



A SHIFT IN THE LONG-TERM MODE OF FORAMINIFERAN SIZE EVOLUTION CAUSED BY THE END-PERMIAN MASS EXTINCTION

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Size is among the most important traits of any organism, yet the factors that control its evolution remain poorly understood. In this study, we investigate controls on the evolution of organismal size using a newly compiled database of nearly 25,000 foraminiferan species and subspecies spanning the past 400 million years. We find a transition in the pattern of foraminiferan size evolution from correlation with atmospheric pO_2 during the Paleozoic (400–250 million years ago) to long-term stasis during the post-Paleozoic (250 million years ago to present). Thus, a dramatic shift in the evolutionary mode coincides with the most severe biotic catastrophe of the Phanerozoic (543 million years ago to present). Paleozoic tracking of pO_2 was confined to Order Fusulinida, whereas Paleozoic lagenides, miliolids, and textulariids were best described by the stasis model. Stasis continued to best describe miliolids and textulariids during post-Paleozoic time, whereas random walk was the best supported mode for the other diverse orders. The shift in evolutionary dynamics thus appears to have resulted primarily from the selective elimination of fusulinids at the end of the Permian Period. These findings illustrate the potential for mass extinction to alter macroevolutionary dynamics for hundreds of millions of years.

KEY WORDS: Extinction, fossils, macroevolution, morphological evolution, paleobiology.

Variation in size across species is a central component of biodiversity and ecosystem function (Hutchinson 1959; Kerr and Dickie 2001). Consequently, identifying controls on evolutionary patterns through the analysis of body size data may also shed light on the factors underlying variation in taxonomic diversity. However, controls on body size evolution, and the extent to which they remain constant across time and taxa, remain poorly understood. Size evolution in terrestrial mammals may be driven largely by ecological interactions (Alroy 1998; Clauset and Erwin 2008; Sookias et al. 2012) with climate change being relatively unimportant (Alroy et al. 2000). In contrast, climate change has significantly impacted the size evolution of diatoms, dinoflagel-

lates, and deep-sea ostracods through the Cenozoic (Schmidt et al. 2004; Finkel et al. 2005, 2007; Hunt and Roy 2006; Hunt et al. 2010). Taken together, these studies suggest a limited applicability for more general theories because controls on size evolution have varied substantially across taxa and habitats.

Ecological change may cause temporal variation in the dominant controls on size evolution. Long-term changes in the taxonomic composition and ecological structure of the global biota indicate increases in the frequency and intensity of competitive and predatory interactions among organisms between the Paleozoic and post-Paleozoic (Vermeij 1977; Kowalewski et al. 1998, 2005; Bambach 1999; Bambach et al. 2002; Baumiller and

Gahn 2004; Wagner et al. 2006; Bush et al. 2007). At the population level, competition and predation are important influences on size (Chilton and Bull 1981; Kingsolver and Pfennig 2004; Olsen et al. 2004); but it is unclear how shifts in these pressures over time have influenced the evolution of organismal size.

Incomplete understanding of controls on size evolution results, in large part, from a paucity of quantitative data. In comparison to taxonomic diversity, the raw pattern of size evolution is poorly documented. Stage-level compilations of family and genus diversity are available for all well-fossilized animal, plant, and protistan taxa (Sepkoski 1993, 2002; Benton 1995; Alroy et al. 2008), facilitating quantitative assessment of physical, chemical, and biological controls on taxonomic diversity (Sepkoski 1978, 1979, 1981, 1984; Raup and Sepkoski 1982; Stanley 2007; Peters 2008; Alroy 2010; Hannisdal and Peters 2011). In contrast, existing genus- and species-level size data are taxonomically, temporally, and geographically incomplete. The most extensive datasets cover North American terrestrial mammals (Alroy 1998) and the dominant diatom and dinoflagellate species through the Cenozoic (Finkel et al. 2005, 2007). For marine invertebrate animals, compilations of size data have focused on individual higher taxa, specific environments, or intervals associated with extinctions and radiations. These studies typically span a few stages or at most a few periods (Jablonski 1997; Roy et al. 2000; Dommergues et al. 2002; Lockwood 2005; Payne 2005; Twitchett 2007; Novack-Gottshall 2008; Novack-Gottshall and Lanier 2008). Differences in age, geographic scope, and data type (occurrence vs taxon-based size metrics) across these datasets further limit the potential for comparative analysis.

In addition to the uncertainties resulting from limited data, analysis of existing datasets is incomplete because nearly all prior analyses have focused either on ecological (Alroy 1998; Clausen and Erwin 2008) or environmental controls (Schmidt et al. 2004; Hunt and Roy 2006; Finkel et al. 2007) rather than explicitly assessing statistical support for both simultaneously. To our knowledge, the two exceptions are recent studies of deep-sea ostracods from the Indian Ocean spanning the past 40 million years (Hunt et al. 2010) and fusulinoidean foraminifera (Order Fusulinida; Superfamily Fusulinoidea) spanning the Late Paleozoic (Payne et al. 2012). In each of these studies, environmental covariates explained patterns of size evolution better than alternative models of random walk, consistent directional change, or stasis. Water temperature was the best predictor of size evolution in the ostracods whereas atmospheric oxygen concentration was the best predictor for the fusulinoidean foraminifera. Variability in the primary environmental control on size may result from differences in the physical or ecological nature of shallow-marine versus deep-marine habitats, intrinsic ecological and physiological differences between foraminifera and ostracods, or differences related to biological and environmental differences between the Paleozoic

