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Knowledge Gaps and Missing Links in Understanding Mass Extinctions: Can Mathematical Modeling Help?
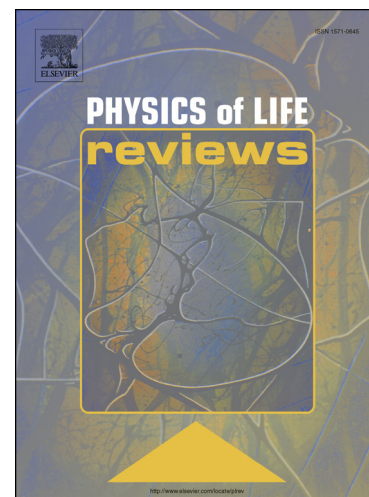
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Highlights

- A thorough revision of the mass extinction science is provided.
- An overview of relevant models is provided with a brief outline of their use for modelling mass extinctions.
- It is argued that mass extinction develops through a cascade of processes of different origin.
- Several missing links and extinction pathways have been identified.

Knowledge Gaps and Missing Links in Understanding Mass Extinctions: Can Mathematical Modeling Help?

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Abstract

Extinction of species, and even clades, is a normal part of the macroevolutionary process. However, several times in Earth history the rate of species and clade extinctions increased dramatically compared to the observed "background" extinction rate. Such episodes are global, short-lived, and associated with substantial environmental changes, especially to the carbon cycle. Consequently, these events are dubbed "mass extinctions" (MEs). Investigations surrounding the circumstances causing and/or contributing to mass extinctions are on-going, but consensus has not yet been reached, particularly as to common ME triggers or periodicities. In part this reflects the incomplete nature of the fossil and geologic record, which – although providing significant information about the taxa and paleoenvironmental context of MEs – is spatiotemporally discontinuous and preserved at relatively low resolution. Mathematical models provide an important opportunity to potentially compensate for missing linkages in data availability and resolution. Mathematical models may provide a means to connect ecosystem scale processes (i.e., the extinction of individual organisms) to global scale processes (i.e., extinction of whole species and clades). Such a view would substantially improve our understanding not only of how MEs precipitate, but also how biological and paleobiological sciences may inform each other. Here we provide suggestions for how to integrate mathematical models into ME research, starting with a change of focus from ME triggers to organismal kill mechanisms since these are much more standard across time and spatial scales. We conclude that the advantage of integrating mathematical models with standard geological, geochemical, and ecological methods is great and researchers should work towards better utilization of these methods in ME investigations.

Keywords: extinction triggers; extinction kill mechanisms; climate change; population dynamics; metapopulation; Allee effect

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1 Introduction

Mathematical models have long been successfully used to elucidate the processes behind patterns in biological and ecological systems [58, 81, 115, 151, 173, 263]. However, rarely have these methods been applied to broader scale phenomena such as major increases and decreases in global taxonomic diversity over geologic timescales. As we argue below, understanding phenomena of this ilk can strongly benefit from the new perspective provided by mathematical models. Here we focus specifically on the record, patterns, processes, and substantial remaining questions associated with Mass Extinction Events.

The phenomenon of Mass Extinctions (MEs) in Earth history has been a challenging and fascinating topic for many generations of scientists [233]. Rigorous, quantitative research into extinction mechanisms did not begin until the 1980s. This resulted from the landmark publication of Alvarez et al. [12], who hypothesized that an extraterrestrial impact was the cause of the Cretaceous-Paleogene (K-Pg) ME event 66 million years ago. Following this, a surge of scientific interest brought the topic to the attention of the wider scientific community and the public, with the recognition of the "Big Five": five MEs and a host of lesser biodiversity crises during the last 541 Myrs of Earth history (the Phanerozoic Eon) when the majority of species were wiped out over geologically short intervals of time [22, 244]; see Fig. 1. The recognition that anthropogenic climate and environmental change is likely driving modern extinction rates to levels well above background, and possibly approaching those of ancient mass extinctions has added strong societal concern for this subject [25, 118].

