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Press-pulse: a general theory of mass extinction?

Nan Crystal Arens and Ian D. West

Abstract.—Previous discussions of mass extinction mechanisms generally focused on circumstances unique to each event. However, some have proposed that extensive volcanism combined with bolide impact may offer a general mechanism of mass extinction. To test this hypothesis we compared generic extinction percentages for 73 stages or substages of the Mesozoic and Cenozoic. We found that the highest frequency of intervals with elevated extinction occurred when continental flood basalt volcanism and bolide impact co-occurred. In contrast, neither volcanism nor impact alone yielded statistically elevated extinction frequencies. Although the magnitude of extinction was uncorrelated with the size of the associated flood basalt or impact structure, crater diameter did correlate with extinction percentage when volcanism and impact coincided. Despite this result, case-by-case analysis showed that the volcanism-impact hypothesis alone cannot explain all intervals of elevated extinction. Continental flood volcanism and impact share important ecological features with other proposed extinction mechanisms. Impacts, like marine anoxic incursions, are pulse disturbances that are sudden and catastrophic, and cause extensive mortality. Volcanism, like climate and sea level change, is a press disturbance that alters community composition by placing multigenerational stress on ecosystems. We propose that the coincidence of press and pulse events, not merely volcanism and impact, is required to produce the greatest episodes of dying in Phanerozoic history.

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Although there is consensus that episodes of elevated extinction have happened in Earth's past (Raup and Sepkoski 1982; Signor and Lipps 1982; Stanley and Yang 1994; May et al. 1995; Jablonski 1996; Hallam 1998; Racki and Wrzolek 2001; Peters and Foote 2002; Bambach et al. 2004; Taylor 2004a; Wignall 2004; Bambach 2006; Peters 2006; Foote 2007; Wang and Everson 2007), their causes remain vigorously debated and anecdotal. Five broad categories of mass extinction mechanisms have been proposed: bolide impact, volcanism, sea level change, marine anoxia/dysoxia, and climate change. Biotic interactions (e.g., Hallam 1979; Dott 1983; Sepkoski et al. 2000) have also been implicated, but these biocentric hypotheses commonly involve only a single lineage and do not generally mow a broad swath through biological diversity. However, Roopnarine (2006) has shown that potentially catastrophic secondary extinctions can occur when food webs are perturbed.

Extinction scenarios that invoke more than one mechanism have emerged as detailed studies of extinction intervals revealed previously unappreciated complexity. For example, the end-Ordovician extinction has been attributed to a combination of sea level regression, rapid climate change, and fluctuations in deep ocean circulation (Sheehan 2001). Global warming that contributed to the formation of extensive marine anoxia has been suggested for the Late Devonian (Bond et al. 2004), Permian (Huey and Ward 2005), and Triassic (McElwain et al. 1999; Bottjer 2004) extinctions. The end-Cretaceous extinction—long the icon for a single impact cause (Alvarez et al. 1980)—may also be a candidate for a multifaceted explanation. Keller and colleagues (e.g., Keller 2003, 2005; Keller et al. 2003) continue to argue for the synergy of volcanism, climate change, and impact. Others (e.g., Racki and Wrzolek 2001; Glikson 2005) proposed, anecdotally, that the combination of impact and extensive volcanism explained high extinction at various intervals. White and Saunders (2005) modeled the statistical frequency of impact, volcanism, and elevated extinction to show that these events were likely to have coincided three times during the last

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300 Myr. They further noted that three of the traditional ''big five'' (Raup and Sepkoski 1982) Phanerozoic mass extinctions (Permian, Triassic, and Cretaceous) occurred within this temporal window. However, their analysis did not systematically evaluate the temporal coincidence of impact, volcanism, and mass extinction, nor did they consider the wider range of elevated extinction intervals that have been identified (MacLeod 2004; Bambach 2006; Wang and Everson 2007).

In this paper, we present a quantitative test of the impact-volcanism hypothesis. We propose that intervals of elevated extinction occur more frequently when extensive volcanism and impact coincide. In corollary, neither volcanism nor impact alone increases the frequency of elevated extinction.

Methods

To test the hypothesis that the coincidence of bolide impact and flood basalt volcanism is associated with elevated extinction, we required three coordinated, yet independent, data sets: extinction percentages, a geologic record of impacts, and a similar record of continental flood basalts.

Extinction Percentages.—Extinction intensity data used in this study were taken from the data set compiled by Rohde and Muller (2005) to look for cyclic variation in the record of diversity through time. Their compilation was reduced from the late Jack Sepkoski's (2002) *Compendium of Fossil Marine Animal Genera*. In their reduction of Sepkoski's data set, Rohde and Muller (2005) chose a conservative subset of genera, for which both first and last appearance datums were known and resolved to stage or substage. From these data, they calculated extinction percentages (for a given time stratigraphic unit, percent extinction = number of genera making last appearances/standing diversity) (Rohde and Muller 2005), which quantify the magnitude of extinction. They binned data into stages or substages following the 2004 timescale (Gradstein et al. 2005). Bambach (2006) rebinned the data to resolve several inconsistencies between Sepkoski's original stratigraphic bins and those of the 2004 timescale. We agreed with Bambach's (2006) stratigraphic treatment and used that in our analysis (reproduced in Appendix 1).