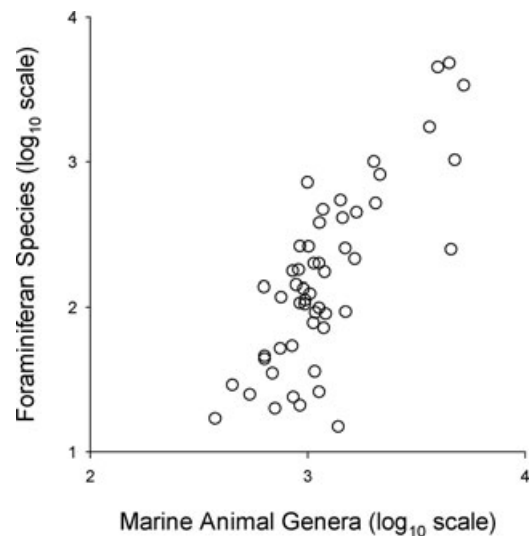


Figure 1. Scatterplot of foraminiferan species diversity from our dataset versus the genus diversity of marine animals from Sepkoski (2002), illustrating the close similarity of foraminiferan diversity to marine animal diversity since the Givetian (Middle Devonian). Species diversity represents only those species whose type material derives from that stage, whereas genus diversity is calculated from observed stratigraphic ranges. Linear regression of log-transformed diversity data indicates a significant correlation (slope = 1.89, SE = 0.21, $P = 5.4 \times 10^{-12}$, adjusted $R^2 = 0.61$).

(543–252 million years ago) and Cenozoic (65–0 million years ago). To identify the most important factors underlying differences in size evolution, we require a larger, more taxonomically and temporally inclusive primary dataset that can be systematically examined across time and taxa.

In this study, we use the fossil record of foraminifera to assess global ecological and environmental controls on the dynamics of size evolution across the great majority of Phanerozoic time. Foraminifera are an ideal study group because they have been diverse and abundant components of marine ecosystems and associated fossil assemblages since the middle of the Devonian Period, soon after the acquisition of calcification in Order Fusulinida. Their fossil record is extensively documented (Ellis and Messina 1940–2006; Loeblich and Tappan 1988) due to their importance in biostratigraphy and petroleum geology. In addition, foraminifera exhibit similar trends to marine animals in taxonomic diversity over Phanerozoic time (Fig. 1; Buzas et al. 2002), suggesting macroevolutionary patterns and processes in this clade may be shared by at least some marine invertebrate animals.

Materials and Methods

FORAMINIFERAN SIZE DATA

We measured the length, width, and height, and determined the geological age of the type material for each foraminiferan species

and subspecies included in the Ellis and Messina catalogue (Ellis and Messina 1940–2006), a nearly comprehensive compilation of species descriptions from the primary taxonomic literature. The catalogue was initially published in 1940, but has been continually updated with additional records. Our compilation includes all records through 2006. Although the scope of this catalogue (>40,000 records) prohibits comprehensive taxonomic standardization, size trends in data designated as from the Superfamily Fusulinoidea in Ellis and Messina corresponded well with trends in a taxonomically and stratigraphically standardized North American dataset (Payne et al. 2012). Analyses of size variation among specimens within species and species maxima within genera for Triassic foraminifera from south China show that the great majority of size variation is among species and genera rather than within them (Rego et al. 2012). Comparison of monograph illustrations and bulk samples for bivalves and brachiopods shows that monographed specimens correlate with but are typically larger than the median or mean size of the bulk population (Krause et al. 2007). Type specimens of bivalves and gastropods also correlate with the sizes of the largest specimens in bulk collections (Kosnik et al. 2006). Thus, it appears likely that broad trends in the size evolution of foraminifera can be captured through the measurement of type specimens. Raw data are archived at Dryad (doi:10.5061/dryad.5pr86).

To calculate test volume, we assumed all specimens were approximately three-dimensional ellipsoids so that: $\text{volume} = 4/3 \cdot \pi \cdot a \cdot b \cdot c$, where a , b , and c are the radii of the test in each dimension. Because all analyses were conducted using the logarithm of volume, errors introduced by this approximation are small relative to the more than eight orders of magnitude variation in size we observe across species. For example, even a very poor match such as approximating the volume of a cube by calculating the volume of a sphere of equivalent radius would result in less than 0.3 log units difference in size.

Our analysis focuses on the interval from the Givetian Stage (Middle Devonian, 392 million years ago) to the Recent because Early Paleozoic diversity is too low to provide statistically significant results. In total, our analysis includes 24,933 species and subspecies.

TIME SCALE

We converted all geological information to the geochronologic ages (referred to hereafter as geological stages) listed in the Ogg et al. (2008) geological time scale. We further merged data for the Kasimovian with the Ghzelian, Artinskian with Kungurian, and Wordian with Capitanian due to stratigraphic uncertainties in the reporting of many foraminifera of Permian age. The size for each species or subspecies was assigned to one of the 52 geological stages based upon the age of the type material.

ENVIRONMENTAL AND GEOLOGICAL COVARIATES

We considered several potential geological covariates of foraminiferan size. Some were chosen due to hypothesized direct or indirect influences on organism size (e.g., atmospheric $p\text{O}_2$, $p\text{CO}_2$, and sea level) and others were chosen to determine whether covariation of numerous aspects of the Earth system and its geochemical cycles may produce widespread correlation among biological and geological processes and their associated proxies (e.g., amount of preserved sedimentary rock and carbon, oxygen, and strontium isotopes).

