

A new ecological-severity ranking of major Phanerozoic biodiversity crises

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

^a Department of Earth and Planetary Sciences, Wright-Rieman Laboratories, Rutgers University, New Brunswick, NJ 08903, USA

^b Department of Earth and Planetary Sciences, University of California, Santa Cruz, CA 95064, USA

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

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

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

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ABSTRACT

A new ecological-severity ranking of the major Phanerozoic biodiversity crises is proposed in which the Capitanian crisis is ranked lesser than the Frasnian (Late Devonian) but greater than the Serpukhovian (end-Mississippian), and the Famennian (end-Devonian) crisis is ranked as equal in ecological impact to the Hirnantian (end-Ordovician). Two new decouplings between taxonomic severity and ecological severity are revealed in these analyses, the Capitanian and Famennian crises, in which the ecological impact of the biodiversity loss was markedly different from the magnitude of the biodiversity loss. These analyses also reveal that the “Great Devonian Interchange” (GDI) invasive-species event in the Givetian biodiversity crisis may provide an important palaeoecological analog for the study of present-day extinction and homogenization in ecosystems produced by modern invasive species.

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1. Introduction

Two separate analyses of the taxonomic severity of biodiversity crises in marine ecosystems since the beginning of the Ordovician, measured in terms of the percentage of marine genera lost in those crises, are given in [Table 1](#). Eleven biodiversity crises are listed, including the well-known Big Five ([Raup and Sepkoski, 1982](#)): the end-Permian (Changhsingian), the end-Ordovician (Hirnantian), end-Triassic (Rhaetian), end-Cretaceous (Maastrichtian), and Late Devonian (Frasnian). The first six of the biodiversity crises have nearly the same taxonomic-severity ranking in the two studies: only the rankings of the Rhaetian and Maastrichtian events are reversed. The taxonomic-severity ranking of the remaining five biodiversity crises varies considerably in the two studies: the Givetian (late Middle Devonian) is ranked seventh and the Serpukhovian (end-Mississippian) ranked tenth, along with the Ludfordian (Late Silurian), by [Sepkoski \(1996\)](#) whereas [Bambach et al. \(2004\)](#) rank the Serpukhovian seventh and the Givetian eighth. The Famennian (end-Devonian) is ranked higher than the Eifelian (early Middle Devonian) by both [Sepkoski \(1996\)](#) and [Bambach et al. \(2004\)](#), although their relative position in the total ranking varies between the two studies ([Table 1](#)).

However, taxonomic severity is only one measure of the biotic impact of a biodiversity crisis—the other is the ecological severity of the crisis. Two measures of the ecological severity of a biodiversity crisis have been developed: a three-level ranking of the magnitude of the ecological disruption produced by the crisis ([McGhee et al., 2004](#)) and a four-level ranking of the ecological impact of the crisis ([Droser et al., 2000](#)). Using these ranking systems, it has been demonstrated that the magnitudes of taxonomic severity and ecological severity of several of the major biodiversity crises are decoupled ([Droser et al., 2000](#); [McGhee et al., 2004, 2012](#)). The most striking example of this decoupling is the Maastrichtian mass extinction: in terms of taxonomic severity it is ranked fifth by [Sepkoski \(1996\)](#) and fourth by [Bambach et al. \(2004\)](#), well below the ranking of the Hirnantian mass extinction ([Table 1](#)). In contrast, in terms of ecological severity ([Table 2](#)) the Maastrichtian mass extinction is the second most severe event in the entire Phanerozoic ([McGhee et al., 2004](#)). A second striking example of the decoupling is the Hirnantian mass extinction. In terms of taxonomic diversity loss, the Hirnantian mass extinction is ranked as the second most severe ([Table 1](#)) in the Phanerozoic by both [Sepkoski \(1996\)](#) and [Bambach et al. \(2004\)](#). In terms of ecological severity, the Hirnantian mass extinction had a minimal ecological impact, less than that of the Serpukhovian ([McGhee et al., 2012](#)), and is ranked sixth in terms of ecological severity ([Table 2](#)).

The object of the present paper is to analyze the relative ecological impacts of the remaining five biodiversity crises listed in [Table 1](#), and

* Corresponding author. Tel.: +1 732 445 8523; fax: +1 732 445 3374.
E-mail address: mcghee@rci.rutgers.edu (G.R. McGhee).

Table 1

Taxonomic-severity ranking of the eleven largest Phanerozoic biodiversity crises since the beginning of the Ordovician, ranked by the percentage loss of marine genera that occurred during the crises in the analyses of Sepkoski (1996, Fig. 3) and Bambach et al. (2004, Fig. 2). The traditional “Big Five” biodiversity crises (Raup and Sepkoski, 1982) are indicated in parentheses and the modern Geologic Stage names are from Walker and Geissman (2009).

Sepkoski (1996) ranking:		Bambach et al. (2004) ranking:	
1. Changhsingian (end-Permian)	–58%	1. Changhsingian (end-Permian)	–57%
2. Hirnantian (end-Ordovician)	–49%	2. Hirnantian (end-Ordovician)	–43%
3. Capitanian	–47%	3. Capitanian	–36%
4. Rhaetian (end-Triassic)	–40%	4. Maastrichtian (end-Cretaceous)	–34%
5. Maastrichtian (end-Cretaceous)	–39%	5. Rhaetian (end-Triassic)	–33%
6. Frasnian (Late Devonian)	–35%	6. Frasnian (Late Devonian)	–22%
7. Givetian	–30%	7. Serpukhovian	–13%
8. Famennian	–28%	8. Givetian	–10%
9. Eifelian	–24%	9. Famennian, Ludfordian	–7%
10. Serpukhovian, Ludfordian	–23%	10. Eifelian	–6%

to propose a new ranking of the ecological severity of the eleven most severe Phanerozoic biodiversity crises since the beginning of the Ordovician.

2. Ecological impact of the Capitanian crisis

The Capitanian (late Middle Permian or Guadalupian) biodiversity crisis is ranked third in taxonomic severity (Table 1) by both Sepkoski (1996) and Bambach et al. (2004). However, it can be shown that estimates of the taxonomic severity of the Capitanian crisis are particularly unstable. Both the analyses of Sepkoski (1996) and Bambach et al. (2004), as well as the extensive analysis of Stanley (2007), are based on versions of the Sepkoski Large Data Base (SLDB) compilation of Sepkoski (2002). The taxonomic severity of the traditional eleven biodiversity crises given in Table 1 were re-calculated in terms of extinction probabilities (Alroy, 2010) using the sampling-standardized occurrence data in the Paleobiology Database (PBDB, www.paleodb.org), and are given in Table 3. The most radical difference between the taxonomic-severity rankings given in Tables 1 and 3 is in that of the Capitanian: it drops from third-most severe in Table 1 to ninth-most severe in the eleven traditional biodiversity crises in Table 3 (in actuality, the Capitanian is ranked still lower at 32 in a total of 66 mid-Ordovician through Cretaceous stages). This radical difference is largely due to updated age assignments in the Paleobiology Database, reflecting improvements to the Permian timescale in the last decade.

We here wish to propose an alternative measure of the severity of the Capitanian biodiversity crisis by analyzing its ecological impact using the ranking of the hierarchy of palaeoecological changes of Droser et al. (1997, 2000). In the ecological-impact ranking system the magnitudes of ecological changes are ranked in four levels (Table 4): changes that occur between ecosystems (first level), within ecosystems (second level), within community types (third level), and within communities (fourth level; for a full discussion of the ranking system see Droser et al., 1997). Using this ranking system it has been demonstrated that the Changhsingian, Maastrichtian, Rhaetian, Frasnian, and Serpukhovian biodiversity crises (Table 2) all triggered second-level

Table 2

Ecological-severity ranking of six of the eleven Phanerozoic biodiversity crises listed in Table 1 (modified from McGhee et al., 2012).

1. Changhsingian (end-Permian)
2. Maastrichtian (end-Cretaceous)
3. Rhaetian (end-Triassic)
4. Frasnian (Late Devonian)
5. Serpukhovian
6. Hirnantian (end-Ordovician)

Table 3

Revised taxonomic-severity estimations of the traditional eleven largest Phanerozoic biodiversity crises since the beginning of the Ordovician (Table 1), based on three-timer extinction probability (Alroy, 2010) calculated from sampling-standardized occurrence data in the Paleobiology Database (www.paleodb.org). Standardization was based on the shareholder quorum subsampling method outlined by Alroy (2010) at a quorum of 0.7.

