis of sediment packages that formed continuously at a specified scale of temporal resolution and that are bound by gaps recognizable at that same scale. The temporal ranges of gap-bound packages, compiled separately for different geographic locations, permit area-weighted, survivorship-based measures of rock quantity and spatio-temporal environmental continuity to be measured. Analytical basin fill models suggest that the parameters controlling sedimentation and sequence stratigraphic architecture, such as base level and sediment supply, can be detected quantitatively by macrostratigraphy.

Macrostratigraphic analysis of the marine sedimentary rock record in the United States at a temporal resolution of  $\sim 10^6$  years reproduces most of the well-known Sloss sequences, but it also identifies two prominent megasequences, the Paleozoic and Modern megasequences, which are separated by a Permian-Triassic discontinuity and Phanerozoic minimum in rock quantity. Many short- and long-term features of the macroevolutionary history of marine animals are reproduced by macrostratigraphy, including 1) many patterns in genus richness, 2) patterns in rates of genus extinction and, to a lesser degree, rates of origination, and 3) patterns of extinction selectivity and the shifting relative richness of Sepkoski's Paleozoic and Modern evolutionary faunas. The extent to which macrostratigraphy reproduces the macroevolutionary history of marine animals transcends what is expected by geologically-controlled sampling biases. Instead, the processes which control the spatio-temporal dynamics of shelf sedimentation, including expansions and contractions of shallow epicontinental seas, have probably exerted a consistent influence on the macroevolutionary history of marine animals. Exploring the common cause hypothesis by putting fossils back into rocks and rocks into a new quantitative framework for physical environmental change holds considerable promise for paleobiology.

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## INTRODUCTION

Sedimentary rocks are the most widespread and voluminous of geological materials exposed at the earth's surface. Approximately 75% of the present-day global land area is covered by sedimentary rock (Fig. 1; Ronov, 1978). In addition to being widespread, the average thickness of mappable sedimentary cover is substantial. If all of the approximately  $640 \times 10^6$  km<sup>3</sup> of Phanerozoic-aged sediment on the emergent land masses (excluding Antarctica; Ronov et al., 1980) were distributed evenly, it would form a blanket nearly 5 km thick. If, in turn, this 5 km were evenly distributed through time, approximately 9 m would represent each one million year time interval in the Phanerozoic.

The total quantity of sediment preserved on the continents is sufficient to record a rich history of Phanerozoic life and environment, but assuming that sediments are uniformly distributed in time and space is a radical departure from reality. At my home institution in Madison, Wisconsin, for example, less than 250 m of late Cambrian to early Ordovician sediments overlie Precambrian crystalline basement. There are no other sediments, save those left behind during the retreat of the last Pleistocene ice sheet, some 14,000 years ago. Just 350 km to the east, near the center of the Michigan Basin, Jurassic red-beds cap an almost 5 km thick succession of sediments, the oldest being Cambrian sandstones similar to those found beneath Madison (Precambrian sediments associated with the mid-continent rift are also locally present in the Mich-



Figure 1—Land area in North America covered by mappable sediments, including those that have been metamorphosed. Sediments on submerged continental shelves not shown. Modified from the 2003 USGS Tapestry of Time and Terrain.

igan Basin subsurface, Van Schmus and Hinze, 1985). Thus, over a short distance in a continental interior that has been relatively stable for one billion years, sedimentary cover differs in thickness by a factor of 20 and in temporal coverage by more than 200 million years.

Rigorously quantifying such spatial and temporal variation in the distribution and character of sedimentary rocks is important for three primary reasons. First, the rock record dictates how earth history must be sampled and this can overprint empirical patterns in paleontological data, both globally (Raup 1972, 1976; Peters and Foote 2001, 2002; Smith 2001, 2007; Smith and McGowan, 2007; McGowan and Smith, 2008) and locally (e.g., Holland, 1999, 2000; Holland and Patzkowsky, 1999; Smith et al., 2001; Crampton et al., 2003). Second, temporal and spatial variation in the rock record is controlled by a number of inter-related phenomena, such as climate change, sea level fluctuation, and tectonic uplift/subsidence (e.g. Sloss, 1976; Ronov, 1978; Berry and Wilkinson, 1994), and therefore quantifying the rock record can help to constrain how these earth systems have changed over time (e.g., Gregor, 1968; Blatt and Jones, 1975; Ronov, 1978;

Ronov et al., 1980; Wold and Hay, 1990). Finally, the accumulation of sediment not only chronicles aspects of earth's history, but it also influences the evolution of earth systems by interacting with the atmosphere, biosphere, and lithosphere. Thus, quantifying the large-scale sedimentary record can enhance our understanding of some of the factors that may have contributed to biotic evolution and physical environmental change.

In this short course, I briefly outline the range of processes that can influence the distribution and character of sediments and describe how their accumulation might influence earth systems, particularly in biologically relevant ways. I then describe a new approach to characterizing the architecture of the sedimentary rock record which may add a new quantitative dimension to stratigraphy and sedimentology. Finally, I conclude with a review of how macrostratigraphic analyses relate to the macroevolutionary history of marine animals and suggest several new research directions that will help to unite stratigraphy and paleobiology in ways that will make it possible to test a number of new and long-standing evolutionary and environmental hypotheses.

### SEDIMENTS AS PRODUCTS, PROXIES, AND DRIVERS

That the distribution and character of sediments respond, both directly and indirectly, to tectonics, climate, and biological evolution is a fundamental principle of sedimentary geology and many fine texts have been written on the subject (e.g., Allen and Allen, 2005; Coe, 2003; Einsele, 2000; Leeder, 1999; Miall, 1999). However, a brief outline of some of the primary drivers and consequences of sedimentation helps to frame the motivation for this work and illustrates the important relationship between scale and process in the sedimentary record. Figure 2 provides a general representation of the topics and interactions that are briefly outlined in the following sections.

#### Solid Earth

The solid earth, which here encompasses lithospheric and crustal motion as well as the composition and structure of igneous and metamorphic crustal rock, is perhaps the most important factor governing sedimentation (e.g., Allen and Allen, 2005). Solid earth attri-

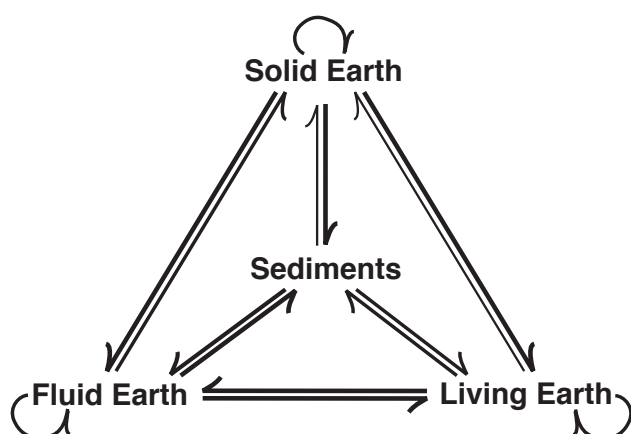


Figure 2—Network of interactions and feedbacks related to the accumulation of sediment. Solid Earth includes geomorphology and the motion and chemical composition of the crust, Fluid Earth includes the hydrosphere and atmosphere, Living Earth includes all living organisms and their metabolic pathways and products, Sediments include the process of sedimentation and resultant sedimentary deposits. Sediments are centrally located in this diagram, which is perhaps best represented by a tetrahedron, because of the role they play in both archiving and influencing earth systems. See text for discussion.

butes that are most relevant to sedimentation include the formation and destruction of sediment source regions and accommodation space via dynamic topography, crustal flexure and faulting, and thermal uplift and subsidence, as well as the petrologic characteristics of sediment source areas and the structural and geometric properties of sedimentary basins (e.g., Leeder, 1999).

The solid earth also exerts a number of important indirect controls on sedimentation by mediating the fluid earth. Examples include 1) changes in the mean elevation of the continents and ocean basin volume (Miller et al., 2005; Zhang, 2005; Müller et al., 2008), both of which drive changes in sea level and continental flooding, 2) the formation of mountain belts, which affect patterns of precipitation and sediment transport pathways, 3) the movement of tectonic plates beneath the circulation structure of the atmosphere and ocean (Allison and Briggs, 1993; Ziegler et al., 2003; Walker et al., 2002), and 4) changes in global climate via volcanic emissions, uplift and exposure of rocks to weathering, and changes in the configuration of the continents and oceans. The solid earth also indirectly affects sedimentation by influencing the biosphere,

which plays out primarily in terms of the extent and productivity of the carbonate factory (e.g., Kiessling et al., 2003; Wright and Burgess, 2005). The role that tectonics plays in directly mediating biological evolution has been discussed extensively elsewhere (e.g., Valentine, 1971; Miller and Mao, 1995; Coblenz and Riitters, 2004).

Although there is a tendency to view sediments as passive recorders of solid earth processes, sediment accumulation also directly affects the solid earth. For example, sediments deform the crust isostatically, resulting in a positive feedback that can amplify accommodation space created by other means (e.g., Reynolds et al., 1991). Earth's sedimentary shell also weakens the lithosphere and thermally insulates the lower crust, thereby changing its mechanical properties (Lavie and Steckler, 1997) and affecting the evolution of orogens (e.g., Cobbold et al., 1993; Bonnet et al., 2007). Sedimentary rocks also contain anisotropies that often determine how strain is accommodated and how fluids flow, and sediments incorporated into magmas can affect how they behave in the lithosphere and volatilize in the atmosphere (e.g., Maruoka et al., 2002).

The timescales over which the solid earth controls sedimentation, and vice versa, vary considerably. For example, large-scale cycles of continental coalescence and breakup, which play a critical role in determining sea level and average sedimentary basin characteristics, occur on timescales of  $10^8$  years or more (Vail et al., 1977; Heller and Angevine, 1985), whereas movements along individual faults can instantaneously change local accommodation space, perturb recently deposited sediments (Allen, 1986; McLaughlin and Brett, 2004), and redirect drainage systems. Nevertheless, solid earth processes tend to be dominant on timescales that are comparable to the lifetimes of individual sedimentary basins (Woodcock, 2004).

### Fluid Earth

The ocean-atmosphere system is intricately complex, but in terms of its direct influence on sedimentation, sea level (or, more precisely, continental flooding; Fig. 3) is probably the most important component of the system. This is because sea level determines long-term sediment base level (the point at which transport potential approaches zero) for all but internally drained continental areas, and because sea level influences lo-

cal and global climate by changing surface albedo and by distributing thermal energy and moisture sources. Sea level change also occurs over a wide range of temporal scales, from long-term tectonic cycles ( $10^8$ - $10^6$  yrs.) to Milankovitch-band and shorter-term ( $10^1$ - $10^5$  yrs.) oscillations in global temperature and ice volume (e.g., Miller et al., 2005). For these reasons, tectonically and climatically driven changes in sea level are expected to exert a dominant control on sedimentation both globally (Fig. 3) and within individual sedimentary basins (e.g., Vail et al., 1977; Van Wagoner et al., 1988; Leeder, 1999; Coe, 2003).