Paleobiological research into MEs over the last forty years has made considerable progress in understanding their causes and consequences. Yet, there are many aspects of these events that remain poorly understood. For instance: what are the temporal scales of extinctions and associated phenomena? It has been convincingly shown that mass extinction of marine and terrestrial biota is usually associated with a perturbation of the global carbon cycle [111, 288, 325]. However, the duration, magnitude, frequency, and even direction of this perturbation – seemingly critical to determine whether the consequence is a mass extinction or part of the 'background' turnover of species – is not consistent across events [256]. This makes even distinguishing pe-
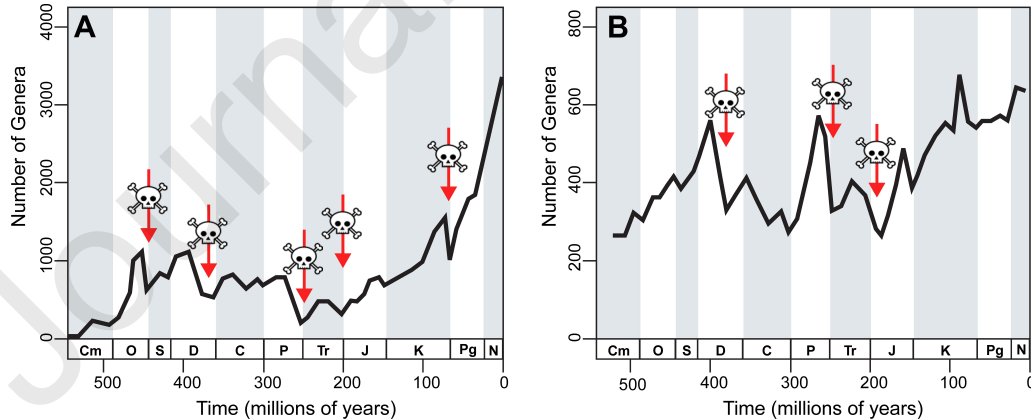
Figure 1: Phanerozoic biodiversity curves. (A) after Sepkoski [274] compilation based on raw data analysis of marine animal genera. (B) after Alroy et al. [11] compilation based on sample standardized data analysis. Arrows indicate mass extinction events observable in the respective curves. Cm = Cambrian, O = Ordovician, S = Silurian, D = Devonian, C = Carboniferous, P = Permian, Tr = Triassic, J = Jurassic, K = Cretaceous, Pg = Paleogene, N = Neogene. Modified from [2].

riods of elevated extinction from background levels challenging [326]. The response of global ecosystems, populations and/or communities, and individual species to any environmental perturbation is often nonlinear and may have its own characteristic timescale, e.g., see [224, 305]. The temporal resolution of paleo-data is rarely better than a 100 Kyrs timescale, whereas extinction occurs within a population as the last individual (or mating pair) dies. Consequently, there is a substantial gap in our understanding of the temporal scaling of MEs from the individuals that die to the species and clades that go extinct.

In spite of the broad array of tools and high-precision methods that are currently utilized by paleobiologists, geochemists and geologists, the standard approaches of empirical and statistical techniques have not provided a way forward to link these scaled phenomena. Specific mechanisms and scenarios of extinction often remain obscure. This is in part a matter of the geologic record, which has lower spatial and temporal resolution with increasing age. The consequences include more time-averaging and spatial discontinuities that both contribute to increased uncertainty in the age and geographic structure of organisms/species and the environments they lived in. The spatiotemporal incompleteness of the fossil archive may result from lack of deposition of sediments in an area, subsequent erosion of deposited sediments, geochemical overprinting of the rocks by geological processes leading to destruction of archived fossils, lack of exposure of rock packages, or simply lack of adequate sampling of strata in a given area. While some of these issues can be mitigated by study design, such as drilling cores to sample buried strata, others – such as erosion – cannot. These challenges make precise estimation of the actual extinction magnitude, selectivity, and duration difficult, as well as the Earth system conditions associated with these events.

Mathematical modelling can help to bridge this gap in our understanding by creating a 'virtual laboratory' where specific hypotheses can be tested, and various scenarios investigated, under controlled conditions [58]. Here we argue that some of the mathematical approaches that are successfully used in ecology and population dynamics (e.g., networks and food webs, metapopulation models, population dynamics models, etc.) can be used to address questions in paleobiology, in particular improving our understanding of mass extinctions. This is not an entirely new idea (e.g., see [62, 220, 285, 298]), however, very little progress has been made in the past two decades linking the potential of mathematical models to the processes causing mass extinction (but see [95, 254]). Here we revisit several relevant modelling techniques and consider how their application may be instrumental in facilitating further progress in understanding MEs.

2 Mass Extinction: definitions, causes, mechanisms

2.1 Mass Extinction definitions and examples

Despite their recurrence and clear importance in the evolution of life on our planet, no precise definition of what constitutes a Mass Extinction (ME) is agreed upon in the literature. One of the most commonly used definitions by Earth scientists is that of Sepkoski [272]:

"A mass extinction is any substantial increase in the amount of extinction (i.e., lineage termination) suffered by more than one geographically widespread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity".

This purposefully vague definition was derived to be flexible in covering the variety of extinction events recorded in the Phanerozoic fossil record, each of which exhibits differing properties in rate, magnitude, duration and, importantly, even in driving mechanism (e.g., see Table 1 in

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[118]). However, because of its ambiguity, a few questions immediately arise: What increase in mortality rate is "substantial"? What does "relatively short" mean? How should "geographically widespread" be defined?

