

Within- and among-genus components of size evolution during mass extinction, recovery, and background intervals: a case study of Late Permian through Late Triassic foraminifera

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Abstract.—One of the best-recognized patterns in the evolution of organismal size is the tendency for mean and maximum size within a clade to decrease following a major extinction event and to increase during the subsequent recovery interval. Because larger organisms are typically thought to be at higher extinction risk than their smaller relatives, it has commonly been assumed that size reduction mostly reflects the selective extinction of larger species. However, to our knowledge the relative importance of within- and among-lineage processes in driving overall trends in body size has never been compared quantitatively. In this study, we use a global, specimen-level database of foraminifera to study size evolution from the Late Permian through Late Triassic. We explicitly decompose size evolution into within- and among-genus components. We find that size reduction following the end-Permian mass extinction was driven more by size reduction within surviving species and genera than by the selective extinction of larger taxa. Similarly, we find that increase in mean size across taxa during Early Triassic biotic recovery was a product primarily of size increase within survivors and the extinction of unusually small taxa, rather than the origination of new, larger taxa. During background intervals we find no strong or consistent tendency for extinction, origination, or within-lineage change to move the overall size distribution toward larger or smaller sizes. Thus, size stasis during background intervals appears to result from small and inconsistent effects of within- and among-lineage processes rather than from large but offsetting effects of within- and among-taxon components. These observations are compatible with existing data for other taxa and extinction events, implying that mass extinctions do not influence size evolution by simply selecting against larger organisms. Instead, they appear to create conditions favorable to smaller organisms.

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Introduction

Beyond altering the taxonomic and ecological composition of the global biota (Sepkoski 1981; Bambach et al. 2002; McGhee et al. 2004), mass extinction events and subsequent recovery intervals have substantially affected the evolution of organism size. Size reduction is commonly associated with biotic catastrophes (Végh-Neubrandt 1982; Stanley and Yang 1994; Arnold et al. 1995; Smith and Jeffery 1998; Fraiser and Bottjer 2004; Lockwood 2005; Payne 2005; Twitchett 2007; Borths 2008; Holland and Copper 2008; Morten and Twitchett 2009; Huang et al. 2010; Payne et al. 2011;

Song et al. 2011), although there are exceptions (e.g., Lockwood 2005). Recovery intervals are typically characterized by return to larger sizes (e.g., Arnold et al. 1995; Fraiser and Bottjer 2004; Payne 2005; Twitchett 2007; Payne et al. 2011; Song et al. 2011). Because body size correlates with many important ecological and physiological characteristics, such as geographic range, life span, reproductive rate, and metabolic rate (Thompson 1942; Peters 1983; Schmidt-Nielsen 1984; Damuth 1991; Brown 1995), the pattern of size change can potentially shed light on the causes of mass extinction events and controls on subsequent

recovery, beyond what can be gleaned from diversity data alone.

The overall pattern of size change across extinction events includes both among- and within-taxon components. Size tends to be inversely related to population size, so larger species are often assumed to be at elevated extinction risk due to small population size (e.g., Stanley 1986; Brown 1995). Therefore size-selective extinction among lineages provides an attractive explanation for size reduction across extinction events. However, there is also evidence for within-genus and within-species trends toward smaller size across some mass extinction horizons (Smith and Jeffery 1998; Payne 2005; Twitchett 2007; Metcalfe et al. 2011). Similarly, subsequent recovery toward larger size likely reflects both the origination of new taxa with larger-than-average sizes, as well as size increase within surviving taxa (e.g., Payne 2005; Lockwood 2005; Song et al. 2011; Payne et al. 2011).

Despite the importance of size evolution for understanding extinction and recovery processes, the relative contributions of within- and among-taxon components of size evolution during extinction and recovery, and the extent to which they differ from background intervals, remain poorly quantified. Some studies have reported only the pre- and post-extinction size distributions for a higher taxon, without distinguishing the contributions of extinction, subsequent origination, and size change within surviving taxa (e.g., Arnold et al. 1995; Fraiser and Bottjer 2004). Other studies have examined only the size selectivity of extinction (e.g., Jablonski and Raup 1995; McRoberts and Newton 1995), and still others have focused on within-lineage size change (e.g., Smith and Jeffery 1998; Twitchett 2007; Morten and Twitchett 2009). Size recovery is comparatively less studied, but similar issues exist; some studies have focused on among-taxon processes (e.g., Lockwood 2005) whereas others have focused on within-lineage trends (e.g., Twitchett 2007). Even those studies that have addressed both within- and among-lineage effects during extinction and recovery (e.g., Payne 2005; Song et al. 2011) have not quantified their relative contributions to overall size change.

Most studies of background size patterns over longer time scales also fail to distinguish within- and among-taxon effects. Some have focused exclusively on among-taxon trends (e.g., Norris 1991; Lockwood 2005; Novack-Gottshall and Lanier 2008) whereas others have focused only on within-taxon trends (e.g., Hallam 1975; Jablonski 1997; Roy et al. 2000). Even those studies that have addressed both among- and within-taxon effects during background intervals (e.g., Budd and Johnson 1991; Alroy 1998; Hunt and Roy 2006; Hunt et al. 2010) have not quantified the relative contributions of these components to overall size trends within the larger clade. Consequently, models of evolutionary size dynamics that include extinction, origination, and within-lineage components (e.g., Alroy 1998; Clauset and Erwin 2008) are incompletely constrained by data. Moreover, the extent to which underlying parameters vary during extinction and recovery intervals remains unknown.

In this study, we explore the macroevolutionary dynamics of size evolution in foraminifera from the Late Permian through the Late Triassic. Foraminifera are an ideal study group because they have an exceptional and long-studied fossil record and are diverse and abundant in Upper Permian through Upper Triassic strata. We explicitly quantify the relative contributions of extinction, origination, and within-taxon trends to changes in the overall size distribution, using both species and genera as operational taxonomic units. By including a major mass extinction event, the associated recovery interval, and subsequent background stages, we are able to identify differences and commonalities of size evolution patterns and processes.

Data and Methods

We compiled a global database of the sizes of Late Permian (Changhsingian) through Late Triassic (Rhaetian) benthic foraminifera from the published literature (Table 1). We standardized genus- and species-level taxonomic identifications following Rettori (1995) and Zaninetti (1976). Species described more recently were standardized by one of us (D. Altiner).