1. Changhsingian	–83%
2. Rhaetian	–73%
3. Hirnantian	–52%
4. Famennian	–50%
5. Maastrichtian, Frasnian	–40%
6. Serpukhovian	–39%
7. Givetian	–36%
8. Eifelian	–32%
9. Capitanian	–25%
10. Ludfordian	–9%

palaeoecological changes in the marine realm, and we shall argue that the Capitanian did so as well.

2.1. Second-level palaeoecological changes in the Capitanian crisis

The Capitanian crisis had a major impact on reef ecosystems: it caused the demise of the large sponge-microbial reefs that characterized the tropics in the Capitanian (Weidlich, 2002) and triggered severe extinctions among the reef-building hypercalcified demosponges (Kiessling and Simpson, 2011). Following the “end-Guadalupian crisis” in reef evolution (Weidlich, 2002), with the exception of some small biostromes and bryozoan reefs, no significant reef-building occurred until the recovery of reef ecosystems some five to seven million years later in the late Wuchiapingian and Changhsingian (Fan et al., 1990; Flügel and Kiessling, 2002; Weidlich, 2002). The global loss of the Capitanian reef masses and the several-million-year gap in significant reef-building until the Changhsingian reef recovery (Weidlich, 2002), although not as severe as the Frasnian or Changhsingian reef crises, are argued here to constitute a second-level “loss/appearance of metazoan reefs” structural change within marine ecosystems (Table 4).

The Capitanian crisis severely affected the very large, photosymbiotic foraminiferal ecosystems (Stanley and Yang, 1994; Bond and Wignall, 2009). All of the species of the fusulinacean families Neoschwagerinidae and Verbeekinae were driven to extinction, removing all of the large-bodied and morphologically-complex species that had specialized test morphologies for photosymbiosis. Only the smaller and morphologically-simpler species of the staffelid and schubertellid foraminifera survived (Vachard et al., 2010). This loss of the dominant photosymbiotic fusulinacean families, and the reduction

Table 4

Definition of palaeoecological levels and characteristic signals for each level (from Droser et al., 2000).

Level	Definition	Signals
First	Appearance/disappearance of an ecosystem	1. Initial colonization of environment
Second	Structural changes within an ecosystem	1. First appearance of, or changes in ecological dominants of higher taxa 2. Loss/appearance of metazoan reefs 3. Appearance/disappearance of Bambachian megaguilids
Third	Community-type level changes structure	1. Appearance and/or disappearance of within an established ecological community types 2. Increase and/or decrease in tiering complexity 3. “Filling-in” or “thinning” within Bambachian megaguilids
Fourth	Community-level changes	1. Appearance and/or disappearance of communities 2. Taxonomic changes within a clade

in size and in morphological complexity of the surviving foraminifera, is argued here to constitute a second-level structural change “of ecological dominants of higher taxa” within marine ecosystems (Table 4).

The Capitanian crisis had a major ecological impact on ammonoid faunas, in which “radical changes led to a complete replacement of Paleozoic ammonoid communities by Mesozoic ones” in marine ecosystems (Leonova, 2009, p. 858). Ammonoids of the order Ceratitida first appeared at the Early–Middle Permian boundary but by the Capitanian only five genera of the order Ceratitida existed, representing 18% of the ammonoid diversity. Following the Capitanian crisis, the diversity of ceratite genera jumped to 55% in the Wuchiapingian and further increased to 74% in the Changhsingian (Leonova, 2009). The shift in abundance, as quantified by the number of reported fossil occurrences of each order in the Paleobiology Database, was as or more abrupt than the shift in diversity that occurred between the Capitanian and Wuchiapingian (Fig. 1), coincident with the Capitanian extinction. These taxonomic diversity changes are reflected in an ecological shift in marine ecosystem structure from nektobenthic ammonoid faunas to pelagic ammonoid faunas, a shift to a more Mesozoic-style ecosystem structure that occurred some 10 million years before the end of the Palaeozoic and the Changhsingian mass extinction. This fundamental change in the dominance of ammonoid life habits is argued here to constitute a second-level structural change in the “first appearance of, or changes in ecological dominants of higher taxa” within marine ecosystems (Table 4).

2.2. Ecological ranking of the Capitanian crisis

In ecological recovery time the Frasnian and Serpukhovian crises (Table 2) are more similar to one another than to the Capitanian. It took 25 million years for reef carbonate productivity to return to Frasnian levels following the Frasnian crisis (in the Viséan), and 30 million years for reef carbonate productivity to return to Serpukhovian levels following the Serpukhovian crisis (in the Asselian). In contrast, reef carbonate productivity returned to Capitanian levels in seven million years following the crisis (in the Changhsingian; Flügel and Kiessling, 2002). Also, the drop in the global carbonate production of reefs was more similar in the Frasnian and Serpukhovian crises (−98.9% and −97.1%, respectively) than in the Capitanian (−88.7%). However, Flügel and Kiessling (2002, p. 691) issue the caveat in their study that changes in reef carbonate production “may be linked to mass extinctions defined by global biodiversity decreases, but are not necessarily so.” For example, the Hirnantian crisis is ranked third in terms the magnitude of decline in reef carbonate production (Flügel and Kiessling, 2002) but is ranked sixth in terms of ecological impact (Table 2) as reefs regained their dominance

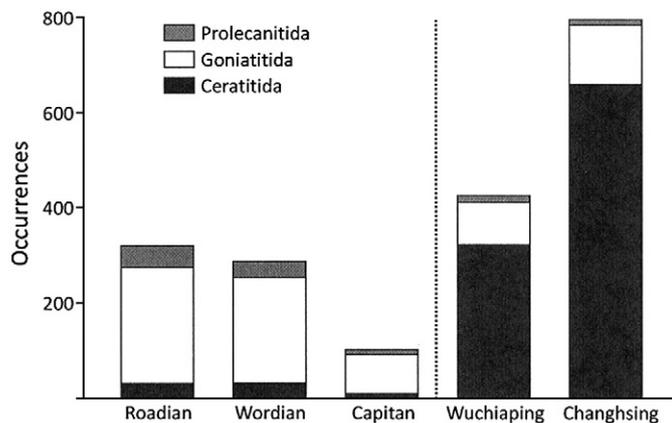


Fig. 1. Occurrence counts for the three late Palaeozoic ammonoid orders from data in the Paleobiology Database (www.paleodb.org). An occurrence is the record of a species from a single fossil collection, and is a proxy for abundance. The Capitanian biodiversity crisis is marked by the vertical dotted line. Abbreviations: Capitan = Capitanian, Wuchiaping = Wuchiapingian, Changhsing = Changhsingian.

in the Early Silurian without major ecological reorganization (to be discussed in Section 3 of this paper).

On the other hand, the Capitanian and Frasnian biodiversity crises share several ecological similarities in their effect on reef ecosystems. Flügel and Kiessling (2002) point out that the most significant changes observed in the constructional guild structures of reefs during the entire Phanerozoic occurred in five events: at the Early–Middle Cambrian boundary and in the Frasnian, Capitanian, Changhsingian, and Rhaetian crises. These crises triggered an abrupt drop in the number of species in the constructor guild, a sharp decline in species in the baffler guild, and an abrupt post-crisis increase of species in the binder guild. The Changhsingian, Rhaetian, and Frasnian crises have been ranked first, third, and fourth in terms of ecological severity in our previous study (Table 2), and the ecological similarity of the Capitanian to these other crises suggests a possible similar ranking range. In contrast, both the Hirnantian and Serpukhovian crises had the reverse ecological effect: a decline in the number of species in the binder guild and a post-crisis increase in the number of species in the constructor and baffler guilds. The Serpukhovian has been ranked fifth, and Hirnantian sixth, in terms of ecological severity (Table 2), and the ecological dissimilarity of the Capitanian to these crises suggests a possibly higher ranking.

Likewise, only five events in the Phanerozoic history of reefs triggered “a clear switch from a metazoan-dominated ecosystem to a microbe-dominated ecosystem” (Flügel and Kiessling, 2002, p. 698): the Early–Middle Cambrian, Frasnian, Capitanian, Changhsingian, and Pliensbachian. In contrast, in both the Hirnantian and Serpukhovian crises the microbial reefs suffered major losses in biota and abundance, rather than experiencing increases as in the five other crises (Flügel and Kiessling, 2002, Fig. 8). Once again, the Capitanian was more ecologically similar to the Changhsingian and Frasnian (ranked first and fourth, Table 2) than to the Serpukhovian and Hirnantian (ranked fifth and sixth).