Because many of the proximate controls on sedimentation are linked to climate and hydrology, even rather subtle changes in precipitation and temperature can affect the accumulation and characteristics of sediments, a supposition that forms a cornerstone of cyclostratigraphy (e.g., House and Gale, 1995). The fluid earth also indirectly affects sedimentation through erosional modification of the solid earth and by numerous climate-related effects on biological productivity (e.g., Behrenfeld et al., 2006).

Similar to solid earth processes, the sedimentary record is often viewed as a passive recorder of sea level and climate. However, sedimentation directly affects sea level by displacing water, albeit by modest amounts, and mediates global climate through the burial and release of climate-changing elements, primarily carbon and sulfur. For example, over 66 million gigatons of carbon are currently stored in sediments (Ruddiman, 2007), primarily in the form of carbonate but also as organic carbon. This is equivalent to approximately 1,500 times the present-day ocean, atmosphere, biosphere, and soil carbon reservoirs combined (Ruddiman, 2007). Thus, at some timescales (generally assumed to be  $10^6$  yrs. or more; Berner, 2003), the exchange of carbon between the ocean/atmosphere and earth's sedimentary shell must be one of the most important of factors driving atmospheric  $\text{CO}_2/\text{O}_2$  concentration and, therefore, the global carbon cycle and climate system (Berner et al., 2003; Berner and Canfield, 1989).

### Living Earth

Organisms directly affect sedimentation in a variety of ways, including 1) the in situ generation of chemically-precipitated sediment, primarily calcium carbonate and silica, 2) mixing and transport of the up-

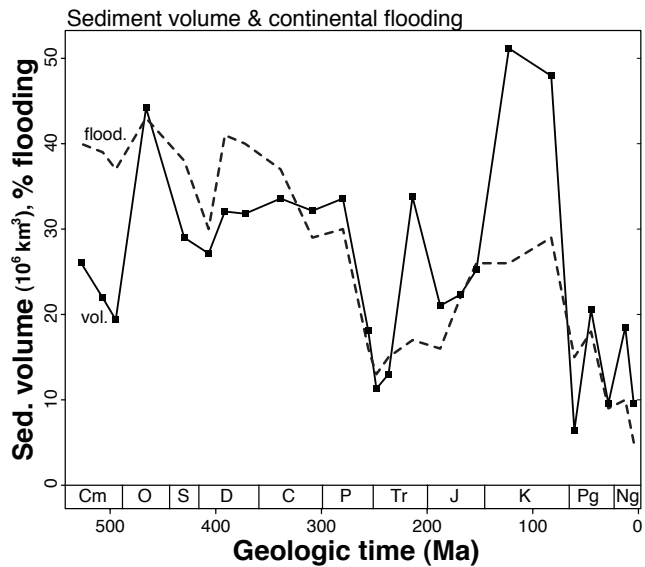


Figure 3—Percent continental flooding (dashed line) and global preserved marine sediment volume in millions of cubic kilometers (solid line) from Ronov et al. (1980).

per sediment volume through bioturbation (e.g., Aller, 1982; Gabet et al., 2003; Meysman and Middelburg, 2006; Amundson et al., 2007; Kosnik et al., 2007), and 3) changing the physical and chemical properties of sediment through disturbance and by the release of metabolic by-products and extracellular polymeric substances (e.g., Burne and Moore, 1987; Patterson, 1994; Gerbersdorf et al., 2008) and bioclasts (Kidwell, 1985). Given the magnitude of human activity in the Recent (Wilkinson, 2005; Wilkinson and McElroy, 2007) and the ability of tetrapods to physically disrupt geomorphic surfaces (e.g., Whitford and Kay, 1999; Neave and Abrahams, 2001), life is also one of the dominant agents of sediment transport and surface destabilization. Vegetation plays an antagonistic role in this regard by physically stabilizing landscapes (e.g., Pimentel and Kounag, 1998) but enhances rates of chemical weathering through  $\text{CO}_2$  injection and enzymatic reactions in soils (Knoll and James, 1987; Chorover et al., 2007). In fact, the effects of life on the solid earth are so pervasive that it has even been suggested that life leaves a statistically distinct topographic signature (Dietrich and Perron, 2006).

Sedimentation, in turn, influences the biosphere through a variety of direct and indirect mechanisms, including some of those discussed above (Fig. 2). Di-

rect effects include physical sediment properties (e.g., grain size, chemistry, and accumulation rates), which can influence community diversity and structure (e.g., Aller et al., 2002; Dashtgard et al., 2007). The input of skeletons as sedimentary particles changes the physical properties of sediment in such a way as to affect both sedimentation and biological communities, an idea encapsulated by sea floor armoring and taphonomic feedback (Kidwell and Jablonski, 1983; Kidwell, 1986). Changes in the character of shallow marine sedimentary environments have also been invoked as drivers of taxonomic and ecological turnover (e.g., Newell, 1952, 1962; Johnson, 1974; Simberloff, 1974; Sepkoski, 1976; Hallam, 1989; Brett, 1998; Peters, 2008).

### Summary

Many biological and physical processes combine to determine the distribution and character of sediments. Given the tight linkage between sea level change and sedimentation, as well as the ability of sea level changes to occur on both tectonic and Milankovitch-band timescales, sea level is expected to exert a dominant control on global patterns of sedimentation (Fig. 3) as well as on the architecture of individual sedimentary sequences (Vail et al., 1977; Coe, 2003). Sediment accumulation does not passively record earth history, but actively shapes it by influencing and causally linking many different earth systems (Fig. 2).

## QUANTIFYING THE ROCK RECORD

### Previous Approaches

The centrality of the sedimentary rock record to geoscience has been recognized for a long time, and this has prompted several different approaches to quantifying its temporal and spatial architecture. Most of these have focused on map area and rock volume, primarily because field geologists have produced high-quality geologic maps for much of the world.

The most important compilations of geologic map area, rock volume, and general lithology are those of Alexander Ronov and coworkers (Ronov, 1978; Ronov et al., 1980; but see also, for example, Cook and Bally, 1975; Sloss, 1976; Ziegler, 1982) and, more recently, Smith and McGowan (2007) and McGowan and Smith (2008). Such compilations continue to con-

tribute greatly to our understanding of the temporal and spatial character of the rock record (Fig. 3), but there are several limitations inherent in most map-based data. First, the minimum temporal resolution that is typically possible on a large geographic scale is often tens of millions of years. Second, geologic maps typically contain little information on lithology and paleoenvironment (but see Smith and McGowan, 2008), which complicates meaningful comparisons of time intervals or regions that might have similar rock quantities. It also makes it difficult for paleontological studies to evaluate the potential importance of, for example, diagenesis (e.g., Cherns and Wright, 2000; Wright et al., 2003), taphonomic variability (e.g., Behrensmeier et al., 2000; Kidwell and Holland, 2002), and differential environmental preservation (Smith et al., 2001; Walker et al., 2002).

The most important limitation of geologic maps, however, is that they provide little or no information on the temporal continuity of the sedimentary record. Here, “temporal continuity” refers to the extent to which sediments preserve an uninterrupted history at a given scale of temporal resolution. Temporal continuity is not the same as stratigraphic completeness (Sadler, 1981; Anders et al., 1987) because sedimentary records with the same overall completeness can have markedly different temporal continuity. As a simplistic example, a sedimentary record that is 50% complete has maximum temporal continuity when half of the time intervals have sediment and all of those time intervals are consecutively adjacent; minimum temporal continuity occurs when 50% of all time intervals have sediment, but each sediment-bearing interval is separated by an interval without any sediment.

The best-known summaries of the large-scale temporal continuity of the sedimentary rock record are grounded in the principles of sequence stratigraphy, which recognizes the importance of unconformities in bounding genetically related sedimentary packages (Vail et al., 1977; Van Wagoner et al., 1988). For example, Sloss (1963, 1976) identified large-scale transgressive-regressive sediment packages in North America and eastern Europe (“Sloss sequences”), and these serve as important organizing frameworks for tectonics and sedimentation. At the scale of sedimentary basins, principles of sequence stratigraphy serve as the preeminent organizational and interpretive framework for stratigraphic data (Vail et al., 1977; Coe, 2003).

However, sequence stratigraphic analyses primarily yield categorical and interpretive summaries of sediment stacking patterns. In order to be comprehensive, any attempt to characterize the rock record must be capable of simultaneously capturing 1) rock quantity, 2) lithology, 3) spatial pattern, 4) paleoenvironment, and 5) temporal continuity, and it must do so quantitatively. Sequence stratigraphy does not satisfy all of these requirements, but it does establish a conceptual framework for an analytical approach that does.

### Macrostratigraphy

At any geographic location, all sediments can be partitioned into discrete packages that formed continuously at a specified scale of temporal resolution and that are bound by gaps recognizable at that same scale of resolution. In the sedimentary record, temporal gaps are the result of non-deposition and/or erosion and form fundamental divisions known as sequence boundaries (Vail et al., 1977; Van Wagoner et al., 1988). The temporal scale of analysis defines the smallest resolvable gap, but there are typically gaps in the record at much finer scales, ranging all the way down to the brief moments that can separate individual bedding surfaces. Because there is a continuum of temporal continuity in the sedimentary record, the specification of a temporal scale is necessary in order to render the sedimentary record into discrete packages. The relationship between temporal scale and gap-bound package structure is related to “order” in sequence stratigraphy (Coe, 2003).