TABLE 1. Summary statistics for data sources. Stages: 0, Changhsingian; 1, Induan; 2, Olenekian; 3, Anisian; 4, Ladinian; 5, Carnian; 6, Norian; 7, Rhaetian.

Reference	No. of specimens	No. of species	No. of genera	Stages
Kobayashi 1997	39	23	20	0
Groves et al. 2007	33	19	12	0, 1
Pronina-Nestell and Nestell 2001	51	45	20	0
Song et al. 2007	44	17	14	0,1
Kobayashi 2005	3	2	2	0
Salaj et al. 1983	776	280	107	1, 3, 4, 5, 6, 7
Rettori 1995	199	33	22	3, 4, 5
Vuks 2007	9	5	3	2
Kobayashi et al. 2005	22	14	11	3
Apthorpe 2003	68	32	24	2,3
Schell and Clark 1960	4	4	3	2
Schroeder 1968	8	8	6	2
Haig et al. 2007	14	7	5	7
Souaya 1976	34	29	18	6,7
Zaninetti 1976	156	112	56	1, 3, 4, 5, 6
Leven and Okay 1996	8	8	6	0
Hauser et al. 2001	29	14	9	4,5,6
Unal et al. 2003	25	17	15	0,1
Pronina 1988	19	18	12	0
Kristan-Tollmann 1986	16	10	7	7
Gazdzicki 1983	50	18	9	6, 7
Song et al. 2009	150	44	29	0,1
Mancinelli et al. 2005	17	12	8	6
Nagy et al. 2010	8	7	6	6
Payne et al. 2011	649	43	28	1, 2, 3, 4, 5, 6

We measured the maximum linear dimension of each specimen from published images using digital calipers. Whenever possible, we measured multiple specimens of the same species to avoid the inclusion of juveniles or specimens that were incomplete and/or poorly oriented. We chose maximum linear dimension as our size metric for analysis because it is correlated with biovolume (Niklas 1994; Novack-Gottshall 2008b), is easily measured from published photographs, and is a practical metric for specimens studied and illustrated from petrographic thin sections. For each stage we followed the accepted practice of using the largest measured specimen of each species for analysis (e.g., Stanley 1973; Jablonski 1997; Lockwood 2005) to minimize the influence of juvenile specimens on estimated size distributions and trends. This approach is further validated by the fact that most size variation in our data set is among species and genera, rather than within them: 78% of the variance in the sizes of all measured specimens is among species and only 22% within species ($F = 11.3$, $df = 580$ and 1850 , $p < 0.00001$); 66% of the variance in size across species is among

genera and only 34% within genera ($F = 3.7$, $df = 198$ and 382 , $p < 0.00001$).

In total, the database we compiled contains 2431 specimens with species-level taxonomic identification and stage-level stratigraphic resolution. Together they include 581 species, 199 genera, 821 unique species-stage combinations, and 409 unique genus-stage combinations compiled from 25 primary sources. Species are distributed unevenly across genera: 48% of genera are monospecific and 90% of genera in the data set contain six or fewer species, while only 4% of genera contain ten or more species. A slight minority of species (46%) occurs in two or more stages and 11% span at least four stages. A large majority of genera (75%) occur in two or more stages and nearly half (47%) span at least four stages in the data set. The full data set of 2431 specimens, as well as summary tables of genus- and species-level sizes and stratigraphic ranges, is available in the online supplementary materials.

Our database permits analyses of within- and among-taxon components of size evolution on multiple taxonomic levels because we measured individuals from the same species

and genera at multiple stratigraphic horizons and within multiple stages, rather than treating size as a taxon-level character. We are thus able to calculate the contributions of extinction, origination, and within-taxon evolution to changes in the overall size distribution from one time interval to the next. Statistical analyses were performed using R (version 2.13.1; R Development Core Team 2011). Relevant computer code is available from the authors upon request.

Results

Foraminiferan Size Trends.—Figure 1 illustrates the size history of foraminifera from the Changhsingian Stage of the Late Permian through the Rhaetian Stage of the Late Triassic using species- and genus-level size metrics. Figure 1A illustrates the size of the largest specimen for each species in each stage. From these data, Figure 1B, 1C, and 1D illustrate the genus-level maximum, mean, and minimum values, respectively. All four treatments show similar long-term patterns, demonstrating that the overall pattern of size change in our data set is not sensitive to the size metric chosen or taxonomic level analyzed. For simplicity, we present all subsequent analyses of within- and among-taxon size changes using the species maximum metric (Fig. 1A) and the genus mean metric (Fig. 1C).

The most prominent change in the overall distribution of foraminiferan sizes illustrated in Figure 1 is a large decrease in maximum and mean size among species and genera across the Permian/Triassic boundary, followed by progressive size increase through the Early Triassic and into the Anisian (early Middle Triassic). Middle and Late Triassic background intervals exhibit a stable size distribution similar to that observed in the Changhsingian, prior to the end-Permian mass extinction event. Although there is little change across foraminifera as a whole, certain subtaxa do exhibit size change; for example, involutinids—aulotortid and triadodiscid foraminifera—exhibit a considerable size increase within the Norian–Rhaetian interval and galeanellids show a size decrease within the Carnian–Norian interval.

The minimum value in Figure 1C, illustrating genus mean sizes, also decreases across the Permian/Triassic boundary. However, Figure 1A (species maxima) shows that smaller species were present in the Changhsingian and consequently that there was likely no decrease in the sizes of the smallest species between the Changhsingian and Induan. The sizes of the smallest species then increased from the Induan to the Anisian before decreasing after the Anisian. There is very little variation in minimum values for the remainder of the Triassic, with the smallest species typically exhibiting maximum dimensions of approximately 100 μm .

Quantifying the Components of Size Change.—Interval-to-interval variation in the overall mean size can result from size bias in extinction and origination or from size trends within boundary-crossing species or genera. We examined the relative contributions of each of these components to the overall change in mean size among genera. For each stage boundary, we separated species and genera into those that went extinct at the end of the preceding stage, those that survived into the succeeding stage, and those that originated in the succeeding stage. For each surviving taxon, we measured its size both before and after the boundary so that we could determine the change in overall genus size across the boundary. We then calculated the effect of the three components (size-biased extinction, within-genus size change, and size-biased origination) on the overall mean size across taxa between adjacent time intervals. These calculations were carried out in the following order, which reflects the likely ordering of events: first, we determined the change in mean size due to the loss of extinction victims (size-biased extinction); second, we determined the change in mean size of survivors across the boundary (within-genus evolution); third, we determined the change in mean size due to the addition of newly originated taxa (size-biased origination).