Last, the Capitanian crisis triggered three second-level palaeoecological changes: within benthic reef ecosystems, benthic photosymbiotic foraminiferal ecosystems, and within pelagic ammonoid ecosystems (Section 2.1). In contrast, the Serpukhovian crisis triggered two second-level palaeoecological changes: within benthic reef ecosystems and within benthic crinoid ecosystems (McGhee et al., 2012). Neither of the reef-ecosystem changes triggered by the Capitanian and Serpukhovian crises were as ecologically severe as that of the Frasnian, which terminated the stromatoporeoid-tabulate component of reef ecosystems and marked a permanent loss in that ecosystem structure (Droser et al., 2000). In summary of this section of the paper, it is here argued that the Capitanian biodiversity crisis had an ecological severity that was lesser than that of the Frasnian crisis, but greater than that of the Serpukhovian.

2.3. Causes of the Capitanian crisis

The Capitanian crisis was also coincident in time (Wignall et al., 2009) with the eruption of the Emeishan Large Igneous Province (LIP) and thus potentially was triggered by the same ecological-disruption mechanism seen in other LIP eruptions: global warming and oceanic acidification (Clapham and Payne, 2011; Payne and Clapham, 2012). The Capitanian crisis may have been more severe ecologically than it was taxonomically because of the environmentally selective nature of the event. For most animal groups, the physiological stresses induced by the Emeishan LIP eruption may not have been sufficiently intense to drive major taxonomic extinctions. In contrast, taxa such as hypercalcified sponges, corals, and larger foraminifera suffered because they had poor physiological buffering and would have been particularly susceptible to the effects of oceanic warming and acidification. The cause of the shift in dominance structure in ammonoid pelagic ecosystems, from the typical Palaeozoic orders of the Goniatitida and Prolecanitida to the more typical Mesozoic order of the Ceratitida, is less clear because the biology of these extinct groups is uncertain but it is of note that the ceratites also survived the

physiologically-driven Changhsingian extinction (also associated with LIP eruptions) whereas goniatites and prolecanitids did not.

3. Ecological impact of the Hirnantian and Famennian crises

It has been previously demonstrated that the severity of taxonomic and ecological losses during the Hirnantian crises was decoupled with other crises, and that only third- and fourth-level palaeoecological changes were triggered (Droser et al., 2000; Brenchley et al., 2001; McGhee et al., 2004, 2012), and that it ranked sixth in terms of the magnitude of its ecological impact in our previous study (Table 2). In this section of the paper, we shall examine in detail the palaeoecological changes that were triggered by the Hirnantian crisis, and compare those changes with those triggered by the Famennian crisis.

3.1. Causes of the Hirnantian and Famennian biodiversity crises

The Hirnantian and Famennian crises appear to have had an equivalent environmental trigger: an intense glaciation phase of geologically short duration within a longer-term glacial period. The Hirnantian intense glaciation phase was less than 1.9 million years in duration (Gradstein et al., 2004) within a longer-term period of glacial advances and retreats in the Late Ordovician and Silurian (Brenchley et al., 1994; Finnegan et al., 2011). The Famennian intense glaciation phase was confined to the last two conodont zones of the Late Devonian within a longer-term glacial period spanning some seven conodont zones in the Late Devonian (Caputo et al., 2008; Isaacson et al., 2008). The Hirnantian intense glaciation phase produced an icecap at least 30,000,000 km² in area (Sheehan, 2001), and the Famennian an icecap at least 16,000,000 km² in area (Isaacson et al., 2008).

Both biodiversity crises also occurred in two pulses: the Hirnantian crisis consisted of an extinction pulse at the beginning of the Hirnantian and a separate extinction pulse at the end of the Hirnantian (Sheehan, 2001). The Famennian consisted of a marine extinction pulse in the middle *praesulcata* conodont zone, followed by a terrestrial extinction pulse in the upper *praesulcata* conodont zone (Streel et al., 2000; Brezinski et al., 2010). Given the equivalency of both the environmental trigger and the two-extinction-pulse structure of the Hirnantian and Famennian crises we wish to see if the two crises had equivalent ecological impacts in the marine realm as well.

3.2. Ecological-impact similarities of the two biodiversity crises

One measure of third-level palaeoecological changes (Table 4) is the degree of “thinning-out” of a Bambachian megaguild (Bambach, 1983) during a biodiversity crisis, and of the “filling-in” of that megaguild post crisis where thinning-out refers to the reduction of the numbers of higher taxa, or to the loss of biodiversity within higher taxa, within a specific Bambachian megaguild and filling-in refers to the reverse phenomenon (Droser et al., 1997). A comparison of third-level palaeoecological changes that were triggered by the Hirnantian and Famennian biodiversity crises is given in Table 5. Five Bambachian megaguilds were affected by both events: the pelagic-filter-feeding, pelagic-carnivore, attached-epifaunal-filter-feeding, mobile-epifaunal-detritivore, and shallow-active-infaunal-detritivore megaguilds.

In the pelagic-filter-feeding megaguild, the chitinozoans and graptolites were the primary zooplankton in the Late Ordovician (Table 5). The chitinozoans suffered significant losses of biodiversity during the Hirnantian crisis (Paris and Nolvak, 1999; Grahn and Paris, 2011) and the graptolites were almost eliminated—only two genera survived (Barnes et al., 1996a) and only the normalograptids reevolved all the major graptolite morphotypes in the Silurian (Chen et al., 2006). Both of these two groups of zooplankton partially recovered post-crisis, but not to the levels of diversity that they had attained in the Late Ordovician. A smaller element of the Late Ordovician zooplankton were the plankton-feeding trilobites of the Ibex and Whiterock trilobite

faunas. The plankton-feeding trilobites were driven to extinction by the Hirnantian crisis and were not ecologically replaced in the Silurian (Fortey and Owens, 1999; Brenchley et al., 2001). Their extinction represents a third-level loss of a community type (Table 4), although the plankton-feeding trilobites played a minor role in the zooplankton of the Late Ordovician.

The primary zooplankton during the Late Devonian had been the tentaculitoids, but they were decimated in the Frasnian biodiversity crisis and had died out before the end of the Famennian (McGhee, 1996; Li, 2000; Wei et al., 2012). The graptolites were not present in significant numbers in the Late Devonian, but the Famennian crisis totally eliminated the chitinozoans (Grahn and Paris, 2011). Similar to the Hirnantian crisis, the extinction of this zooplankton group represents a third-level loss of a community type (Table 4) in the Famennian crisis, although the chitinozoans played a minor role in the zooplankton of the Late Devonian (Grahn and Paris, 2011) just as the plankton-feeding trilobites had played a minor role in this megaguild in the Late Ordovician (Table 5).

In the pelagic-carnivore megaguild (Table 5) the nautiloid orthocerid, lithulitid, and tarphyncerid cephalopods were dominant carnivores in the Late Ordovician (Servais et al., 2010), whereas in the Late Devonian the ammonoid cephalopods and placoderm fishes were the dominant carnivores (McGhee, 1996). The Hirnantian biodiversity crisis reduced the diversity of nautiloid cephalopods to levels not seen since their origination in the Early Ordovician (Crick, 1990) and eliminated the coiled tarphyncerids (Kröger et al., 2009), but by the middle Silurian the nautiloids had rediversified and regained their ecologically prominent position in the pelagic-carnivore megaguild (Crick, 1990; Kröger, 2005; Kröger et al., 2009). In comparison, the Famennian biodiversity crisis also sharply reduced the diversity of cephalopod predators, now ammonoids rather than nautiloids (only two genera survived the crisis; House, 2002), but the ammonoids rediversified in the early Carboniferous, rapidly evolving no less than nine new families (House, 2002).

In both the Late Ordovician and Devonian the conodonts were tiny swimming carnivores that fed on both plankton and on benthic organisms (Jones et al., 2012). The Hirnantian crisis eliminated over 60% of the conodont genera (Sepkoski, 2002) but, post-crisis, they recovered their ecological prominence. The Famennian crisis triggered a major reduction in conodont diversity (40% of their families were lost; Hallam and Wignall, 1997), but the conodonts recovered their diversity post-crisis, just as they did following the Hirnantian crisis.

Predatory fishes, not present in significant numbers in the Late Ordovician, had evolved a position of ecological prominence in the pelagic-carnivore megaguild in the Late Devonian (Table 5). All of the placoderm fish predators were eliminated in the Famennian biodiversity crisis (Young, 2010), but they were ecologically replaced by chondrichthyan fishes in the early Carboniferous with the explosive evolution of no less than 84 new genera (Sallan and Coates, 2010).

It is possible that some larger pelagic trilobites were also carnivores, preying on smaller pelagic trilobites and phyllocarid crustaceans. If so, the extinction of these pelagic-carnivore trilobites during the Hirnantian crisis would represent a third-level loss of a community type (Table 5). In summary, both the Hirnantian and Famennian biodiversity crises triggered major thinning-out of diversity within the pelagic-carnivore megaguild but the structure of the megaguild remained the same as the affected predatory groups either rediversified or, in the case of the placoderms, were ecologically replaced by equivalent predatory groups after the crises had passed. Only the loss of pelagic trilobites that may have been carnivores would represent a third-level loss of a community type within this megaguild.

