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Reply to comment

Mathematical modeling is an efficient research tool to address challenges in mass extinction research

Reply to comments on "Knowledge gaps and missing links in understanding mass extinctions: Can mathematical modeling help?"

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Mass extinctions are dramatic events recorded in the last 540 Myrs of the Phanerozoic Eon when a large proportion of the global biota went extinct over a relatively short time interval [1–3]. The most famous are the "Big Five" when more than 70% of Earth's species were wiped out, but there were also many more mass extinctions of a smaller magnitude [3,4]. Although these are events from Earth history, the meaning and importance of mass extinctions is not limited to deep time. Studies of these events can provide valuable insights into the dynamics of ecosystems and the factors that can cause them to collapse. This links the study of past events to the modern biosphere and its future: indeed, the elevated rate of species extinctions observed during recent centuries is often regarded as the beginning of the "Sixth Mass Extinction" [5]. Understanding past extinction mechanisms and pathways is therefore important for identifying the parameters of habitability of our planet, the vulnerability of particular ecosystems and organisms to perturbation, as well as assessing the current and potential future magnitude of human impact on the biosphere [6].

Mass extinctions are a complex phenomenon, as there are many factors that can contribute to these events, their causes and consequences often being difficult to decipher. In particular, the following challenges in studies on mass extinctions were identified (see [7] and further references there):

- Multiple causes. Mass extinctions are rarely caused by a single factor; instead, they result from a combination of factors and drivers (triggers and kill mechanisms [7]). For instance, volcanic eruptions, climate change, asteroid impacts, and sea level fluctuations are known as triggers that initiated Phanerozoic extinctions. Understanding how these different factors interact and contribute to kill mechanisms that produce mass extinctions, and/or which particular combination of different factors ultimately leads to a mass extinction can be challenging. This is because of the complexity of integrating multiple processes and disparate data such as geological, paleontological, geochemical, ecological, climatic, etc. [8,9].
- Scale and scope. Mass extinctions can occur over different spatiotemporal scales, from regional extinctions that affect a particular ecosystem type or particular region, to global extinctions that impact the entire planet; corre-

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spondingly, these events may occur over days to millions of years. Understanding how these different spatial and temporal scales interact, and how they are influenced by different factors, is challenging. In fact, it is not even clear what exactly a mass extinction is, e.g., how large the biodiversity loss should be in order to be regarded as a mass extinction [2], because commonalities among extinction mechanisms and magnitudes of biodiversity decline are hard to identify. Importantly, this is not just terminological meandering: there is evidence [10] that extinctions of larger and smaller magnitude can correspond to, respectively, over-critical and sub-critical perturbations of the CO_2 cycle and hence can be linked to different kill mechanisms and follow different extinction pathways [7].
- Species interactions and feedback loops. Interspecific interactions aggravated by changes in their local/regional environment can play an important role in mass extinctions, e.g. through competitive exclusion or by disrupting food webs, but these interactions are often poorly understood and difficult to distinguish in the fossil record. Competition between species for resources can intensify during times of stress, potentially leading to the extinction of one or more species. The loss of a key species can have cascading effects throughout an ecosystem, leading to further extinction and trophic webs collapse [11]. Mass extinctions likely create complex feedback loops, in which the loss of one or more species leads to further extinctions, or to changes in the environment that make it more difficult for other species to survive. Understanding and recognizing these feedback loops is challenging, as they can also involve multiple factors and operate on different spatial and temporal scales [12].

Overall, understanding mass extinctions is a complex and challenging task that requires the integration of multiple fields of knowledge, and consideration of many different factors and processes. Tremendous progress has been made over the last few decades, in particular through detailed field work, advancements in radiometric dating, and statistical analysis of the fossil record. However, there are some inherent factors that have complicated research and hamper further progress. One persistent challenge is the limitations of the geological record. Ultimately, all fossils pass through a number of taphonomic filters of various origin, such as geological processes (e.g., erosion and tectonic activity) and biological traits (i.e., whether the organisms were hard-bodied or soft-bodied), as well as biased sampling effort; see Fig.2 in [7] for more details on the limitations among the organisms that are ultimately preserved. Another challenge is recognition that the temporal and spatial resolution of the fossil record is usually inconsistent with observable processes of ecosystem change and extinction for living species [6,13]: while the latter may happen over timeframes of years, decades or centuries, the resolution of the fossil record for many (but not all) mass extinction events is on the order of 10's to 100's Kyrs. Relying on fossil data alone makes it difficult to reconstruct what happened ecologically during past extinction events, in turn making it hard to determine the causes and timing of mass extinctions, and to identify taxa or ecosystems that were most vulnerable to environmental perturbation. Moreover, the prolonged and global nature of mass extinctions may include larger scales of "biosphere" processes that are not currently well-linked to ecosystem dynamics.

Arguably, many of these problems as well as other open questions in mass extinction science can be addressed by means of mathematical modeling [7,13–16]. Mathematical models can help to partially compensate the spatial deficiency of the fossil record, in particular to reveal the effect of environmental heterogeneity [17] and/or species dispersal and migration [18]. Models can help to identify relevant temporal scales of mass extinctions development on the 'subscale' of ecological processes which are much shorter than the temporal resolution afforded by the fossil record [15], for instance by revealing the scaling in the duration of transient dynamics of relevant ecological processes [19,20]. Models can provide insight into 'hidden' yet important processes such as the effect of vegetation on the global energy balance [21,22] and adaptive evolutionary response of a species to an unfavorable environmental change (e.g., caused by an extinction trigger) [16,22].

Models can also help to reveal the role of stochastic factors in mass extinction events. This is particularly important, as both climate and ecosystem dynamics are inherently stochastic [14]. While deterministic models are generally successful in describing the changes in the mean, e.g. a tendency of the average Earth temperature to increase during periods of global warming, they usually fail to account for the effect of fluctuations. However, the variance in the fluctuation magnitude may grow with time resulting, for instance, in an increase in the frequency of extreme climatic events [13]. There is growing awareness that this can be a factor leading to a mass extinction and/or affecting the temporal scales of its development. This can be grasped by stochastic mathematical models. Also, stochastic models are a natural research tool to reveal the role of mutations in mass extinction events [16], another important factor as it can both determine species adaptation to an unfavorable environmental change and contribute to interspecific interactions, e.g. through competitive exclusion. A variety of stochastic models of coupled environment-population dynamics systems have become available over the last decade; although originally developed for somewhat different purposes, arguably, they can be used for modeling mass extinctions [14].

To conclude, there is general agreement that mathematical models are a useful tool for understanding mass extinctions and have a huge potential to facilitate further research in extinction science [6,13–16]. Several examples of possible applications are given in [7]; for more recent advances, see also [18,22]. We take inspiration from the related field of ecology, where mathematical models have now become a standard part of the theoretical ecologist's toolbox. Development of relevant mathematical models and their application to the geological record of Phanerozoic mass extinctions is still at its infancy; in order to realize its full potential, the active involvement of a broader applied mathematics community is needed.

Declaration of competing interest

Herewith, we confirm that the authors have no conflict of interests.

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