To make the above definition more quantitative, several of these parameters have been generalized: MEs typically show over 70% species extinction occurring over 2 Myrs or less that affects the global biota (both land and sea, although often with different intensities), and results in a substantial – Myrs – period of biotic recovery [14, 79, 22, 24, 136, 137, 332]. Depending on how extinction rates are calculated, this results in upwards of 14 [10] to 18 [22] periods of "elevated" extinction, each associated with a unique suite of Earth system conditions that are the basis for the ambiguity in the definition above. They reflect not only the pre-existing conditions of the Earth system at the time (e.g., plate tectonic configuration, Icehouse vs. Greenhouse climate regime, sea level), but also differences in extinction "triggers" (asteroids, volcanoes, etc.) vs. "kill mechanisms" (temperature change , habitat loss, etc.) [158]. For instance, while the large asteroid impact at the end of the Cretaceous Period in and of itself only killed organisms in the blast zone, the impact likely *triggered* global climate change (e.g., changes in temperature and/or precipitation), changes in incident solar radiation, ocean circulation, nutrient cycling, etc. – *kill mechanisms*.

The distinction between extinction triggers and kill mechanisms is not semantic but an important component of deriving a more rigorous understanding of MEs. Extinction triggers are defined as factors that initiate the conditions eventually leading to elevated global extinction [158]. Common hypothesized triggers in the Phanerozoic are events such as the emplacement of Large Igneous Provinces (LIPs) [37] and large bolide impacts [12]. Mass Extinction triggers set off a cascade of environmental and ecosystem changes – kill mechanisms – that directly impact the survival of organisms, populations, species, and communities. Kill mechanisms are thus defined as factors causing the deaths of organisms and lineages [158]. The Phanerozoic fossil record suggests that four major kill mechanisms dominate during times of mass extinction: (1) temperature change (especially associated with warming), (2) ocean acidificiation / acid rain, (3) ocean anoxia, (4) habitat change. Habitat change is itself a complex kill mechanism that may involve loss, fragmentation, and/or degradation (either abiotic or biotic, e.g., invasive species) of habitat at local and regional scales, and plate tectonic configuration at global scales. Collectively, these can be considered the "Four Horsemen of the Evolutionary Apocalypse." Importantly, different triggers may initiate the same or multiple kill mechanisms, e.g., LIPs often cause temperature change, ocean acidification, acid rain, and ocean anoxia as described below [37, 63].

From this perspective, we might consider, for example, that the trigger of the end-Permian ME, which wiped out upwards of 96% of species on Earth (some recent studies estimated it at a somewhat smaller value of upwards of 80%, cf. [289]), was the emplacement of the Siberian Traps. Approximately 252 Ma, this LIP erupted over 3,000,000 km^3 of lava across 7,000,000 km^2 in northern Asia over >100 kyrs [52, 53]. Such massive volcanic outpourings likely released over 30,000 Gt of carbon into the atmosphere (primarily as CO_2 and CH_4) as well as many 1000s of giga-tons of other climate-influencing gases such as sulfates, chlorine and fluorine compounds [89, 158]. The environmental consequences would have included acid rain, large-spatial scale decreases in ocean water pH, anoxia, and atmospheric warming. Thus, despite being triggered by volcanism, the kill mechanisms associated with this event in the marine realm were temperature change (warming), ocean anoxia (via warming and excess atmospheric CO_2), ocean acidification and acid rain (resulting from increased dissolved CO_2 in the ocean and atmospheric reservoirs), as well as habitat change in the terrestrial realm [127, 147]. Each of these mechanisms provides a prediction of extinction susceptibility which are well-supported by

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patterns of extinction selectivity in the marine and terrestrial fossil records. For instance, in the ocean, LIP volcanism is associated with selective extinction of hypercalcifying organisms and those more susceptible to hypoxia, such as corals, brachiopods, crinoids, and some mollusks [158]. Many questions still remain, however, in particular about relative timing of extinction in marine vs. terrestrial settings and the magnitude and relative contributions of warming, anoxia, acidification and hypercapnia in causing the extinctions [323].

