



ELSEVIER

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Palaeogeography, Palaeoclimatology, Palaeoecology 211 (2004) 289–297

PALAEO

www.elsevier.com/locate/palaeo

Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled

George R. McGhee Jr.^{a,*}, Peter M. Sheehan^b, David J. Bottjer^c, Mary L. Droser^d

^a*Department of Geological Sciences, Wright-Rieman Laboratories, Rutgers University, Busch Campus, New Brunswick, NJ 08903, USA*

^b*Department of Geology, Milwaukee Public Museum, 800 West Wells Street, Milwaukee, WI 53233, USA*

^c*Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089, USA*

^d*Department of Earth Sciences, University of California, Riverside, CA 92521, USA*

Received 23 February 2004; received in revised form 30 April 2004; accepted 13 May 2004

Abstract

The past two decades have seen extensive analyses of the taxonomic severity of major biodiversity crises in geologic time. In contrast, we propose here an alternative analysis of the ecological severity of biodiversity crises. It is clear that the ecological impacts of the five Phanerozoic biodiversity crises were not all the same. Ranking the five Phanerozoic biodiversity crises by ecological severity reveals that the taxonomic and ecological severities of the events are decoupled. The most striking example of the decoupling is the end-Cretaceous biodiversity crisis, which is the least severe in terms of taxonomic diversity loss yet is ecologically the second most severe event in the entire Phanerozoic. A second striking example is the end-Ordovician biodiversity crisis: the environmental degradation produced by the end-Ordovician glaciations precipitated a major loss of marine diversity, yet the extinction failed to eliminate any key taxa or evolutionary traits, and was of minimal ecological impact.

We suggest that the decoupled severities indicates that the ecological importance of component species in an ecosystem is at least as important as species diversity in maintaining the integrity of the ecosystem and that this ecological phenomenon operates on geological timescales. The selective elimination of dominant and/or keystone taxa that occurs in the ecologically most devastating biodiversity crises indicates that a strategy emphasizing the preservation of taxa with high ecological value is necessary to mitigate the ecological effects of the current ongoing loss of global biodiversity.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Biodiversity crisis; Mass extinction; Ecosystem evolution; Ecological replacement

1. Introduction: analyzing the severity of biotic crises

Analyses of the taxonomic severity of biodiversity crises have a long history (Phillips, 1860; Newell, 1967; Raup and Sepkoski, 1982; Sepkoski, 1982;

* Corresponding author. Tel.: +1 732 445 3832; fax: +1 732 445 3374.

E-mail address: mcghee@rci.rutgers.edu (G.R. McGhee).

Benton, 1995; see the review of Benton, 1999) and have led to the current recognition of the five most severe losses of biodiversity in Phanerozoic time: the end-Ordovician, Late Devonian, end-Permian, end-Triassic and end-Cretaceous crises (Raup and Sepkoski, 1982). The numerous studies of the taxonomic severity of biodiversity crises in geological time are in part due to the fact that severity magnitudes are easily quantifiable using ratio metrics, even though different metrics will yield different results (McGhee, 1989).

We feel that the time has come to attempt to analyze the ecological impact of biotic crises, rather than the magnitude of the biodiversity loss. The analysis of the ecological severity of a biodiversity crisis is much more difficult due to the fact that there exists no system to measure ecological severity on a ratio scale. It is clear that the ecological impacts of the five Phanerozoic biodiversity crises were not all the same. If the crises differed in ecological severity, then it should be possible to *rank those differences*. In a previous paper, we proposed an ordinal measurement scale to rank ecological changes in marine communities, a scale that we used to compare the marine effects of the end-Ordovician and Late Devonian biodiversity crises (Droser et al., 2000).

We here propose an ordinal measurement scale designed to rank the ecological effects of all five of the Phanerozoic biodiversity crises in a series of impact categories, from greater to lesser (Table 1), and which can be used to analyze both marine and terrestrial ecosystems. As in any ordinal measurement system, such as Mohs Scale of mineral hardness, the ranking is of essence and the interval of change between ranks remains undefined. The primary ecological impact measure is whether a biodiversity crisis triggers an ecosystem collapse and replacement

event: yes (category I) or no (category II). If ecosystems are disrupted but recover (category II), the secondary ecological impact measure is the degree of that disruption: does the biodiversity crisis trigger permanent ecosystem reorganization: yes (category IIa) or no (category IIb). Application of the ecological severity ranking (Table 1) requires a maximum of two binary assessments (I vs. II and IIa vs. IIb). The scale itself has a total of three severity levels (categories I, IIa and IIb; from greatest ecological impact to least ecological impact).

We hope that the proposed scale to measure ecological severity and the preliminary conclusions of this study will stimulate further efforts to assess the ecological impacts of biotic crises in geologic time. The present study considers only the Phanerozoic “Big Five” biotic crises, and further work particularly remains with the less severe biotic crises not included here.