Estimates of $p\text{O}_2$ and $p\text{CO}_2$ at the midpoint of each stage were obtained from Berner's GEOCARBSULF model (Berner 2006). In a sensitivity analysis, we also examined results based upon alternative reconstructions of atmospheric $p\text{O}_2$ developed by Berner and Canfield (1989), Bergman et al. (2004), and Berner (2009) and alternative reconstructions atmospheric $p\text{CO}_2$ developed by Bergman et al. (2004) and Rothman (2001). Briefly, GEOCARBSULF uses measurements of carbon and sulfur isotopes from sedimentary rocks to track the dynamics of the ancient carbon and sulfur cycles over the past 600 million years. In the model, $p\text{O}_2$ and $p\text{CO}_2$ are calculated at 10 million year time steps and so have similar temporal resolution to the stage-level resolution of the foraminiferan size data. The alternative reconstructions of Berner and Canfield (1989) and Bergman et al. (2004) are based on the same basic understanding of the geological carbon and sulfur cycles, but differ in their details. The uncertainty of the model reconstructions varies through geological time, generally improving toward the present day. Sensitivity tests within models generally suggest errors are in the range of 20% of the estimated values. Rather than explore uncertainty within a given model structure, we have addressed the issue of uncertainty by comparing the best estimates across models, as this approach incorporates uncertainty not only in the details of a given model but the assumptions that have been used to build the models as well.

Sea level data were obtained from the Exxon sea level curve (http://hydro.geosc.psu.edu/Sed_html/exxon.sea; accessed July 1, 2011). Mean values for each stage were used in the regression analysis. Radiometric ages from the Ogg et al. (2008) geological time scale were used to obtain mean values and variance in sea level from the Exxon curve for each geological stage. In a sensitivity analysis, we also examined results based upon an alternative reconstruction of eustatic sea level developed by Haq and Al-Qahtani (2005) and illustrated by Miller et al. (2005).

Isotope data for $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $^{87}\text{Sr}/^{86}\text{Sr}$ were obtained from the compilation of Veizer et al. (1999), including later updates (http://mysite.science.uottawa.ca/jveizer/isotope_data/index.html; accessed July 1, 2011). Because the data density is uneven within and among stages, we first calculated a mean value for each 100 ky interval and then calculated a mean value for each stage using the 100 ky means. No data were available in

the Veizer dataset for the Santonian and Cenomanian stages. For these stages, $\delta^{13}\text{C}$ data were taken from Jarvis et al. (2006) and $\delta^{18}\text{O}$ values represent median values between the preceding and succeeding stages.

We examined the completeness of the North American marine sedimentary rock record as a proxy for material available to sample, using data from Heim and Peters (2011) regarding the number of localities containing marine sedimentary rock of a given age. Although it would clearly be preferable to include a global metric of rock area or volume, such data are not currently available with stage-level stratigraphic resolution. However, the North American rock record shows strong correlation to global marine genus diversity (Peters 2005; Heim and Peters 2011) and so is not an unreasonable choice. We applied their Lopingian values to our Changhsingian and Wuchiapingian, their Guadalupian values to our Capitanian and Roadian/Wordian, their Kinderhookian to our Tournaisian, their Osagean plus Meramecan to our Viséan, their Chesterian to our Serpukhovian, their Morrowan to our Bashkirian, their Atokan and Desmoinesian to our Moscovian, their Missourian and Virgilian to our Kasimovian/Ghzelian, and their Wolfcampian to our Artinskian/Kungurian. We applied their Pliocene values to our Pleistocene and Recent as well as to our Pliocene because they reported no values for the Pleistocene or Recent.

Stage-level summary statistics on foraminiferan size and environmental covariates (i.e., all of the inputs to the statistical analyses described below) and the raw foraminiferan size dataset are archived at Dryad (doi:10.5061/dryad.5pr86).

COMPARING EVOLUTIONARY MODELS

We compared statistical support across four general models of change in the mean size across species: random walk, directional trend, stasis, and environmental control. We followed Hunt's methodology (Hunt 2006; Hunt et al. 2010) for fitting ancestor-descendant size changes to compare evolutionary models using the "paleoTS" package (version 0.4-1; Hunt 2011) for R (version 2.13.1; R Development Core Team 2011).

Each statistical model implies a different underlying process of size evolution. Random walk is a null expectation in the absence of selective pressure (McShea 1994). Consistent directional patterns, such as Cope's Rule (size increases within lineages), may result from intrinsic competitive advantages of larger size (Kingsolver and Pfennig 2004). Stasis is expected when size is optimized to invariant physiological, ecological, and/or environmental factors (Eldredge et al. 2005). Size may covary with environmental parameters when these factors significantly influence fitness (Hunt and Roy 2006; Hunt et al. 2010; Payne et al. 2012).

We examined atmospheric oxygen concentration, atmospheric carbon dioxide concentration, and sea level as potential

