Stratigraphic distribution of marine fossils in North America

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ABSTRACT

The stratigraphic distribution of fossils reflects a combination of physical and biological factors. Although many studies have addressed the distribution of fossils at a basin scale and within sedimentary sequences spanning 10^4–10^6 yr, little is known about the distribution of fossils within longer duration sedimentary successions covering broad geographic regions. Here we combine a North American macrostratigraphic database with fossil occurrence data from the Paleobiology Database to quantify the stratigraphic distribution of fossils within hiatus-bound marine sedimentary rock packages that have a mean duration of 10^7 yr. We find that fossil collections and marine genera are, when averaged over all Phanerozoic sedimentary rock packages, more abundant than expected in the top 40% of package durations, and less common than expected in the bottom ~25%. Generic first and last appearance datums (FADs and LADs) in North America are not randomly distributed among fossil collections. Instead, LADs are more common than expected in the top ~20% of package durations, whereas FADs are more uniformly distributed. This result is not consistent with an unconformity-related sampling bias, but is indicative of greater congruence in the temporal scales over which genus extinction and regression occur than genus initiation and transgression. These results support the hypothesis that macroevolution, particularly genus extinction, and large-scale patterns of sedimentation share a common set of forcing mechanisms that are related to the formation and destruction of shallow-marine habitats.

INTRODUCTION

The distribution and abundance of fossils within sedimentary successions are controlled by both physical and biological factors. In the marine realm, physical control is related primarily to transgressive-regressive cycles that cause upsection changes in environmental sampling (e.g., Brett, 1998; Scarponi and Kowalewski, 2004; McLaughlin and Brett, 2007), taphonomic regime (e.g., Brett and Baird, 1993), and the degree of temporal and spatial condensation of biological communities (e.g., Kidwell, 1993, 1997; Kowalewski et al., 1998). Biological controls on the distribution of fossils include real evolutionary and ecological change, which may occur independently of, or in coordination with, transgression and regression (e.g., Scarponi and Kowalewski, 2007). Taxonomic first and last appearance datums (FADs and LADs) are similarly related to large-scale stratigraphic architecture, either as a result of artificial truncation of taxon range endpoints at unconformities and environmental discontinuities (Holland, 1995; Holland and Patzkowsky, 1999; Smith et al., 2001), or as a result of coordinated responses in sedimentation and biological evolution (Newell, 1962; Hallam, 1989; Peters, 2005, 2008).

Determining the extent to which physical versus biological factors control the stratigraphic distribution of fossils is important because a growing body of work has empirically linked large-scale patterns in the sedimentary rock record to macroevolutionary patterns in the fossil record, including biodiversity, faunal composition, and rates of origination and extinction (e.g., Raup, 1976; Smith, 2001; Smith et al., 2001; Peters and Foote, 2001; Peters, 2006, 2008; Smith and McGowan, 2007; Wall et al., 2009). Thus, either physically induced preservation biases (bias hypothesis), biological responses to environmental perturbations associated with transgression and regression (common cause hypothesis), or, more likely, some combination of the two must be responsible for a sig-

nificant component of the temporal variability that is observed in the fossil record. Nevertheless, most analyses to date have treated stratigraphic and paleontological data separately, thereby making it impossible to evaluate the large-scale stratigraphic distribution of fossils or to determine the location of taxon range end points within sedimentary successions. This is a substantive limitation because, at least in some cases, the bias and common cause hypotheses make different predictions regarding how fossils and FADs/LADs should be distributed within sedimentary deposits.

Here we seek to improve upon our understanding of the nature of the Phanerozoic fossil record and the causes of macroevolutionary patterns among marine organisms by measuring the large-scale stratigraphic distribution of fossils and taxon FADs and LADs within hiatus-bound marine sedimentary rock packages in North America. To do this, we use the intersection of two data compilations, the Paleobiology Database (PaleoDB; http://paleodb.org) and Macrostrat (http://macrostrat.geology.wisc.edu), which provide regionally comprehensive summaries of the fossil and rock records. Specifically, we address the following fundamental question: are marine fossils and generic FADs and LADs distributed within sedimentary packages, corresponding roughly to second-order Sloss sequences (Sloss, 1963), in a way that is consistent with preservation-induced sampling biases, or in a way that reflects a biological response to changing environmental conditions during large-scale transgressive-regressive cycles?