Several other compilations of extinction magnitudes are also available (e.g., Bambach et al. 2002; Peters and Foote 2002; Foote 2003, 2005, 2007). All of these compilations are based on Sepkoski's (2002) original data set. However, each group reduced the data in subtly different ways. Peters and Foote (2002) and Foote (2003, 2005, 2007) resolved data only to the stage level in most cases, giving the data coarser stratigraphic resolution. Bambach and colleagues (2002, 2004) and Rohde and Muller (2005) worked with substages. Bambach and colleagues (2002, 2004) interpolated first and last appearance datums for genera that were not resolved to the stage level. Rohde and Muller (2005) and Peters and Foote (2002) included only those genera for which first and last appearances were resolved to the stage level or better. Bambach and colleagues (2002, 2004) and Peters and Foote (2002) also included genera that appeared in only one stage or substage (Peters and Foote [2002] provided a second compilation excluding these so-called singletons). Bambach (2006) noted that including singletons increased both origination and extinction magnitudes because, by definition, singletons have 100% origination and extinction at the time unit boundary. All data sets except that reduced by Foote (2003, 2005, 2007) assumed that the last appearance datum was a good proxy for extinction, which may introduce bias if sampling is incomplete (Foote 2003). We preferred Rohde and Muller's (2005) compilation both for its higher stratigraphic resolution and for its conservative approach to the inclusion of genera, and base our primary conclusions on it. However, for completeness, we repeated our analysis on the other data sets in the form compiled by Bambach (2006). We do not discuss Foote's (2005) data further because its lower stratigraphic resolution (generally stage rather than substage) produced time-averaging in geologic events that created coincidences where none actually occurred. This concern overrode the important benefit of Foote's (2005, 2007) compilation: the mitigation of sampling bias.

Sepkoski's (2002) *Compendium* and its earlier versions have been widely used to study patterns of diversity through time (e.g., Sepkoski 1981, 1993; Sepkoski and Miller 1985; Bush et al. 2004; Lane et al. 2005; Bambach 2006). However, sampling bias is a persistent problem in any such taxon-counting exercise (e.g., Peters and Foote 2001, 2002; Smith 2001; Bush et al. 2004; Bush and Bambach 2004). This is another compelling reason to exclude genera that appear in only one substage: Such temporal singletons are commonly single-locality reports as well, making it likely that they are incompletely sampled. Despite its imperfections, the fossil record appears to show variability in extinction rate that reflects real pattern (Foote 2003). Incompleteness of the record would create noise that would likely obscure structure, biasing the analysis toward the null hypothesis.

Geologic Record of Bolide Impact.—Impacts leave a distinct signature in the geologic record, and an impact structure's diameter can give insight into the magnitude of the event (Melosh 1989). A crater's size may also suggest its extinction potential (Raup 1992), although the geographic and geologic context of an impact may be more important than size in determining ecological consequences (Arthur and Barnes 2006). Importantly, Earth's impact record is independent of the fossil record from which data on extinction were derived. This statistical independence is essential to the analysis we use.

Our compilation of impact structures worldwide is based on the Earth Impact Database (EID) (www.unb.ca/passc/ImpactDatase/) managed by the Planetary and Space Sciences Centre at the University of New Brunswick, Canada. As of January 2008, 174 confirmed impact structures were listed. To be included in the EID, a structure must show the primary macroscopic and microscopic features of hypervelocity impact, including (1) in situ shatter cone, (2) multiple planar deformation fractures in grains of in situ rocks, and (3) high-pressure mineral polymorphs in in situ rocks. From the list of confirmed impact structures, we culled those for which dating was not available. We also removed structures less than 10 km in diameter, because such impacts likely had little global effect. Although the 10 km size cutoff is guided by theory (Raup 1992), it is arbitrary. This resulted in the 33 structures listed in Appendix 2.

This data set is necessarily incomplete. In addition to those structures removed for poor dating, it does not include impacts that occurred in ocean basins, which should account for approximately two-thirds of all impacts. However, definitive evidence of such events is unlikely, and the lethal effects (e.g., dust and rock-based volatiles) may be buffered by ocean water. Thus, it seems appropriate to focus on continental impacts. On the continents, impact structures may be lost to erosion or buried by younger sediments, or they may simply be unrecognized or unstudied. This leads to significant pull of the Recent in the impact record. Incompleteness in the impact record should bias our analysis toward the null hypothesis, making this a conservative approach.

Geologic Record of Continental Flood Basalt Volcanism.—We focus on continental flood volcanism because it has greater potential for environmental disruption than do oceanic events (Rampino and Strothers 1988). Furthermore, the size and timing of continental events is generally better constrained. Our compilation of flood basalts was based on that published by Ernst and Buchan (2001) and updated as an on-line database (www.largeigneouspronvinces.org). We further limit our analysis to the Mesozoic and Cenozoic because many Paleozoic flood basalt provinces are deeply eroded, making size determination impossible, and have yielded equivocal radioisotopic ages. In this decision we follow Rampino and Strother (1988), who noted that despite several well-preserved examples, the record of large igneous provinces was generally poor before the Mesozoic. This yielded the 14 episodes of continental flood basalt volcanism listed in Appendix 3.

Statistical Analyses.—Manipulation of data, visualization, and statistical analyses were performed in Microsoft Excel 11.1.1 (Microsoft Inc.) and Aabel 1.5.8 (Gigawiz Ltd.) both for Macintosh.