As a simple example, a temporal resolution of 400 Myr, when applied to sedimentary record of the Grand Canyon, renders two discrete gap-bound packages of sediment over basement rocks: a continuous package represented by the Proterozoic Grand Canyon Supergroup, and another continuous package comprising the overlying Paleozoic sediment (Fig. 4). These two gap-bound packages are separated by an angular unconformity and represent major phases of continental coalescence and breakup, a “first-order” cycle occurring on timescales of  $10^8$  years (Heller and Angevine, 1985). At a finer temporal resolution of 40 Myr, the Paleozoic package is divided into two continuous packages, one for the Cambrian and another for the Devonian-Permian. This package structure reflects a “second-order” change in accommodation space and a regional tectonic cycle of uplift and subsidence. The Proterozoic

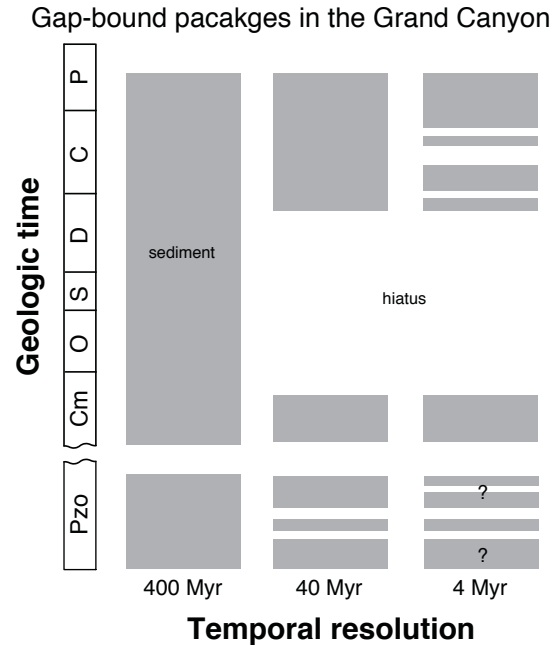


Figure 4—Relationship between the minimum duration of a recognizable gap (temporal resolution) and discrete sedimentary package structure in the Grand Canyon. Gray boxes indicate temporal range of packages of sediment that are continuous at the specified scale of resolution. White areas are intervening hiatuses recognizable at that same scale of resolution. Gap-bound sediment packages constitute the fundamental units in macrostratigraphy. See text for discussion.

package is also subdivided into two gap-bound packages at a temporal resolution of 40 Myr. Sharpening the temporal resolution to 4 Myr further subdivides the upper Paleozoic, and this new package structure reflects shorter-duration, “third-order” depositional cycles controlled by eustatic sea level change and regional tectonic uplift and subsidence. Uncertainties in correlation and age assignments in the Grand Canyon Supergroup prevent the reliable recognition of 4 Myr gaps.

The foregoing example illustrates two important points. First, the packaging of sediment depends upon the scale of temporal resolution. Second, the processes that control the temporal continuity of sedimentation change with temporal resolution such that high-frequency processes have little effect on lower-frequency structure. For example, Milankovitch-band forcing of climate may have exerted a dominant influence on the temporal continuity of Grand Canyon sedimen-

tation, but such forcing is irrelevant to the temporal continuity of sedimentation on timescales of  $10^7$ - $10^6$  years because that is governed by an entirely different set of processes related to tectonics and long-duration climate change. The same is true in the opposite temporal direction, though longer-duration processes will always determine the intervals of time during which higher-frequency signals can be preserved.

Gap-bound packages of sediment, similar to those illustrated in Figure 4, constitute the fundamental units of macrostratigraphy. A simple analogy is to think of rock packages in much the same way that a paleobiologist conceives of taxa in macroevolutionary analyses. Like taxa, gap-bound rock packages have physical/chemical properties and times of initiation and truncation. Thus, many of the same analytical tools that are used to measure the number and persistence of biological entities in the fossil record, such as biodiversity and rates of extinction and origination (Foote, 2000), can be used to measure the number and persistence of sedimentary entities in the rock record, parameters that correspond to area-weighted measures of rock quantity and area-weighted rates of expansion and contraction/erosional truncation of sedimentary environments (Miller, 2000; Peters, 2006a).

Although macrostratigraphy uses parameters that are conceptually related to biological diversity and rates of evolutionary turnover, there are several important differences. For example, fossil occurrences from different locations are usually combined in order to generate a single stratigraphic range for each taxon. Macrostratigraphy, on the other hand, explicitly preserves all spatial information by including gap-bound packages compiled independently for multiple geographic locations (Fig. 5). It is not redundant to sample a single sedimentary rock body at multiple locations because doing so reflects the area over which that sediment accumulated and appropriately weights that unit for macrostratigraphic analysis (Fig. 5).

For the purposes of macrostratigraphy, gaps in sedimentation can be defined as time intervals for which no sediment is preserved, or they can be defined as any break in the record of an environment or lithological subset of the data. For example, some hypotheses might require the temporal and spatial dynamics of carbonate environments to be measured separately from siliciclastics (Peters, 2008). In this case, temporal gaps in sedimentation would include hiatuses that

might correspond to traditional sequence boundaries or to lithostratigraphic and environmental contacts that may be of little or no sequence stratigraphic importance. Thus, it is possible to quantify the spatio-temporal dynamics of sedimentary environments individually or collectively using macrostratigraphic parameters.

### **Relationships Between Macrostratigraphy and Forcing Mechanisms**

Like sequence stratigraphy, macrostratigraphy can be applied at any spatial and temporal scale, but it is perhaps easiest to understand the meaning of macrostratigraphic parameters at the familiar scale of sedimentary basins. Insofar as the the statistical properties of gap-bound packages relate to sequence stratigraphy and to underlying forcing mechanisms, macrostratigraphy should provide a new tool in the description and characterization of sequence architecture as well as the identification and quantification of the processes that control sedimentation.

As a preliminary test of this possibility, the physics-based basin model SEDFLUX 2.0 (Syvitski and Hutton, 2001; Hannisdal, 2006) was used to generate sedimentary successions in response to a known history of sea level change, sediment supply, and subsidence. To parameterize the model used here, a simple four-cycle sinusoidal curve with an amplitude of approximately 80 m, with superimposed higher-frequency, lower-amplitude variation, was used to drive sea level (Fig. 6). Subsidence and sediment supply parameters derive from the empirical record along the New Jersey margin (following Steckler et al., 1999). The model was run forward in time  $10^5$  years and the resultant sedimentary fill was sampled across space for gap-bound packages at a temporal resolution of 500 years, though results are similar for a wide range of temporal resolutions and binning strategies. The model was executed by Bjarte Hannisdal at the University of Bergen. See Hannisdal (2006) for further explanation of the SEDFLUX model and for the ability of these results to be scaled up temporally.

The time series for the total number of packages, as well as rates of package initiation and truncation, provide statistical summaries that reflect the spatio-temporal architecture of sediments in a familiar chronostratigraphic diagram (Fig. 6). That is, when sediments are geographically widespread, the total

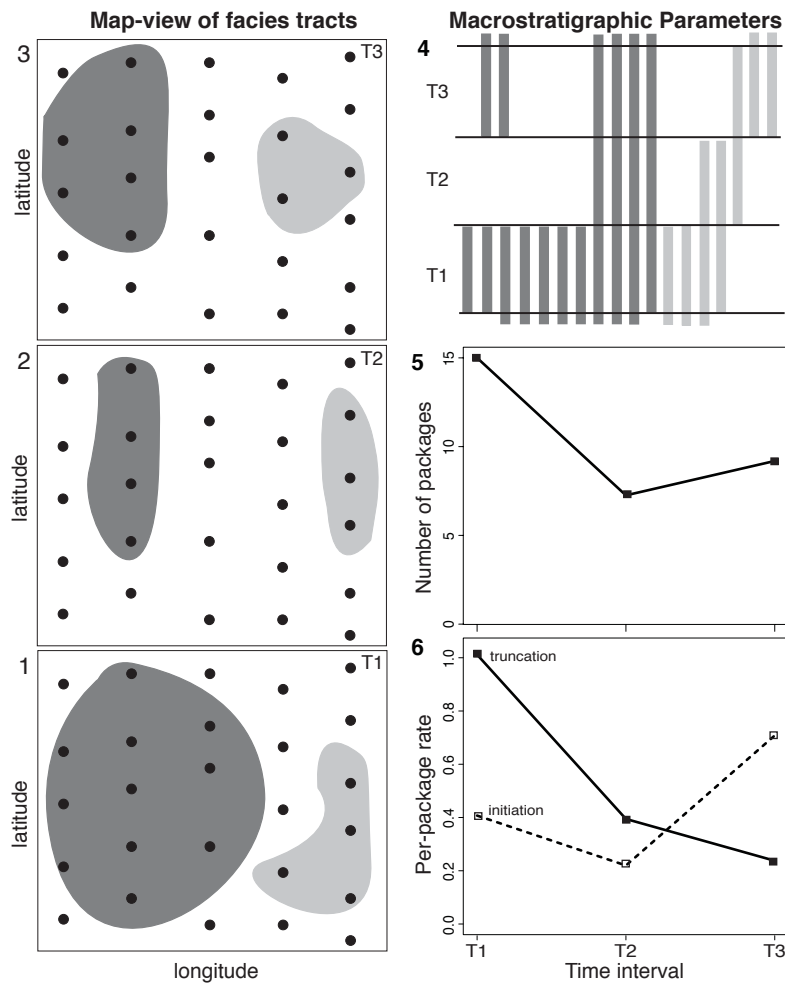


Figure 5—Macrostratigraphy and spatio-temporal patterns for two hypothetical sedimentary facies. 1-3, sampling region, sampling locations (black dots), and map-view showing expansion/contraction of two sedimentary environments (shaded regions) for three time intervals, T1, oldest, to T3. 4, Gap-bound sediment packages from T1-T3 colored by environment. 5, Total number of packages in each time interval irrespective of environment. 6, Per-interval truncation and initiation rates for packages from T1-T3 calculated using Foote's (2001) survivorship-based, per-capita rates (per-package per-interval rates). Separate parameters could be calculated for each environment, but here aggregate macrostratigraphic parameters are shown. Note that package turnover rates reflect spatio-temporal dynamics that rock quantity alone fails to detect (e.g., light gray environment from T2 to T3 is static at points, but undergoes spatio-temporal turnover).

number of packages is large, when sedimentation contracts in area, rates of package truncation increase, and when sedimentation expands geographically, rates of package initiation increase. Average rates of initiation and truncation reflect the overall spatial and temporal volatility of sedimentation and the mean survivorship of sedimentary packages (Fig. 6.1).

In addition to providing a useful quantitative summary of the spatio-temporal architecture of sedimentary deposits, macrostratigraphic parameters are quantitatively related the underlying forcing mechanisms

specified in the model input. For the iteration shown in Figure 6, sea level was the dominant forcing signal and macrostratigraphic parameters accurately reproduce the both the high- and low-frequency components of sea level (Fig. 6.4).