We illustrate the method by working through the calculation of the three components of size change across the Permian/Triassic boundary (Fig. 2). This example also

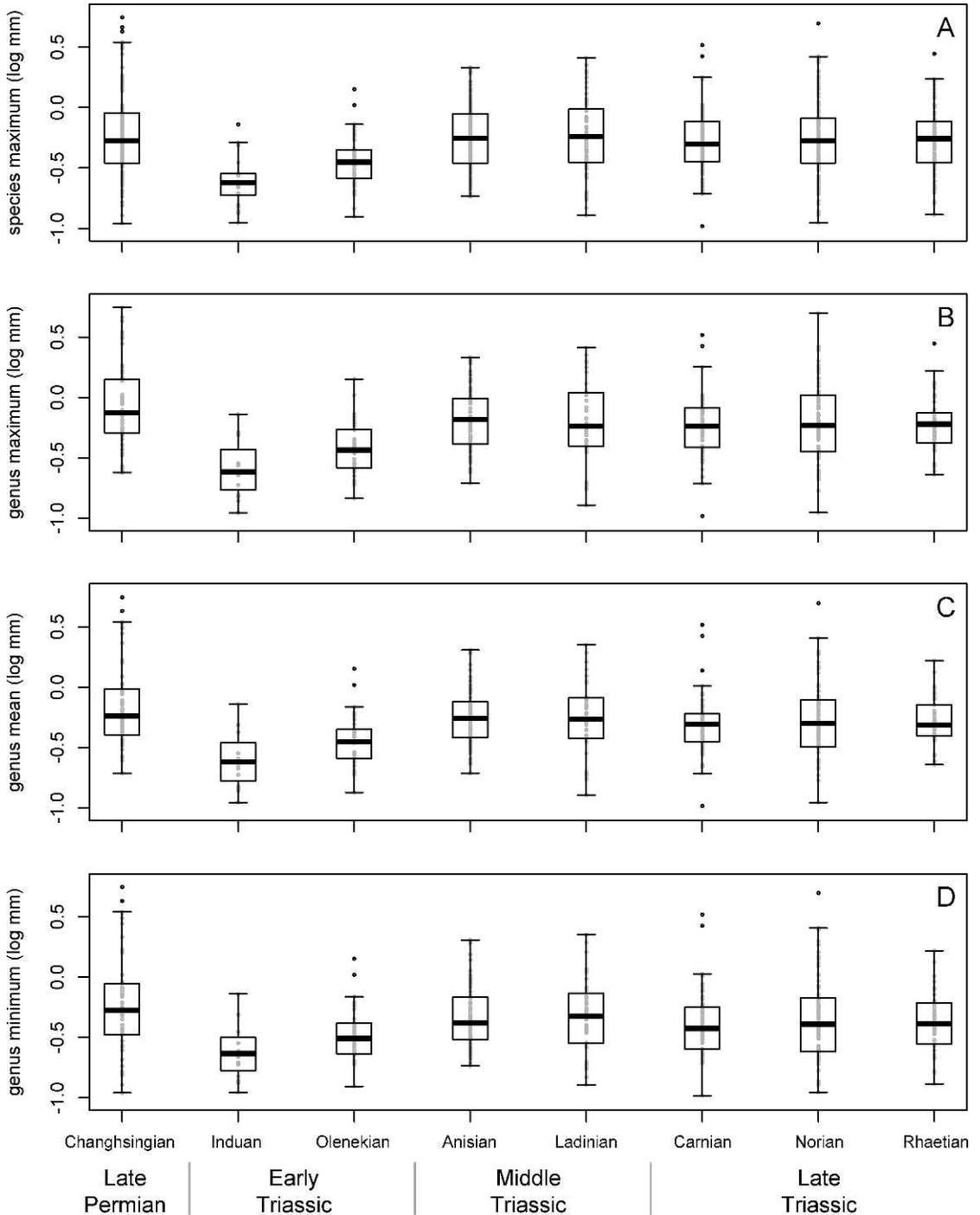


FIGURE 1. Size distribution of foraminifera from the Changhsingian stage of the Late Permian through the Rhaetian Stage of the Late Triassic. A, Largest measured specimen of each species. B, Largest measured specimen of each genus. C, Genus mean (mean of all species maxima within that genus). D, Genus minimum (minimum of all species maxima within that genus). Maximum and mean size decrease dramatically across the Permian/Triassic boundary from the Changhsingian to the Induan, followed by an increase in size during the Early Triassic. The mean size across genera and across species remains stable throughout the remainder of the study interval. All four figures show similar patterns, suggesting that the overall pattern of size evolution is not sensitive to the metric used. Each boxplot displays the 25th percentile, median, and 75th percentile, with whiskers extending to the 5th and 95th percentiles.