To evaluate the hypothesis, we divided the 73 Mesozoic and Cenozoic stages/substages listed in Appendix 1 into four groups: (1) those in which neither continental flood ba-

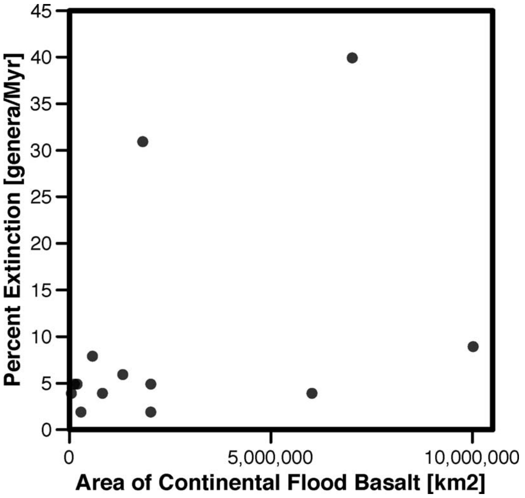

FIGURE 1. Area of Mesozoic and Cenozoic continental flood basalts considered in this study plotted against extinction percentages (percent standing diversity). No statistically significant relationship emerged ($r = 0.34$, $p = 0.25$). Extinction data plotted in this graph were detrended by arithmetic rotation around the mean. This detrending method, as opposed to regression residuals discussed in the text, was used to produce a more intuitive graph, without negative extinction values. Results of statistical analyses were identical to those produced by analysis of extinction residuals.

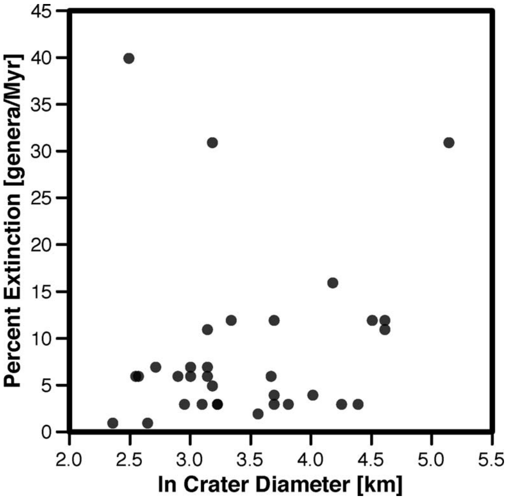

FIGURE 2. Natural log of Mesozoic and Cenozoic impact structure diameters plotted against extinction percentages (percent standing diversity). No statistically significant relationship emerged from these data ($r = 0.13$, $p = 0.45$). Extinction data plotted in this graph were detrended by arithmetic rotation around the mean. This detrending method, as opposed to regression residuals discussed in the text, was used to produce a more intuitive graph, without negative extinction values. Results of statistical analyses were identical to those produced by analysis of extinction residuals.

salts nor impacts were reported ($n = 32$), (2) those in which an impact structure >10 km in diameter but no flood basalt was reported ($n = 15$), (3) those in which continental flood basalts but no impact structures were recorded ($n = 18$), and (4) those in which basalts and impact structures co-occurred ($n = 8$). Next, we regressed percent extinction onto midpoint age for all 165 Phanerozoic stages/substages (Rohde and Muller 2005) and calculated residuals for each extinction percentage. Extinction residuals were used in the subsequent analysis to account for the well-recognized trend toward lower extinction rates through time (Raup and Sepkoski 1982; Bambach 2006). Data were also detrended by arithmetic rotation around the mean. This detrending solution was used for Figures 1 and 2, in which negative values of extinction residuals would seem counterintuitive. The techniques are mathematically equivalent. The nonparametric Mann-Whitney *U*-test (equivalent to the Wilcoxon rank-sum test) was used to assess whether large, positive residuals (higher-than-average extinction percentages) occurred more frequently in one or the other of the four groups of stratigraphic intervals. We used bootstrapping to balance sample sizes ($n = 50$) in the four populations prior to analysis. A balanced design was required because the Mann-Whitney *U* statistic is the product of the sample sizes minus the rank sum, which is also influenced by sample size. Consequently, an unbalanced design artificially weights the test statistic toward the variable with larger sample size (Mann and Whitney 1947). Significance of the test statistic (*p*-values) was calculated from the standard normal deviate (z-score approximation) at $\alpha = 0.01$.

Results

Table 1 presents *p*-values for paired comparisons of extinction residuals between substages when continental flood basalts or impacts occurred alone or coincided, and those devoid of geologic events. In this analysis, neither impacts nor flood basalts alone generated a higher frequency of elevated extinction compared to intervals when neither event occurred. In contrast, the combination of volca-

TABLE 1. Results (*p*-values) of the Mann-Whitney rank-order analysis of four groups of Mesozoic and Cenozoic extinction percentage residuals using the Rohde and Muller (Rohde and Muller 2005; Bambach 2006) data set. ''No events'' included extinction percentages for stages and substages in which neither continental flood basalts nor impact structures were reported. ''Impacts'' included stages and substages in which at least one impact structure >10 km in diameter was reported, but no continental flood basalts occurred. ''Basalts'' included stages and substages in which continental flood basalts were reported, but no impact structure. ''Both'' included stages and substages in which flood basalts and at least one impact structure >10 km in diameter were reported. Data were bootstrapped to a sample size $n = 50$ prior to analysis. Balanced samples are required by the Mann-Whitney statistic. Results statistically significant at $\alpha = 0.01$ are noted with an asterisk.

	No events	Impacts	Basalts	Both
No events	1			
Impacts	0.06	1		
Basalts	0.06	0.38	1	
Both	0.001*	<0.001*	<0.001*	1

nism and impact produced a statistically higher frequency of elevated extinction compared to flood basalts alone, impacts alone, and geologically quiet times.