The results shown in Figure 6 include every output location generated by the SEDFLUX model. Although useful for testing purposes, such complete spatial sampling will rarely be attainable in the field. Nevertheless, even when sampling is incomplete, macrostratigraphic parameters can accurately characterize



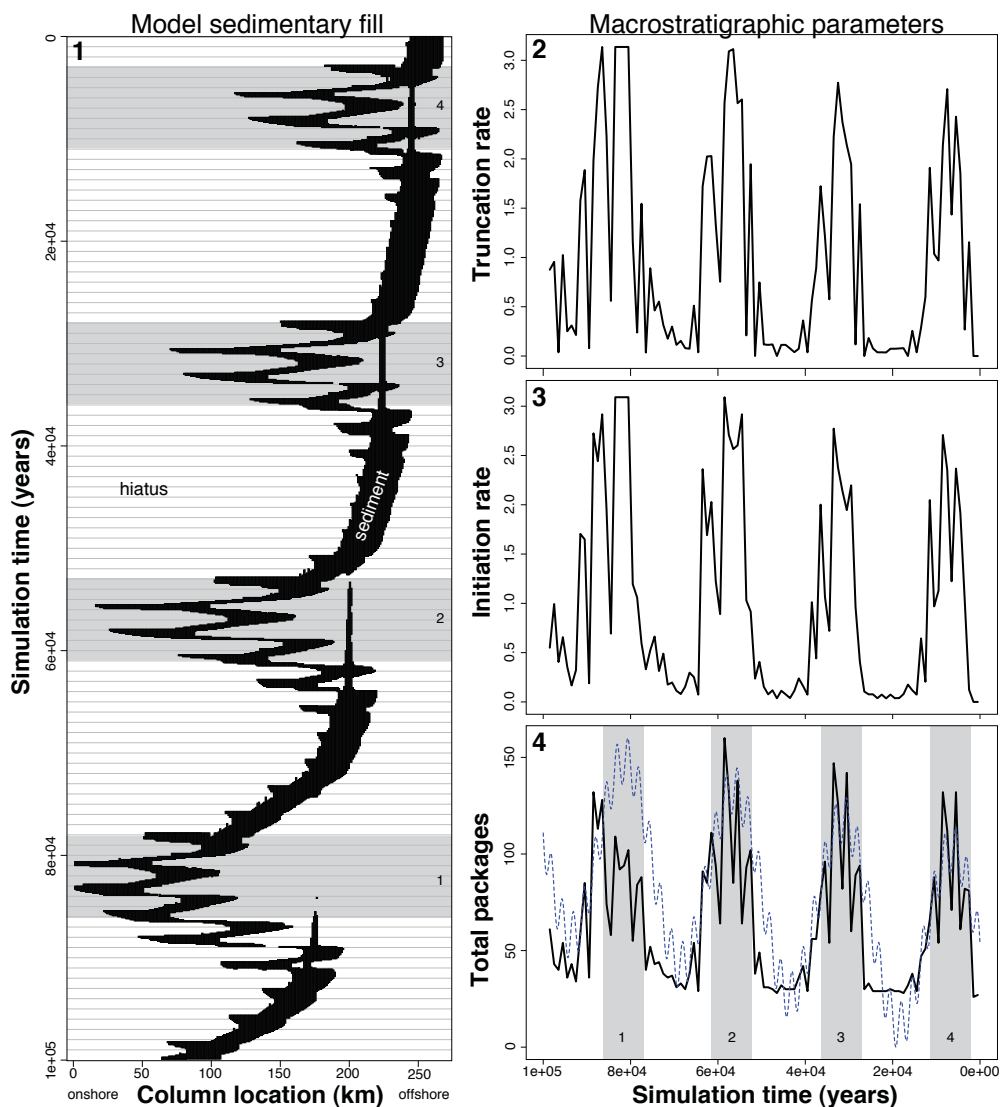


Figure 6—SEDFLUX basin fill model and macrostratigraphic parameters. 1, Chronostratigraphic (Wheeler) diagram. Zero marks end of 100 Kyr model run; horizontal lines are time interval boundaries used to calculate macrostratigraphic parameters. Abscissa shows sampling position in number of kilometers from basin margin along a 2D sampling transect. 2, per-interval per-package truncation rates (Foote, 2000). 3, per-interval per-package initiation rates (Foote, 2000). 4, total number of packages. Dashed curve in 4 shows sinusoidal sea level curve defined in the model input. Shaded and numbered regions in 1 and 4 show time-equivalent sea level highstands. Because sea level has the largest amplitude of all forcing mechanisms in this simulation, the sedimentary fill is controlled primarily by sea level with minor contributions from sediment supply. Macrostratigraphic parameters reflect short- and long-term volatility in these forcing mechanisms (2-4).

patterns of sedimentation and forcing mechanisms. For example, a random subsample of just 2% of the sampling locations used to generate Figure 6 yields results that are statistically similar to the completely sampled model output and the sea level curve (Fig. 7). This is remarkable considering that many time intervals are represented by just one rock package.

**The Distinction Between Package Initiations and Truncations**

Package initiations and truncations correspond to discrete surfaces in the stratigraphic record that are, at least in principle, unambiguous. However, package truncations may reflect non-deposition, the erosional truncation of a longer-duration sedimentary record, or

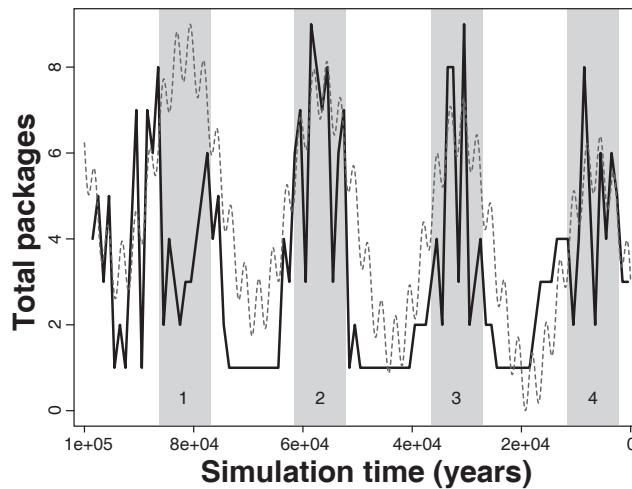


Figure 7—SEDFLUX model results and total number of sedimentary packages, as in 4, but for a random subsample of 2% of the column locations. The maximum number of packages sampled in a given time interval is nine and many time intervals have a single gap-bound package (compare to maximum of 157 in 1). Despite incomplete sampling, the time series for the total number of packages is statistically similar to the time series obtained for 100% spatial coverage (4; for first differences,  $p < 0.0001$ ), and both time series reproduce short- and long-term variation in sea level forcing (gray dashed curve). Results for package truncation and initiation rates are similar (not shown).

some combination of the two (Fig. 8; see also Sloss, 1963; Wheeler, 1964). Package initiations, by contrast, can only be temporally offset by faulting, and therefore most package initiations must represent the times at which sediment actually began to accumulate.

Although both non-deposition and erosion must contribute to sedimentary hiatuses and the apparent timing of package truncations, it is currently impossible to determine the relative importance of these two phenomena. However, there are several reasons to believe that non-deposition might, on average, account for more time than erosion in the majority of sedimentary hiatuses. First, sediments tend to accumulate in areas of low elevation relative to the surrounding landscape. Thus, when sedimentation stops, the unconformity surface should be located in an area with low net rates of erosion. Second, in order to generate a hiatus that is bracketed above and below by sediment, which is the most common scenario at temporal resolutions less than  $10^7$  Myr (e.g., Fig. 4), a region must be at least episodically located in a sediment-catching, and

therefore low-elevation, area. Third, in order to keep pace with non-deposition, erosion must remove sediment at a rate that is comparable to the rate at which the sediment accumulated (Fig. 8). For example, if deposition stopped for 1 Myr, in order for erosion to make an equal contribution to the duration of the resultant hiatus, the equivalent of 1 Myr of underlying sediment would have to be removed before deposition resumed. Finally, the wholesale destruction of a portion of the sedimentary record, although very important in terms of sediment cycling and defining the minimum age of preserved sediments in a region, does not affect the partitioning of time among the hiatuses that remain to be sampled.

### Summary

Discrete, gap-bound packages of sediment constitute a fundamental architecture in the sedimentary rock record. Specification of a temporal scale renders discrete the continuum of temporal continuity that is inherent in the rock record and that discrete structure is related

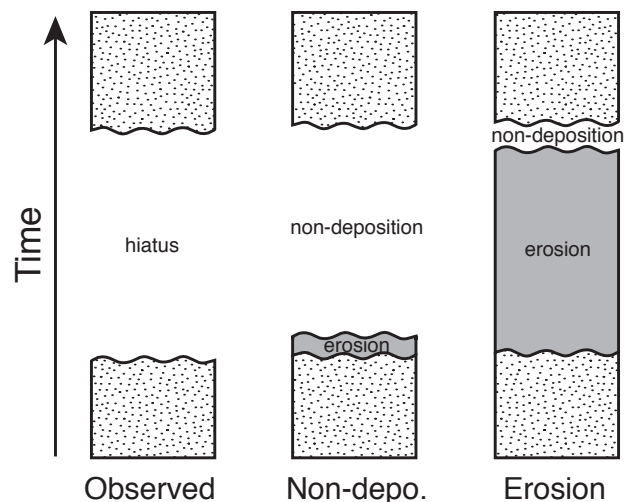


Figure 8—Two possible scenarios for partitioning an observed hiatus (left) into non-deposition and erosion (center, right). Two end-members are shown. “Non-depo.” shows a hiatus in which there is little temporal offset between the termination of deposition and the observed termination of the underlying sedimentary package. “Erosion” illustrates a hiatus in which there is a substantial temporal offset due to the erosion of a significant quantity of sediment that spans a large amount of time. In both scenarios, the timing and duration of the resultant hiatus is identical. See text for discussion.

to the sedimentary processes that operate at that scale. Macrostratigraphy takes advantage of this fundamental architecture by utilizing gap-bound packages compiled separately for different geographic locations as its fundamental units. Area-weighted measures of rock quantity and spatio-temporal environmental continuity derive from these gap-bound packages. Simulation analyses show that macrostratigraphic parameters relate quantitatively to the processes that control sedimentation (e.g., base level, sediment supply, and subsidence) and that these parameters can be estimated even when sampling is incomplete. Because package terminations must always reflect some (generally unknown) combination of erosion and non-deposition, package terminations reflect two distinct and important sets of processes. On long timescales, non-deposition is probably more important than erosion in controlling the apparent duration of sediment-bound hiatuses.

### PHANEROZOIC MACROSTRATIGRAPHY OF NORTH AMERICA

Having described the general analytical approach of macrostratigraphy and outlined the meaning of macrostratigraphic parameters at the familiar scale of sedimentary basins, I now turn to an empirical macrostratigraphic data-set that spans much of a continent and the entire duration of the Phanerozoic. In many ways, this is the scale at which macrostratigraphy is most useful for quantifying the spatio-temporal pattern of sedimentation.

Peters (2006a) compiled gap-bound packages of rock in United States using the COSUNA correlation charts (Childs, 1985), which provide a comprehensive summary of the known rock record, including the subsurface, for 541 geographic locations. The temporal resolution used to recognize these packages varies regionally with knowledge of the record, but it is generally between 1-3 Myr. For the macrostratigraphic results presented here, package data were binned into Phanerozoic stages with a mean duration of about 6 Myr. Here, I focus on marine sediments, even though it is impossible to fully disentangle the marine and terrestrial records at this time (Peters, 2005). See Peters (2006a) for a more general summary that includes known terrestrial sediments as well as igneous rocks.