On the sea bottom, major thinning-out of the attached-epifaunal-filter-feeding megaguild was triggered by both the Hirnantian and Famennian biodiversity crises (Table 5). The Hirnantian crisis eliminated 69% of Late Ordovician non-stromatoporoid sponge species (Carrera and Rigby, 2004) and 73% of stromatoporoid species (Webby, 2004). However, all non-stromatoporoid sponge clades that were ecologically

Table 5

Third-level palaeoecological changes within Bambachian megaguilds (Table 4) triggered by the Hirnantian (end-Ordovician) and Famennian (end-Devonian) biodiversity crises.

1. Pelagic-filter-feeding megaguild
1.1. Crisis thinning-out of Bambachian megaguilds:
1.1.1. Hirnantian crisis:
• Major extinction of chitinozoans (Paris and Nolvak, 1999; Grahn and Paris, 2011)
• Total extinction of plankton-feeding trilobites (Fortey and Owens, 1999)
• Almost total extinction of graptolites (Barnes et al., 1996a; Chen et al., 2006)
1.1.2. Famennian crisis:
• Total extinction of chitinozoans (Grahn and Paris, 2011)
1.2. Post-crisis filling-in of Bambachian megaguilds:
1.2.1. Hirnantian crisis:
• Partial rediversification of chitinozoans (Paris and Nolvak, 1999; Grahn and Paris, 2011)
• Partial rediversification of graptolites (Barnes et al., 1996a; Chen et al., 2006)
2. Pelagic-carnivore megaguild
2.1. Crisis thinning-out of Bambachian megaguilds:
2.1.1. Hirnantian crisis:
• Major extinction of nautiloid cephalopods to diversity levels not seen since their origination in the Early Ordovician and the extinction of advanced coiled nautiloids (Kröger, 2005; Kröger et al., 2009)
• Extinction of pelagic carnivorous trilobites (Fortey and Owens, 1999; Brenchley et al., 2001)
• Major extinction of conodonts (Sheets et al., 2011; Jones et al., 2012)
2.1.2. Famennian crisis:
• Almost total extinction of ammonoid cephalopods (House, 2002)
• Major extinction of conodonts (Hallam and Wignall, 1997)
• Total extinction of placoderm fish predators (Young, 2010)
2.2. Post-crisis filling-in of Bambachian megaguilds:
2.2.1. Hirnantian crisis:
• Rediversification of nautiloid cephalopods to ecological prominence in the megaguild (Crick, 1990; Kröger et al., 2009)
• Rediversification of conodonts (Chen et al., 2006; Sheets et al., 2011)
2.2.2. Famennian crisis:
• Rediversification and recovery of ammonoid cephalopod diversity (House, 2002)
• Rediversification of conodonts (Hallam and Wignall, 1997)
• Major diversification of chondrichthyan fish predators (Sallan and Coates, 2010)
3. Attached-epifaunal-filter-feeding megaguild
3.1. Crisis thinning-out of Bambachian megaguilds:
3.1.1. Hirnantian crisis:
• Major extinction in sponges (Carrera and Rigby, 2004; Webby, 2004)
• Major extinction in corals (Webby et al., 2004)
• Extinction in brachiopods, permanent reduction of strophomenids (Harper and Rong, 2001; Harper, 2010)
• Extinction of <i>Foliomena</i> community brachiopods living in dysoxic habitats (Sheehan, 1977; Rong et al., 1999)
3.1.2. Famennian crisis:
• Almost total extinction of rugose corals (Poty, 1999; Wang et al., 2006)
• Total extinction of stromatoporoid sponges (Hallam and Wignall, 1997)
• Extinction in brachiopods (Simakov, 1993)
3.2. Post-crisis filling-in of Bambachian megaguilds:
3.2.1. Hirnantian crisis:
• Rediversification of sponges (Hallam and Wignall, 1997; Carrera and Rigby, 2004)
• Rediversification of corals (Sheehan, 2001)
• Rediversification of brachiopods, new groups of pentamerids and spiriferids (Harper and Rong, 2001; Harper, 2010)
• Evolution of new dysoxic brachiopod fauna in mid-Silurian (Calef and Hancock, 1974)
3.2.2. Famennian crisis:
• Rediversification of rugose corals (Poty, 1999; Wang et al., 2006)
• Rediversification of brachiopods (Simakov, 1993)
4. Mobile-epifaunal-detritivore megaguild
4.1. Crisis thinning-out of Bambachian megaguilds:
4.1.1. Hirnantian crisis:
• Major extinction in detritus-feeding bivalves (Cope, 2004)
• Extinction in gastropods (Erwin and Signor, 1991; Fryda and Rohr, 2004)
• Major extinction in ostracodes, especially palaeocopes (Sheehan, 2001; Sepkoski, 2002)
• Extinction in jawless fishes (Turner et al., 2004)
4.1.2. Famennian crisis:
• Extinction in gastropods (Erwin and Signor, 1991)
• Extinction in benthic ostracodes (Hallam and Wignall, 1997)
• Total extinction of all non-petromyzontiform jawless fishes (Benton, 2005)
4.2. Post-crisis filling-in of Bambachian megaguilds:
4.2.1. Hirnantian crisis:
• Rediversification of detritus-feeding bivalves (Cope, 2004)
• Rediversification of gastropods (Erwin and Signor, 1991; Fryda and Rohr, 2004)
• Rediversification of benthic ostracodes (Hallam and Wignall, 1997)

4.2.1. Hirnantian crisis:

- Rediversification of jawless fishes with new advanced morphologies (Turner et al., 2004)

4.2.2. Famennian crisis:

- Rediversification of gastropods (Erwin and Signor, 1991)
- Rediversification of benthic ostracodes (Hallam and Wignall, 1997)
- Major diversification of actinopterygian fishes (Sallan and Coates, 2010)

5. Shallow-active-infaunal-detritivore megaguild

5.1. Crisis thinning-out of Bambachian megaguilds:

5.1.1. Hirnantian crisis:

- Extinction of Cambrian EF trilobites (Adrian et al., 1998)

5.1.2. Famennian crisis:

- Almost total extinction of trilobites (Caplan and Bustin, 1999)

5.2. Post-crisis filling-in of Bambachian megaguilds:

5.2.1. Hirnantian crisis:

- Diversification of Palaeozoic EF trilobites (Adrian et al., 1998)

5.2.2. Famennian crisis:

- Rediversification of trilobites (Caplan and Bustin, 1999)
-

dominant in the Late Ordovician rediversified and regained their dominance in the early Silurian (Carrera and Rigby, 2004), and the stromatoporoids rediversified as well (Hallam and Wignall, 1997; Nestor and Stock, 2001). In contrast, all stromatoporoid sponges were driven to extinction in the Famennian crisis (Hallam and Wignall, 1997). The stromatoporoids had previously suffered massive extinctions in the Frasnian biodiversity crisis (McGhee, 1996), some 15 million years earlier and, unlike in the Hirnantian crisis, the surviving stromatoporoid lineages did not survive the Famennian crisis. The extinction of the stromatoporoids represents a third-level loss of a community type (Table 4) as they were not replaced by ecologically-equivalent filter-feeding organisms in the Early Carboniferous.

Globally, the rugose corals lost about half their generic diversity in the Hirnantian crisis, although corals in the Baltoscandian region lost only about a quarter of their genera (Webby et al., 2004). The tabulate corals lost their ecological dominance and the tetradiid corals were driven to extinction (Webby et al., 2004). However, post-crisis rugose corals rediversified and surpassed their former diversity in the Silurian (Sepkoski, 2002). In the Famennian crisis the rugose corals were almost driven to extinction (Poty, 1999), with only one genus surviving of the once-diverse rugosan fauna in China (Wang et al., 2006). Post-extinction, two surviving species of Famennian rugose corals began to rediversify, and a major radiation of new Carboniferous-type rugosans occurred later in the Tournaisian (Poty, 1999; Wang et al., 2006).