We repeated the analysis described above with data from Bambach and colleagues (Bambach et al. 2002, 2004) and from Peters and Foote (2002). The data sets of Bambach and Peters (using both the compilations including and excluding singletons) were calibrated to a single timescale and republished by Bambach (2006). We used these numbers for our analysis. Data sets including singletons did not produce statistically significant differences in the frequency of substages with elevated extinction. This reflects heterogeneity in the distribution of singletons throughout the Mesozoic and Cenozoic. Intervals with a large proportion of singletons had artificially elevated extinction percentages, by definition, because singletons have 100% extinction at the stratigraphic boundary (Bambach 2006). In both data sets that excluded singletons, however, we reproduced the pattern of more frequent intervals of elevated extinction when volcanism and impact coincided, and a similar level of statistical significance.

Magnitude, rather than simply presence or absence, of continental flood volcanism or impact might determine extinction magnitude (Raup 1992). To test this hypothesis we regressed the area of each continental flood basalt onto the extinction percentage of each time stratigraphic unit during which volcanism was active (Fig. 1). Area values, which were available for most continental basalts, are proportional to the amount of magma erupted and might be related the environmental consequences of the event. Basalt volume would be a better choice, but many large igneous provinces are deeply eroded, making volume estimates unreliable. There is no relationship between the area of flood basalts and co-occurring extinction residuals ($r = 0.34$, $p = 0.25$). To test the converse hypothesis that impact magnitude predicts extinction percentage, we regressed the natural log of crater diameter onto extinction percentage for the substage in which the impact occurred (Fig. 2). Natural log of crater diameter linearized the distribution of impact structure sizes before we applied the regression model. As with flood basalts, we found no significant relationship between crater size—a proxy for impact magnitude (Melosh 1989)—and extinction residuals ($r = 0.13$, $p = 0.45$).

However, when the interaction of volcanism and impact was modeled, the results differed. A multivariate regression of extinction residuals on the linear combination of continental flood basalt size and natural log transformed diameter of the impact structure was statistically significant ($r = 0.37$, $p = 0.01$). In the multivariate regression, crater diameter explained the greater percentage of the observed variance, suggesting that impact magnitude does influence extinction intensity, but only when the impact occurred within the context of a biosphere already disturbed by major continental flood volcanism.

Discussion

Within the limitations of the available data, we confirm the hypothesis that elevated extinction occurred more frequently during intervals when continental flood basalt volcanism and bolide impact coincided. This result is consistent with qualitative suggestions by various authors (e.g., Racki and Wrzolek 2001; Glikson 2005; Keller 2005; White and Saunders 2005) that single events are insufficient to explain the complexity of the stratigraphic and fossil records surrounding extinction events. Some (e.g., Racki and Wrzolek 2001; Glikson 2005; White and Saunders 2005) have specifically suggested that extensive volcanism combined with bolide impact may be required to produce episodes of major extinction. White and Saunders (2005) further argued that the co-occurrence of impact, volcanism, and major extinction is unlikely to be merely coincidental. They contended that volcanism produced climate change, altered marine circulation, and stressed biotic communities. Our analysis showed that volcanism-induced stress alone appeared insufficient to produce more than anecdotal extinction. To produce an episode of elevated extinction, an additional trigger, such as an impact, may be required to eliminate species already endangered by environmental stress. This hypothesis is supported by our analysis.

Episodes of Elevated Extinction in the Mesozoic and Cenozoic.—In his reanalysis of Phanerozoic extinction data, Bambach (2006) noted that different data tabulation methods produced different extinction percentages, but that 18 time stratigraphic units emerged consistently as intervals of elevated extinction. Seven of these intervals occurred during the Mesozoic and Cenozoic. These were (from oldest to youngest): late Norian/Rhaetian (end-Triassic), late Pliensbachian/early Toarcian (Early Jurassic), late Tithonian (end-Jurassic), late Cenomanian (early Late Cretaceous), late Maastrichtian (end-Cretaceous), Late Eocene, and Pliocene. All of these intervals produced positive extinction residuals in our analysis. We consider the relationship between volcanism and impact in each of these intervals.

The end-Triassic extinction appears confined to a single interval (Rhaetian, 29% generic extinction [Rohde and Muller 2005]), although Bambach (2006) combined this stage with the late Norian to resolve concerns with time stratigraphic correlation in the underlying data (40% extinction, Appendix 1). This event registered the highest extinction residuals (0.31) in our analysis, making it the most severe extinction in the Mesozoic/Cenozoic, after correction for the declining trend in extinction rate through the Phanerozoic. This extinction coincided with extrusion of Central Atlantic Magmatic Province (Marzoli et al. 1999b; Palfy et al. 2000, 2002). Two small North American impact structures formed during the Rhaetian: the 9 km diameter Red Wing structure in North Dakota (47°36′N, 103°33′W [Sawatzky 1977]), which was not considered in the analysis, and the Wells Creek structure in Tennessee (36°23′N, 87°40′W [Stearns et al. 1968]), 12 km in diameter (Appendix 2). Both dated to about 200 Ma, although there is significant uncertainty in the Wells Creek structure's age. No attempt has been made to link these structures to a single event, and neither impact structure has previously been associated with the end-Triassic extinction, probably because of their small size and presumably regional effects. A modest iridium anomaly of purported impact origin has been reported at the close of the Triassic in the Newark Basin (285 ppt Ir [Olsen et al. 2002]). Iridium was associated with fern spore enrichment and significant turnover in both flora and fauna of the Newark Basin, all hallmarks of extinction linked to catastrophic disturbance (Tschudy et al. 1984; Vijda et al. 2001).

The late Pliensbachian shows mildly elevated extinction (10%, Appendix 1, residual = 0.02) and the early Toarcian somewhat less (9%, residual = 0.01). Thus, they do not emerge as intervals of strongly elevated extinction in our data set. The late Pliensbachian is a substage devoid of flood basalt activity and impact structures. The early Toarcian coincides with the Karoo-Ferrar flood basalts in southern Africa (Appendix 3) (Marsh et al. 1997; Jourdan et al. 2005) but contains no impact structure.