METHODS

Fossil collections consisting of 1 or more taxonomic occurrences in the PaleoDB were matched to 1 of 16,322 pre-Pleistocene sedimentary lithostratigraphic rock units in Macrostrat using the procedure described by Peters and Heim (2010). Of 4152 hiatus-bound sedimentary rock packages from 814 geographic locations in the United States and Canada, a total of 1415 packages (34%) contain at least 1 lithostratigraphic rock unit that has been matched to 1 or more of 27,239 PaleoDB fossil collections. This study utilizes the 900 marine sediment packages that span >1 time interval (median package duration 5 stages, 30 m.y.; mean duration 6 stages, 40 m.y.), that have >1 lithostratigraphic rock units (median 7 units), and that also have at least 1 matched fossil collection. Lithostratigraphic units that are known to be nonmarine in origin are excluded from the analysis and from the definition of packages. Nearly all of the sedimentary packages analyzed here accumulated in shallow continental shelf settings.

The distribution of fossils within hiatus-bound sedimentary rock packages was quantified using the following procedure. First, the duration of each sediment package was estimated from the ages of its top and bottom boundaries using 86 time intervals (primarily stages) in the Phanerozoic (see the GSA Data Repository[1]). Each package duration was then scaled to unity. Lithostratigraphic units within each package were then distributed within the scaled package based on the estimated ages of their top and bottom boundaries (temporal overlap is possible due to nomenclatural hierarchy and binning resolution; Fig. 1A). Next, the number of fossil collections, occurrences, and the number of genera in each lithostratigraphic unit were tabulated as a function of their scaled durations. In all cases, fossils were assumed to span the entire duration of their matched

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[1]GSA Data Repository item 2011093, supplemental materials and figures, is available online at www.geosociety.org/pubs/ft2011.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.
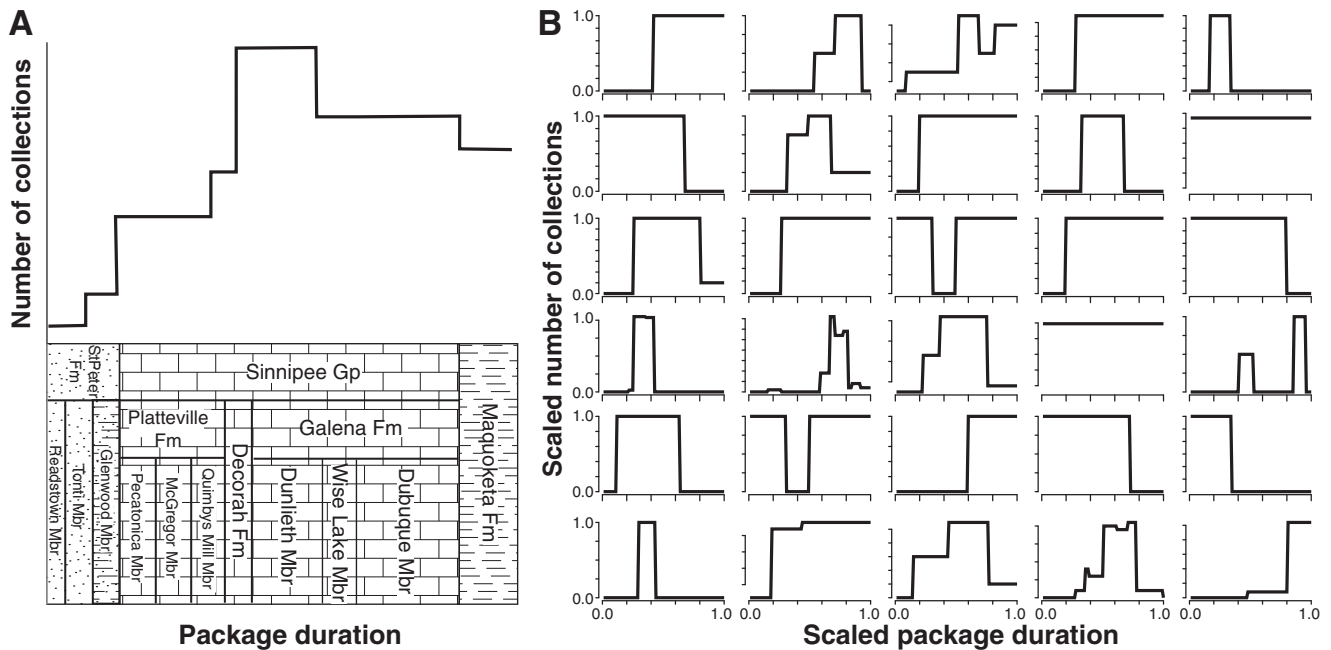