Brachiopods lost over half of their generic diversity in the Hirnantian crisis, with the ecologically dominant strophomenid and orthid brachiopods suffering the greatest diversity losses (Harper and Rong, 2001). Post-crisis, however, the orthids recovered their ecological prominence but strophomenids did not (Harper and Rong, 2001). Instead, new spiriferid and pentamerid brachiopods, rare in the latest Ordovician, diversified in the early Silurian (Harper et al., 2004). Specialized dysoxic-habitat brachiopods of the *Foliomena* and related communities were driven to extinction in the Hirnantian crisis, probably due to the ventilation of the global ocean by the sinking of oxygenated, cold, and dense water masses from near the glacial margin. However, in the mid-Silurian the extinct brachiopods in this community type were ecologically replaced by new, morphologically similar brachiopods that occupied this unique dysoxic habitat (Calef and Hancock, 1974; Hancock et al., 1974; Sheehan, 1977).

The Famennian crisis did not have as great an impact on brachiopod diversity as the Hirnantian, perhaps due to the fact that the brachiopod faunas had been decimated in the Frasnian crisis some 15 million years earlier (McGhee, 1996). Simakov (1993) does note that the typical inner-shelf Devonian brachiopod species and ephemeral species of the Eastern European province were driven to extinction in the Famennian crisis, and these two groups also suffered varying diversity losses in the Kazakhstan-Altayan and Eastern-Siberian provinces as well. Post-crisis, brachiopod diversity was recovered by speciation of typical Carboniferous taxa (Simakov, 1993).

In the mobile-epifaunal-detrivore megaguild (Table 5) the benthic trilobites, ostracods and gastropods were dominant in the Late Ordovician (Servais et al., 2010) whereas in the Late Devonian the jawless fishes were the dominant vagrant detritivores (McGhee, 1996). Bivalve diversity was still relatively low in the Ordovician but the detritus-feeding nuculoids were particularly hard hit in the Hirnantian crisis (only 3 of 9 genera survived; Cope, 2004) but recovered post crisis. Bivalves survived the Famennian crisis unusually well with the exception of the nuculoids which experienced a slight loss of diversity (Sepkoski, 2002). Both crises appear to have produced equivalent diversity drops in gastropods (Erwin and Signor, 1991; Sepkoski, 2002), but post-crisis gastropods recovered their diversity. Particle-feeding and filter-feeding ostracodes lost 60% of their genera during the Hirnantian crisis, and palaeocope ostracodes were hit particularly hard (Sepkoski, 2002), but podocope ostracodes began a gradual expansion in diversity post crisis. Benthic ostracodes lost 17% of their familial diversity in the Famennian (Hallam and Wignall, 1997), but recovered post crisis.

Detritivorous jawless fishes are present in the Late Ordovician (Pteraspidomorphi: Astraspida, Arandaspidia, and Heterostraci; Benton, 2005) but apparently they were rare and not ecologically prominent (Servais et al., 2010). By the Late Devonian the jawless fishes had evolved a position of ecological prominence in the mobile-epifaunal-detrivore megaguild (Table 5). Even at low diversity, however, the Hirnantian biodiversity crisis appears to have elevated extinction rates in jawless fishes and other vertebrates, and that extinction pulse was then followed by “a post-Hirnantian recovery indicating major innovation in the thelodonts, pteraspidomorphs, and possibly the acanthodians” (Turner et al., 2004, p. 334). All of the non-petromyzontiform jawless fishes were eliminated in the Famennian biodiversity crisis (three entire clades: the Pteraspidomorphi, Anaspida, and Osteostraci; Benton, 2005), but they were replaced by the explosive evolution of no less than 70 new genera of actinopterygian fishes in the Early Carboniferous (Sallan and Coates, 2010). Thus both the Hirnantian and Famennian biodiversity crises triggered thinning-out of diversity within the mobile-epifaunal-detrivore megaguild but the structure of the megaguild remained the same as the affected detritivorous groups either rediversified or, in the case of the non-petromyzontiform jawless fishes in the Famennian, were ecologically replaced by equivalent detritivore groups after the crises had passed.

Both the Hirnantian and Famennian biodiversity crises triggered major thinning-out of diversity within the shallow-active-infaunal-detrivore megaguild, followed by post-crisis ecological recovery of the infaunal detritivores with no change in the megaguild structure itself (Table 5). The Hirnantian crisis eliminated all of the Cambrian “Evolutionary Fauna” (EF; sensu Sepkoski, 1984) detritivorous trilobites, but these trilobites were ecologically replaced by the diversification of Palaeozoic EF detritivorous trilobites post-crisis (Adrian et al., 1998). Likewise, the Famennian biodiversity crisis almost eliminated trilobite detritivores (Feist, 1991; Hallam and Wignall, 1997; Caplan and Bustin, 1999), but the few surviving trilobites experienced a final Palaeozoic rediversification pulse post-crisis.

3.3. Ecological-impact dissimilarities of the two biodiversity crises

Both crises triggered third-level terminations of two community types that were not ecologically replaced post crisis, but two of the megaguilds affected by this thinning-out were different: both the Hirnantian and Famennian crises terminated lineages in the pelagic-filter-feeding megaguild (filter-feeding trilobites and chitinozoans, respectively), but the Hirnantian crisis terminated an ecological group in the pelagic-carnivore megaguild (carnivorous trilobites) whereas the Famennian crisis terminated an ecological group in the attached-epifaunal-filter-feeding megaguild (stromatoporoid sponges). The latter two thinning-out events represent two non-equivalent ecological changes in megaguild structure produced by the two crises.

3.4. Summary

The overwhelming number of ecological changes produced by these two crises was very similar: a total of 22 ecologically-equivalent thinning-out and post-crisis rediversifications or replacement couplets in the same five Bambachian megaguilds (Table 5), megaguilds that overwhelmingly retained their same ecological structure post crisis. When megaguild structures were changed, both crises produced a permanent thinning-out change in the same megaguild: the pelagic-filter-feeding megaguild. Only in the pelagic-carnivore and attached-epifaunal-filter-feeding megaguilds did two non-equivalent ecological changes occur in the two crises (see Section 3.3). Thus it is argued that the Hirnantian and Famennian biodiversity crises had an essentially equivalent ecological severity: that is, that neither crisis is demonstrably more ecologically severe or less ecologically severe than the other.

4. A preliminary ecological ranking of the Ludfordian, Eifelian, and Givetian crises

4.1. The Givetian crisis

The Givetian biodiversity crisis consisted of two separate extinction events: an earlier event within the Givetian variously named the Taghanic Event (House, 1985), the *Pharciceras* Event (Walliser, 1983), and the Late Givetian Event (Walliser, 1996), and a later event at the end of the Givetian variously named the Frasnian Event (House, 1985), the *Manticoceras* Event (Walliser, 1985), the Ense Event (Ebert, 1993), and the Givetian–Frasnian Boundary Event (Walliser, 1996). House (2002, p. 15) noted that the “Taghanic Event covers a long time span” and that it was a phased event. Ebert (1993) also demonstrated that different animal groups experienced their greatest diversity losses at the different times: for example, the corals and stromatoporoids in the upper *varcus* conodont zone, and the brachiopods near the lower-upper *hermanni-cristatus* conodont zonal boundary. Walliser (1996) stated that diversity losses in the event began in the middle *varcus* conodont zone, became more pronounced in the upper *varcus* conodont zone, and continued through the lower and upper *hermanni-cristatus* conodont zones. Thus the Taghanic Event in the Givetian crisis was spread over four conodont zones and the Frasnian Event in the crisis started at the base of the lower *falsiovalis* conodont zone and may be confined to that single conodont zone.

House (1985, 2002) and Walliser (1996) argued that both the Taghanic and Frasnian Events were triggered by major and rapid sea-level rises, and that reefal species in particular suffered extinction by drowning in that reef growth could not take place fast enough to keep up with the deepening of marine waters. Episodic and cumulative sea-level rises continued throughout the entire Frasnian Age, peaking with a maximum onlap of the continents at the end of the Frasnian (Johnson et al., 1985). While the extinction of many reefal species may have been due to drowning, reefal and other marine species also suffered extinction due to a quite different phenomenon: the arrival of invasive species.

The progressive marine onlap onto the continents from the Givetian through the Frasnian triggered one of the largest invasive-species episodes in the marine realm during the Palaeozoic, the “Great Devonian Interchange” (GDI; McGhee, 1997), comparable to the Pleistocene interchange of terrestrial species between North and South America. Early Devonian and Eifelian marine faunas were highly endemic and divided into three major biogeographic realms: the “Old World Realm” (OWR) in eastern, northern, and western Laurussia and the eastern margin of Gondwana, the “Eastern Americas Realm” (EAR) in central Laurussia and the margin of Gondwana to the south, and the cooler southern “Malvinokaffric Realm” (MR) in most of Gondwana (Boucot et al., 1968; Boucot, 1988; Oliver, 1977). Sea-level rise throughout the Givetian and Frasnian led to the progressive breaching of previous land barriers to marine species migration, bringing an end to the

older endemic faunas and the establishment of a cosmopolitan marine fauna by the end of the Frasnian (Johnson, 1970). The GDI invasive-species event triggered wholesale extinction via ecological relays, where geographically-restricted endemic species were replaced by ecologically equivalent invasive species (Johnson, 1970; McGhee, 1981, 1997; Stigall, 2010).