The end-Jurassic (late Tithonian) extinction was also modest (13%, Appendix 1, residual = 0.06) and occurred during a time when neither continental flood basalt volcanism nor impact occurred.

The late Cenomanian also showed minor extinction (8%, Appendix 1, residual = 0.01). This event coincided with the second pulse of the Rajmahal flood volcanism in India (Eldholm and Coffin 2000). No impact structure has been dated to this substage.

The end-Cretaceous extinction is arguably the most extensively studied, and its causes have been widely debated. It emerged as the second largest Mesozoic/Cenozoic extinction in our data set (31% extinction, Appendix 1, residual = 0.25). The 170 km diameter Chicxulub crater (21°20′N, 89°30′W) in the Yucatán peninsula of Mexico (Hildebrand et al. 1991) formed during extrusion of India's Deccan Trap flood basalts (Eldholm and Coffin 2000).

The late Eocene (12% extinction, Appendix 1, residual = 0.07) had the fourth highest extinction residual in our analysis. No continental flood basalts occurred during this interval. However, the 90 km diameter Chesapeake Bay structure in Virginia (37°17′N, 76°1′W) and the 100 km diameter Popigai structure in Russia (71°39′N, 111°11′E) are dated at 37.7 Ma (McHugh et al. 1998) and 35.5 Ma (Bottomley et al. 1997) respectively (Appendix 2).

The Pliocene also showed modest extinction (6%, Appendix 1, residual = 0.02) that coincided with the 18 km diameter El'gygytgyn impact structure in Russia (67°30′N, 172°5′E). Several smaller impact structures are also reported from the Pliocene; these were not included in our analysis: 10 km Karla structure in Russia, 8 km Bigache structure in Kazakhstan, and 2.5 km Roter Kamm structure in Namibia (LIP database, January 2008).

Our analysis also revealed intervals in which continental flood basalts and impacts coincided but elevated extinction was not reported. These included early Barremian (Early Cretaceous, 4% extinction, Appendix 1, residual = −0.03), the late Aptian (Early Cretaceous, 6% extinction, residual = −0.005), the Thanetian (late Paleocene, 6% extinction, residual = 0.004), and the Middle Miocene (5% extinction, residual = −0.002). During the Barremian, the Paraná-Etendeka flood basalts (134–129 Ma) were active in the region straddling the rift between South America (Brazil, Paraguay) and Africa (Namibia, Angola) (Eldholm and Coffin 2000). The most intense period of volcanism occurred between 133 and 131 Ma (Marzoli et al. 1999a). The 55 km diameter Tookonooka impact structure (27°7′S, 142°50′E) also formed during the early part of this stage (Gostin and Therriault 1997). In the late Aptian, the first phase of Rajmahal volcanism was active in India and Bangladesh (116–113 Ma) (Kent et al. 1997). The Carswell (39 km diameter) impact structure (58°27′N, 109°30′W) in Saskatchewan, Canada formed during this substage. During the Thanetian, the North Atlantic Volcanic Province was active (62–58 Ma) and the small (12.7 km) Marquez impact structure (31°17′N, 96°18′W) formed in Texas. In the middle Miocene, outpourings of the Colombia River flood basalt coincided with formation of the Ries impact structure (24 km in diameter, 48°53′N, 10°37′E) in Germany.

Although our results demonstrate that intervals of elevated extinction occurred more frequently when continental flood volcanism and impact coincided, the simple volcanism-impact model (White and Saunders 2005) cannot explain the entire pattern of elevated extinction in the Mesozoic and Cenozoic. A wide variety of other extinction mechanisms have been proposed, including sea level change (Cohen and Hallam 1989; Hallam 1998; Sheehan 2001; Sandberg et al. 2002; Shen and Shi 2002; Bond et al. 2004), marine anoxia/dysoxia (House 1985, 1992; Cohen and Hallam 1989; Joachimski and Buggisch 1993; McGhee 1996; Sheehan 2001; Bond et al. 2004; Kump et al. 2005; Riccardi et al. 2007), and global climate change (McElwain et al. 1999; Norris et al. 2001; Sheehan 2001; Berry et al. 2002; Bralower et al. 2002; Johnson 2002; Bottjer 2004; Kiehl and Shields 2005). Like the volcanism-impact model, some of these scenarios require the interaction of multiple mechanisms. For example, sea level change may require an additional proximal trigger such as marine anoxia/dysoxia (Cohen and Hallam 1989; Sheehan 2001; Bond et al. 2004) to generate elevated extinction. Similarly, mechanisms involving climate change commonly require some additional agent of mortality to produce more than anecdotal extinction (Keller 2003; Bottjer 2004).

As in the volcanism-impact model, most proposed extinction agents act either as ecologically long-term environmental stress (e.g., sea level and climate change) or as sudden, catastrophic disturbance (e.g., incursion of anoxia/dysoxia waters). To generalize, we propose that some form of environmental stress must be coupled with a catastrophic disturbance to produce elevated extinction. However, environmental stress need not be produced by volcanism, nor must disturbance be the result of impact. Other agents are possible.