2. Ecological impact of marine biodiversity crises

In seeking an ecological ranking of the five Phanerozoic biodiversity crises, we consider first the marine realm, and then the terrestrial. In the marine realm (Table 2), we propose that category I ecological impacts correspond to changes at the level of Evolutionary Faunas (EFs, sensu Sepkoski, 1984, 1990), and category II ecological impacts correspond to changes at the level of Ecological Evolutionary Units (EEUs, sensu Sheehan, 1996).

Sepkoski (1984, 1990) has argued that the Phanerozoic marine biosphere can be divided into three Evolutionary Faunas: the Cambrian EF, which dominated the Cambrian Period; the Paleozoic EF, which was dominant from the Ordovician through the Permian; and the Modern EF, which was dominant in the Mesozoic and Cenozoic. Sepkoski (1984, 1990) has demonstrated that each successive EF has a slower rate of diversification and turnover but a higher level of maximum diversity. Sepkoski and Miller (1985) have demonstrated not only that the three EFs can be reconstructed from ecological community data, but also that the three EFs have characteristic ecological distributions along an onshore–offshore environmental gradient, and thus are recurrent associations in space as well as time. Bambach (1983, 1985) has

Table 1
A classification of the ecological impacts of a biodiversity crisis

Impact category	Ecological effects
Category I	Existent ecosystems collapse, replaced by new ecosystems post-extinction
Category II	Existent ecosystems disrupted, but recover and are not replaced post-extinction
Subcategory IIa	Disruption produces permanent loss of major ecosystem components
Subcategory IIb	Disruption temporary, pre-extinction ecosystem organization reestablished post-extinction in new clades

Table 2
Signals for each ecological impact category in the marine realm

Impact category	Marine ecological signals
Category I	Collapse of one Evolutionary Fauna (sensu Sepkoski, 1984, 1990) and its passive replacement by another Evolutionary Fauna
Category IIa	Collapse of metazoan reef ecosystems, triggering the replacement of one Ecological Evolutionary Unit (sensu Sheehan, 1996) by another within an Evolutionary Fauna; second-level paleoecological changes (sensu Droser et al., 2000)
Category IIb	Transition of one Ecological Evolutionary Unit to another via community reorganization; third-level paleoecological changes (sensu Droser et al., 2000)

demonstrated that each of the three EFs has a unique and characteristic guild structure, with each of the successive EFs occupying more “ecospace” and having more guilds in total. Bottjer and Ausich (1986) have demonstrated that each EF has its own tiering structure, both above and below the sediment–water interface, and Sheehan (1996) has shown that each of the EFs is characterized by a unique series of periods of ecological structural stability, or EEUs.

The Paleozoic EF, a stable ecological structure that had persisted in the oceanic realm for over 200 million years, collapsed during the end-Permian biodiversity crisis and was passively replaced by the Modern EF, an ecological structure that persists to the present day (Sepkoski, 1984, 1990; Sheehan, 1996; in ecological contrast, the earlier Cambrian EF was actively, competitively, replaced by the Paleozoic EF). It has also been demonstrated that the Permian crisis reset the global pattern of both extinction rates (Van Valen, 1984) and speciation rates (Sepkoski, 1998) in marine ecosystems.

We propose that the collapse of the Paleozoic EF, and its replacement by the Modern EF, meets the criterion of existent ecosystem collapse and replacement post-extinction by a new ecosystem (Tables 1 and 2), and that the end-Permian biodiversity crisis had a category I ecological impact (Table 3). We further argue that the four remaining Phanerozoic biodiversity crises did not trigger existent ecosystem collapse and replacement (Tables 1 and 2), and that these crises did not have a category I ecological impact. The Paleozoic EF persisted, following a

recovery interval, after both the end-Ordovician and Late Devonian crises (Sepkoski, 1984, 1990; Sheehan, 1996), thus the ecological structure of the Paleozoic EF was disrupted but not replaced. Likewise, the Modern EF persisted after both the end-Triassic and end-Cretaceous crises (Sepkoski, 1984, 1990; Sheehan, 1996).

In contrast to the end-Permian, we propose that the four remaining Phanerozoic biodiversity crises instead represent category II ecosystem disruptions (Table 1), or perturbations, of the oceanic realm’s ecological structure, and resulted only in the replacement of one EEU by another (Table 2). However, we also argue that the four remaining Phanerozoic biodiversity crises were not of equal ecological severity. Category IIa ecosystem disruptions result in the permanent loss of major ecosystem components (Table 1); typically, the collapse of metazoan reefs in the marine realm (Table 2), triggering second-level paleoecological changes (sensu Droser et al., 2000). In contrast, category IIb ecosystem disruptions result only in the replacement of one EEU by another through community reorganization without the permanent loss of major ecosystem components, triggering only third-level paleoecological changes (sensu Droser et al., 2000).