environmental controls on size (Fig. 2). Atmospheric $p\text{O}_2$ has been widely hypothesized as a control on size evolution because molecular oxygen is required by all aerobic organisms and oxygen transport can therefore limit organism size and geometry (reviewed in Payne et al. 2011). Although evolutionary responses to changing oxygen availability are undoubtedly complex (e.g., Mossabua 2003; Williams et al. 2011), oxygen availability has been shown to influence the sizes of aerobic organisms in laboratory studies (Klok and Harrison 2009; Klok et al. 2009; Owerkowicz et al. 2009; Harrison 2010) and to correlate with organism size in both space and time (Graham et al. 1995; Chappelle and Peck 1999), even within foraminifera (Kaiho 1994, 1998; Payne et al. 2012). Low $p\text{CO}_2$ has been proposed to favor large size in foraminifera because many larger living species harbor symbiotic algae and symbiotic associations may be particularly advantageous to algae when CO_2 is scarce (Lee and Kugrens 2000). Moreover, carbon dioxide is an important greenhouse gas and one of the strongest controls on Earth's climate over geological time. Many groups of organisms show correlation between size and ambient temperature. Typically, this relationship is expressed as an inverse relationship between size and temperature, commonly known as Bergmann's Rule (Ashton et al. 2000). Although Bergmann's Rule was initially formulated based upon mammals, similar patterns characterize at least some marine animals (Chappelle and Peck 1999) and climate change has been proposed to explain temporal change in organism size as well (Hunt and Roy 2006; Hunt et al. 2010). Larger foraminifera also tend to inhabit tropical, shallow-marine environments and harbor photosymbionts (Hallock 1999). Consequently, temporal variation in shallow-marine habitat area may be an important control on the distribution of size across species. We use global sea level as a proxy for shallow-marine shelf area because higher sea level tends to produce broad areas of flooded continental shelf. Habitat area has been shown to influence maximum size in terrestrial vertebrates (Burness et al. 2001; Smith et al. 2010). In a supplementary analysis, we also examined models of size evolution predicted by rock volume, geochemical records (carbon, oxygen, and strontium isotopes), and alternative reconstructions of atmospheric $p\text{O}_2$, atmospheric $p\text{CO}_2$, and sea level (see above for the sources of these data). We examined the geological records of carbon, oxygen, and strontium isotopes because they are proxies for the behavior of long-term biogeochemical cycles that may have indirectly impacted the evolution of foraminiferan size or been governed by common controls. Carbon isotopes record changes in the geological cycling of carbon between reduced and oxidized forms (i.e., organic matter vs calcium carbonate), oxygen isotopes record changes in global seawater temperature and glacial ice volume, and strontium isotopes record variation in tectonic activity, especially the chemical weathering of continental versus oceanic crust, which varies as supercontinents

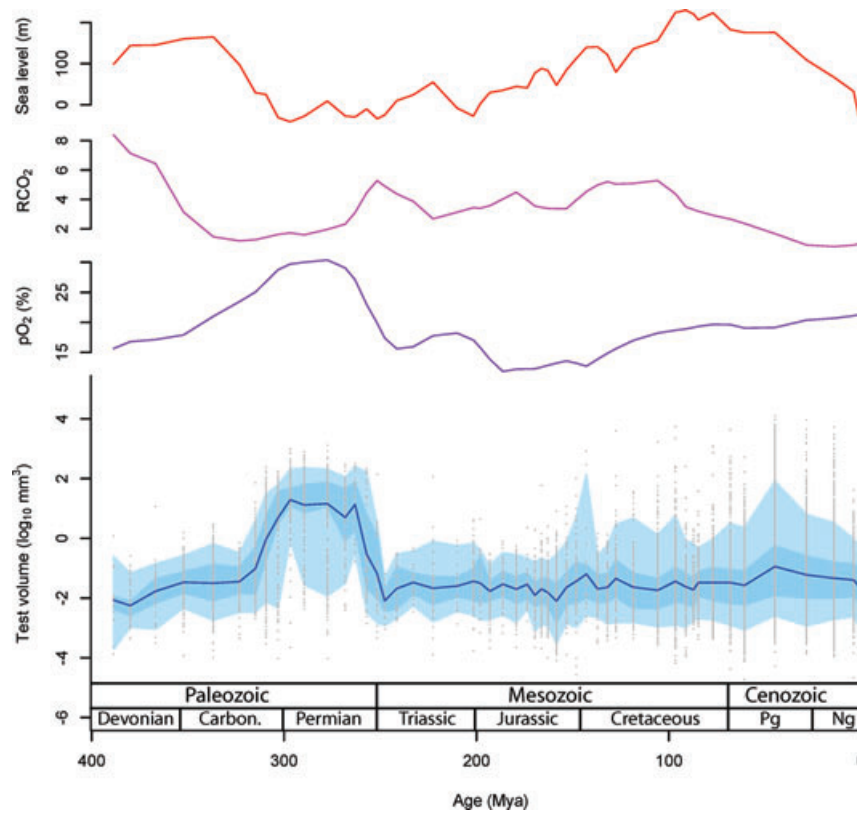


Figure 2. Histories of foraminiferan size and environmental predictors, illustrating close correspondence between Paleozoic maxima in foraminiferan size and atmospheric pO_2 . pCO_2 is presented as the ratio of past CO_2 to an approximate current value (360 ppm). Sea level is presented in meters relative to present day. In the graph of foraminiferan sizes, gray dots illustrate the sizes of individual species, and the blue line illustrates the mean size across species. Dark blue shading covers the 25th through 75th percentiles. Light blue shading covers the 5th through 95th percentiles. Stage-level summary data and raw size data are provided as online appendices.

form and then break up. We examined rock volume as a proxy for the amount of material available to sample.

L₁-REGRESSION

L_1 -regression analysis was performed using the R package “glm-path” (version 0.95; Park and Hastie 2011). Briefly, the L_1 -regression package performs a multiple linear regression in which the L_1 -norm (i.e., the sum of the absolute values) of the coefficients for the predictor variables is penalized (Park and Hastie 2007). Because predictors are measured on different scales, each was rescaled to mean zero and unit variance prior to analysis. The model was then evaluated by incrementally increasing the L_1 -norm until all predictors were incorporated into the model. To choose the preferred model from this class of models, we minimized the Akaike’s information criterion (AIC), the Bayesian information criterion, and the cross-validated error. If multiple criteria had different minima, we chose the simplest model.

Results

Figure 2 illustrates the Phanerozoic histories of foraminiferan size and three potential environmental forcing variables: atmospheric

pO_2 , atmospheric pCO_2 , and sea level. Mean size increased from the Late Devonian to an Early Permian maximum, subsequently declined from the Middle Permian through the Early Triassic, and remained relatively stable thereafter. Lower quantiles of the data are relatively more stable than the mean, whereas upper quantiles exhibit greater variability. The 95th percentile size exhibits post-Paleozoic maxima in the Cretaceous and Paleogene and the overall maximum trends broadly upward from the Triassic through Paleogene.