Press and Pulse Disturbances.—Working within the framework of community ecology, Bender and colleagues (1984) introduced a distinction between ''press'' and ''pulse'' disturbances to make explicit the consequences of differing experimental treatments. In pulse experiments, a single perturbation alters the density of a target species. Following the perturbation, all species in the community are allowed to respond and recover (Bender et al. 1984). In press experiments, a target species is reduced or eliminated from the community, and the target's new density is maintained throughout the experiment. As a consequence of continued manipulation, the community recovers to a new compositional equilibrium (Bender et al. 1984). Community ecology has embraced this distinction and applied it broadly to both natural and human-designed experiments (Underwood 1989, 1994). In natural experiments—such as those we might observe in the fossil record—pulse disturbances are events that cause significant mortality. In contrast, press events are long-term stresses that may not cause immediate mortality, but instead alter population densities and shift the community into a new equilibrium. In studies of living systems, the press-pulse paradigm has been broadly applied to the marine benthos (Elias et al. 2005; Morello et al. 2005; Lilley and Schiel 2006; Scheibling and Gagnon 2006), freshwater communities (Marshall and Bailey 2004; Parkyn and Collier 2004; Lottig et al. 2007; Alexander et al. 2008), soil invertebrates (Bengtsson 2002), terrestrial animals (Alterio and Moller 2000), plants (Inchausti 1995), and conservation theory (Parasiewicz 2007).

The pulse-press model has been be extended to the evolutionary scale and applied to discussions of extinction (Erwin 1996, 2001). At the macroevolutionary level, pulse disturbances are geologically instantaneous events that disrupt biological communities and produce high mortality (e.g., bolide impact or rapid incursion of anoxic marine waters). If mortality is high enough to render populations non-viable, extinction results. However, if enough individuals can endure the pulse event and its immediate aftermath, survival is ensured because the physical and biotic environments eventually recover to their pre-disturbance equilibria.

In contrast, press mechanisms exert long-term stress on biological communities (Erwin 1996), thereby altering the adaptive landscape. Such mechanisms include changes in the mixing ratios of atmospheric gasses, sea level variation, and climate change. Although these may be of geologically short duration, they occur over many generations of the organisms involved and qualify as ecologically long-term stresses. Press disturbances promote extinction by reducing populations to non-viable levels through habitat loss, range restriction, and curtailed reproduction. In the fossil record, such proximal mechanisms may be impossible to distinguish. However, unlike pulse disturbances, press mechanisms force the biological community into a new equilibrium, in which previously important species may have no place. The mechanism of extinction in press events may not be mortality but rather changes that prevent growth and reduce carrying capacity until populations are rendered non-viable. Furthermore, press disturbances change the trajectory of evolution both directly (by eliminating players) and indirectly (by shifting the adaptive landscape for surviving species). Press disturbances also differ from pulse in that their ecologically longer duration permits adaptation of affected species (Erwin 1996). However, when press disturbances are of sufficient magnitude, they may exceed the adaptive potential of a lineage and lead to its extinction (Erwin 1996).

Clearly, both press and pulse disturbances can produce extinction. Many proposed extinction scenarios have focused on single, large magnitude press or pulse events. However, as more episodes of elevated extinction have been studied in detail, some researchers have recognized that singe-mechanism scenarios do not fit all of the available data (e.g., Racki and Wrzolek 2001; Glikson 2005; Keller 2005; White and Saunders 2005). Thus, a variety of multiple-cause hypotheses have been proposed. White and Saunders (2005) moved beyond the anecdotal to suggest a generalized extinction mechanism: the combined effects of flood volcanism and bolide impact. Recognizing the contingent nature of history, most geologists and paleontologists resist such generalizations. However, ecologists agree that extinction, even in the face of large-scale catastrophe, is more likely when species are already endangered (Breininger et al. 1999; Hakoyama and Iwasa 2000), and that recovery from disturbance is less likely when ecosystems are stressed (Dolbeth et al. 2007; Nelson et al. 2007). We propose the press-pulse hypothesis to offer an ecologically meaningful framework in which to pose and test multiple-mechanism scenarios for individual extinction events in Earth's history.

Temporal Scale Critique.—Moving any concept from neoecology to deep time invites criticism of temporal scale. There is little question that pulse events, such as large bolide impacts, are instantaneous on both ecological (within one or a few generations of the organisms involved) and evolutionary (a time sufficient for change to occur and become fixed in a population) time scales. However, the direct consequences of a major impact may linger for days or months (Pope et al. 1997; Toon et al. 1997). For most organisms, this remains an ecological time scale. The crucial observation: pulse disturbances exert extinction power through mortality in the immediate aftermath of the event.

Questions of temporal scale are more challenging for press disturbances. For example, a large igneous province may be emplaced over several million years (see Appendix 3), but is generally characterized by episodes of peak eruption that last for one million years or less (Silver et al. 2006). Within peak periods, eruption may be sporadic or continuous. However, the global extinction power of flood basalts comes not from the eruptions themselves, but from secondary effects. Flood basalts have been linked to climate change (Wignall 2001; Chenet et al. 2005; Jolley and Widdowson 2005) and carbon cycle disruption (Wignall 2001; Palfy et al. 2002; Berner 2004). Flood basalts may also record levels of tectonic activity that drive some sea level change (Adatte et al. 2001). All of these consequences will continue through, and probably beyond, the period of peak eruptive activity—about 1 Myr. For most organisms this constitutes the evolutionary time scale that typifies a press disturbance. The key observations: (1) press disturbances need not kill outright, but can instead exert extinction power through curtailed reproduction, lost habitat, geographic range contraction, and the long-term decline of population size; and (2) press disturbances occur over evolutionary time scales, making adaptation possible.