Of the four remaining biodiversity crises, the Late Devonian, end-Triassic and end-Cretaceous crises had category IIa ecological impacts, whereas the end-Ordovician crisis did not and thus is of category IIb impact (Table 3). The category IIa impact of the Late Devonian and end-Triassic crises is indicated by the virtual elimination of the global reef component of marine ecosystems that was triggered by both events (Erwin, 1998). The Late Devonian crisis triggered the demise of the largest reef ecosystem ever seen in Earth history (Copper, 1994), as stromatoporoid-tabulate-

Table 3
Ecological severity ranking of Phanerozoic biodiversity crises

Rank	Event	Ecological severity category	
		Marine	Continental
1	End-Permian	I	I
2	End-Cretaceous	IIa	I
3	End-Triassic	IIa	I or IIa
4	Late Devonian	IIa	IIb
5	End-Ordovician	IIb	n.a. ^a

^a n.a.=not applicable.

rugosan reefal constructs shrank in geographic extent by a factor of 5000 from the Frasnian Stage to the Famennian Stage (McGhee, 1996). Although Triassic scleractinian-calcsponge reefs did not have the areal extent of those of the Frasnian Stage in the Late Devonian, the end-Triassic crisis likewise eliminated the global reef component of marine ecosystems and has been judged to be “as dramatic as the much-discussed disappearance of reef ecosystems at the end of the Frasnian” by Hallam and Wignall (1997).

It has long been assumed that the rudist-scleractinian reefal ecosystems of the Cretaceous declined in a stepwise fashion during the Maastrichtian Stage. This assumption has been challenged by Steuber et al. (2002), whose analyses demonstrate that robust rudist-scleractinian reefs persisted into the latest Maastrichtian in the Caribbean. Steuber et al. (2002) argue for a catastrophic demise of rudist-scleractinian reefal ecosystems, related to the Chicxulub impact.

Beyond the collapse of rudist-scleractinian reefs and, in contrast to the benthic effects of the Late Devonian and end-Triassic biodiversity crises, the end-Cretaceous crisis most severely affected biota in the water column, where primary production was essentially eliminated (Zachos et al., 1989). The end-Cretaceous crisis triggered permanent, category IIa, changes in the ecological structure of animals in the water column: in the nektonic megafauna, the marine reptiles that had been abundant throughout the Mesozoic were lost with the exception of marine turtles, and were ecologically replaced by marine mammals in the Cenozoic. Likewise in the nektonic invertebrates, the abundant ammonite faunas of the Mesozoic were eliminated and were replaced by the post-extinction expansion of fishes (Sheehan et al., 1996). Last, Bambach et al. (2002) argue that permanent changes in major aspects of the ecological structure of marine communities following the end-Cretaceous crisis were second only to those triggered by the end-Permian crisis, as seen in the increase in physiologically buffered taxa, predators and motile species in post-Cretaceous marine communities.

In contrast to the Late Devonian, end-Triassic and end-Cretaceous crises, the end-Ordovician biodiversity crisis did not result in the permanent loss of major components of the marine ecosystem, triggered only the replacement of the P2 EEU by the P3 (Sheehan et al., 1996; Erwin, 1998; Droser et al., 2000; Sheehan,

2001; Brenchley et al., 2001), and thus only had a category IIb ecological impact (Table 3). The end-Ordovician crisis produced no change at all in the paleoenvironmental distribution of marine communities of the Paleozoic and Modern EFs, in marked contrast to the Late Devonian crisis (Droser et al., 2000, Fig. 1). In reefal (Copper, 1994; Copper and Brunton, 1991), pelagic (Underwood, 1998) and benthic marine ecosystems (Brenchley et al., 2001) the end-Ordovician crisis produced only a thinning-out of diversity within Bambachian megaguilds (third-level paleoecological changes, Droser et al., 2000), and the Ordovician ecological structure of marine communities re-emerged unchanged following the Early Silurian diversification (Erwin, 1998; Sheehan, 2001; Brenchley et al., 2001).

3. Ecological impact of terrestrial biodiversity crises

At present, there exists no analytical division of the terrestrial animal biosphere into Evolutionary Faunas and Ecological Evolutionary Units equivalent to those produced for the marine animal biosphere by Sepkoski (1984, 1990) and Sheehan (1996). However, Sepkoski (1990) considered the three terrestrial tetrapod assemblages of Benton (1985) to be similar in ecological nature to his marine EFs: (1) the Paleozoic labyrinthodont-anapsid-synapsid assemblage that was terminated in the end-Permian crisis; the (2) diapsid-dinosaur-pterosaur assemblage that was terminated in the end-Cretaceous crisis; and the (3) Cenozoic assemblage of lissamphibians, turtles, lizards, crocodiles, birds and mammals. As such, both the end-Permian and end-Cretaceous biodiversity crises would be classified as category I events, as each triggered the collapse of a terrestrial faunal equivalent of a marine EF (Table 2).