Environmental forcing of size evolution by variation in atmospheric pO_2 is the best supported model (Table 1), receiving 98.6% of the AIC weight support across the six models considered (random walk, directional trend, stasis, oxygen forcing, carbon dioxide forcing, sea level forcing). Support for oxygen forcing comes primarily from the correlated increases in foraminiferan size and atmospheric pO_2 from the Devonian through Early Permian and correlated decreases from the Middle Permian through Early Triassic (Fig. 2). Three of the four reconstructions of pO_2 we examined overwhelmingly outperform all other environmental drivers (including alternative reconstructions of pCO_2 and sea level) as well as random walk, directional trend, and stasis (Table S1). Importantly, these analyses were conducted on first

Table 1. Support (AICc weights) for models of size evolution for foraminifera as a whole and within major subclades. Weights indicate relative support among models examined and are therefore constrained to sum to one. Models receiving more than 85% of the total weight are indicated in bold. Measures of sample size are presented in italics. Scythian (Early Triassic) species (17 total) are included in both Paleozoic and post-Paleozoic tabulations because the analysis is based upon changes in size between intervals. Thus, Scythian data are required for calculating the last Paleozoic change in size and the first post-Paleozoic change in size.

Model	Phanerozoic	Paleozoic only						
	All species	All species	Fusulinida	Globigerinida	Lagenida	Miliolida	Rotaliida	Textulariida
<i>Stages</i>	52	17	16		9	10		13
<i>Species</i>	24,933	3013	2633		58	55		246
pO_2	0.986	0.988	0.973		0.008	0.008		0.101
Sea level	0.004	0.006	0.011		0.032	0.009		0.084
pCO_2	0.008	0.005	0.012		0.010	0.009		0.121
Random walk	0.001	0.001	0.003		0.030	0.051		0.181
Trend	0.001	0.000	0.001		0.005	0.010		0.059
Stasis	0.000	0.000	0.000		0.916	0.913		0.454
		Post-Paleozoic only						
<i>Stages</i>		36		22	35	33	27	36
<i>Species</i>		21,937		1693	4911	2408	8540	3874
pO_2		0.010		0.132	0.159	0.001	0.013	0.000
Sea level		0.011		0.113	0.189	0.000	0.029	0.000
pCO_2		0.005		0.165	0.157	0.000	0.018	0.000
Random walk		0.077		0.422	0.023	0.000	0.710	0.000
Trend		0.025		0.141	0.008	0.000	0.221	0.000
Stasis		0.871		0.027	0.465	0.998	0.009	1.000

differences, which remove the effects of long-term trends that might produce spurious correlation between predictors and body size. A multiple linear regression (L_1 regression) of size on environmental predictors produces similar results, which are described below. Berner's (2006, 2009; Berner and Canfield 1989) oxygen reconstructions are by far the three best environmental predictors of mean size across foraminifera among all covariates examined (Table S2). Moreover, the most recent reconstruction (Berner 2009), which incorporates the greatest range of geological and geochemical data and our best understanding of the relevant biogeochemical processes is also the reconstruction that best predicts variation in foraminifera size (Tables S1 and S2). These findings indicate that the correlation between size and pO_2 is robust within the range of uncertainty inherent in such reconstructions.

Despite the fact that forcing by atmospheric pO_2 or its close correlates is far better than the alternatives we explored, closer examination suggests this association is driven largely by Paleozoic data. A plot of mean size versus pO_2 (Fig. 3) shows that the slope of correlation is substantially greater in the Paleozoic data (slope = 0.22, 95% CI = [0.18, 0.27], adjusted R^2 = 0.87, p = 8.7×10^{-8}) than the post-Paleozoic data (slope = 0.02, 95% CI = [-0.003, 0.05], adjusted R^2 = 0.06, p = 0.09). Separate linear models of size as a function of pO_2 for the Paleo-

zoic and post-Paleozoic are statistically superior to a single linear model (log-likelihood -6.71 for the two-interval model vs -36.0 for the single model; AICc > 99% vs \ll 1%). This finding shows there was a change in the controls on size evolution between the Paleozoic and post-Paleozoic rather than a simple reduction in the magnitude of variation in pO_2 .

To further assess whether a change in evolutionary dynamics may have occurred within the study interval, we explored statistical support for scenarios in which evolutionary dynamics changed at some point during the study interval. Allowing for a shift in evolutionary size dynamics greatly improves the overall model fit, even after penalizing the additional parameters (AICc 25.78 for the best two-phase model vs 45.74 for the best one-phase model; model support > 99% vs \ll 1%). Figure 4 illustrates statistical support for two-phase models as a function of the assumed time of the shift in evolutionary mode. The optimal position for the shift in evolutionary dynamics is at the beginning of the Triassic Period (~248 million years ago; Fig. 4). The fit of two-phase models declines substantially as the transition moves away from the Permian-Triassic boundary, strongly constraining the timing of the transition. The Scythian (Early Triassic) receives 43% of the AICc support across all possible break points and support decreases away from this stage such that 97% of all support for

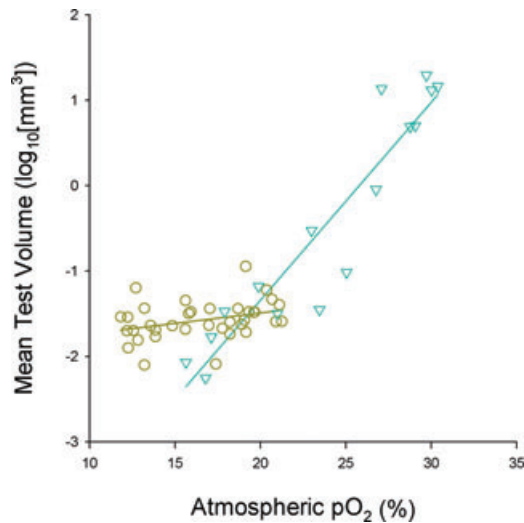


Figure 3. Scatterplot of foraminiferan mean size versus atmospheric pO_2 , illustrating the strong positive correlation during the Paleozoic and weak positive correlation during the post-Paleozoic. Triangles—Paleozoic stages; circles—post-Paleozoic stages; lines represent best single-variable linear regressions to the data. Summary statistics for the regression analysis are presented in the text.