The total number of marine sediment packages in North America varies considerably from stage-to-stage and on longer time scales during the Phanerozoic (Fig. 9). The spatial scale of this analysis is similar to that of Sloss (1963), who used large-scale unconformities to define six “first-order” cratonic sequences in North America. Not surprisingly, most Sloss sequences register very clearly in these macrostratigraphic data (Fig. 9), but there are two notable discrepancies. First, Sloss’ longest duration sequence, the Pennsylvanian-Jurassic Absaroka sequence, is not clearly represented in the macrostratigraphic data. Instead, macrostratigraphy supports the division of Sloss’ Absaroka sequence into three shorter-duration sequences that reflect expansions and contractions in deposition that are similar to those observed in the other sequences (Fig. 9). The second mismatch occurs in the Cenozoic, when package data indicate little change at the same time that Sloss indicates a large decline. This divergence is probably due to the inclusion of some unknown number of terrestrial units in the macrostratigraphic data. Because terrestrial sediments increase in abundance towards the recent (Peters, 2006a) and cannot be fully disentangled from the marine record, the number of Cenozoic marine packages is likely biased in an upward direction.

Macrostratigraphy complements Sloss’ summary of sedimentation by adding a new quantitative dimension, but it also reveals longer-term (and shorter-term) variations that Sloss did not emphasize. In particular, macrostratigraphy clearly identifies two prominent 250-300 Myr cycles of sedimentation in North America. In terms of the total number of sedimentary packages, these cycles are defined by minima in the Lower Cambrian and end-Paleozoic, and maxima in the Late Ordovician and Late Cretaceous (Fig. 9). In terms of the temporal continuity of sedimentation, macrostratigraphy shows a fundamental break that defines two major depositional cycles, which are herein referred to as the Paleozoic and Modern megasequences (Fig. 10). The Paleozoic megasequence has a volatile, long-duration plateau in the number of through-ranging packages after a sharp Cambrian increase, whereas the Modern megasequence has a more sustained Mesozoic increase in the number of through-ranging packages (Fig. 10).

The average duration of marine sediment packages is approximately 25 Myr, and the durations are ap-

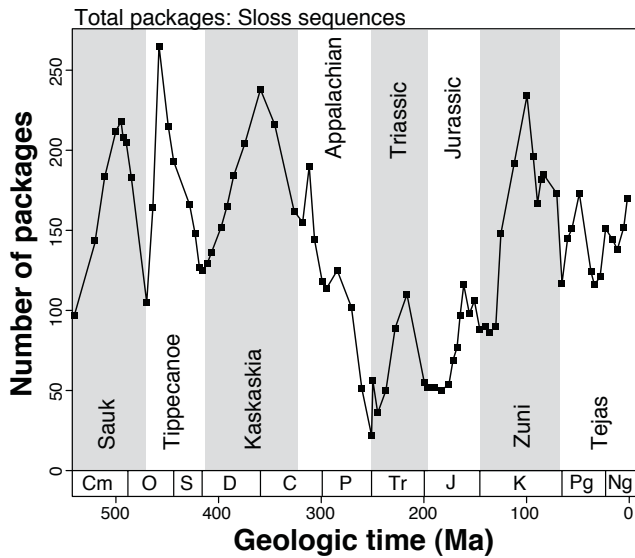


Figure 9—Total number of marine sedimentary rock packages in the USA. Data are binned into stratigraphic stages with a mean duration of approximately 6 Myr. Alternating gray and white fields show sequences, including Sloss' (1963) Sauk, Tippecanoe, Kaskaskia, Zuni (modified), and Tejas sequences. Sloss' (1963) Absaroka sequence, which spans the Pennsylvanian-Jurassic is not well supported by package data. Instead, three new sequences are recognized: the Appalachian, Triassic, and Jurassic sequences. Note Phanerozoic low in the late Permian to early Triassic, and local maxima in the Ordovician and Cretaceous. See also Figure 10.

proximately exponentially distributed (Peters, 2005). However, there is considerable temporal variability in package longevity. Forward survivorship curves (*sensu* Raup, 1978; Foote, 1988) for marine sediment cohorts are shown in Figure 11, and aggregate per-interval rates of package truncation are summarized in Figure 12.1. The largest increase in area-weighted rates of truncation occurs at the end-Permian and this is followed immediately by the second of two large pulses of package initiation (Fig. 12.2). This Permian-Triassic turnover pulse reflects the temporal discontinuity in sedimentation that separates the Paleozoic and Modern megasequences (Fig. 10). Other significant pulses of package truncation mark the upper boundaries of many Sloss sequences (Figs. 9, 12), in particular the Sauk, Triassic, and Zuni sequences. An additional large pulse of truncation, driven by eustatic sea lev-

el fall associated with the end-Ordovician glaciation (Brenchley et al., 1994), occurs within the Tippecanoe sequence, but this truncation and recovery is too short in duration to cause a Sloss-scale sequence break.

At this scale of analysis, no other factor is probably more important than sea level (or, more precisely, continental flooding, Fig. 3) in controlling patterns of sedimentation and the turnover of sedimentary environments. Although published Phanerozoic sea level estimates differ in detail and in absolute magnitude, the familiar “M-curve” (Fig. 13) is a recurring feature in most compilations (Miller et al., 2005; Müller et al., 2008). The lowstand during the end-Permian to early Triassic, as well as highstands in the Ordovician and Cretaceous, define two major cycles of continental flooding and these are closely mirrored by macrostratigraphic patterns. Shorter-duration changes in continental flooding correspond to Sloss sequences, though some of the short-term sea level fluctuations recognized by Hallam (1992) and others do not register in the macrostratigraphic data of North America (Fig. 13).

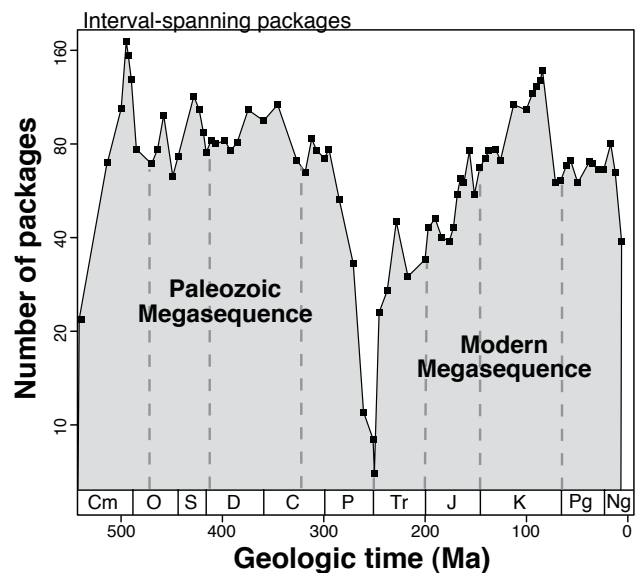


Figure 10—Total number of through-ranging marine sedimentary packages plotted on a logarithmic ordinate. Sequence boundaries from Figure 9 are shown by vertical dashed lines. There are two major Phanerozoic depositional cycles, or “megasequences,” in North America. Note the volatile Paleozoic plateau and the post-Paleozoic increase on a logarithmic scale.

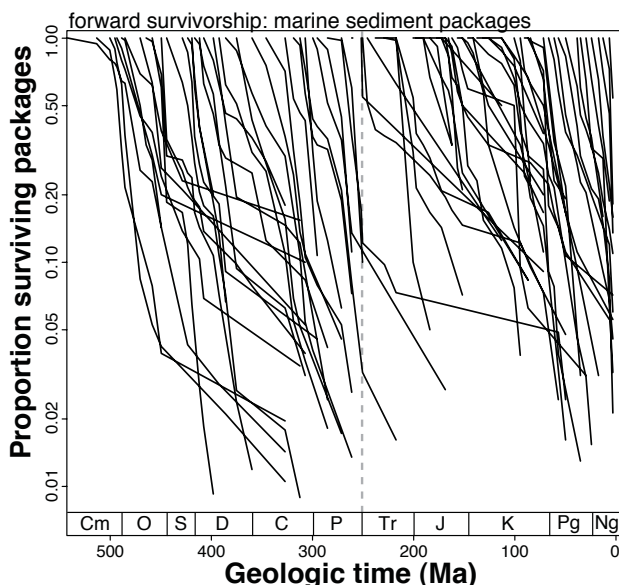


Figure 11—Forward survivorship curves for marine sediment package cohorts. Vertical dashed line separates Paleozoic and Modern megasequences.

**Summary**

Macrostratigraphic analysis conducted at a temporal resolution of approximately 1-3 Myr reveals important large-scale variation in rock quantity and temporal continuity in the marine sedimentary record. The most striking features are two distinct, large-scale cycles of sedimentation that are here called the Paleozoic and Modern megasequences. Five main pulses in package truncation punctuate the Phanerozoic sedimentary record, most of which occur at the Sloss-type sequence boundaries. The largest truncation pulse occurs at the end-Permian and this defines the top of the Paleozoic megasequence. Only two pulses of package initiation stand out above all others and these mark the base of each megasequence. At the spatial scale of North America and a temporal scale of approximately one million years, the most important proximal controls on sedimentation are probably the draining and flooding of continents (Figs. 3, 13) via tectonics and long-duration changes in global climate.

**MACROSTRATIGRAPHY AND  
MACROEVOLUTION**

In 1952, Norman D. Newell suggested that “successive expansions and restrictions of shallow epi-

continental seas” were the most likely causes of mass extinctions in the fossil record (Newell, 1952, 1962, 1967). Newell’s hypothesis stemmed from the observation that most of the large declines in biodiversity, which he first termed “mass extinctions,”

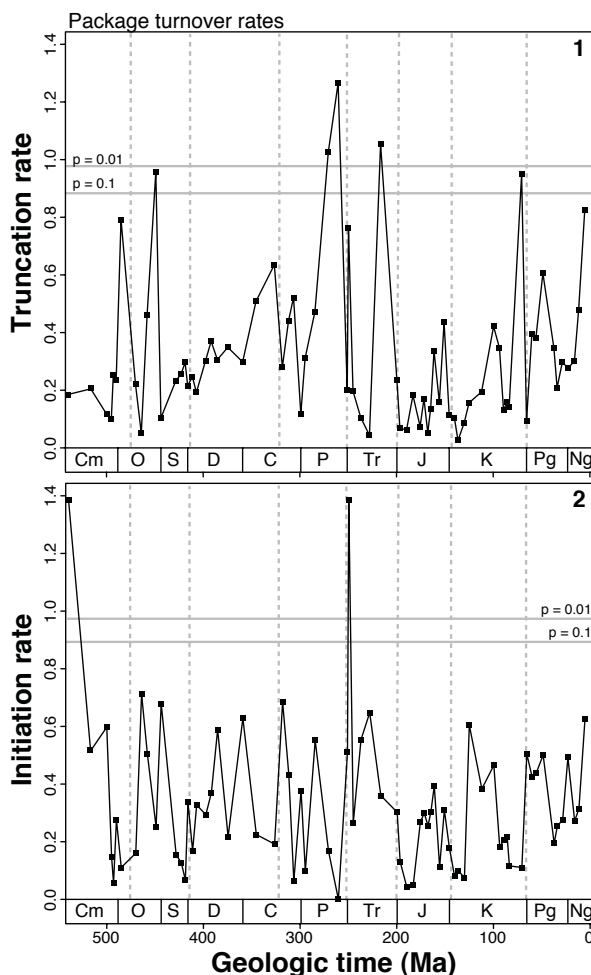


Figure 12—Per-package rates of turnover measured per-interval (Foote, 2000). 1, truncation rates. 2, initiation rates. For reference, Sloss sequence boundaries from Figure 9 are shown by vertical dashed lines. Horizontal gray lines show probability of obtaining at least one rate peak  $\geq$  to the indicated value based on 1000 randomizations of package data. Many peaks below the horizontal lines are also significant relative to adjacent intervals. In general, rates of truncation increase and rates of initiation decrease within Sloss sequences. The Paleozoic and Modern megasequences are defined by prominent pulses of initiation at their base and a large pulse of truncation at the end of the Paleozoic.