Assessment of the ecological impact of the end-Permian crisis on terrestrial ecosystems has changed dramatically in the past decade (Benton, 1995; Hallam and Wignall, 1997; Wignall, 2001). Similar to its ecological effects in the oceans (category I, Table 3), on the continents the end-Permian crisis initiated the ecological replacement of terrestrial “faunas of Palaeozoic-style tetrapods to modern faunas” (Benton, 1997). The Permian mammal-like reptiles were

particularly hard hit in the extinction, and they lost “their key adaptive zones to two new groups—the archosaurs and rhynchosaurs” (Benton, 1997). In addition to ecological replacement of the tetrapod fauna, paleoecological analyses of both terrestrial plants and fossil soils demonstrate that the end-Permian crisis triggered a collapse of the floral component of continental ecosystems as well (Retallack, 1995; Ward et al., 2000). Floral ecosystem destruction is indicated by the global cessation of peat accumulation (Retallack et al., 1996) and catastrophic soil erosion associated with deforestation (Retallack, 1999; Ward et al., 2000). Floral ecosystem destruction is further indicated by the global distribution of abundant fungal and fern spores in strata at the Permian–Triassic boundary, indicating a planet-wide die-off and rotting of the continental flora (Visscher et al., 1996).

Insect faunas suffered the only major crisis in their evolutionary history during the end-Permian crisis (Labandeira and Sepkoski, 1993). Insects play a major role in modern ecosystems in breaking down plant matter, and their unusual decline during the Permian crisis may have allowed the massive spread of fungi in the extraordinary landscapes of rotting vegetation that apparently had a world-wide distribution in the aftermath of the Permian event (Hallam and Wignall, 1997). We propose that the synchronous collapses of both marine and terrestrial ecosystems (Twitchett et al., 2001), and their subsequent ecological replacements in the Triassic, meet the criterion of existent ecosystem collapse and replacement post-extinction by a new ecosystem (Table 1). They are signals that the end-Permian biodiversity crisis had a category I ecological impact both in the sea and on the land (Table 3).

In contrast to the oceanic realm, we argue that the end-Cretaceous crisis clearly had a category I ecological impact on the continents (Table 3), where it destroyed dinosaur-dominated ecosystems, terminating an evolutionary fauna that had characterized the terrestrial realm for some 140 million years (Benton, 1997; Sereno, 1999). Following the collapse of Cretaceous dinosaur-dominated ecosystems, the terrestrial niches and adaptive zones previously occupied by dinosaurs were reoccupied by newly and rapidly evolving mammalian faunas in the Paleocene. The ecological net result of the end-Cretaceous biodiver-

sity crisis in the terrestrial realm was one of the most dramatic examples of ecosystem collapse and replacement (category I, Table 1) in the geological record (Benton, 1997; Sereno, 1999; Pearson et al., 2001).

We consider the impact of the end-Triassic crisis on the continental biota to be more problematic in terms of an ecological characterization. A major tetrapod replacement does occur from the Triassic to the Jurassic: Early to Middle Triassic terrestrial vertebrate ecosystems are dominated by mammal-like reptiles, rhynchosaurs and basal archosaurs, whereas Jurassic terrestrial ecosystems are dominated by dinosaurs (Benton, 1997). The question is the manner and timing of the replacement of the typical Triassic vertebrate fauna by the dinosaurs. Previous workers have maintained that the ecological replacement was gradual and represented active competitive replacement (Charig, 1984). More recent studies suggest that the ecological replacement was rapid: that the Triassic terrestrial vertebrate fauna of mammal-like reptiles and rhynchosaurs was first decimated in the end-Triassic crisis, and that their subsequent replacement by the dinosaurs was ecologically passive and opportunistic (Benton, 1997; Sereno, 1999; Olsen et al., 2002). In summary, the ecological effect of the end-Triassic biodiversity crisis may have been either of category I or IIa magnitude (Table 3). A more definitive assignment depends upon the outcome of the debate concerning the active versus passive ecosystem replacement hypotheses.

The end-Triassic crisis may not be ecologically equivalent to the end-Cretaceous, but we argue that it clearly had more effect on the continental biota than the Late Devonian crisis (Table 3), which did not trigger any permanent loss in major components of the terrestrial ecosystem (category IIb, Table 1). Freshwater mollusc, arthropod and fish groups experienced a thinning-out of diversity in the Late Frasnian, but the ecological structure of freshwater communities re-emerged essentially unchanged in the Famennian diversification (McGhee, 1996). Terrestrial floral communities experienced a diversity minimum across the Frasnian–Famennian boundary (Raymond and Metz, 1995) but also re-established the same ecosystem structure in the Famennian recovery. In contrast to the Late Frasnian, the much smaller event (in terms of taxonomic diversity loss) that occurred at the end of the Famennian produced a more marked change in the

ecological structure of continental floral ecosystems (Streele et al., 2000).