the position of the breakpoint is within two stages of the Scythian (Table S3). In the optimal two-phase model, size evolution is forced by atmospheric pO_2 during the Paleozoic (98.8% of support), but post-Paleozoic size evolution is characterized by stasis (87.1% of support). The only stages to receive more than 1% support as the transition point are those closely preceding and following the Scythian, and in all cases the favored two-phase model consists of forcing by atmospheric pO_2 during the earlier phase and stasis during the later phase. These findings do not result from our decision to restrict the analysis to environmental covariates with clear potential links to body size evolution. No geochemical predictor or alternative reconstruction of sea level or atmospheric pCO_2 approaches pO_2 in explaining foraminiferan size evolution during the Paleozoic and no environmental covariate approaches stasis as a model for post-Paleozoic size evolution (Table S2). Three of the four best environmental predictors of foraminiferan size come from reconstructions of pO_2 (Tables S1 and S2). The most recent pO_2 reconstructions of Berner (2006, 2009) explain nearly 90% of the variation in mean size across foraminifera during the Paleozoic; in contrast, no environmental predictor explains more than 23% of size variation in post-Paleozoic foraminifera (Table S2).

Three classes of explanation, not mutually exclusive, may account for the end-Permian transition in evolutionary size dynamics: (1) a change in the nature of fossil preservation or sampling; (2) cell biological differences between Paleozoic and post-Paleozoic foraminifera; or (3) a change in the selective pressures on size.

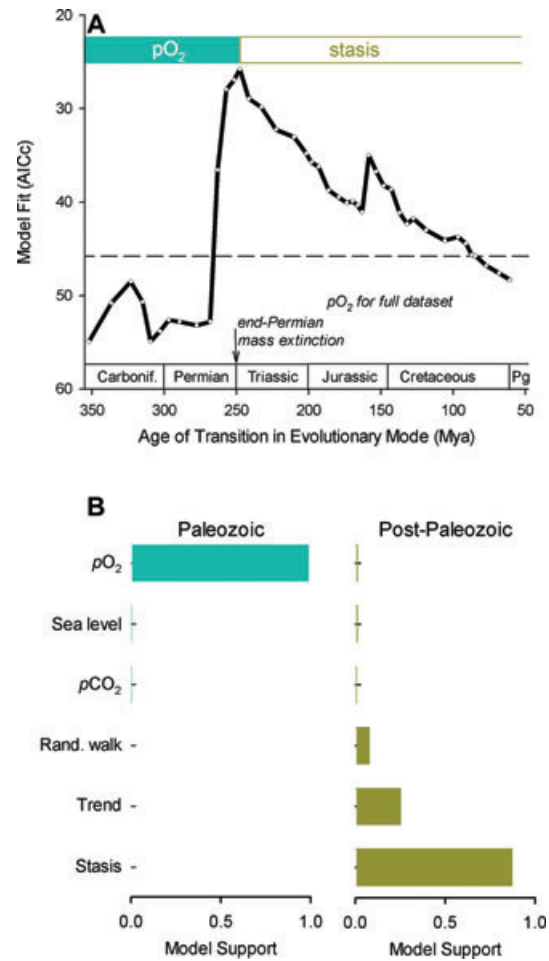


Figure 4. Model support versus timing of the shift in evolutionary dynamics, illustrating that the best supported two-phase model is a shift from pO_2 control to stasis at the beginning of the Triassic. Each point along the horizontal axis indicates a placement of the transition in evolutionary dynamics, with one model fit to the interval before that point and a different model fit to the interval following that point. Note: y-axis decreases toward the top of the figure. The highest point in the graph (i.e., the lowest AICc value) indicates the optimal placement of the transition in evolutionary dynamics. The best two-phase model is overwhelmingly supported (>99%) relative to a single model for the entire Phanerozoic (AICc 25.78 vs 45.74). (A) Proportional model support calculated from AIC adjusted for small sample sizes (AICc) is plotted for all possible break points in a two-phase model. In the first phase, mean test volume is regressed against pO_2 , whereas in the second phase mean test size is a constant. The optimum breakpoint is the Early Triassic (~248 million years ago). (B) Relative support for all Paleozoic and post-Paleozoic models, showing that pO_2 control is overwhelmingly supported as the best Paleozoic model and stasis as the best post-Paleozoic model.

The Paleozoic and post-Paleozoic fossil records differ substantially in environmental coverage, which could potentially explain the shift in evolutionary dynamics. The Paleozoic record of foraminifera is dominated by shallow-marine deposits from water

depths of a few hundred meters or less. At these shallow depths, wind mixing can maintain oxygen concentrations in seawater near equilibrium with the atmosphere. In contrast, the post-Paleozoic fossil record includes a greater proportion of deep-sea and infaunal species, which occupy local environments largely decoupled from global atmospheric composition and sea level. In addition, the Late Paleozoic record is numerically dominated by Superfamily Fusulinoidea, which were epifaunal inhabitants of shallow shelf environments and therefore influenced by ambient seawater oxygen levels rather than low-oxygen microenvironments within the sediment. In general, larger foraminifera tend to inhabit shallow-marine environments likely to be near equilibrium with atmospheric pO_2 . If the Paleozoic correlation between size and pO_2 results because most Paleozoic foraminiferan species (predominantly Order Fusulinida) were epifaunal inhabitants of shallow-marine settings in which seawater was generally equilibrated with atmospheric pO_2 , then a similar correlation might be expected if the post-Paleozoic analysis could be restricted to species inhabiting similar environments.