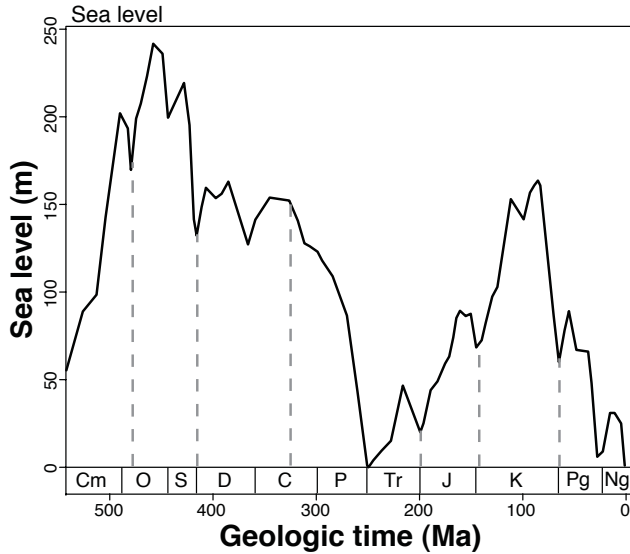


Figure 13—Phanerozoic sea level, roughly adapted from Hallam (1992). Vail and Haq curves are broadly similar. The classic “M-curve” in sea level, with minima in the lower Cambrian, Permian-Triassic, and Neogene, and maxima in the Ordovician and Cretaceous, has left a strong quantitative signal in the macrostratigraphy of North America and global sediment area. Sequence boundaries from Figure 9 are shown by vertical dashed lines. Compare to Figures 9 and 10.

corresponded to the draining of epicontinental seas. Newell’s hypothesis was revisited by Hallam (1989) and Hallam and Wignall (1999), who corroborated the correlation between drops in sea level and extinction but also highlighted additional complexities related to the spread of anoxic bottom water during marine transgressions (e.g., Johnson et al., 1985; Smith et al., 2001; Wignall et al., 2005; Bond and Hallam, 2008) and perturbations to the carbon cycle (e.g., Payne et al., 2004; Maslin et al., 2004; Knoll et al., 2007).

Despite the empirical evidence in favor of Newell’s hypothesis, and modifications thereon, the link between sea level change and macroevolution has been downplayed, often in favor of other, more explosive environmental perturbations (e.g., Alvarez et al., 1980). Bambach (2006), Hallam and Wignall (1997), Erwin (2006) and others provide good overviews of the factors that have been proposed as mass extinction mechanisms, which are so diverse that Andrew Bush (2006) identified a jocular “Third Law of Mass Extinctions:” for every proposed explanation, there is an equal and opposite explanation.

Although sea level change is still widely cited as a possible extinction mechanism (e.g., Erwin, 2006), there are two main reasons for the recent relegation of Newell’s hypothesis to the background. First, in trying to understand the causes of mass extinctions, which were originally identified in large-scale compilations (Newell, 1952; Raup and Sepkoski, 1982), the tendency has been to seek out and study stratigraphic sections that straddle the boundary interval. This is a necessary and important approach that has contributed greatly to our growing body of knowledge of mass extinctions (e.g., Payne, 2005), but it has several substantial limitations in terms of testing Newell’s specific hypothesis. For example, it has been pointed out that Permian-Triassic boundary sections show an abrupt sea level rise, not a fall (e.g., Wignall and Hallam, 1992; Wignall et al., 1995). This observation has been used to argue against Newell’s hypothesis for the end-Permian mass extinction (see also Johnson, 1974; Simberloff, 1974). However, field studies that rely on individual sections or basins are necessarily removed from the larger context of Phanerozoic sea level change. In the case of the Permian-Triassic, it is incontrovertible that the late Permian witnessed the withdrawal of the large epicontinental seas that had dominated shallow marine environments for almost 300 Myr. The sea level fall at the end-Permian was so great, in fact, that paleobiologists have been forced to travel far and wide in search of complete marine boundary sections. Moreover, the biological relationship between sea level change fossil first and last occurrences is always confounded by sequence stratigraphic architecture (Holland, 1999, 2000; Holland and Patzkowsky 1999, 2002), and this has yet to be adequately accounted for in the case of the Permian-Triassic boundary interval and end-Permian sea level rise.

Second, and more importantly, there is a natural tendency to equate the phrase “expansions and restrictions of shallow epicontinental seas” in Newell’s original hypothesis with eustatic sea level, if for no other reason than some sort of quantification is required in order to test the idea. However, sea level change per se was never the primary mechanism for extinction in Newell’s hypothesis. Instead, the direct link to biological turnover was the expansion and restriction of epicontinental seas, environmental changes which will often coincide with eustatic sea level rise and fall, but not uniformly so. This disconnect occurs because

of nonlinearities and threshold effects with respect to the environmental consequences of sea level change, which are especially prevalent in epicontinental seas (e.g., Algeo et al, 2007). As a simple example, re-examine Figure 6. Note that the amplitude of the high-frequency sea level curve does not change (Fig. 6.4), but that the effect of this forcing on the volatility of shallow shelf sedimentation (and, therefore, shelf environments) is much greater when overall sea level is high. Although simplistic, this result is indicative of the fact that the environmental effects of a given sea level change depend on the state of the system.

Perhaps the biggest reason for the relegation of Newell's hypothesis to the background, however, has been the lack of rigorous methods with which to quantify the environmental consequences of sea level change. One of the most valuable aspects of macrostratigraphy is that it is sensitive to sea level change (Fig. 6), but based on the area-weighted survivorship of marine sedimentary environments. Thus, macrostratigraphic analyses permit Newell's hypothesis to be more precisely tested than do estimates of sea level change per se.

Macrostratigraphy has already been used to examine the relationship between short-term changes in sedimentation and macroevolutionary patterns, primarily because of the statistical advantages of first differences (Brockwell and Davis, 1991). These results show that macrostratigraphy predicts, without modeling, transforming or culling, much of the observed variance in three of the most important macroevolutionary patterns in the marine animal fossil record: 1) genus richness (Peters, 2005), 2) rates of genus extinction and origination, including the mass extinctions (Peters, 2005, 2008), and 3) turnover among Sepkoski's (1981) Paleozoic and Modern Evolutionary Faunas (Peters, 2008). The similarities between macrostratigraphy and macroevolution are not the result of unconformity-related sampling biases in fossil data (Holland, 1999) because the macrostrat-macroevolution correlations tend to improve or remain similar after adjusting taxonomic rates to account for incomplete and variable fossil preservation (Foote, 2003; Peters, 2005, 2008) and because the "gappiness" of the rock record does not predict turnover in a way that is consistent with the bias hypothesis (Peters, 2006b). For these reasons, sampling bias and its effects on paleobiological patterns will not be discussed further here.

### The "M" in Macroevolution

The dominant long-term features in the marine sedimentary rock record of North America are two megasequences that reflect the large-scale flooding and draining of the continent during two cycles of supercontinent breakup and coalescence ("Wilson Cycle"; Fig. 10). Each megasequence corresponds to one of the lobes of the familiar "M-curve" of Phanerozoic sea level (Fig. 13). If Newell's hypothesis is correct, then long-term variation in the expansion and contraction of epicontinental seas (as well as shorter-term changes) should register in the macroevolutionary history of marine animals. Here I use Jack Sepkoski's (2002) global genus compendium (available at <http://strata.geology.wisc.edu/jack>) to estimate all macroevolutionary parameters. Loess regression, a linear regression technique that uses subsets of the data to compute local distance-weighted fits (R Development Core Team, 2006), was used to measure the long-term trajectories in both genus and package data.

The most basic macroevolutionary feature in the marine animal fossil record is the temporal trajectory of taxonomic richness (biodiversity). Although the extent to which global biodiversity has actually changed during the Phanerozoic remains rather contentious (e.g., Alroy et al., 2001; Bush et al., 2004; Stanley, 2007), there is little disagreement over the empirical pattern (Fig. 14), and this pattern has several prominent features in common with macrostratigraphic data. First, both the total number of packages and genus diversity achieve maxima in the Ordovician and then decline to post-Cambrian lows in the early Triassic (Fig. 14). Second, both the genus and rock package data increase during the Mesozoic. In fact, the only major discrepancy between the genus and package data occurs in the Cenozoic, when biodiversity increases dramatically at the same time that rock packages remain steady or decline.

On the shorter, but still relatively long, temporal scales of Sloss-sequences, the match between biodiversity and rock packages is also very good, particularly from the Carboniferous to the Cretaceous (Fig. 9). It is worth pointing out that the average duration of a Sloss sequence (as redefined here) is 67 Myr, which is close enough to the 62 Myr periodicity in diversity reported by Rhode and Muller (2005) that I concur with Smith and McGowan (2005); the rock record

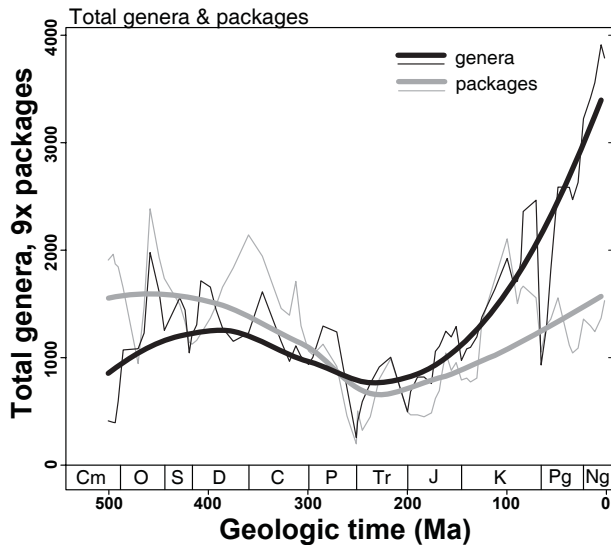


Figure 14—Total number of marine animal genera in Sepkoski’s global compendium and 9x total number of marine sedimentary packages. To emphasize longer-wavelength patterns, loess regressions with alpha smoothing coefficients of 0.75 are shown by bold lines. Fine lines show raw data. Note broadly similar temporal trajectories that include a decline during the mid-Paleozoic to a low in the Triassic and a post-Paleozoic increase. First differences, which only address interval-to-interval changes in the original time series, are positively correlated ( $r = 0.58$ ;  $p = 1.1 \times 10^{-7}$ ). Drop in genus diversity across K/Pg boundary is exaggerated due to a decrease in the number of genera resolved to Sepkoski’s Cenozoic subepochs, which are plotted here.

must be considered in the context of any discussion of cycles in fossil diversity.