Figure 1. Example distributions of Paleobiology Database (PaleoDB; see text) fossil collections within hiatus-bound sedimentary packages. A: Single sedimentary package showing lithostratigraphic units and number of PaleoDB fossil collections. Fm—formation; Mbr—member. B: 30 examples of scaled collection occupancy curves.

rock unit. For example, the fossils in a PaleoDB collection resolved to a group-level unit were assumed to be representative of the entire duration of that group, whereas collections resolved to a single formation within a group were assumed to range only through the duration of that formation (Fig. 1A). Although this procedure introduces error because the actual distribution of PaleoDB fossil collections can be limited to a single stratigraphic level, this is currently the best possible stratigraphic resolution. Tests for significant patterns in fossil distribution will explicitly account for this uncertainty as well as for the exact nature of the distribution of lithostratigraphic units within rock packages (see the following).

Having established the stratigraphic distribution of fossil collections within each sediment package, the total number of collections, occurrences, and genera in each scaled time increment were tabulated and then scaled to the maximum value. The result for each package is a dimensionless curve ranging from zero to unity. Packages with a uniform distribution of fossils are represented by a horizontal line at a value of unity (Fig. 1B). Packages with only one fossil-bearing lithostratigraphic unit have a single flat-topped peak at unity (width determined by proportional duration of rock unit) surrounded by values of zero. The distribution of fossils within many hiatus-bound rock packages can, therefore, be summarized independent of the effects of package duration and the total number of fossil collections. Here we focus on the mean distribution of fossils by summing the occupancy values for each proportional time increment over all packages and then dividing each time increment by the total number of packages. This procedure is similar to the method used by Foote (2007) and Liow and Stenseth (2007) to tabulate the occupancy of collections within the ranges of taxa.

Determining the stratigraphic distribution of generic FADs and LADs within packages followed a similar procedure, but with one important difference. The age of the FAD and/or LAD for any given genus in North America may be defined by multiple collections from many different rock packages. To account for this, a separate occupancy curve was calculated for each package containing a range-defining collection and then a mean occupancy curve for each of 9066 marine genera was calculated by pooling the results.

To test for statistically significant patterns in the observed distribution of fossils, the stratigraphic position of fossil collections was randomized among lithostratigraphic units within each package and then occupancy curves were calculated for the randomized data. Each randomized data set contains the same packages and the same number of collections as the original data set. Because our objective is to test for a nonrandom distribution of fossils within package durations, not for clustering of collections within lithostratigraphic units, groups of fossil collections assigned to the same unit were randomized with respect to all of the units in that package. This procedure is conservative because it preserves, on average, the observed distribution in the number of collections per unit. Results for the alternative randomization procedure, in which individual collections are randomly assigned to lithostratigraphic units, pertains primarily to the clustering of collections within packages (for results, see the Data Repository) (collections are generally more clustered within units than expected).

The randomization procedure was repeated 1000 times for the entire data set to generate a null distribution for the stratigraphic distribution of fossils; if lithostratigraphic units were uniformly distributed within packages, then the expected pattern of fossil occupancy would be a flat line. Thus, this randomization procedure simultaneously accounts for any patterns in the empirical fossil occupancy curve that could reflect the non-uniform distribution of lithostratigraphic units within packages and the specific nature of the lithostratigraphic and temporal binning scheme that is employed in this study. The randomization procedure for FADs and LADs was similar, but involved shuffling the identity of the collections that define FADs and LADs, not the position of those collections within packages. This randomization procedure is conservative because it preserves the original positional information of fossil collections within packages, making it is possible for fossil collections to be nonrandomly distributed within packages, but for FADs and LADs to be randomly or nonrandomly distributed among those same collections.