To test the hypothesis that changes in evolutionary dynamics result from changes in sampling frequency between shallow and deep-sea foraminifera, we examined data for the largest foraminifera, which are predicted to be epifaunal because the largest extant species are almost all epifaunal inhabitants of shallow-marine environments (Hallock 1999). We conducted an L_1 -regression of the 95th percentile in size against the geological and geochemical predictors discussed above as well as sampled diversity and radiometric age. Radiometric age was also included as a predictor to capture any tendency of the data simply to exhibit a consistent trend through time. Atmospheric pO_2 and sea level exhibit the strongest associations with 95th percentile size during the Paleozoic (Fig. 5A). The association of pO_2 with size is consistent with physiological prediction whereas the observed inverse association between sea level and size is opposite our expectation that larger species would be more common during intervals of high sea level and expanded shallow-marine habitat area. Atmospheric pO_2 exhibits a similarly strong association with mean size during the Paleozoic, whereas sea level is only weakly associated with mean size in our multiple regression analysis (Fig. 5B). No predictor exhibits a similarly strong association with size during the post-Paleozoic (Fig. 5C and D), consistent with our finding from model comparison that stasis is the best supported model for this interval (Table 1; Fig. 4). Thus, the reduced importance of pO_2 in the size evolution of foraminifera during post-Paleozoic time appears unlikely to be the result of secular variation in the range of sampled environments.

To test the alternative hypothesis that the shift in evolutionary dynamics arose from cell biological differences in Paleozoic versus post-Paleozoic foraminifera, we examined size evolution of major orders (>1000 species). Size evolution within Fusulinida,

the dominant Paleozoic order, is best modeled as controlled by atmospheric pO_2 (97% support; Table 1). In contrast, stasis is the best supported model for Lagenida, Miliolida, and Textulariida for both the Paleozoic and post-Paleozoic. Random walk is the best supported model for Globigerinida and Rotaliida, the other two diverse post-Paleozoic orders while environmental models receive very little support for all clades (Table 1).

Comparative analysis of major orders of foraminifera suggests that patterns of extinction and survival during the end-Permian mass extinction played an important role in shifting evolutionary dynamics within foraminifera as a whole. The short-term survivorship patterns of marine animals across the extinction horizon and resulting long-term shifts in the taxonomic and ecological structure of marine animal communities help to explain the temporal correspondence between mass extinction and the change in evolutionary dynamics of foraminiferan size.

The end-Permian mass extinction preferentially eliminated heavily calcified marine animals with limited physiological capacity to tolerate prolonged changes in ambient pCO_2 , pO_2 , pH, and temperature (Knoll et al. 1996, 2007; Kiessling and Simpson 2011). This selectivity can account, at least in part, for the lasting effect of this event on foraminiferan size evolution. The extinction of the large, heavily calcified fusulinids as opposed to the survival and subsequent radiation of the agglutinated textulariids suggests that the mass extinction was similarly selective within foraminifera (Knoll et al. 1996). Contrasting Paleozoic evolutionary dynamics of Fusulinida, which were nearly eliminated by end-Permian extinction, versus Lagenida, Miliolida, and Textulariida, which were less affected by the end-Permian crisis, indicates that the physiological traits that made fusulinid size evolution sensitive to variation in pO_2 also made them vulnerable to end-Permian environmental changes. This interpretation is also consistent with the selective extinction of larger fusulinids during a Middle Permian episode of environmental change (Stanley and Yang 1994) and associated selectivity patterns across marine animals similar to those observed during the end-Permian mass extinction (Clapham and Payne 2011).

In addition to physiology, dramatic changes in external ecological pressures following the mass extinction event may have contributed to the shift in dynamics of foraminiferan size evolution. In particular, increased influence of competition and predation pressure during the post-Paleozoic may have played a role in decoupling size evolution from global environmental change. Paleozoic marine communities were dominated by sessile, filter-feeding animals, the relative diversity and abundance of mobile predators was low, and sediment bioturbation was limited in depth and intensity (Ausich and Bottjer 1982; Bush et al. 2007). The proportional diversity and abundance of predators and motile organisms increased permanently across the Permian-Triassic transition (Bambach et al. 2002; Bush et al. 2007). Even if