4. Nonequivalency of ecological and taxonomic severity rankings

We here compare the proposed ecological severity ranking of the five Phanerozoic biodiversity crises (Table 3), obtained in the previous sections, with the taxonomic severity ranking based upon the magnitude of familial diversity loss obtained from the Large Data Bases (LDBs) of Sepkoski (1982) and Benton (1995) (see Benton, 1999 for a discussion of the LDBs of paleontology). The LDB of Sepkoski (1982) is for marine families only (Table 4). It clearly indicates that the end-Permian crisis saw the largest loss of marine diversity and the end-Cretaceous saw the least (Table 4). Between these two extremes, however, the end-Ordovician, Late Devonian and end-Triassic crises sequentially differ only by 1% in the magnitude of their respective diversity losses. Thus, although the end-Ordovician, Late Devonian and end-Triassic crises are ranked second, third and fourth in terms of diversity loss (Table 4), this ranking of the respective taxonomic severities of these three biodiversity crises is not robust in the marine LDB of Sepkoski (1982).

The greatest difference between the taxonomic severity ranking of Sepkoski (1982) and the ecological severity ranking proposed in this study is in the differential ranking of the end-Cretaceous biodiversity crisis (Table 4), which is the least severe in terms of taxonomic diversity loss yet is ecologically the second most severe event in the entire Phanerozoic. The

Table 4

Comparison of Phanerozoic biodiversity crises by ecological and taxonomic severity, where taxonomic severity is measured by familial diversity loss

Ecological severity ranking	Familial diversity loss (%)	
Event	Event	Marine
1. End-Permian	1. End-Permian	–50
2. End-Cretaceous	2. End-Ordovician	–22
3. End-Triassic	3. Late Devonian	–21
4. Late Devonian	4. End-Triassic	–20
5. End-Ordovician	5. End-Cretaceous	–15

Familial diversity data from Sepkoski (1982) and are for the marine realm only.

Table 5

Comparison of Phanerozoic biodiversity crises by ecological and taxonomic severity, where taxonomic severity is measured by familial diversity loss

Ecological severity ranking	Familial diversity loss (%)		
Event	Event	Marine	Continental
1. End-Permian	1. End-Permian	–47.5	–61.5
2. End-Cretaceous	2. Late Devonian	–27.8	–43.6
3. End-Triassic	3. End-Ordovician	–24.3	n.a. ^a
4. Late Devonian	4. End-Triassic	–23.4	–21.7
5. End-Ordovician	5. End-Cretaceous	–14.7	–6.3

Familial diversity data are the most conservative and robust minimum figures reported by Benton (1995) for both the marine and continental realms.

^a n.a. = not applicable.

second greatest difference is in the differential ranking of the end-Ordovician biodiversity crisis. Ecologically, it is the least severe of the five biodiversity crises, whereas it is ranked second in terms of taxonomic severity (Table 4). Given that the ranking of the end-Ordovician, Late Devonian and end-Triassic crises sequentially differ only by a 1% diversity loss, it is possible that the end-Ordovician crisis may rank as low as fourth place in terms of taxonomic severity, yet this is still greater than the ecological severity ranking, where it is ranked last (Table 4).

The LDB of Benton (1995) is for both marine and terrestrial families (Table 5). Where multiple pulses of extinction are reported to occur within the span of a biodiversity crisis (see Benton, 1995), the percentages given in Table 5 represent the most severe loss of diversity reported. The LDB of Benton (1995) corroborates the Sepkoski (1982) ranking of the end-Permian crisis as the most severe loss of diversity and the end-Cretaceous as the least severe (Table 4). Furthermore, the LDB of Benton (1995) indicates that the taxonomic severity ranking of end-Permian as first, and end-Cretaceous as fifth, holds true for both marine and continental realms (Table 5). The LDBs of both Sepkoski (1982) and Benton (1995) yield a fourth-place rank for the taxonomic severity of the end-Triassic crisis (cf. Tables 4 and 5). However, the taxonomic severity ranking of the end-Ordovician and Late Devonian crisis is reversed between the two LDBs. In the Benton (1995) LDB, the Late Devonian crisis is ranked second in terms of diversity loss, both in the marine and continental realms (Table 5).

The most striking example of the decoupling of ecological and taxonomic severities is the end-Cretaceous crisis (Tables 4 and 5). This event is the least severe in terms of taxonomic diversity loss, both in the oceans and on the continents, yet ecologically it is the second most severe. The second-most striking example of the severity decoupling is the end-Ordovician crisis. Clearly, whether it be ranked in second (Table 4) or third (Table 5) place, a significant loss of diversity occurred in the end-Ordovician crisis. Yet ecologically, it is the least severe of the five crises (Sheehan et al., 1996; Erwin, 1998; Droser et al., 2000; Sheehan, 2001; Brenchley et al., 2001).