RESULTS

Marine fossils in the PaleoDB are not randomly distributed within hiatus-bound sedimentary rock packages in North America. On average,

there are fewer fossils than expected in the bottom 25% of package durations and more than expected in the top 40% (Fig. 2). This is true for collections, occurrences, and the total number of genera (results for occurrences not shown, but not significantly different). The null distribution of fossils within packages (gray area, Fig. 2) is not uniform because lithostratigraphic rock units are not uniformly distributed. This irregularity likely reflects changes in environmental heterogeneity and, therefore, lithological variability during the evolution of large-scale transgressive-regressive cycles, such that peak lithological heterogeneity is typically achieved at ~60% of package duration. Alternatively, the peaked null distribution could reflect edge effects, whereby the probability of lithostratigraphic binning and nomenclatural overlap (Fig. 1A) is higher near the middle part of a package than it is at its terminations. Regardless of the reason for the peaked null distribution, the observed distribution of collections within packages diverges significantly, indicating that fossils are nonrandomly distributed among the available rock units. Results are similar if we exclude the paleontologically heavily sampled Late Cretaceous, which also has many package truncations (Heim and Peters, 2011; see the Data Repository).

Mean fossil occupancy for the entire Phanerozoic is shown in Figure 2, but there is temporal variation (see the Data Repository). Although understanding the cause of temporal heterogeneity in fossil distribution requires more detailed, time-specific analyses, we suspect that the boundary conditions and environmental characteristics that characterize each large-scale sedimentary succession in North America are responsible for differences in fossil occupancy patterns. For example, marine packages that initiate in the Cambrian tend to have more fossil collections in the bottom 50% of their duration than in their upper half, which is consistent with the occurrence of many unfossiliferous rock units in the Late Cambrian and Early Ordovician (Peters, 2007; Pruss et al., 2010; see the Data Repository).

It is possible for taxon range end points to be randomly distributed among fossil collections even though collections are, on average, non-

randomly distributed within hiatus-bound packages; this is, however, not what we observe. FAD and LAD distributions differ significantly from one another and from their respective null distributions (Fig. 3). Specifically, LADs are more prevalent than expected in the top ~20% of packages and less common than expected in the bottom. FADs, by contrast, are generally more uniformly distributed than LADs and are only less common than expected in the top ~20% of package durations. The null distributions for FADs and LADs differ because the packages that contain genus FADs and LADs are only a partially overlapping set and have slightly different distributions of fossils and lithostratigraphic units.
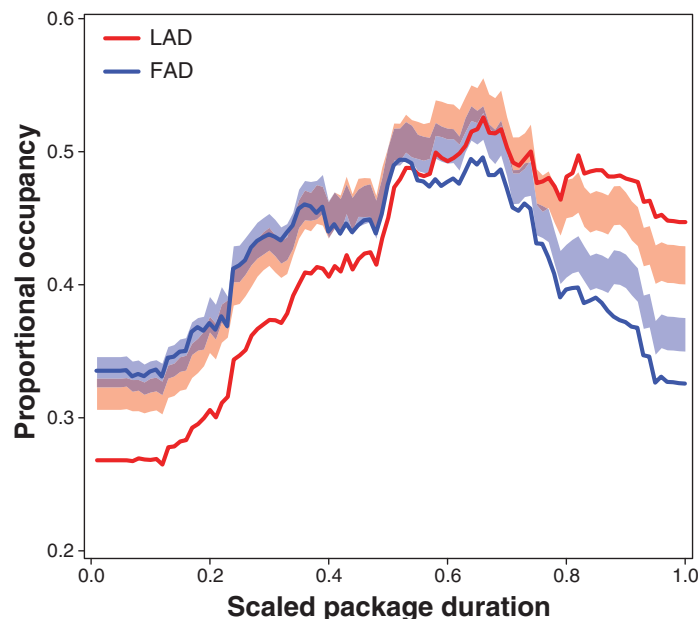
Figure 3. Mean stratigraphic distribution of generic first and last appearance datums (FADs and LADs) in North American marine sediment packages. Shaded regions encompass all outcomes for 1000 randomizations of FADs and LADs among collections. Null distributions differ because packages containing FAD- and LAD-defining collections are a partially overlapping subset of all fossil-bearing packages. See text for discussion.