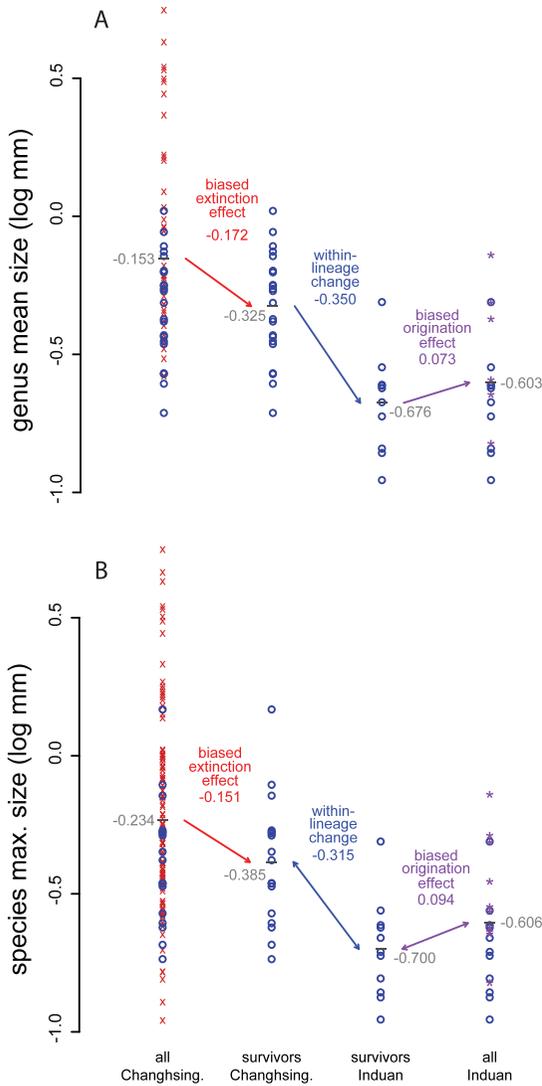


FIGURE 2. Explanatory plot describing the calculation of the three component values (biased extinction, biased origination, and within-lineage evolution). A, Genus-level analysis using the mean size across species for each genus in each stage. B, Species-level analysis using the largest specimen for each species in each stage. Interpretation of this figure works as follows, using Figure 2A as an example: The mean size of Changhsingian genera was -0.153 log mm. For genera that survived into the Induan (blue \circ ; red X denotes extinction victims), their mean size in the Changhsingian was -0.325 log mm—smaller than the overall mean, so the extinction was size biased. The change in mean size due to this size-biased extinction was $-0.325 - (-0.153) = -0.172$ log mm. Of the surviving genera with Induan size data (blue points), their mean size in the Induan was -0.676 log mm. Thus the estimated change in size due to within-genus evolution is $-0.676 - (-0.325) = -0.350$. The mean size of all Induan genera—including the survivors from the Changhsingian (blue) plus new Induan originations (purple $*$)—was -0.603 log mm, so origination brought the mean size of Induan genera up from

illustrates the strong concordance between genus- and species-level results. Figure 2A illustrates the genus-level results. In the Changhsingian, 58 genera were extant; their mean size was -0.153 log mm. Of these 58 genera, 36 went extinct by the end of the stage, and 22 survived into the Induan. The mean size of these 22 survivors in the Changhsingian was -0.325 log mm. Thus the survivors were, on average, smaller than the extinction victims. In other words, extinction was size-biased, with larger genera more likely to go extinct. The change in mean size due to this size-biased extinction was $-0.325 - (-0.153) = -0.172$ log mm. Of the 22 surviving genera, we have size data for ten of them in the Induan; their mean size is -0.676 log mm. Thus the estimated change in size due to within-genus evolution is $-0.676 - (-0.325) = -0.350$. By the end of the Induan, six new genera originated; their mean size is -0.480 . The mean size in the Induan of all 16 genera (ten survivors from the Changhsingian and six originators) for which we have size data is -0.603 . Thus the six new originators changed the mean size of genera extant in the Induan from -0.676 to -0.603 , a difference of $-0.603 - (-0.676) = 0.073$. In summary, the mean size of Changhsingian taxa is -0.153 , and the mean size of Induan taxa is -0.603 , a change of $-0.603 - (-0.153) = -0.450$. This change of -0.450 is partitioned into a size-biased extinction component of -0.172 , a within-genus evolution component of -0.350 , and a size-biased origination component of 0.073 . Note that $-0.172 + (-0.350) + 0.073 = -0.450$.

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 -0.676 to -0.603 , a difference of $-0.603 - (-0.676) = 0.073$. In summary, the mean size of Changhsingian taxa was -0.153 log mm, and the mean size of Induan taxa was -0.603 log mm, a change of $-0.603 - (-0.153) = -0.450$. This change of -0.450 is partitioned into a size-biased extinction component of -0.172 , a within-genus evolution component of -0.350 , and a size-biased origination component of 0.073 . In summary, the decrease in size from the Changhsingian to the Induan is attributable to within-genus evolution and size-biased extinction. Origination of new genera during the Induan slightly mitigated the size decrease imposed by the other two components of size change.

Because some species and genera are unsampled from stages within their stratigraphic ranges, it is necessary to address the potential effect of these “Lazarus” genera on the components of size evolution. The calculation above for the effect of within-genus evolution includes Lazarus taxa. For instance, there are 22 known Changhsingian survivors, of which ten are known from the Induan, and the other 12 are Lazarus taxa known from later stages but not found in the Induan itself. In calculating the effect of within-genus evolution, we subtract the mean of the ten surviving genera known in the Induan from the mean of the 22 survivors in the Changhsingian (not just the Changhsingian representatives of those ten non-Lazarus survivors). This is necessary to make the overall size change equal the sum of the three individual components; the implicit assumption is that the 22 observed Changhsingian genera are representative of all Changhsingian genera, and that the ten observed Induan genera are representative of all Induan genera. However, our procedure could introduce bias if species tend to become Lazarus taxa as a function of their size (e.g., if survivors missing in the Induan tend to be missing because they are smaller). To address this possibility, we repeated our calculations excluding Lazarus taxa. This excludes taxa for which we have the pre-extinction size but not the immediate post-extinction size (i.e., taxa missing in the succeeding stage but found in later stages), and taxa for which we have the post-extinction size but not the immediate pre-extinction size (i.e., taxa missing in the initial stage but found in earlier stages). The results for both the species- and genus-level analyses are only minimally affected by excluding Lazarus taxa (results not presented), so we have chosen to keep our original calculation method, as it preserves the decomposition of the total interval-to-interval change into the three components of size-biased extinction, within-taxon evolution, and size-biased origination.

We emphasize that what we are calculating is not the mean size of victims or originators, nor is it the change in the mean size of victims or originators compared to other genera extant in the interval. Rather, we are estimating the

effects of extinction, origination, and within-genus evolution on the change in mean size among taxa from one interval to the next. In other words, we are estimating the effect of each component on mean size, not its degree of selectivity. It is possible, for instance, for origination to be strongly size-biased, yet for the effect of size-biased origination to be minimal. This could occur if there were a small number of originators at large size but a large number of genera already extant; in that case, the few genera originating at large size would have relatively little effect on the mean size given the large number of smaller genera. This distinction is appropriate, because we are estimating how observed size distributions are affected by size-biased extinction and origination and within-genus evolution, rather than the inherent magnitudes of these factors. The overall importance of extinction, within-genus change, and origination depends both on the per capita magnitude of each effect and the relative numbers of taxa in each category. Our approach thus differs from logistic regression (e.g., Payne and Finnegan 2007; Finnegan et al. 2008), which attempts to estimate the degree of bias rather than its effect on the distribution of the parameter of interest.