The GDI invasive-species event has been intensively studied using Geographic Information System technology by Rode and Lieberman (2004). Although their data base included only 28 of the most common genera of brachiopods and bivalves of the EAR and OWR, the results of this modern-technology approach to the analysis of invasive-species phenomena are instructive. In the Taghanic Event, Rode and Lieberman (2004) document three invasion events in the lower *hermanni-cristatus* conodont zone and two in the upper *hermanni-cristatus* conodont zone whereas in the Frasnian Event, the single lower *falsiovalis* conodont zone, that number jumped to seven. The invasion continued episodically through the span of the Frasnian, peaking with 15 invasion events in the late Frasnian (Rode and Lieberman, 2004). Each of the observed spikes in the number of invasion events are argued by Rode and Lieberman (2004) to correspond with pulses of sea-level rise.

In the attached-epifaunal-filter-feeding megaguild (Table 6) a major extinction of rugose corals and the beginning of the collapse of Middle Devonian reefal ecosystems took place during the Taghanic Event (18 families were lost; House, 2002). However, Oliver and Pedder (1994, p. 186) noted that the coral extinctions were selective in that all of the endemic coral genera of the EAR were driven to extinction and the “Frasnian coral genera in the area of the former EAR were all widespread or cosmopolitan forms of OWR origin;” that is, they were genera of invasive species. A major extinction of brachiopods also took place during the Taghanic Event (14 families were lost; House, 2002). However, Johnson (1970, p. 2077) noted the selectivity of many brachiopod extinctions in that the Taghanic Event started the “end of North American Devonian provinciality” in brachiopod faunas with the replacement of endemic EAR faunas with invasive, geographically-widespread OWR faunas throughout the Frasnian (McGhee, 1981, 1997; Stigall, 2010). Unlike the EAR coral species, which were all driven to extinction (Oliver and Pedder, 1994), a few EAR brachiopod species managed to migrate out of the EAR region into the OWR to the west (*Pseudatrypa devoniana* for example; see Rode and Lieberman, 2004). In the same megaguild, the stalked echinoderms were hard-hit in the Frasnian Event: this

event reduced crinoid generic diversity by approximately 33% (Sallan et al., 2011) and blastoid generic diversity by 86% (Waters, 1990). Only one genus of blastoid, *Hyperblastus*, survived into the Frasnian in the EAR in the Appalachian basin and it was an invasive species from the OWR in New Mexico (Waters, 1990). A major refugium from extinction for both blastoids and crinoids appears to have existed in the OWR northwestern region of China (Waters and Webster, 2009).

In the mobile-epifaunal-detritivore megaguild (Table 6) the Taghanic Event triggered a major extinction of trilobites, globally eliminating four families and two subfamilies (Feist, 1991). However, Feist (1991, p. 208) noted that the trilobites that were eliminated were largely endemic, being found in “numerous and varied habitats in palaeogeographically distinct domains,” an endemism that “vanishes at the Taghanic Event.” In the Frasnian Event, trilobite faunas outside of the MR did not experience “any notable trilobite extinction with the probable exception of the koneprusiins” (Feist, 1991, p. 199). In the cold-water MR of Gondwana the Frasnian Event did trigger a drop in species diversity of calmonioid trilobites from 22 to five: a 77% reduction in biodiversity (Abe and Lieberman, 2009). Abe and Lieberman (2009, p. 232) further demonstrate that this loss of biodiversity was linked to “a decline in speciation rates associated with a decline in geographic provincialism,” that is, the decline of endemic species in the MR and the survival of invasive species with low speciation rates.

Last, in the mobile-epifaunal-carnivore megaguild the global species diversity of phyllocarid crustaceans dropped from 23 at the end of the Givetian to 10 in the early Frasnian (Rode and Lieberman, 2005), thus the Frasnian Event triggered a 56% reduction in species diversity. However, this diversity loss was selective as Rode and Lieberman (2005) also demonstrate an increase in the mean area of geographic range of species in the Frasnian as opposed to those in the Givetian, an increase that reflects the replacement of endemic Givetian species by cosmopolitan, geographically-widespread invasive species.

Not all of the species extinctions that occurred in the Givetian biodiversity crisis can be attributed to the GDI invasive-species event. As noted previously, both House (1985, 2002) and Walliser (1996) argue that many coral and stromatoporoid reefal species suffered extinction by drowning during rapid sea-level rises during the Taghanic and Frasnian Events. In addition, Stock (1990) further attributes the local extinction of Givetian stromatoporoids in the Appalachian Basin of the EAR to the increased influx of silt and mud into the basin that was generated by the uplift of the Acadian Mountains, noting that stromatoporoid faunas still existed in the Missouri and Iowa basins to the west in the Frasnian, at a distance removed from the Acadian Mountains. In the pelagic-carnivore megaguild (Table 6) the goniatite cephalopods exhibit an extinction–diversification–extinction pattern in the Taghanic and Frasnian Events interval that appears to be unrelated to geographic migrations of these nektonic, bottom-swimming species. Barnes et al. (1996b) attributed both of these Givetian extinction events to environmental changes triggered by sea-level rise, and House (1985, 2002) stressed the role of the onset of oxygen depletion and anoxia in marine bottom waters following major marine transgressions as a causal extinction mechanism.

4.2. The Ludfordian crisis

The Ludfordian crisis consisted of three separate events: the early Ludfordian (upper *leintwardiensis* graptolite zone), middle Ludfordian (upper *bohemius-kozłowski* graptolite zone), and the late Ludfordian (upper *formosus* graptolite zone) extinctions (Kaljo et al., 1996). The Ludfordian Age spanned some 2.6 million years of time (Gradstein et al., 2004), thus the Ludfordian crisis was a stepped, protracted ecological event.

The Ludfordian biodiversity crisis principally affected four Bambachian megaguilds of marine animals (Table 7). In the pelagic-filter-feeding megaguild the early Ludfordian Event eliminated many diverse and specialized monograptid graptolites and all of the plectographids, but

Table 6

Third-level palaeoecological changes within Bambachian megaguilds (Table 4) triggered by the Givetian (late Middle Devonian) biodiversity crisis.

1. Pelagic-carnivore megaguild
1.1. Crisis thinning-out of Bambachian megaguilds:
1.1.1. Taghanic Event:
• Extinction of all maeniceratid and agoniatitid goniatite cephalopods (House, 2002)
1.1.2. Frasnian Event:
• Extinction of all petteroceratid and pharciceratid goniatite cephalopods (House, 2002)
1.2. Post-crisis filling-in of Bambachian megaguilds:
1.2.1. Taghanic Event:
• Diversification of pharciceratid goniatite cephalopods (House, 2002)
2. Attached-epifaunal-filter-feeding megaguild
2.1. Crisis thinning-out of Bambachian megaguilds:
2.1.1. Taghanic Event:
• Major extinction in endemic rugose corals (Oliver and Pedder, 1994)
• Major extinction in endemic brachiopods (Johnson, 1970; McGhee, 1997)
2.1.2. Frasnian Event:
• Major extinction in endemic stalked echinoderms (Waters, 1990)
3. Mobile-epifaunal-detritivore megaguild
3.1. Crisis thinning-out of Bambachian megaguilds:
3.1.1. Taghanic Event:
• Major extinction in endemic trilobites in the EAR and OWR (Feist, 1991)
3.1.2. Frasnian Event:
• Major extinction in endemic trilobites in the MR (Abe and Lieberman, 2009)
4. Mobile-epifaunal-carnivore megaguild
4.1. Crisis thinning-out of Bambachian megaguilds:
4.1.1. Frasnian Event:
• Major extinction in endemic phyllocarid crustaceans (Rode and Lieberman, 2005)

Table 7

Third-level palaeoecological changes within Bambachian megaguilds (Table 4) triggered by the Ludfordian (Late Silurian) biodiversity crisis.

