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On the causes of mass extinctions

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ABSTRACT

The temporal link between large igneous province (LIP) eruptions and at least half of the major extinctions of the Phanerozoic implies that large scale volcanism is the main driver of mass extinction. Here we review almost twenty biotic crises between the early Cambrian and end Cretaceous and explore potential causal mechanisms. Most extinctions are associated with global warming and proximal killers such as marine anoxia (including the Early/Middle Cambrian, the Late Ordovician, the intra-Silurian, intra-Devonian, end-Permian, and Early Jurassic crises). Many, but not all of these are accompanied by large negative carbon isotope excursions, supporting a volcanogenic origin. Most post-Silurian biocrises affected both terrestrial and marine biospheres, suggesting that atmospheric processes were crucial in driving global extinctions. Volcanogenic-atmospheric kill mechanisms include ocean acidification, toxic metal poisoning, acid rain, and ozone damage and consequent increased UV-B radiation, volcanic darkness, cooling and photosynthetic shutdown, each of which has been implicated in numerous events. Intriguingly, some of the most voluminous LIPs such as the oceanic plateaus of the Cretaceous were emplaced with minimal faunal losses and so volume of magma is not the only factor governing LIP lethality. The missing link might be continental configuration because the best examples of the LIP/extinction relationship occurred during the time of Pangaea. Many of the proximal kill mechanisms in LIP/extinction scenarios are also potential effects of bolide impact, including cooling, warming, acidification and ozone destruction. However, the absence of convincing temporal links between impacts and extinctions other than the Chicxulub-Cretaceous example, suggests that impacts are not the main driver of extinctions. With numerous competing extinction scenarios, and the realisation that some of the purported environmental stresses may once again be driving mass extinction, we explore how experimental biology might inform our understanding of ancient extinctions as well as future crises.

1. Introduction

The past three decades have seen major advances in our understanding of mass extinctions, and yet consensus has not been reached on the causes of each of Earth's greatest biotic catastrophes, and much less so its numerous lesser calamities. The past decade in particular has seen research efforts directed toward understanding the context and nature of environmental changes associated with extinction events. This has resulted in significant new data and observations from the fields of geochronology, geochemistry, mineralogy, palaeontology, sedimentology, stratigraphy, palaeomagnetism, volcanology and geophysics, several of which are the focus case studies in this Special Issue. Mass extinction theories have developed from the simple death-by-sea-level-change hypothesis first proposed almost fifty years ago (Newell, 1967) into ever more complex, multicausal scenarios. The body of evidence associated with mass extinctions lends much support to proximal kill mechanisms that include anoxia (e.g. House, 1985; Buggisch, 1991; Wignall and Hallam, 1992; Brenchley et al., 1994, 2001; Isozaki, 1994, 1997; Wignall and Twitchett, 1996; Bond et al., 2004; Grice et al., 2005; Bond and Wignall, 2010; Shen et al., 2016; Wang et al., 2016), global warming (e.g. McElwain et al., 1999, 2005; Beerling and Berner, 2002; Wilf et al., 2003; Joachimski et al., 2009, 2012; Gómez and Goy, 2011; Sun et al., 2012, 2015; Punekar et al., 2014; Petersen et al., 2016), and ocean acidification (e.g. Hautmann, 2004; Payne et al., 2007; Hautmann et al., 2008a, 2008b; Clapham and Payne, 2011; Montenegro et al., 2011; Beauchamp and Grasby, 2012; Greene et al., 2012; Hinojosa et al., 2012; Martindale et al., 2012; Heydari et al., 2013; Clarkson et al., 2015) coupled with changes in atmospheric greenhouse gases, notably CO_2, to name just a few. Advances in analytical capabilities have led to the identification of new kill mechanisms, such as toxic metal poisoning (e.g. Sanei et al., 2012; Sial et al., 2013, 2014; Grasby et al., 2015, 2016; Percival et al., 2015; Font et al., 2016; Thibodeau et al., 2016). It is increasingly widely thought that large igneous province (LIP) eruptions might be the driver of many of the purported proximal kill mechanisms, and the temporal link

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between volcanism and extinction is now well-established (Courtillot, 1999; Wignall, 2001; Courtillot and Renne, 2003; Bond and Wignall, 2014). However, the link between the two phenomena is still not fully understood. Whilst the deleterious effects of LIP volcanism are implicated in many extinction scenarios, a role for extra-terrestrial drivers should not be ignored. Bolide impact is of course famously implicated in the end-Cretaceous crisis (Alvarez et al., 1980; Hildebrand et al., 1991), and a role for deadly bursts of cosmic gamma rays also has advocates (Piran and Jimenez, 2014), notably for the Late Ordovician extinction (Melott et al., 2004).