The two severity measures of the Late Devonian crisis also appear to be decoupled, but not as markedly as for the end-Cretaceous and end-Ordovician. Sepkoski (1982) ranks the taxonomic severity of the Late Devonian crisis in third place, whereas Benton (1995) ranks it higher in second place, yet in ecological impact it ranks only fourth (cf. Tables 4 and 5). In reverse, the ecological severity of the end-Triassic event is ranked higher (third place) than the consistent fourth-place taxonomic severity ranking given it by both Sepkoski (1982) and Benton (1995). In summary of this comparison, only the end-Permian crisis has an ecological severity and a taxonomic severity that is equivalent, namely the highest magnitude in both systems of measurement.

We also compare here the ecological severity ranking (Table 3) with the recent taxonomic ranking of Phanerozoic biodiversity crises by extinction rate severity (Table 6). Considering the extinction intensity per time interval of marine genera during the Phanerozoic, Bambach and Knoll (2001) have argued that only four of the five Phanerozoic biodiversity crises can be accurately designated as “mass ex-

tinctions”, characterized by extinction rates that differ from an exponential continuum of ranked extinction intensities. These are the end-Permian, end-Cretaceous, end-Ordovician and end-Triassic mass extinctions. Neither the Frasnian Stage of the Late Devonian nor its two flanking stages have extinction intensities that depart from the main trend (Bambach and Knoll, 2001).

The two severity rankings are identical for the end-Permian and end-Cretaceous crises, which are respectively the first and second most severe events in both ecological impact and extinction rate (Table 6). However, the end-Ordovician crisis is again ranked highly, third in extinction rate severity, whereas ecologically it is the least severe. Both the end-Triassic and Late Devonian biodiversity crises are ecologically more severe than the end-Ordovician crisis, but the extinction severity of the end-Triassic event is ranked less, and the Late Devonian crisis is not ranked at all, being judged non-anomalous (Bambach and Knoll, 2001).

5. Implications of decoupled ecological and taxonomic severities

What are the causes of the decoupled severities? We suggest that the rate at which taxa go extinct during a biodiversity crisis is only part of its severity (Table 6). Biodiversity loss is not simply the result of elevated extinction rates, it can also be triggered by depressed speciation rates (and, of course, by a combination of the two). It has long been known that the Late Devonian biodiversity crisis was triggered in large part by a precipitous decline in speciation rates at the end of the Frasnian (McGhee, 1988). The ecological severity of this event may be a direct result of its ecological complexity, in that biodiversity loss in the Late Devonian crisis was triggered by elevated extinction rates and depressed speciation rates operating in concert. The ecological impact of the loss of biodiversity in the Late Devonian crisis was much greater than that of the end-Ordovician (Droser et al., 2000; Brenchley et al., 2001).

Likewise, we suggest that the number of taxa lost during a biodiversity crisis is only part of its severity (Tables 4 and 5). The ecological importance of the taxa that are lost provides an important control on

Table 6

Comparison of Phanerozoic biodiversity crises by ecological and taxonomic severity, where taxonomic severity is measured by the extinction rate of marine genera

Ecological severity ranking	Extinction rate severity ranking
1. End-Permian	1. End-Permian
2. End-Cretaceous	2. End-Cretaceous
3. End-Triassic	3. End-Ordovician
4. Late Devonian	4. End-Triassic
5. End-Ordovician	

Extinction rate severity ranking from Bambach and Knoll (2001).

the degree to which the crisis disrupts the ecological architecture of life (Bottjer et al., 2001), and selective removal of specific biological traits or higher taxa may trigger much larger ecological changes than if traits or taxa are eliminated at random (McKinney, 2001; Jablonski, 2001). The environmental degradation produced by the end-Ordovician glaciations precipitated a loss of marine diversity much greater than that of the end-Cretaceous crisis (Tables 4 and 5), and the third largest extinction rate in Earth history (Table 6), yet the extinction failed to eliminate any key taxa or traits, and was of minimal ecological impact. In contrast, the end-Cretaceous crisis produced the least loss of diversity (Tables 4 and 5), but the elimination of key taxa within the dinosaurs, marine reptiles and ammonites triggered the end of the Mesozoic Era of life. We, the mammals, owe our current ecological dominance to that event.

Modern ecological studies recognize the importance of dominant taxa in communities, which have a very high biomass and hence a greater ecological impact on directions and rates of community processes (Power et al., 1996). Other types of taxa, such as keystone species, have a relatively low biomass within a community but have a relatively large ecological impact, commonly as great as that of dominants (Paine, 1969; Power et al., 1996). It is not clear if the value of these modern traits or taxa-types, which exist in ecological time scales, can be scaled up temporally to geological time scales.