-
1. Pelagic-filter-feeding megaguild
 - 1.1 Crisis thinning-out of Bambachian megaguilds:
 - 1.1.1. Early Ludfordian Event:
 - “Leintwardienensis extinction event” in graptolites (Kaljo et al., 1996)
 - 1.1.2. Middle Ludfordian Event:
 - “Podoliensis extinction event” in graptolites (Kaljo et al., 1996)
 - 1.1.3. Late Ludfordian Event:
 - “Spineus extinction event” in graptolites (Kaljo et al., 1996; Sadler and Cooper, 2011)
 - 1.2. Post-crisis filling-in of Bambachian megaguilds:
 - 1.2.1. Early Ludfordian Event:
 - Partial rediversification of graptolites (Kaljo et al., 1996; Sadler and Cooper, 2011)
 2. Pelagic-carnivore megaguild
 - 2.1. Crisis thinning-out of Bambachian megaguilds:
 - 2.1.1 Early Ludfordian Event:
 - Major extinction in conodonts (Kaljo et al., 1996)
 - 2.1.2 Middle Ludfordian Event:
 - Major extinction of nautiloids (Kröger, 2005)
 3. Attached-epifaunal-filter-feeding megaguild
 - 3.1. Crisis thinning-out of Bambachian megaguilds:
 - 3.1.1. Middle Ludfordian Event:
 - Extinction in corals (Kaljo et al., 1996)
 - 3.1.2. Late Ludfordian Event:
 - Almost total extinction of pentamerid and subrianid brachiopods (Kaljo et al., 1996)
 - 3.2. Post-crisis filling-in of Bambachian megaguilds:
 - 3.2.1. Late Ludfordian Event:
 - Diversification of gypidulid brachiopods (Kaljo et al., 1996)
 4. Mobile-epifaunal-detritivore megaguild
 - 4.1. Crisis thinning-out of Bambachian megaguilds:
 - 4.1.1. Early Ludfordian Event:
 - Extinction in ostracoderm fishes (Kaljo et al., 1996)
 - 4.1.2. Middle Ludfordian Event:
 - Extinction in ostracoderm and acanthodian fishes (Kaljo et al., 1996)
 - 4.2. Post-crisis filling-in of Bambachian megaguilds:
 - 4.2.1. Middle Ludfordian Event:
 - “Hedei event” diversification of fishes (Kaljo et al., 1996)
-

was followed by the diversification of the *Monograptus dalejensis*, *Monograptus uncinatus*, *Cucullograptus*, *Polonograptus* groups (Kaljo et al., 1996). However, fewer graptolite species survived the middle Ludfordian Event and, following the late Ludfordian Event, graptolite diversity dropped to two to three species (Kaljo et al., 1996).

In the pelagic-carnivore megaguild, the conodonts lost 85% of their species assemblages in the early Ludfordian Event and only a few subspecies variants of *Ozarkodina eosteinhornensis* survived until the end of the Silurian (Kaljo et al., 1996). A major extinction of nautiloids occurred in the middle Ludfordian Event, of equal or greater magnitude to that that occurred in the Hirnantian (Kröger, 2005).

In the attached-epifaunal-filter-feeding megaguild (Table 7), the rugose, tabulate, and heliolitid corals lost around 45 genera in the middle Ludfordian Event (Kaljo et al., 1996). The late Ludfordian Event almost eliminated the pentamerid and subrianid brachiopods, but these were ecologically replaced by a post-crisis diversification of gypidulid brachiopods in the same benthic assemblages (Kaljo et al., 1996).

In the mobile-epifaunal-detritivore megaguild (Table 7), several genera of ostracoderm fishes were lost in the early Ludfordian Event and both ostracoderm and acanthodian fishes were lost in the middle Ludfordian Event (Kaljo et al., 1996). However, this extinction event was followed by a “profound innovation” or “hedei event” evolutionary diversification in fishes (Kaljo et al., 1996, p. 183) with the evolution of new thelodont, heterostracan, anaspid, acanthodian, and osteichthyan fishes. The radiation of these fishes may be an example of ecological release following an extinction event when loss of ecological constraints permits survivors to radiate into vacated ecospace, as in the replacement of dinosaurs by mammals following the Maastrichtian crisis. A decrease in mobile benthos and/or herbivores which restrict formation of microbial mats is indicated by the local expansion of microbial mats and stromatolites following the Ludfordian crisis (Calner, 2005).

In their own ranking system of diversity-change impacts, Kaljo et al. (1996) rank the middle Ludfordian Event as taxonomically more severe than the early Ludfordian, and the early Ludfordian Event as taxonomically more severe than the late. Thus Kaljo et al. (1996) propose that the Ludlow biodiversity crisis started with moderately-severe diversity losses (early Ludfordian “third-order bio-event,” Dimitri Kaljo in Barnes et al., 1996b, p. 328) which then intensified in the middle Ludfordian (“second-order bio-event”) but significantly waned by the late Ludfordian (“fifth-order bio-event”).

However, the largest carbon-isotope excursion in the marine realm during the entire Silurian occurred during the late Ludfordian Event, not the middle (Munnecke et al., 2003). Munnecke et al. (2003) have demonstrated an interesting lag-time effect in marine extinctions in the Silurian: the extinctions consistently began before major positive stable-isotope excursions, geochemical perturbations that are argued to indicate the onset of arid, and perhaps colder, palaeoclimatic periods. They further noted that pelagic-planktonic, hemipelagic-nektonic, and nektonic floating and swimming organisms were most strongly affected, and benthic reefal organisms like corals and brachiopods to a lesser extent, and thus argued that this “indicates the mechanism for the extinctions first acted in the deeper ocean realm and then extended into the shallower marginal seas” (Munnecke et al., 2003, p. 119). On the other hand, while noting that isotopic excursions in the global carbon cycle were more frequent and of higher magnitude in the Silurian than in any other period in the Phanerozoic, Munnecke et al. (2010, p. 391) also noted that “there is no general agreement on the palaeoenvironmental changes responsible for these excursions.”

4.3. The Eifelian crisis

The Eifelian biodiversity crisis consisted of two separate extinction events: an earlier event within the Eifelian that has been named the Lower Kačák Event (also known as the *Otomari* Event; Walliser, 1996) after the Kačák Black Shale Member of the Srbsko Formation in Bohemia, and a later event that has been named the Upper Kačák Event (Walliser, 1996) at the Eifelian-Givetian boundary. Walliser (1996) indicates the Lower Kačák Event to have occurred in the *ensensis* conodont zone, and Walliser (1996) and House (2002) indicate that the Upper Kačák Event occurred in the *ensensis-hemiansatus* conodont zonal interval around the Eifelian-Givetian boundary, thus the Eifelian crisis spanned two conodont zones.

The Eifelian crisis primarily affected four Bambachian megaguilds (Table 8). In the pelagic-carnivore megaguild Walliser (1996) noted that only one genus of goniatites, *Exopinacites*, went extinct in the Lower Kačák Event but that four genera were eliminated in the Upper Kačák Event. On the other hand, House (2002) stated that five entire families of nautiloid cephalopods went extinct in the Eifelian, but it is not known if these families were lost in the Lower Kačák Event, Upper Kačák Event, or both. In the pelagic-filter-feeding megaguild (Table 8), Walliser (1996) noted that a large number of typical Eifelian conodont species vanished in the Lower Kačák Event, but that these species were ecologically replaced post-crisis by new species within the *Polygnathus* and *Icriodus* conodont lineages. In contrast, in the Upper Kačák Event the conodonts “do not show a major turnover” (Walliser, 1996, p. 232).

On the sea bottom, in the attached-epifaunal-filter-feeding megaguild (Table 8), House (2002) noted that seven families of tabulate corals, six families of rugose corals, and 12 families of brachiopods are estimated to have gone extinct in the Eifelian Age, but that it is uncertain whether these extinctions occurred in the Lower Kačák Event, Upper Kačák Event, or both. Last, in the mobile-epifaunal-detritivore megaguild (Table 8), Feist (1991) noted the extinction of one family and seven sub-families of trilobites in the Lower Kačák Event.

The Lower Kačák extinctions have been attributed by many authors to the sudden and global onset of anoxic, oxygen-deficient conditions in marine shelf environments that smothered benthic organisms

Table 8

Third-level palaeoecological changes within Bambachian megaguilds (Table 4) triggered by the Eifelian (early Middle Devonian) biodiversity crisis.