This special issue of *Palaeogeography, Palaeoclimatology, Palaeoecology* is thematically dedicated to understanding mass extinction events through the Phanerozoic. Ordered chronostratigraphically, Ernst and Youbi (2017-in this issue) examine the record and climatic effects of LIP volcanism through Earth history; Faggetter et al. (2017-in this issue) explore enigmatic trilobite losses and concomitant carbon isotope shifts in the Cambrian; Beard et al. (2017-in this issue) study the less well-known of the two Late Devonian Kellwasser Events and the role of anoxia in the Frasnian-Famennian crisis; Lindström et al. (2017-in this issue) present a new correlation scheme and event stratigraphy for the Triassic-Jurassic extinction; Martindale and Aberhan (2017-in this issue) and Mateo et al. (2017-in this issue) investigate extinction losses and the record of volcanism in the Early Jurassic and Cretaceous-Paleogene catastrophes, whilst Tobin et al. (2017-in this issue) model the effects of Deccan Traps eruptions in that latter crisis; and finally, Keller et al. (in this issue) compare that last, great extinction with events at the Paleocene-Eocene boundary - a further LIP-induced global warming event.

In this introductory paper we evaluate the most commonly implicated extinction mechanisms, and summarise the role of each in each of the major extinctions, and several lesser crises (Tables 1 and 2). While one or more of these mechanisms might be sufficient to explain marine extinctions, there is typically a coincident terrestrial extinction that requires teleconnection between the two environments to explain coeval extinction processes. The atmosphere is the obvious linkage between the two biospheres, and we explore atmospheric drivers of extinction that may hold the key to catastrophes of global scale.

The realisation that Earth is once again facing some of the stresses implicated in its past crises has intensified debate over the cause(s) of mass extinctions and yet we have very limited understanding of *how* either terrestrially-generated (e.g. LIP-derived) or extra-terrestrial (e.g. bolide impact-derived) stresses actually affect ecosystems. We do not know *why* stress (e.g. global warming or ocean acidification) might sometimes lead to such a profound collapse in Earth's ability to support life as occurred at the Permian-Triassic boundary, and yet at other times in Earth's history the same perceived stress had apparently little effect on the biosphere. We explore biology as the missing link in our understanding of extinction scenarios and suggest ways in which the Earth and biological sciences might be integrated in future to solve the riddles of mass extinctions, and inform our understanding of Earth's future.

2. Extinction records and proximal kill mechanisms

A wide variety of terrestrially, and a few extra terrestrially-derived proximal kill mechanisms have gained support over the past few decades. Some, discussed below, have become leading contenders for the cause(s) of Earth's greatest extinctions as increasingly sophisticated proxies and dating methods have implicated them in one or more of

Table 1

Summary of data and proposed causal mechanisms implicated in mass extinctions since the Early Cambrian.

Extinction (*age*)	Associated LIP	Associated impact structure	Global warming or cooling?	Ocean acidification?	Marine anoxia?	Carbon isotope shift	Notes and other postulated causes
Early/Middle Cambrian (Botomian)	Kalkarindji	None	?	?	Yes	−4‰	ROECE Event in carbon isotope stratigraphy. Maybe several extinction events – poorly constrained.
Dresbachian	None	None	Warming?	?	Yes	+5‰	SPICE Event in carbon isotope stratigraphy.
End Ordovician	Speculated	None	Cooling (phase 1) and warming (phase 2)	?	Partly	+7‰ followed by −7‰	Gamma-ray burst?
Ireviken Event	None	None	Cooling?	?	Yes	−4‰ imposed on a positive trend	
Mulde Event	None	None	Cooling?	?	Yes	+4‰	Starvation amongst planktonic larvae driven by severe drop in primary planktonic productivity
Lau Event (Ludfordian)	None	None	Cooling?	?	Yes	+6‰	
Kačák Event (Eifellian)	None	None	Warming?	?	Yes	+2‰	
Thaganic Event (Givetian)	None	None	Warming?	?	Yes	+2‰	
Frasnian-Famennian	Viluy Traps, PDD?	Siljan Ring?	Warming (+9 °C) imposed on cooling pulses	?	Yes	up to +4‰	
Hangenberg Event (End Devonian)	PDD?	Woodleigh, Western Australia?	Warming and cooling (including glaciation)	?	Yes	up to +6‰	A prolonged and diachronous extinction (several 100kyr) on par with the "big 5" but poorly understood
Capitanian	Emeishan Traps	None	? both have been invoked	Possibly	Yes (only regionally)	−6‰ (in China)	Volcanic darkness and photosynthetic shutdown; toxic metal (Hg) poisoning
End Permian	Siberian Traps	Bedout? Wilkes Land?	Warming (+10 °C)	Probably	Yes	up to −8‰	Acid rain; toxic metal (Hg) poisoning; UV-B damage
Smithian/Spathian	Siberian Traps (late stages)	None	Warming (+6 °C)	?	Yes	−6‰ followed by +6‰	Toxic metal (Hg) poisoning
Carnian	Wrangellia	None	Warming (+7 °C)	?	Yes	−5‰	Major radiations as well as extinctions
End Triassic	CAMP	None	Warming (+6 °C)	Probably	?	−5‰	Seismite at the extinction level: CAMP or bolide? Toxic metal (Hg) poisoning
Early Jurassic	Karoo/Ferrar	None	Warming (+7 °C)	?	Yes	−7‰ in $\delta^{13}C_{org}$ −3‰ in $\delta^{13}C_{carb}$	Toxic metal (Hg) poisoning
End Cretaceous	Deccan Traps	Chicxulub	Warming (+4 °C)	?	No	−2‰	Toxic metal (Hg) poisoning