However, the results of this study do suggest that there are taxa that are ecologically more significant than others and that removal of these taxa results in major ecological change. That is, the ecological value of component species in an ecosystem is at least as important as species diversity in maintaining the integrity of the ecosystem (Hooper and Vitousek, 1997), and this ecological phenomenon operates on geological timescales as well.

Acknowledgements

This work was supported in part by grants from the National Science Foundation (McGhee, Sheehan, Bottjer, Droser), the National Geographic Society (Bottjer, Droser) and the Petroleum Research Fund,

administered by the American Chemical Society (McGhee, Bottjer, Droser).

References

- Bambach, R.K., 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In: Tevesz, M.J.S., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum, New York, pp. 719–746.
- Bambach, R.K., 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. In: Valentine, J.W. (Ed.), *Phanerozoic Diversity Patterns*. Princeton Univ. Press, Princeton, pp. 191–253.
- Bambach, R.K., Knoll, A.H., 2001. Is there a separate class of “mass” extinctions? *Abstr. Programs-Geol. Soc. Am.* 33 (6), A141.
- Bambach, R.K., Knoll, A.H., Sepkoski, J.J., 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proc. Natl. Acad. Sci. U. S. A.* 99, 6854–6859.
- Benton, M.J., 1985. Patterns in the diversification of Mesozoic non-marine tetrapods and problems in historical diversity analysis. *Spec. Pap. Palaeontol.* 33, 185–202.
- Benton, M.J., 1995. Diversification and extinction in the history of life. *Science* 268, 52–58.
- Benton, M.J., 1997. *Vertebrate Palaeontology*. Chapman and Hall, London.
- Benton, M.J., 1999. The history of life: large databases in palaeontology. In: Harper, D.A.T. (Ed.), *Numerical Palaeobiology*. John Wiley, London, pp. 249–283.
- Bottjer, D.J., Ausich, W.I., 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology* 12, 400–420.
- Bottjer, D.J., Droser, M.L., Sheehan, P.M., McGhee, G.R., 2001. The ecological architecture of major events in the Phanerozoic history of marine invertebrate life. In: Allmon, W.D., Bottjer, D.J. (Eds.), *Evolutionary Paleocology*. Columbia Univ. Press, New York, pp. 35–61.
- Brenchley, P.J., Marshall, J.D., Underwood, C.J., 2001. Do all mass extinctions represent an ecological crisis? Evidence from the Late Ordovician. *Geol. J.* 36, 329–340.
- Charig, A.J., 1984. Competition between therapsids and archosaurs during the Triassic period: a review and synthesis of current theories. *Zool. Soc. London, Symp.* 57, 597–628.
- Copper, P., 1994. Ancient reef ecosystem expansion and collapse. *Coral Reefs* 13, 3–11.
- Copper, P., Brunton, F., 1991. A global review of coral reefs. *Spec. Pap. Palaeontol.* 44, 225–299.
- Droser, M.L., Bottjer, D.J., Sheehan, P.M., McGhee, G.R., 2000. Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass extinctions. *Geology* 28, 675–678.
- Erwin, D.H., 1998. The end and the beginning: recoveries from mass extinctions. *Trends Ecol. Evol.* 13, 344–349.
- Hallam, A., Wignall, P.B., 1997. *Mass Extinctions and Their Aftermath*. Oxford Univ. Press, Oxford.

- Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277, 1302–1305.
- Jablonski, D., 2001. Lessons from the past: evolutionary impacts of mass extinctions. *Proc. Natl. Acad. Sci. U. S. A.* 98, 5393–5398.
- Labandeira, C.C., Sepkoski, J.J., 1993. Insect diversity in the fossil record: myth and reality. *Science* 261, 310–315.
- McGhee, G.R., 1988. The Late Devonian extinction event: evidence for abrupt ecosystem collapse. *Paleobiology* 14, 250–257.
- McGhee, G.R., 1989. Catastrophes in the history of life. In: Briggs, D.E.G., Allen, K.C. (Eds.), *Evolution and the Fossil Record*. Belhaven, London, pp. 26–50.
- McGhee, G.R., 1996. *The Late Devonian Mass Extinction*. Columbia Univ. Press, New York.
- McKinney, M.L., 2001. Selectivity during extinctions. In: Briggs, D.E.G., Crowther, P.R. (Eds.), *Palaeobiology*, vol. II. Blackwell Science, Oxford, pp. 198–202.
- Newell, N.D., 1967. Revolutions in the history of life. *Special Paper - Geological Society of America* 89, 63–91.
- Olsen, P.E., Kent, D.V., Sues, H.-D., Koeberl, C., Huber, H., Montanari, A., Rainforth, E.C., Fowell, S.J., Szajna, M.J., Hartline, B.W., 2002. Ascent of dinosaurs linked to an Iridium anomaly at the Triassic–Jurassic boundary. *Science* 296, 1305–1307.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *Am. Nat.* 103, 65–75.
- Pearson, D.A., Schaefer, T., Johnson, K.R., Nichols, D.J., 2001. Palynologically calibrated vertebrate record from North Dakota consistent with abrupt dinosaur extinction at the Cretaceous–Tertiary boundary. *Geology* 29, 39–42.
- Phillips, J., 1860. *Life on Earth: Its Origin and Succession*. Macmillan, London.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *Bioscience* 46, 609–620.
- Raup, D.M., Sepkoski, J.J., 1982. Mass extinctions in the marine fossil record. *Science* 215, 1501–1503.
- Raymond, A., Metz, C., 1995. Laurussian land-plant diversity during the Silurian and Devonian: mass extinction, sampling bias, or both? *Paleobiology* 21, 74–93.
- Retallack, G.J., 1995. Permian–Triassic life crisis on land. *Science* 267, 77–80.
- Retallack, G.J., 1999. Postapocalyptic greenhouse paleoclimate revealed by earliest Triassic paleosols in the Sydney Basin, Australia. *Geol. Soc. Amer. Bull.* 111, 52–70.
- Retallack, G.J., Veevers, J.J., Morante, R., 1996. Global coal gap between Permian–Triassic extinction and Middle Triassic recovery of peat-forming plants. *Geol. Soc. Amer. Bull.* 108, 195–207.
- Sepkoski, J.J., 1982. Mass extinctions in the Phanerozoic oceans: a review. *Special Paper - Geological Society of America* 190, 283–289.
- Sepkoski, J.J., 1984. A kinematic model of Phanerozoic taxonomic diversity: III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267.
- Sepkoski, J.J., 1990. Evolutionary faunas. In: Briggs, D.E.G., Crowther, P.R. (Eds.), *Palaeobiology: A Synthesis*. Blackwell Scientific, Oxford, pp. 37–41.
- Sepkoski, J.J., 1998. Rates of speciation in the fossil record. *Philos. Trans. R. Soc. Lond.* 353 (B), 315–326.
- Sepkoski, J.J., Miller, A.I., 1985. Evolutionary faunas and the distribution of Paleozoic marine communities in space and time. In: Valentine, J.W. (Ed.), *Phanerozoic Diversity Patterns*. Princeton Univ. Press, Princeton, pp. 153–190.
- Sereno, P.C., 1999. The evolution of dinosaurs. *Science* 284, 2137–2147.
- Sheehan, P.M., 1996. A new look at Ecologic Evolutionary Units (EEUs). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127, 21–32.
- Sheehan, P.M., 2001. The Late Ordovician mass extinction. *Annu. Rev. Earth Planet. Sci.* 29, 331–364.
- Sheehan, P.M., Coorough, P.J., Fastovsky, D.J., 1996. Biotic selectivity during the K/T and Late Ordovician extinction events. *Special Paper - Geological Society of America* 307, 303–317.
- Steuber, T., Mitchell, S.F., Buhl, D., Gunter, G., Kasper, H.U., 2002. Catastrophic extinction of Caribbean rudist bivalves at the Cretaceous–Tertiary boundary. *Geology* 30, 999–1002.
- Streel, M., Caputo, M.V., Loboziak, S., Melo, J.H.G., 2000. Late Frasnian–Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth-Sci. Rev.* 52, 121–173.
- Twitchett, R.J., Looy, C.V., Morante, R., Visscher, H., Wignall, P.B., 2001. Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis. *Geology* 29, 351–354.
- Underwood, C.J., 1998. Population structure of graptolite assemblages. *Lethaia* 31, 33–41.
- Van Valen, L.M., 1984. A resetting of Phanerozoic community evolution. *Nature* 307, 50–52.
- Visscher, H., Brinkhuis, H., Dilcher, D.L., Elsik, W.C., Eshet, Y., Looy, C.V., Rampino, M.R., Traverse, A., 1996. The terminal Paleozoic fungal event: evidence of terrestrial ecosystem destabilization and collapse. *Proc. Natl. Acad. Sci. U. S. A.* 93, 2135–2158.
- Ward, P.D., Montgomery, D.R., Smith, R., 2000. Altered river morphology in South Africa related to the Permian–Triassic extinction. *Science* 289, 1740–1743.
- Wignall, P.B., 2001. End-Permian extinction. In: Briggs, D.E.G., Crowther, P.R. (Eds.), *Palaeobiology*, vol. II. Blackwell Science, Oxford, pp. 226–229.
- Zachos, J.C., Arthur, M.A., Dean, W.F., 1989. Geochemical evidence for suppression of pelagic marine productivity at the Cretaceous/Tertiary boundary. *Nature* 337, 61–64.