The volatile Paleozoic plateau (which is actually better described as a gentle decline after an Ordovician peak) as well as the subsequent rise during the Mesozoic is strikingly similar in both the macrostratigraphic and genus data, but there are some noteworthy differences. In particular, there is an overall negative genus diversity residual in the Paleozoic, and an overall positive diversity residual in the post-Paleozoic (difference between black and gray lines in Fig. 14). This raises the possibility of a true long-term increase in biodiversity, perhaps driven by an increase in diversity at the community level (Bambach, 1977; Bush and Bambach, 2004; Kowalewski et al., 2006), which would be decoupled from the environmental dynamics captured by macrostratigraphy. However, determining

the biological meaning of this residual variation requires further investigation, if for no other reason than package data include subsurface rocks and genus data ignore sampling/preservation effects and the Pull of the Recent (see below).

As suggested by long-term trends in total genus diversity (bold lines, Fig. 14), the total number of through-ranging genera reveals two distinct phases in the temporal continuity of the marine animal fossil record: a Paleozoic plateau following a large Cambrian-Ordovician increase, and a sustained post-Paleozoic increase after a minimum in the early Triassic (Fig. 15). This long-term temporal pattern is strikingly similar to the sedimentary megasequences discussed above (Figs. 10, 15), but there are two notable discrepancies.

First, the number of through-rangers for both packages and genera have an abrupt early Paleozoic increase, but the increase for packages is completed by the late Cambrian whereas the increase for genera continues into the Ordovician. Thus, there is a negative genus residual in the Cambrian and early Ordovician (Fig. 15), and this may reflect a Cambrian explosion and Ordovician radiation (e.g., Droser and Finnegan, 2003) that lags or is completely decoupled from the environmental dynamics related to macrostratigraphy. Alternatively, the disconnect could reflect relatively high rates of extinction in this interval, which would suppress the number of through-ranging genera in this interval (Foote, 2000; Stanley, 2007). The second discrepancy is that the total number of through-ranging genera more than doubles after the late Cretaceous, whereas through-ranging sediment packages decrease in number (Fig. 10). A Cenozoic divergence between through-ranging genus and package data (Fig. 10) is consistent with the expectations of the Pull of the Recent, which refers to the “pulling” of genus last occurrences forward to the relatively well-sampled present-day even if those taxa have no fossil occurrences after their first fossil appearance (Raup, 1972, 1979). However, the observed divergence is also consistent with a real biological increase in diversity after the Cretaceous (Jablonski et al., 2003; Stanley, 2007).

Recent work has questioned the importance of the Pull of the Recent (Jablonski et al., 2003; Stanley, 2007), but one way to minimize the problem is to tabulate the number of events that are actually observed in each time interval rather than the number



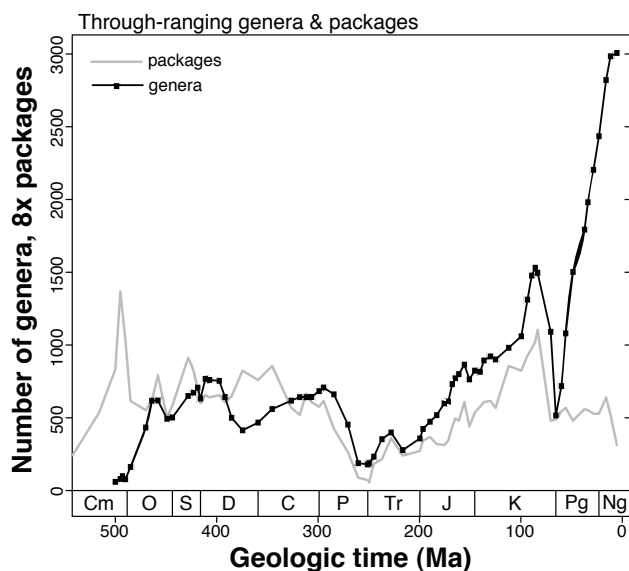


Figure 15—Total number of through-ranging genera in Sepkoski's genus database and sedimentary packages in North America (8x raw data, gray line; from Fig. 10). Note similarities in overall temporal trajectories, including a large early Paleozoic increase, a Paleozoic plateau, and a post-Paleozoic increase. First differences are also correlated ( $r = 0.40$ ;  $p = 0.002$ ). Drop in genera at the K/Pg boundary is exaggerated due to a decrease in the number of genera resolved to Sepkoski's Cenozoic subepochs, which are plotted here. Last datapoint shown is Pliocene.

of entities that may or may not actually occur (i.e., through-rangers). In the case of genera and sediment packages, some of the relevant "events" are genus first and last occurrences and package initiations and truncations (Fig. 16). The number of genus first occurrences in each time interval is unaffected by the Pull of the Recent. Thus, it is notable that the long-term trajectory in the number of genus first occurrences is very similar to that for package initiations throughout the entire Phanerozoic, including the Cenozoic (Fig. 16.2). The number of genus last occurrences, on the other hand, is expected to be distorted by the Pull of the Recent, but to a lesser degree than through-rangers because some fossil genera do not survive to the Recent and, therefore, are counted as last occurrences. Thus, the fact that genus last occurrences diverge less from sediment packages (Fig. 16.2) than the number of through-rangers (Fig. 15), but more than genus first occurrences (Fig. 16.1), is expected if the Pull of the Recent is significant.

Given the overall similarity between macrostratigraphic parameters and short- and long-term patterns in total genus diversity (Fig. 14), the number of through-ranging genera (Fig. 15), and genus first and last occurrences (Fig. 16), one might expect long-term rates of genus extinction and origination to similarly resemble long-term rates of package truncation and initiation. However, this is not the case (Fig. 17). Rates of genus extinction decline during the Phanerozoic, a robust (Foote, 2003) and long-recognized pattern in the fossil record (e.g., Raup and Sepkoski, 1982; Van Valen, 1984; Flessa and Jablonski, 1985; Gilinsky and Bambach, 1987; Bambach et al., 2004; Stanley, 2007), whereas package truncation rates show a sinusoidal long-term trajectory (Fig. 17.1). Genus origination rates also decline during the Phanerozoic, but there is rather little change in average origination rates after the Silurian. Package initiation rates also decline during the early Paleozoic, but the overall long-term temporal pattern is not otherwise strikingly similar to genus origination rates.

Some of the discrepancy between long-term patterns of genus and package turnover rates could be controlled by the Cenozoic and early Paleozoic divergences discussed above. For example, the Pull of the Recent is expected to artificially suppress apparent extinction rates in the Cenozoic (Foote, 2000). However, accounting for this effect by adjusting taxonomic rates to account for sampling does not substantively change the long-term trend (Foote, 2003). Another factor contributing to divergent long-term structure, but similar short-term variability, may be the paucity of Cambrian-Ordovician through-ranging genera in comparison to sedimentary packages (Fig. 15). This discrepancy could enhance the volatility of taxonomic rates relative to the macrostratigraphic rates. Finally, it is also possible that my current inability to completely separate the marine and terrestrial records at this time has artificially elevated mean rates of sediment package turnover in the Cenozoic. This could, in principle, mask a longer-term decline in rates of package turnover and contribute to a divergence between genera and packages without affecting short-term variation (i.e., first differences). Nevertheless, even if all of these possible effects could be fully accounted for, it is likely that the secular decline in rates of genus extinction and origination will remain one of the few

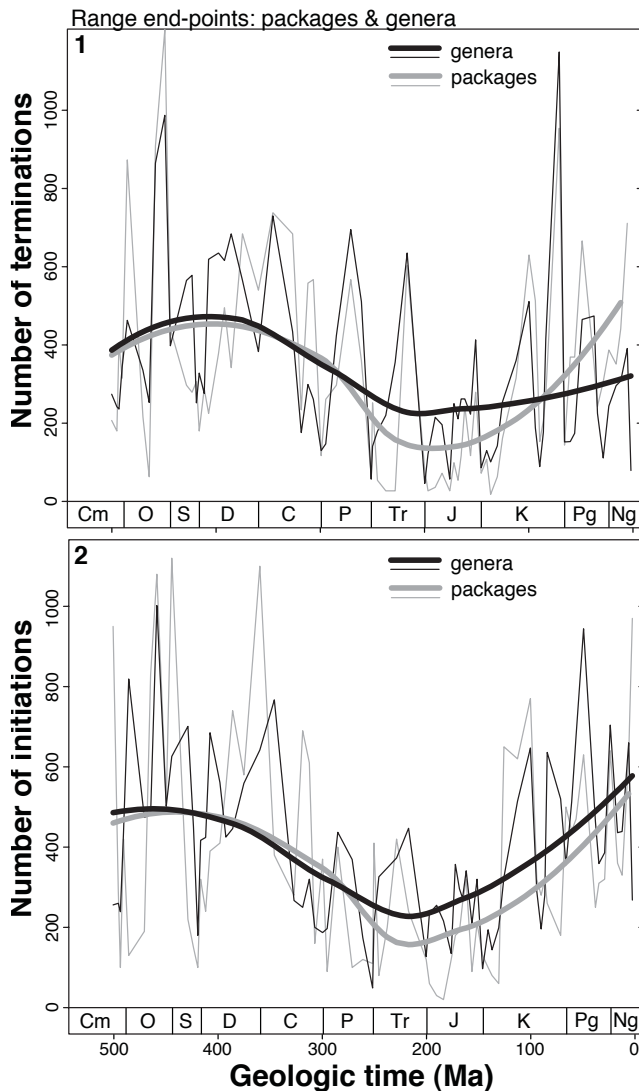


Figure 16—First and last occurrences of genera and sedimentary rock package initiations and truncations. 1, total number of genus last occurrences and 9x total package truncations. 2, total number of genus first occurrences and 9x total package initiations. To emphasize longer-wavelength patterns in each time series, loess regressions with alpha smoothing coefficients of 0.75 are shown by thick lines. Fine lines show raw data. Note broadly similar long-term trajectories. On an interval-to-interval basis (thin lines), genus last occurrences and package terminations are strongly positively correlated (first differences,  $r = 0.76$ ;  $p = 3 \times 10^{-14}$ ); the correlation between first differences in genus first occurrences and package initiations is weaker ( $r = 0.33$ ;  $p = 0.006$ ).