Implicit in this analysis is an assumption that species and genera are monophyletic. In principle, poor correspondence between Linnean taxonomic assignments and true phylogenetic relationships could obscure the effects of within- and among-lineage processes or even, under the right circumstances, create patterns that are simply artifacts of taxonomic practice. For example, pseudo-extinction associated with no other change in size within taxa should produce perfectly balancing effects of extinction and origination. Purely random taxonomy should partition most size evolution into the within-taxon component, because extinction and origination will be random with respect to size. Although pseudoextinction and polyphyly undoubtedly exist in our data set to some extent, the decomposition of size trends is not consistent among intervals and does not follow the expectations of either of these scenarios, suggesting that genuine evolutionary patterns dominate the signal in our data set.

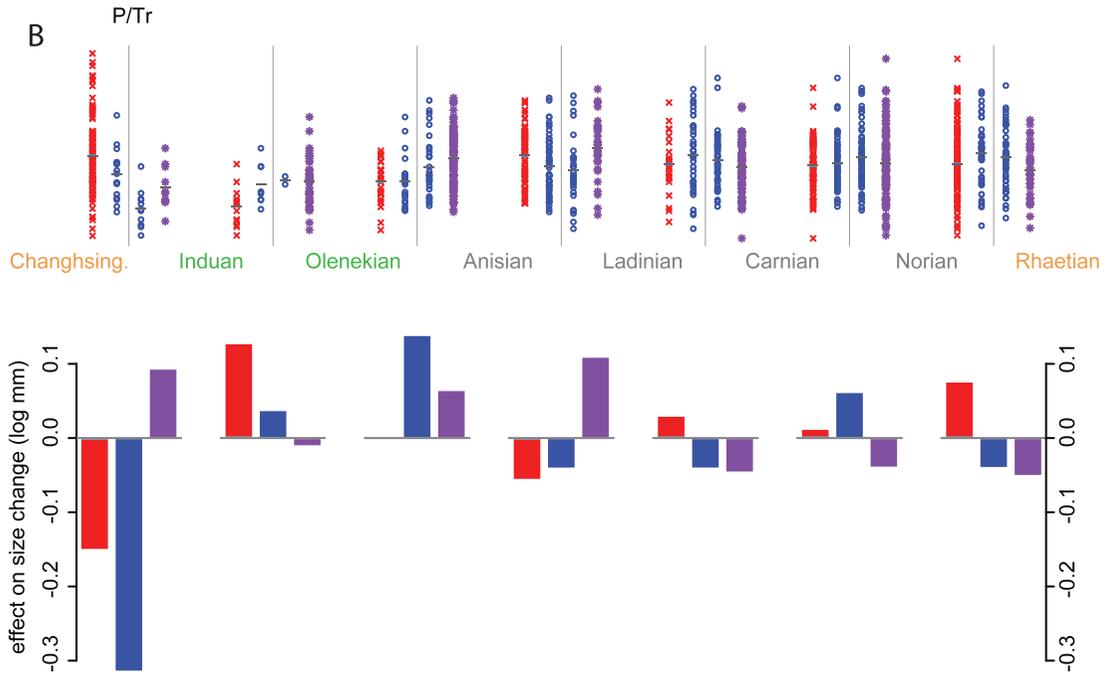
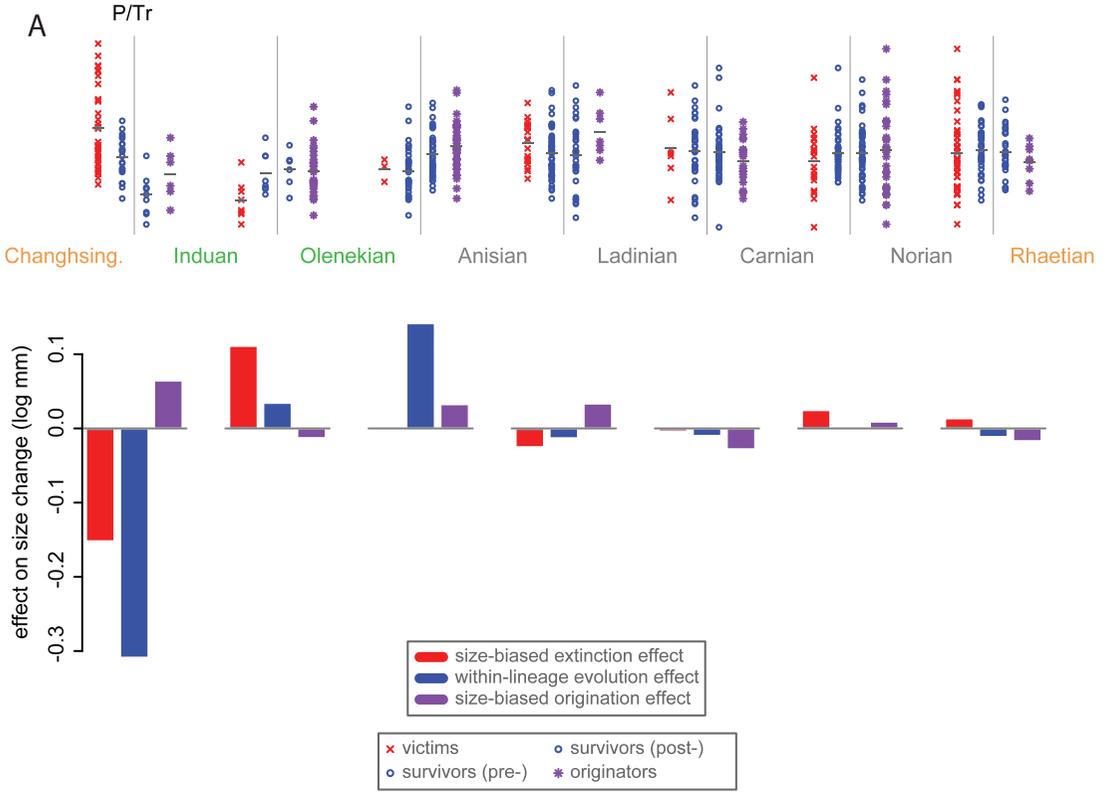
Contributions of Within- and Among-Taxon Components to Size Changes.—Figure 3A and 3B show the extent to which the three components of foraminiferan size change influenced the overall pattern throughout the study interval for genera and species, respectively. Results of the genus- and species-level analyses are largely concordant. Despite the loss of large taxa during the end-Permian mass extinction, the size reduction across the Permian/Triassic boundary cannot be explained by size-biased extinction alone (red bar). In fact, most of the reduction in mean size among species and genera resulted from size reduction within survivors (blue bar). Size increase during the Early Triassic was more complex. Increase in mean size among taxa from the Induan to Olenekian resulted largely from the extinction of smaller taxa, whereas size increase from the Olenekian to the Anisian was driven almost exclusively by within-genus and within-species size increase.