In our analysis, we chose independent press and pulse disturbances. However, a single event may—for some organisms—constitute both press and pulse. For example, planktonic foraminifera experienced significant extinction at the Cretaceous/Tertiary boundary (D'Hondt et al. 1996). Certainly, the direct effects of the terminal-Cretaceous impact produced major mortality in planktonic communities. However, plankton are well adapted to a bloom-and-bust lifestyle (Mohiuddin et al. 2005), where only a few survivors give rise to rapid population recovery once favorable conditions return. Nonetheless, high-resolution stratigraphic sections showed that recovery after the terminal-Cretaceous impact was curtailed and extinction resulted (Keller 1988; Fornaciari et al. 2007), with some last appearances occurring above the impact's iridium signature (Keller 1988). In this case, we speculate that pulse mortality reduced populations, and that long-term (press) disruption of the open ocean ecosystem inhibited recovery and promoted extinction (D'Hondt et al. 1998). Only when both the press and pulse disturbances are articulated do the geochemical, biological, ecological, and stratigraphic data come into accord. Keller and colleagues (1988, 2003, 2005) have long argued that mantle plume volcanism is the press behind the extinction of foraminifera at the Cretaceous/Tertiary boundary. In this case, explicitly articulating the press mechanism, and its temporal relationship to the pulse disturbance, allows these two hypotheses to be clearly distinguished and tested.

This example also illustrates a conundrum facing students of extinction. The stratigraphic record, in which time is imperfectly recorded and last appearances only approximate extinction, does not always offer sufficient resolution to separate the effects of press and pulse disturbances. However, where stratigraphic resolution is sufficient, the press-pulse model poses clear, testable, ecologically meaningful hypotheses that may better capture the complexity underlying intervals of elevated extinction.

In conclusion, our analysis suggests that single causes for mass extinction—although appealing in their simplicity—may be inadequate to explain the detailed data now available for many episodes of mass extinction. Instead, a geologic one-two punch of press and pulse disturbances may be required to generate elevated extinction. The press-pulse model provides an ecologically realistic framework in which to investigate such hypotheses at the moments of great dying in Earth's history.

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Appendix 1

Extinction as a percent of standing diversity for marine animal genera during the Mesozoic and Cenozoic based on Sepkoski's (2002) *Compendium of Fossil Marine Animal Diversity*, reduced by Rohde and Muller (2005) and republished by Bambach (2006), who consolidated some stages to better reflect the temporal resolution of the original data. Only genera for which first and last appearance data were known and for which first and last appearance data can be resolved to stage or substage were used to calculate extinction rate. Singletons excluded.

Age (Ma)	Stage	Extinction magnitude (% Genera)	Age (Ma)	Stage	Extinction magnitude (% Genera)
0–1.8	Pleistocene	1.25	148.2–150.8	Early Tithonian	8.37
1.8–5.3	Pliocene	6.19	150.8–153.3	Late Kimmeridgian	6.15
5.3–11.6	Late Miocene	4.13	153.3–155.7	Early Kimmeridgian	6.30
11.6–16	Middle Miocene	4.64	155.7–157.5	Late Oxfordian	5.68
16–23	Early Miocene	3.55	157.5–159.4	Middle Oxfordian	2.82
23–28.4	Late Oligocene	1.60	159.4–161.2	Early Oxfordian	4.55
28.4–33.9	Early Oligocene	4.98	161.2–162.4	Late Callovian	5.59
33.9–37.2	Late Eocene	12.37	162.4–163.5	Middle Callovian	4.79
37.2–48.6	Middle Eocene	6.70	163.5–164.7	Early Callovian	5.66
48.6–55.8	Early Eocene	3.40	164.7–165.7	Late Bathonian	4.77
55.8–60.2	Thanetian	6.14	165.7–166.7	Middle Bathonian	2.87
60.2–65.5	Danian	7.55	166.7–167.7	Early Bathonian	3.17
65.5–68.1	Late Maastrichtian	30.90	167.7–169.7	Late Bajocian	5.92
68.1–70.6	Early Maastrichtian	16.15	169.7–171.6	Early Bajocian	6.77
70.6–77.1	Late Campanian	6.36	171.6–175.6	Aalenian	3.50
77.1–83.5	Early Campanian	6.12	175.6–179.3	Late Toarcian	5.55
83.5–85.8	Santonian	5.24	179.3–183	Early Toarcian	8.78
85.8–89.3	Coniacian	2.44	183–186.3	Late Pliensbachian	10.29
89.3–91.4	Late Turonian	3.15	186.3–189.6	Early Pliensbachian	6.22
91.4–93.5	Early Turonian	3.87	189.6–193.1	Late Sinemurian	3.22
93.5–95.5	Late Cenomanian	7.73	193.1–196.5	Early Sinemurian	2.86
95.5–97.6	Middle Cenomanian	4.11	196.5–199.6	Hettangian	2.41
97.6–99.6	Early Cenomanian	5.98	199.6–207.9	U. Norian/Rhaetian	39.97
99.6–103.7	Late Albian	6.63	207.9–212.2	Middle Norian	9.96
103.7–107.9	Middle Albian	4.45	212.2–216.5	Early Norian	11.11
107.9–112	Early Albian	3.92	216.5–222.3	Late Carnian	11.69
112–118.5	Late Aptian	6.39	222.3–228	Early Carnian	12.15
118.5–125	Early Aptian	7.66	228–232.5	Late Ladinian	6.01
125–127.5	Late Barremian	3.70	232.5–237	Early Ladinian	6.24
127.5–130	Early Barremian	3.81	237–239.7	Late Anisian	4.91
130–133.2	Late Hauterivian	2.41	239.7–242.3	Middle Anisian	3.73

Appendix 1

Continued.