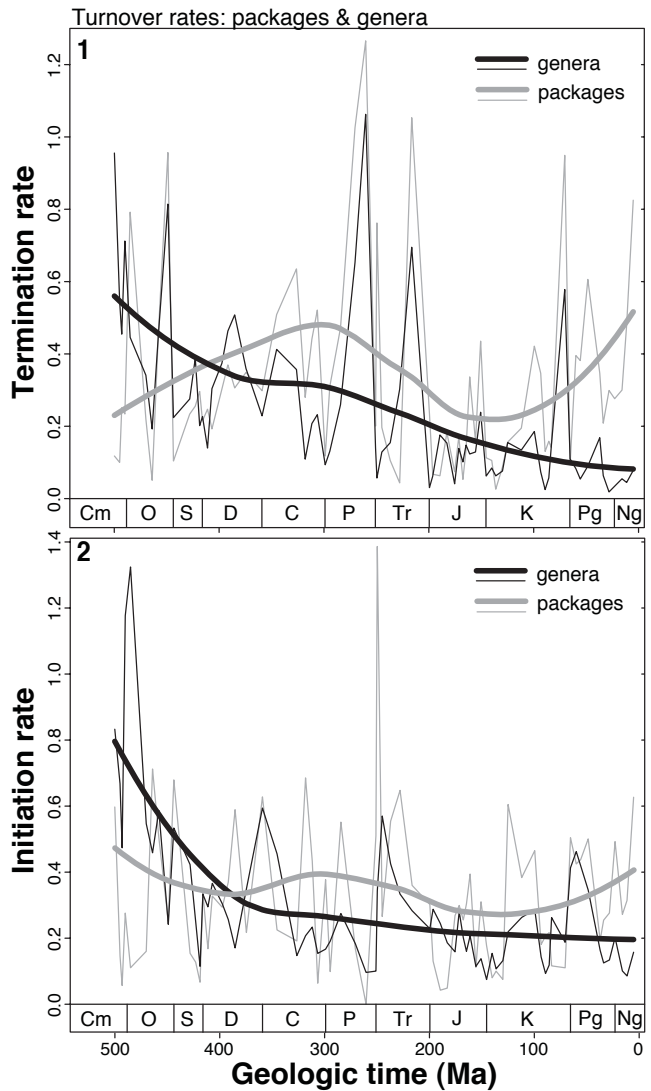


Figure 17—Per-interval rates of turnover for marine animal genera and marine sedimentary packages. 1, Genus extinction rates and sedimentary package truncation rates. 2, Genus origination rates and sedimentary package initiation rates. To emphasize longer-wavelength patterns in each time series, loess regressions with alpha smoothing coefficients of 0.75 are shown by bold lines. Fine lines show raw data. Note that long-term trends in genus and package turnover rates (thick lines) are not well correlated. Short-term patterns (thin lines) in rates of truncation are, however, strongly positively correlated ( $r = 0.73$ ;  $p = 6 \times 10^{-13}$ ); the correlation between genus origination and package initiation is substantially weaker, but significant ( $r = 0.24$ ;  $p = 0.04$ ).

major macroevolutionary features in Sepkoski's database that is not reproduced by macrostratigraphy.

### Summary

Norman D. Newell (1952) hypothesized that mass extinctions were caused by the expansions and withdrawals of epicontinental seas. Because sea level change has nonlinear and threshold environmental effects, particularly in epicontinental seas, only some fluctuations in sea level are expected to drive biologically relevant environmental changes. Macrostratigraphy is well suited to testing Newell's hypothesis because it is sensitive to sea level change yet responds to the expansions and contractions of sedimentary environments. As predicted by Newell's hypothesis, many long-term macroevolutionary patterns in the marine animal fossil record are closely reproduced by macrostratigraphy. Some of these patterns relate to the two Phanerozoic sedimentary megasequences and the "M-curve" in sea level, but variation at the scale of Sloss sequences (~67 Myr) is also similar in both the fossil and sedimentary records. Most of the discrepancies between macrostratigraphic and macroevolutionary data occur in the early Paleozoic and in the Cenozoic. The former may reflect a temporal decoupling between biodiversification and marine shelf environments prior to the establishment of what appears to be an equilibrational relationship throughout most of the Paleozoic and Mesozoic. The later may reflect the Pull of the Recent, which explains several aspects of the rock-fossil agreement that are not otherwise easily explained, or it may reflect a real biological increase in diversity that is exceptional in comparison to the entire post-Ordovician Phanerozoic history of life.

### BACK TO BEDROCK

It may seem incredible that the draining and flooding of continents may predict much of the macroevolutionary history of marine animals, but the environmental causes and consequences of changes in continental flooding have biological impacts that go far beyond simple species area effects (e.g., Sepkoski, 1976; Johnson, 1974; Simberloff, 1974). Sea level both responds to and interacts with the climate system and tectonics in numerous important ways (Fig. 2, dis-

ussion above). Sea level can also serve as a trigger for many types of environmental change. For example, the destabilization of methane clathrates on shelf margins can occur during large sea level falls, which lowers hydrostatic pressure on the shelves (e.g., Rothwell et al., 1998; Maslin et al., 2004), and the formation of stratified or restricted epicontinental seas during changes in sea level are common (Hallam, 1989; Johnson et al., 1985; Allison and Wright, 2005; Algeo et al., 2007, in press). Moreover, the drivers of fluctuations in sea level, such as climate change caused by perturbations to the carbon cycle, are often important macroevolutionary forces in their own right. Thus, it is likely that the correlation between macrostratigraphy and macroevolution reflects both the direct effects of shrinking and expanding epicontinental seas, as predicted by Newell, and covariation that is forced by a third (or more) mechanism. A likely candidate for a two-phase scenario is the end-Permian mass extinction. In this case, the first pulse of extinction could have been driven by sea level fall and the loss of epicontinental sea environments and a second pulse could reflect associated environmental changes, such as perturbations to the carbon cycle, which in turn can affect sea level, carbonate sedimentation patterns, and biological diversity (Payne et al., 2007).

The linkage between sea level, tectonics, and climate is strong enough for the expansions and contractions of epicontinental seas to register important effects in terrestrial settings. For example, the draining of the Cretaceous interior seaway that occurred near the end of the Maastrichtian would have affected the climate throughout much of North America. Similarly, the end-Permian sea level fall would have affected local hydrologic conditions (primarily by decreasing precipitation) within terrestrial depositional basins. The tectonic consequences of suturing Pangaea would have affected sea level and directly affected terrestrial climate and evolution, albeit on longer timescales. Because of the linkage between sea level change and other earth systems, the coincidence of biological turnover on land and in the sea does not, by itself, detract from the importance of continental flooding as a potential cause of mass extinctions and macroevolutionary change.

Some may perceive a single suite of causal mechanisms, all related to the formation and draining of epi-

continental seas, to be a rather uninspiring hypothesis for the cause turnover in the biosphere. However, the possibility that macroevolution has been uniformly and tightly linked to the same set of environmental forcing mechanisms for most of the Phanerozoic is surprising, particularly in light of the numerous and dramatic physical perturbations, such as asteroid impacts, that are known to have occurred. Thus, if the common cause hypothesis could be shown to be a dominant factor in the macroevolutionary history of marine life, then our perception of the biosphere might be transformed from that of a fragile, idiosyncratic vessel that is always teetering on the edge of disaster, to a predictable, durable entity that moves only when a consistent suite of physical environmental changes occur, almost regardless of what other large perturbations may occur.

Although the macrostratigraphic results summarized here suggest that the expansion and contraction of epicontinental seas has been a dominant factor in controlling the macroevolutionary history of marine animals, many other types of environmental perturbations and biological interactions must also be important. For example, Stanley (2007, 2008) recently argued that exponential biological diversification at “characteristic” rates, along with mass extinctions of unspecified causes, were the sole drivers of Phanerozoic biodiversity. The only role that he allowed for physical environmental forcing of any kind involved mass extinction events and a late Paleozoic glaciation, but Stanley’s point is well taken. Predation and many other biotic factors affect macroevolutionary patterns. However, all such hypotheses should be considered within the empirical constraints provided by macrostratigraphy. Or, at the very least, work advocating biotic hypotheses should acknowledge that a large proportion of the variance in biodiversity and rates of turnover on several different timescales is accounted for by the physical environmental record of sedimentation. The same is true for hypotheses that address the roles of physical perturbations, such as bolide impacts and volcanism, that may not be related to expansions and contractions of epicontinental seas. Such events must have been very important at various times in earth history, but their quantitative effects on macroevolution should be framed within the context of Newell’s hypothesis, which successfully predicts not only specific peaks in extinction, but also statisti-

cal patterns of extinction at all times in the Phanerozoic, rates of origination, many short- and long-term patterns of diversity, and shifts in faunal composition.

### The Next Steps

Ground-breaking research continues to define the new field of stratigraphic paleobiology. Some of this research includes 1) modeling the sequence stratigraphic distribution of fossils (Holland, 1999, 2000; Holland and Patzkowsky, 1999) and morphology (Hannisdal, 2006), 2) efforts to integrate multivariate paleoecology, sequence stratigraphy, and sedimentary basin analysis (e.g., Holland et al., 2001; Miller et al., 2001; Holland and Patzkowsky, 2004; Holland, 2005; Scarponi and Kowalewski, 2007; Brett et al., 2007), 3) advances in quantitative biostratigraphy (Sadler, 2004), high-resolution faunal analysis (Holland et al., 2000; Brett et al., 2006; Bonelli et al., 2006), and taphonomic microstratigraphy (e.g., Gaines and Droser, 2003; Hunda et al., 2006; Webster et al., 2008;), and 4) efforts to quantify time averaging and temporal resolution in the fossil record (e.g., Kowalewski et al., 1998; Kidwell et al., 2005; Kosnik et al., 2007). Continuing to advance this work is necessary for accurately calibrating macroevolutionary patterns in the fossil record and for understanding the link between physical environment change and biotic evolution.

The results of this analysis, and others that have focused on short-term patterns rather than long-term trends, provide a good starting point for testing Newell’s hypothesis for mass extinctions and for extending it to include other types of macroevolutionary change. However, the work accomplished thus far serves only as an outline for what should come next. Macrostratigraphy holds considerable promise for paleobiology not because it reproduces many classic patterns in Sepkoski’s database, but because it provides an analytical framework for measuring the rich history of environmental turnover that is encoded in the rock record. Combined with the critical ongoing efforts of the Paleobiology Database and other occurrence-based paleontological initiatives, it will be possible to express evolutionary and biogeographical dynamics in the fossil record using precisely the same quantitative currency as spatio-temporal environmental dynamics in the sedimentary record, and to document the physical intersection of sedimentary environments and the fossil record. With this level of temporal and spatial

integration of physical environmental and biological data, it will be possible to not only fully test Newell's idea and the common cause hypothesis, but also to formulate and test a promising new generation of evolutionary and ecological hypotheses.

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