In addition to the dramatic size changes across the Permian/Triassic boundary and during the subsequent recovery, the other clearly apparent result is the overall size stasis during Middle and Late Triassic background intervals. This stasis, which is apparent in all treatments of the data (Fig. 1), occurs because no component contributes much of a pull on the overall size trend, rather than because one component offsets or balances out the others (Fig. 3A,B).

Size change across each stage boundary can be characterized by three component values of size change, associated with extinction bias, within-taxon size change, and origination bias. Figure 4A and 4B show the data for the seven observed stage boundaries displayed in

a three-dimensional space, with each stage represented by a single point, for the genus- and species-level data, respectively. It is apparent that the seven transitions (named according to the stage below the boundary) tend to fall in a small region of the entire size dynamics space, with much of the space being empty (e.g., no stages fall into the region for which biased extinction is $<0.1 \log(\text{mm})$ and within-genus change is $<0.1 \log[\text{mm}]$). Another way to visualize the size dynamics space is given in Figure 4C and 4D, which show the seven observed stage boundaries using a parallel coordinates plot (Inselberg 1985; Wegman 1990), analogous to the “spider diagram” used commonly in geochemistry. In this plot, the three axes, corresponding to the three components, are plotted parallel to each other rather than orthogonally as in Figure 4A. For each stage, the three component values are plotted on implicit vertical axes and then connected with line segments. Thus each point in Figure 4A or 4B is represented as a pair of line segments in Figure 4C or 4D, respectively. Here it is apparent that the background stages (gray) cluster together in that they have values for all components that are close to zero, which accounts for the pattern of stasis observed in these stages. The Changhsingian has substantially more extreme values for both extinction bias and within-taxon change, indicating both selective loss of larger taxa and selective pressure towards small size in surviving lineages. The recovery stages (Induan and Olenekian, plotted in green) have very large positive values for change due to preferential extinction of small taxa (Induan) and within-taxon size increase (Olenekian). The Induan pattern appears to reflect the

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 FIGURE 3. Relative magnitudes of the three components of foraminiferan size change (biased extinction, biased origination, and within-genus evolution) from the Late Permian to the Late Triassic. A, Components of size evolution from genus-level analysis using genus mean values for each stage. B, Components of size evolution from species-level analysis using species maximum values for each stage. Top row of A and B: For each stage, each set of four dotplots show the size distribution of (from left to right) victims in that stage (red), survivors (boundary crossers) in that stage (blue), survivors (boundary crossers) in the succeeding stage (blue), and new originators in the succeeding stage (purple). (Note that this is not the same format as in Fig. 2.) Horizontal line denotes the mean of each distribution. Bottom row of A and B: For each stage boundary, bars denote magnitude of size change accounted for by biased extinction (red), within-lineage evolution (blue), and biased origination (purple), calculated using the steps described in Figure 2.