Age (Ma)	Stage	Extinction magnitude (% Genera)	Age (Ma)	Stage	Extinction magnitude (% Genera)
133.2–136.4	Early Hauterivian	3.56	242.3–245	Early Anisian	4.04
136.4–138.3	Late Valanginian	3.67	245–247.4	Late Olenekian	6.03
138.3–140.2	Early Valanginian	4.34	247.4–249.7	Early Olenekian	2.11
140.2–142.9	Late Berriasian	3.33	249.7–250.4	Late Induan	4.56
142.9–145.5	Early Berriasian	2.60	250.4–251	Early Induan	8.95
145.5–148.2	Late Tithonian	13.14			

Appendix 2

Impact structures used in this analysis. The data set was culled from the Earth Impact Database managed by the Planetary and Space Sciences Centre at the University of New Brunswick, Canada (data drawn 1 January 2008). To be included in this data set, an impact structure must be larger than 10 km in diameter and dated to a Mesozoic or Cenozoic stage. Key citations are provided below; additional references for each structure are available at www.unb.ca/passc/impactDatabase/.

Impact structure	Location	Diameter (km)	Age (Ma)	Reference
Zhamanshin	Kazakhstan	14	0.9	Izokh 1991
Bosumtwi	Ghana	10.5	1.07	Jones et al. 1981
El'gygytgyn	Russia	18	3.5	Feldman et al. 1981
Ries	Germany	24	15.1	Kavasch and Kavasch 1986
Chesapeake Bay	Virginia, USA	90	35.5	Koeberl et al. 1996
Popigai	Russia	100	35.7	Hodge 1994
Mistastin Lake	Labrador, Canada	28	36.4	Taylor and Dence 1968
Haughton	Nunavut, Canada	23	39	Robinson 1988
Logancha	Russia	20	40	Hodge 1994
Logoisk	Belarus	15	42.3	Grieve 1991
Kamensk	Russia	25	49	Hodge 1994
Montagnais	Nova Scotia, Canada	45	50.5	Jansa and Pe-Piper 1987
Marquez Dome	Texas, USA	12.7	58	Hodge 1994
Chicxulub	Yucatán, Mexico	170	64.98	Hildebrand et al. 1991
Boltysh	Ukraine	24	65.17	Grieve et al. 1987
Kara	Russia	65	70.3	Koeberl et al. 1990
Lappajärvi	Finland	23	73.3	Reimold 1982
Manson	Iowa, USA	35	73.8	Izett et al. 1993
Dellen	Sweden	19	89	Muller et al. 1990
Steen River	Alberta, Canada	25	91	Carrigy 1968
Deep Bay	Saskatchewan, Canada	13	99	Sander et al. 1963
Carswell	Saskatchewan, Canada	39	115	Hodge 1994
Tookoonooka	Queensland, Australia	55	128	Gostin and Therriault 1997
Mjølinir	Norway	40	142	Dypvik et al. 1996
Gosses Bluff	N. Territory, Australia	22	142.5	Milton et al. 1972; Milton and Sutter 1987
Morokweng	South Africa	70	145	Corner et al. 1997; Reimold et al. 2002
Puchezh-Katunki	Russia	80	167	Masaitis and Mashchak 1990
Obolon	Ukraine	20	169	Masaitis et al. 1976
Wells Creek	Tennessee, USA	12	200	Stearns et al. 1968
Rochechouart	France	23	214	Lambert 1977
Manicouagan	Quebec, Canada	100	214	Dence 1964
Saint Martin	Manitoba, Canada	40	220	Robinson and Grieve 1975
Araguainha	Brazil	40	244.4	Hammerschmidt and Engelhardt 1995

Appendix 3

Continental flood basalt events used in this analysis. The data set was culled from the Large Igneous Provinces database managed by the LIPs Commission, under the auspices of the International Association of Volcanology and Chemistry of the Earth's Interior (data drawn 1 January 2008). Only well-dated, continental events were included in this study. Key references are provided; additional references are available at www.largeigneousprovinces.org/record.html/.

Igneous province	Location	Area (km^2)	Age range (Myr)	Reference
Columbia River	USA	164,000	14.5–16.5	Zoback et al. 1994; Hooper 1997
Afar	NW Africa, Arabia	2,000,000	29–31	Hofmann et al. 1997; Menzies et al. 1997; George et al. 1998
North Atlantic Volcanic Province	UK, Greenland	1,300,000	58–62	Saunders et al. 1997
Deccan	India	1,800,000	66	Rampino and Strothers 1988; Haggerty 1996; Eldholm and Coffin 2000
Madagascar	Madagascar	260,000	84–90	Storey et al. 1997; Eldholm and Coffin 2000
Queen Elizabeth Is.	Canada, Greenland	550,000	95	Embry and Osadetz 1988; Ernst and Buchan 1997
Rajmahal	India	6,000,000	86–110	Kent et al. 1997; Eldholm and Coffin 2000
Marie Byrd	Antarctica	undetermined	107–110	Storey et al. 1999
Paraná-Etendeka	South America, W. Africa	2,000,000	129–134	Peate 1997
Greenland Trap	Greenland	20,000	133–138	Nielsen 1987; Larsen et al. 1999
Gascoyne Margin	NW Australia	800,000	136–140	Eldholm and Coffin 2000
Argo Basin Margin	E. Indian Ocean	100,000	155–160	Eldholm and Coffin 2000
Karoo-Ferrar	Southern Africa	10,000,000	179–183	Marsh et al. 1997; Jourdan et al. 2005
Central Atlantic Magmatic Province	USA, South America, Africa	7,000,000	199–201	Marzoli et al. 1999b