1. Pelagic-filter-feeding megaguild
1.1 Crisis thinning-out of Bambachian megaguilds:
1.1.1. Lower Kačák Event:
• Extinction of numerous conodont species (Walliser, 1996)
1.2. Post-crisis filling-in of Bambachian megaguilds:
1.2.1. Lower Kačák Event:
• Radiation of new polygnathid and icriodid conodont species (Walliser, 1996)
2. Pelagic-carnivore megaguild
2.1. Crisis thinning-out of Bambachian megaguilds:
2.1.1. Lower Kačák Event:
• Extinction of one genus of goniate cephalopods (Walliser, 1996)
2.1.2. Upper Kačák Event:
• Extinction of four genera of goniate cephalopods (Walliser, 1996)
2.1.3. Uncertain Lower or Upper Kačák Event?:
• Extinction of four families of nautiloid cephalopods (House, 2002)
3. Attached-epifaunal-filter-feeding megaguild
3.1. Crisis thinning-out of Bambachian megaguilds:
3.1.1. Uncertain Lower or Upper Kačák Event?:
• Extinction of corals (House, 2002)
• Extinction of brachiopods (House, 2002)
4. Mobile-epifaunal-detritivore megaguild
4.1. Crisis thinning-out of Bambachian megaguilds:
4.1.1. Lower Kačák Event:
• Extinction of trilobites (Feist, 1991)

(House, 1985; Feist, 1991; Walliser, 1996; Barnes et al., 1996b), but an anoxic event that also extended up into the water column as both pelagic conodonts and cephalopods were affected. The extinctions that occur in the Upper Kačák Event are more enigmatic, as they occur with the waning of marine anoxia and the cessation of black-shale sedimentation.

4.4. Summary

The Hirnantian and Famennian biodiversity crises were short-term events (see Section 3 above). In contrast, the Givetian, Eifelian, and Ludfordian biodiversity losses were the result of protracted, multi-event crises. The Givetian Taghanic and Frasnian Events together spanned a total of five conodont zones, the Eifelian Lower and Upper Kačák Events spanned two conodont zones, and the early, middle, and late Ludfordian Events spanned a total of 2.6 million years.

The Givetian crisis was a long-term series of stepped invasive-species events linked to episodic and cumulative sea-level rises that progressively breached the land barriers that had existed between formerly isolated palaeobiogeographic realms. Thus the Givetian biodiversity crisis had a marked palaeobiogeographic impact in the marine realm: the GDI invasive-species event marked the beginning of the transition of the global marine biosphere from diverse endemic faunas distributed in palaeogeographically distinct realms and subrealms, to a less diverse but cosmopolitan marine fauna in the Frasnian. Rather than the numerous crisis thinning-out and post-crisis filling-in of Bambachian megaguilds seen in the Hirnantian and Famennian crises (Table 5), the Givetian crisis produced only thinning-out of biodiversity within marine megaguilds (Table 6) due to the loss of previously diverse endemic faunas. The structure of the megaguilds themselves was not altered, however, as the new lower-diversity cosmopolitan faunas were ecologically equivalent to the extinct endemics.

The Ludfordian and Eifelian crises were ecologically distinct in that the Ludfordian crisis primarily affected animals living in the water column (Munnecke et al., 2003, 2010), and the Eifelian crisis had a greater affect on animals living on the sea bottom (although the differential magnitude of this effect has yet to be completely documented; House, 2002). Both crises, however, appear to have been caused by primary environmental triggers, not secondary ones as in the Givetian crisis where the primary environmental effect of rising sea level made possible the secondary invasion events that previously had been blocked by land barriers.

In conclusion, the Givetian crisis was a long-term, transitional palaeobiogeographic event producing a homogenization of marine faunas within megaguilds that we argue was less ecologically severe than the major and numerous extinction and rediversification or replacement ecological couplets triggered within megaguilds by both the Hirnantian and Famennian glacial pulses (cf. Tables 5 and 6). On the other hand, the Givetian crisis did produce a larger ecological change – global cosmopolitanism in marine megaguild compositions – than did either of the Ludfordian or Eifelian crises, thus it is argued that the Givetian crisis had an ecological impact that was greater than either the Ludfordian or Eifelian crises.

Last, the Ludfordian and Eifelian crises need more refined data and study. Both the Ludfordian and Eifelian crises affected four Bambachian megaguilds (Tables 7 and 8), thus one could argue on that basis that the two crises had an equivalent ecological impact. On the other hand, three of the four affected Bambachian megaguilds in the Ludfordian crisis also experienced at least partial filling-in and ecological relays within megaguilds (Table 7) whereas only one did so in the Eifelian crisis (Table 8), thus it could be argued that the Ludfordian crisis was ecologically more complex and that it had a greater ecological impact (particularly in the post-crisis diversification of fish faunas; see Section 4.2). The counter argument would be that the Eifelian crisis was almost entirely a thinning-out of ecological diversity, and hence of greater ecological impact than the Ludfordian. Thus we at present cannot convincingly demonstrate whether either event was more or less ecologically severe than the other.

5. Conclusions

A new ecological ranking of the traditional eleven taxonomically-most-severe Phanerozoic biodiversity crises (Table 1) is proposed in which the Capitanian biodiversity crisis is ranked with an ecological impact that was lesser than that of the Frasnian crisis, but greater than that of the Serpukhovian (Section 2.2 of the paper), and thus is ranked fifth in terms of ecological severity (Table 9). The Famennian crisis is ranked as equal in ecological impact to the Hirnantian (Section 3.3 of the paper), and thus is ranked seventh in terms of ecological severity (Table 9). It is proposed that the Givetian crisis had an ecological impact that was lesser than that of the Hirnantian and Famennian, but that was greater than that of the Ludfordian and Eifelian crises (Section 4.4), thus is ranked eighth in terms of ecological severity (Table 9). Last, the Ludfordian and Eifelian crises need more data and study, thus we cannot at present demonstrate whether either event was more or less ecologically severe than the other. Until more refined data are obtained for these events, we have tentatively ranked them as equal in ecological impact, but of a lesser ecological impact than the Givetian crisis, thus they are ranked ninth in terms of ecological severity (Table 9).

Two taxonomic-severity versus ecological-severity decouplings appear in this new analysis that are not present in previous analyses (McGhee et al., 2012): the Capitanian and the Famennian (Table 9).

Table 9

Ecological-severity ranking of the traditional eleven largest Phanerozoic biodiversity crises since the beginning of the Ordovician (Table 1) compared with the new taxonomic-severity ranking given in Table 3; see text for discussion. The traditional “Big Five” biodiversity crises (Raup and Sepkoski, 1982) are indicated in parentheses.

Ecological-severity ranking:	Taxonomic-severity ranking (Table 3):
1. Changhsingian (end-Permian)	1. Changhsingian
2. Maastrichtian (end-Cretaceous)	2. Rhaetian
3. Rhaetian (end-Triassic)	3. Hirnantian
4. Frasnian (Late Devonian)	4. Famennian
5. Capitanian	5. Maastrichtian, Frasnian
6. Serpukhovian	6. Serpukhovian
7. Famennian, Hirnantian (end-Ordovician)	7. Givetian
8. Givetian	8. Eifelian
9. Eifelian, Ludfordian	9. Capitanian
	10. Ludfordian

The Capitanian crisis is ranked with an ecological severity of fifth-most-severe, in the middle of the ecological severity ranking range (Table 9). In contrast, in both of the traditional taxonomic-severity rankings using the Sepkoski Large Data Base (SLDB, Table 1) the Capitanian is ranked as third-most-severe, a higher severity ranking than its ecological severity of fifth-most-severe, thus the two Capitanian severities are decoupled. On the other hand, in the Paleobiology Late Data Base (PBDB) and using the recalculated extinction probabilities, the Capitanian crisis is ranked as ninth-most-severe, a lower severity ranking than its ecological severity of fifth-most-severe (Tables 3 and 9). Thus the Capitanian ecological severity is decoupled from its taxonomic severity in these severity comparisons as well, but in the opposite direction!

Unlike both of the traditional taxonomic-severity rankings using the SLDB (Table 1), in which the Hirnantian crisis is ranked as the second-most-severe loss of biodiversity in the Phanerozoic, both Hirnantian and Famennian crises are equally ranked as the seventh-most severe in terms of ecological impact (Table 9). Given the equivalency of the environmental trigger (a short-term, intense glacial pulse) and the two-extinction-pulse structure of both the Hirnantian and Famennian crises it is perhaps not surprising that the two crises had equivalent ecological impacts in the marine realm. That causal and ecological equivalency is decoupled from taxonomic severity and is not apparent in the SLDB taxonomic-severity rankings (Table 1) in which the two events would appear to have been markedly different, but in fact were not. Only in the PBDB, and in the recalculated extinction probabilities, do the Hirnantian and Famennian appear to have similar taxonomic severities (Tables 3 and 9).

In the Givetian biodiversity crisis, the Great Devonian Interchange (GDI) invasive-species event triggered the replacement of diverse endemic faunas distributed in palaeogeographically distinct realms and subrealms by a much less diverse but cosmopolitan marine fauna in the Frasnian, and a global homogenization of marine faunas within Cambachian megaguilds. Thus the GDI invasive-species event may provide an important palaeoecological analog for the study of present-day extinction and homogenization in ecosystems produced by modern invasive species with “a few winners replacing many losers” (McKinney and Lockwood, 1999, p. 450).

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