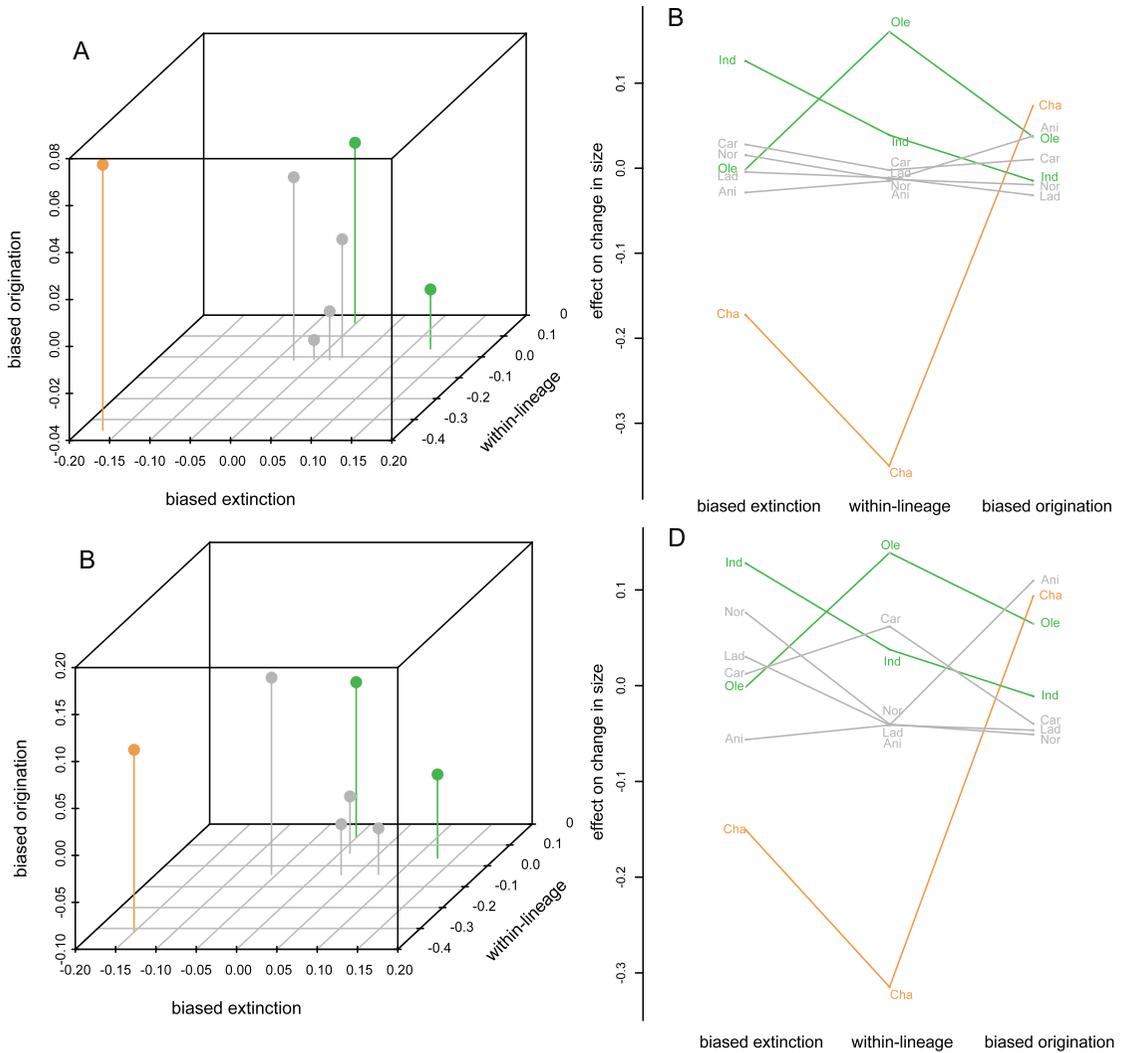


FIGURE 4. Theoretical “size dynamics space” showing where the seven observed stage boundaries fall within the space of all possible combinations of size change component values. Units are $\log(\text{mm})$ of size change accounted for by each component: biased extinction, biased origination, and within-genus evolution. Tan denotes the mass extinction stage (Changhsingian), green denotes recovery stages (Induan and Olenekian), and gray denotes background stages. A, B, Three-dimensional scatterplots for genus- and species-level analyses, respectively. Large regions of the space are empty; actual stages are limited to a small region of the space rather than being spread throughout. Note differences in scale across the three axes. C, D, Parallel coordinates plots for the genus- and species-level analyses, respectively. Line segments connect values for each stage on each of the three component axes. Background stages have all three component values near zero, particularly in the genus-level analysis; the mass extinction stage has large negative values for within-lineage change and size-biased extinction; the recovery stages have large positive values for biased extinction of smaller lineages (Induan) and within-lineage change (Olenekian).

extinction of several very small species that proliferated in the immediate aftermath of the mass extinction event but did not participate in the long-term recovery (e.g., *Rectocornuspira kalthori*). Finally, it is clear from the parallel coordinates plot that changes in size were driven primarily by within-taxon and extinction dynamics and that the origination of new

taxa contributed little to size shifts between stages.

Discussion

Size Dynamics during Extinction, Recovery, and Background Intervals.—The patterns of size evolution in Late Permian through Late Triassic foraminifera suggest qualitative dif-

ferences in evolutionary process among mass extinction, recovery, and background intervals. This observation adds to a series of previous findings pointing toward similar conclusions. Mass extinction events commonly differ in selectivity from nearby background intervals (Jablonski 1986, 2005; Payne and Finnegan 2007; Kiessling and Simpson 2011; Clapham and Payne 2011), and genera that originated during recovery intervals show enhanced survivorship relative to those originating during nearby background times (Miller and Foote 2003).

The importance of within-genus and within-species size change in driving overall size reduction in foraminifera during mass extinction events is in accord with a more limited previous study of foraminifera. In a study of the end-Permian extinction interval in the Meishan section in south China, Song et al. (2011) observed decrease in the mean size across all specimens within two surviving genera and four surviving species—the only taxa that they analyzed in this fashion. Importantly, their data were not included in this study because they were not reported at specimen or species level; thus these results provide independent confirmation of the results we observe at the global scale.

The patterns observed in foraminifera appear to be consistent with observations of other taxa and other extinction events, even though explicit decomposition of size reduction into within- and among-lineage components has not been reported previously. For example, there is little evidence for size-selective extinction at the genus level in Changhsingian gastropods, but surviving genera show pronounced size reduction (Payne 2005). In addition to the evidence from gastropods, Twitchett (2007) observed size reduction across the Permian/Triassic boundary within the phosphatic brachiopod *Lingula* and the bivalves *Claraia* and *Unionites*. Data for the Triassic/Jurassic boundary are more limited. Bivalve extinctions were not size selective (McRoberts and Newton 1995), but megalodont bivalves show a dramatic decrease in maximum size (Végh-Neubrandt 1982). However, comprehensive size data were not presented, so analysis of within- vs. among-

lineage change is not possible. Similarly, Maastrichtian (latest Cretaceous) bivalves and gastropods show little evidence for size-selective extinction (Jablonski and Raup 1995; Lockwood 2005), whereas surviving echinoids exhibit substantial size reduction (Smith and Jeffery 1998). Because previous studies have not explicitly decomposed size change into within- and among-genus components across mass extinction events and most have not even reported the data required to do so, it is at present impossible to determine whether the greater importance of within-genus size reduction for the overall trend in our data set is shared across time and taxa.

The importance of within-species and within-genus size increase during biotic recovery in foraminifera is also consistent with observations of other taxa and other time intervals. Gastropod survivors of the end-Permian mass extinction event show substantial size increase from the Early Triassic to the Anisian (earliest Middle Triassic) (Payne 2005) and *Lingula*, *Claraia*, and *Unionites* all show size increase even within the Griesbachian (earliest Early Triassic) (Twitchett 2007). Detailed examination of foraminifera from southern China shows a significant prevalence of within-species and within-genus size increase during the Early Triassic, as well as a tendency for progressively larger genera to originate through time (Payne et al. 2011; Song et al. 2011). Within-genus size increase also appears to have been important during recovery of cephalopods and bivalves from the Pliensbachian/Toarcian ocean anoxic event (Morten and Twitchett 2009), but the importance of origination for size increase following this event remains unknown.

The small magnitudes and inconsistent directions of the within- and among-genus components of size change during background intervals suggests that overall stasis results from the fact that none of these factors have strong or consistent effects during background time. This finding contrasts with the widespread assumption that extinction risk is size biased under most circumstances (e.g., Brown 1995). It also differs from a recent model for the size evolution of Cenozoic terrestrial mammals, in which within-lineage size change is

assumed to consistently favor increase while extinction risk is biased against larger taxa (Clauset and Erwin 2008). In contrast, we find no consistent tendency for within-lineage increase to be offset by extinction bias against larger taxa, nor any consistent tendency for the effect of origination to be small relative to those of within-genus change and genus extinction. Rather, all components have small effects of inconsistent sign during background intervals, indicating that overall stasis results from non-selective extinction and origination and that there is no typical, strong trend within survivors. Body size evolution appears to be constrained by upper and lower adaptive limits during background intervals, consistent with—though not requiring—the hypothesis of a physiological optimum near the modal size (Brown et al. 1993; Sebens 2002).

Controls on Size Evolution.—The dynamics of size evolution in foraminifera were altered by the environmental and biological circumstances associated with mass extinction and the early phases of subsequent recovery. Similarities between the patterns of size change seen in our end-Permian data and those observed in other taxa and in association with other events indicate common controls linking mass extinction to size evolution.