DISCUSSION

This study demonstrates that fossils and generic FADs and LADs in the PaleoDB are, on average, nonrandomly distributed within hiatus-bound sedimentary rock packages in North America. There are two possible explanations for this result: (1) fossil distribution reflects a combination of taphonomic and sequence stratigraphic factors that govern the preservation and sampling of biological communities and taxon range end points, and (2) environmental changes occurring during the deposition of second-order sedimentary sequences and the formation of intervening hiatuses influence the diversity of biological communities and macroevolution. Although both factors are likely to be relevant, the results of this study suggest an important role for biological control on the distribution of fossils and generic FADs and LADs.

Principles of sequence stratigraphy predict that fossil concentration should be highest during periods of relatively low rates of sediment accumulation. Such conditions occur most commonly during the deposition of transgressive systems tracts (e.g., Kidwell, 1997), which occupy the base of most hiatus-bound marine sediment packages. Thus, the fact that fossil concentration is highest in the upper ~60% of package durations (Fig. 2) may seem contradictory. However, the temporal and spatial scale of this
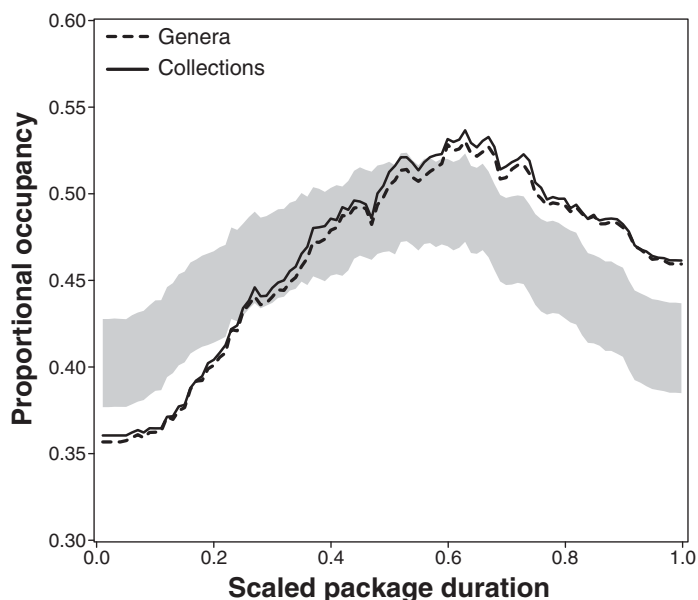

Figure 2. Mean Phanerozoic distribution of fossil collections and diversity of 9066 genera within hiatus-bound sedimentary packages. Shaded region shows 95% confidence limits around expected distribution based on 1000 randomizations. See text for discussion.

analysis is much larger than that of other analyses examining the stratigraphic distribution of fossils. Thus, our results are more likely to reflect wholesale changes in the environmental characteristics of marine shelves during the accumulation of second-order sedimentary successions rather than changing rates of sediment supply that concentrate or dilute skeletal remains within individual beds or bed sets. This possibility is reinforced by the peaked null distribution of fossil occupancy (Fig. 2), which may indicate changes in lithological and environmental heterogeneity during the accumulation of packages.

One of the most compelling aspects of our results is the difference between the stratigraphic distribution of generic FADs and LADs. Although principles of sequence stratigraphy imply that FADs and LADs should cluster around unconformities and the sampling gaps that define sediment package boundaries, the expectation is that FADs and LADs should be similarly influenced. That is, a hiatus in sedimentation should result in the artificial clustering of LADs at the top of the underlying sequence and a comparable artificial clustering of FADs in the bottom of the overlying sequence (Holland, 1995). This is, however, not what we observe. LADs are more asymmetrically distributed within packages than FADs. This difference implies that environmental changes resulting in the truncation of sedimentary successions (i.e., marine regression) often correspond to the truncation of locally occurring genera. The environmental changes associated with marine transgression do not, however, correspond to a similarly well coordinated pulse of taxon FADs (Fig. 3). Thus, the consistent ability of the rock record to better predict extinction than origination (Foote, 2003; Peters, 2005; Heim and Peters, 2011) is likely related to a disconnect between the temporal scales over which biological extinction and origination operate and the environmental changes to which each respond.

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