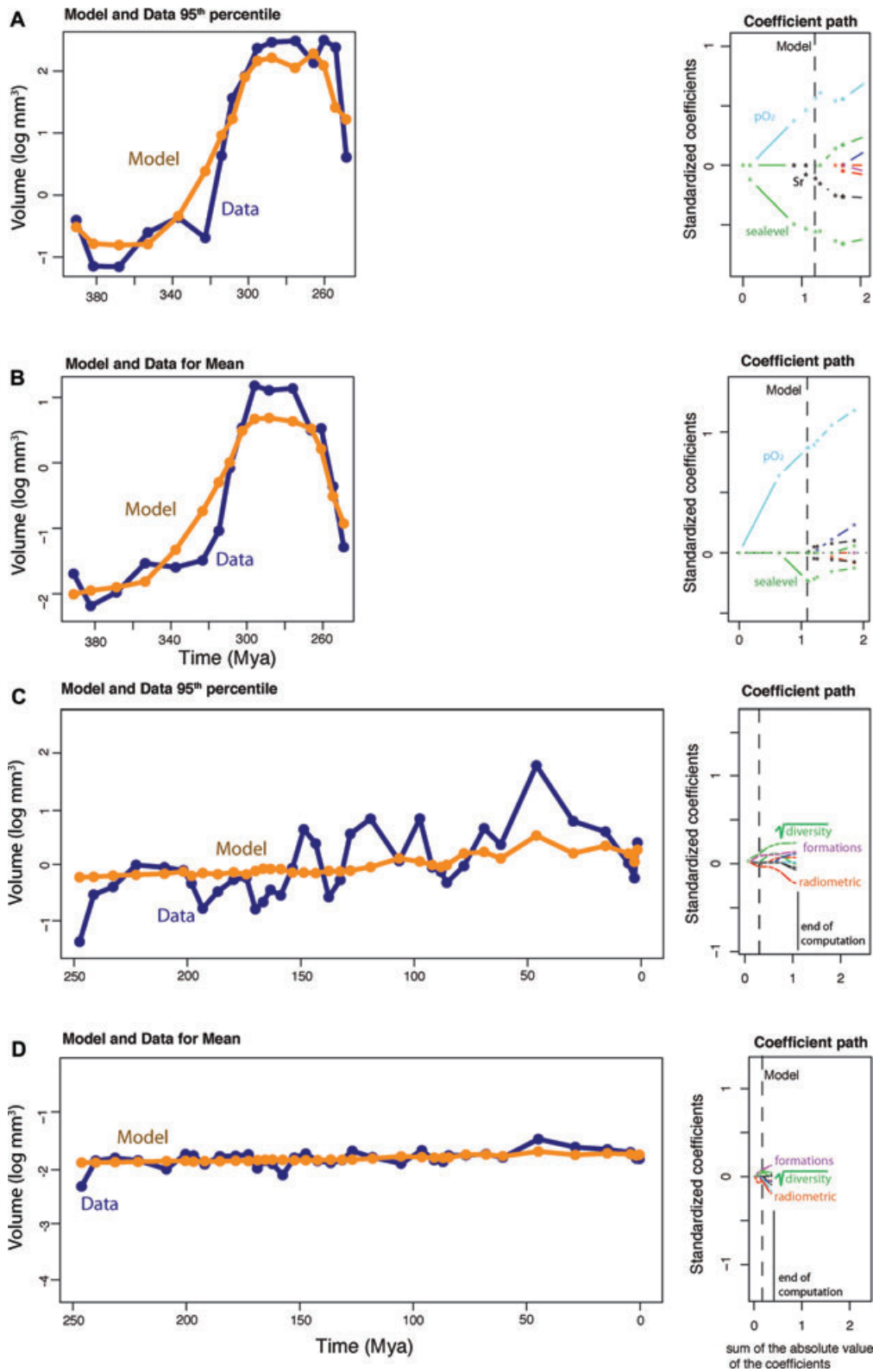


Figure 5. Regression results using L₁-regularization show that atmospheric *p*O₂ and sea level are the strongest predictors of 95th percentile (A) size and atmospheric *p*O₂ is the strongest predictor of mean (B) size for Paleozoic time. No predictor exhibits a large coefficient for predicting post-Paleozoic 95th percentile (C) or mean (D) size. The left-hand panels compare the data with the corresponding optimal linear model. The right-hand panels illustrate the corresponding coefficient paths, that is, the regressor coefficients for the best model as a function of the sum of the absolute values of all coefficients. The optimal model, indicated by the vertical dashed line, minimizes the Akaike and Bayesian information criteria and cross-validation error.

environmental factors continued to constrain the minimum or maximum possible size for foraminifera as a whole, increased competition and predation are likely to have reduced the relative importance of physical environmental change for species with sizes far from environmentally imposed bounds. A similar scenario of post-Paleozoic decoupling of size evolution from environmental change has been hypothesized to explain size evolution in flying insects. The post-Paleozoic reduction in the maximum size of flying insects (dragonflies) is too large to be explained by physiological effects resulting from a decrease in pO_2 and has been attributed to post-Paleozoic competition with flying vertebrates (Okajima 2008; Clapham and Karr 2012).

Conclusions

The evolutionary history of foraminifera suggests the extent to which environmental variation influences size evolution depends upon the physiological characteristics of the taxon and the ecological context in which its member species are evolving. This finding may help to explain why marine phytoplankton and deep-sea organisms respond clearly to climate change (Kaiho 1998; Schmidt et al. 2004; Finkel et al. 2005, 2007; Hunt and Roy 2006; Hunt et al. 2010) whereas terrestrial mammals exhibit comparatively little sensitivity (Alroy et al. 2000; Prothero et al. 2011). We remain far from a predictive model that accounts for ecological and environmental context, but comparative studies across time and taxa are clearly essential to build a comprehensive model of size evolution accounting for both environmental and ecological factors.

Our findings further highlight the potential for short-term geological catastrophes to influence evolutionary patterns long after the immediate environmental perturbations have dissipated. The end-Permian mass extinction has long been recognized for its lasting influence on the taxonomic and ecological structure of marine communities (Bambach et al. 2002; Wagner et al. 2006). Our analysis demonstrates that this biotic crisis also permanently altered evolutionary size dynamics in a diverse and ecologically important marine clade. The close similarities in the taxonomic diversity histories of foraminifera and marine animals suggest fundamental differences in evolutionary dynamics between the Paleozoic and post-Paleozoic may extend across much of the marine biosphere.

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Supporting Information

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Table S1. AICc measures of model support across the primary models considered in the paper, geochemical covariates, and alternative reconstructions of environmental covariates.

Table S2. Model fit (adjusted R^2) for simple linear regression of body size on a wide range of environmental covariates.

Table S3. Model results and AICc weights for all possible transitions in the two-phase model of foraminiferan size evolution, showing that the Scythian (Early Triassic: 247.7 million years ago) is strongly favored as the transition point, with atmospheric pO_2 as the best Paleozoic model and stasis as the best post-Paleozoic model.