Broadly, size reduction may result from changes in the abiotic and/or biotic environment. For example, size reduction following the end-Permian mass extinction has been attributed to persistence of hypoxia (Fraiser and Bottjer 2004; Twitchett 2007), reduced food availability (Twitchett 2001; He et al. 2010), and changes in pressures from competition and predation (Payne 2005). Below we discuss the extent to which each of these factors may account for size change in association with individual events, and the likelihood that each could represent a unifying cause of the general phenomenon of size reduction following mass extinction and size increase during recovery.

In the case of the end-Permian mass extinction, there is evidence for environmental constraint on maximum size. The Early Triassic has long been recognized as an interval of environmental instability, characterized by several large perturbations of the global

carbon cycle (Payne et al. 2004), and shallow marine hypoxia, especially during the Induan (Wignall and Hallam 1992, 1993; Wignall and Twitchett 2002; Grice et al. 2005; Cao et al. 2009). The Hettangian (Early Jurassic) is similarly characterized by continued carbon isotope variation (Williford et al. 2007; van de Schootbrugge et al. 2008) and widespread evidence for anoxia (Clémence et al. 2010). However, there is no evidence for persistent marine anoxia in the aftermath of the end-Cretaceous mass extinction. Thus, although it is possible, if not likely, that oxygen stress played a role in size reduction during some of these events, it appears unlikely that hypoxia is the only cause of size reduction.

Food shortage has been proposed as a cause of size reduction across the end-Permian mass extinction (Twitchett 2001). This hypothesis is consistent with carbon isotope evidence for reduced export productivity following the end-Cretaceous mass extinction (Arthur et al. 1987; D'Hondt et al. 1998). However, geochemical models indicate that Hettangian (Lower Jurassic) sediments resulted from elevated productivity, not reduced productivity (Meyer et al. 2008; Ozaki et al. 2011). A recent carbon isotope study along a depth gradient in Lower Triassic limestones reveals a large gradient in $\delta^{13}\text{C}$ from shallow to deep water, consistent with a high productivity scenario (Meyer et al. 2011) and in direct contrast to the reduced $\delta^{13}\text{C}$ gradient observed following the end-Cretaceous mass extinction (Arthur et al. 1987; D'Hondt et al. 1998). Bacterial dominance of primary production during intervals of anoxia (Xie et al. 2007; Luo et al. 2011) may have reduced the nutritional value of available food for animal consumers (Payne and Finnegan 2006; Payne and van de Schootbrugge 2007), but it appears unlikely that a simple reduction in the rate of photosynthesis can account for the prevalence of size reduction in survivors of mass extinction, because prolonged anoxia requires high rates of primary production.

The ubiquity of size reduction within survivors of (1) the end-Permian and end-Triassic mass extinctions, which are widely viewed to have been triggered by flood basalt volcanism (Wignall 2001; Benton and Twitch-

ett 2003; Erwin 2006; Ganino and Arndt 2009; Schoene et al. 2010; Payne and Clapham 2012); (2) the end-Cretaceous mass extinction, which is widely viewed to have been triggered by bolide impact (Schulte et al. 2010); and (3) the end-Ordovician mass extinction, which is widely viewed to have been triggered by glaciation (Sheehan 2001; Finnegan et al. 2011), suggests that loss of biodiversity may directly produce selective pressures favoring smaller size. Several mechanisms may link diversity to selective pressures on body size. Ecological modeling predicts that the recovery of diversity and population sizes will be slower at higher trophic levels (Solé et al. 2002). Thus, to the extent that large size is a refuge from predation pressure (e.g., Paine 1976; Harper et al. 2009), then this selective pressure against smaller individuals may be differentially reduced in the aftermath of major extinction events. Alternatively, given that fecundity increases with size in foraminifera (Hallock 1985), the loss of large-bodied species could reflect an increased risk of mortality due to environmental stress.

Existing data are not sufficient to clearly distinguish the relative importance of environmental and biological factors in shifting selective pressures on organism size that account for size reduction within survivors and subsequent size increase during recovery. However, the prevalence of size reduction within surviving lineages across the Late Ordovician, end-Permian, end-Triassic, Pliensbachian/Toarcian, and end-Cretaceous mass extinctions points toward shared controls. If so, links between biodiversity and selective pressures from competition and predation appear to be the best candidate, as neither reduced primary productivity nor shallow-marine anoxia occurs in the aftermath of all four events.

The relative stasis of foraminiferan size during background intervals is not consistent with any inherent directionality associated with foraminiferan size evolution. Moreover, stasis does not simply result from size-biased extinction counteracting the tendency for size to increase within genera, indicating there is no inherent competitive advantage associated with larger size for foraminifera over geolog-

ical time scales. These findings are consistent with evidence from marine invertebrates that long-term patterns of size increase (i.e., Cope's Rule) or decrease are exceptions rather than the rule (Jablonski 1997; Roy et al. 2000; Lockwood 2005). Moreover, observed instances of Cope's Rule tend to be associated with either evolutionary radiations (Novack-Gottshall 2008a; Novack-Gottshall and Lanier 2008) or environmental controls on size evolution (Hunt and Roy 2006; Hunt et al. 2010), consistent with evidence from planktonic marine protists for environmental control on size evolution (Schmidt et al. 2004; Finkel et al. 2005, 2007). Evidence from benthic foraminifers suggests that maximum size in this group may also often respond to environmental change (Kaiho 1998; Payne et al. 2012).

Summary

Explicitly calculating the contributions of within- and among-taxon components of size evolution in Late Permian through Late Triassic foraminifera reveals several unexpected phenomena that shed light both on the nature of size evolution across these critical intervals of global change and on fundamental differences in evolutionary dynamics between extinction, recovery, and background intervals. Size decrease across major extinction events was driven more by size reduction within surviving species and genera than by selective extinction of larger genera. Similarly, size recovery was produced mostly by the extinction of small taxa that flourished in the immediate aftermath of the event and subsequent size increase within surviving species and genera that contributed to long-term recovery. Size stasis during background intervals results from the small magnitude and variable direction of influences from extinction, origination, and within-taxon size change rather than from offsetting effects between within- and among-taxon processes. These findings are largely consistent with those from previous studies of size evolution across major extinction events. They imply that mass extinctions do not influence size evolution simply by selecting against larger organisms; mass extinctions also create conditions that

explicitly favor smaller sizes in their immediate aftermath. Whether the selective pressures favoring smaller size in the aftermath of extinction result primarily from changes in the physical or biological context remains unclear. The consistent observation of size reduction in numerous taxa across extinction events thought to differ substantially in geological triggering mechanism implies control by the biological environment.

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