Alternatively, although the trigger of the end-Cretaceous ME, which wiped out 75% of species[2] and all of the non-avian dinosaurs, was most likely an asteroid impact, we have a much less precise picture of the kill mechanisms involved (at least for those species not in the immediate vicinity of the impact site). A favored kill mechanism, perhaps summarized as "the darkness", involves short-lived cooling ("impact winter") and trophic collapse associated with the global spread of impact ejecta, debris, and volatiles from impacted target rocks and consequent decrease in solar radiation reaching the Earth's surface [48, 61, 71, 110, 162, 300]. Although there exists no direct evidence of impact winter or decreased incidence of solar radiation (but see [320]), this kill mechanism is supported by discovery of impact debris and geochemical markers for volatile release and biomass burning in deep ocean cores and land-based geological sections [184], as well as climate modelling of the effects of extensive aerosol release from volatilized surface rocks (e.g. [61]). It is also indirectly supported by patterns of extinction selectivity. That is, photosynthesizing species, those that depend on them, and species without a resting stage were disproportionately likely to go extinct [162, 320]. In spite of recent findings and the progress made by integrating datasets, the specific kill mechaisms remains a focus of debate and some controversy [5]. Thus, the end-Cretaceous ME is an example where application of mathematical modeling may significantly push the field forward, in particular by identifying alternative and/or most likely kill mechanism(s) resulting from various extinction triggers. This will also lead to a more rigorous understanding of the ways in which kill mechanisms scale from organismal to global ecosystem declines.

Notably, all of the "Four Horsemen" are in play in current and predicted future environmental change [55]. Greenhouse gas inputs (especially those from CO_2) have already contributed to $1.19°C$ warming since pre-Industrial Revolution averages [138, 222]. This is already being associated with areas of increasing ocean anoxia [21, 43], decreases in ocean pH [54, 104, 109], drought, and weather intensification [159, 223]. Moreover, the very immediate, direct effects of human activities on habitat loss, fragmentation, and degradation are strikingly apparent in modern population- and species-level health: remarkably, the majority of recent species extinctions are associated with this kill mechanism alone [44, 85, 91, 329]. Therefore, application of well-estabished and new modeling approachces that are used to model the effect of habitat loss in the contemporary ecological context to similar situations in the deep past can be both useful and insightful.

2.2 Historical context

The phenomenon of Mass Extinction in Earth's past was first considered by the French zoologist Georges Cuvier in 1813, based on his studies of Cenozoic (66 million years ago to present) marine and terrestrial rocks in the Paris Basin, France. Cuvier noted apparent sudden changes in the fossil record, with many species abruptly disappearing across particular rock layers. He postulated these were wiped out by sudden extinction events: episodic geological 'calamities' that occurred rapidly following long periods of environmental stasis. In the early-mid 19th century,

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[2]Stanley [289] estimated it as 67% of species and 40% of genera.

it was recognized that fossils could be used to correlate rock strata across great distances and establish a relative geologic time scale [283]. This also led to the first attempts at estimating past diversity using counts of species in the fossil record. Thus when John Phillips [233] defined the three main subdivisions of the last 541 million years of Earth history (the Paleozoic, Mesozoic, and Cenozoic eras), the boundaries between these intervals were characterized by rapid changes in the composition of the fossil record and the apparent sudden loss of many animal groups.

Cuvier's 'catastrophist' approach and the theory of rapid, periodic mass extinction events fell out of favor in the latter part of the 19th century, following the influential work of the British geologist Charles Lyell. Lyell advocated a more 'gradualist' reading of the rock and fossil record, with slow natural processes such as erosion responsible for shaping both the Earth's surface and evolution of life over millions of years [183]. The gradualist approach also emphasized 'imperfections' or erosional breaks in the record of Earth history, whereby "rapid" extinction events observed in the fossil record were instead interpreted as artifacts of missing time (rock outcrop) due to erosion or nondeposition. Lyell's thinking had a huge influence on Charles Darwin during his formation of the theory of evolution by natural selection, as typified by the oft-cited quote:

"I look at the geological record as a history of the world imperfectly kept and written in a changing dialect. Of this history we possess the last volume alone, related only to two or three countries. Of this volume, only here and there a short chapter has been preserved, and of each page, only here and there a few lines." [73].

Mass extinctions (if acknowledged at all) were thus seen as gradual, non-catastrophic, and Earth-bound events well into the twentieth century. Renewed interest came in the 1960's, when researchers such as Norman Newell in the United States and Otto Schindewolf in Germany used updated quantitative counts of biodiversity through time to argue that mass extinctions were real events, and separate from a 'constant'[3] level of background extinction [214, 267]. Schindewolf invoked cosmic radiation as the kill mechanism of sudden mass extinctions, while Newell suggested that sea level changes and habitat loss drove mass extinctions in both marine and terrestrial realms.

This quantitative approach was expanded in the 1980's, capitalizing on the interest generated by Alvarez et al. [12], and resulting from the pioneering statistical work of David Raup and Jack Sepkoski [242, 244, 245, 271, 272, 273, 276]. This work was based upon an exhaustive database of the Phanerozoic fossil record of marine families and genera derived from the published literature (now compiled under the Paleobiology Database, PBDB, https://paleobiodb.org/). Large dataset approaches clearly demonstrated, for the first time, five distinct periods of biodiversity decline during the Phanerozoic, that were subsequently labeled "The Big 5", and included extinction events at the end-Ordovician, late Devonian, end-Permian, end-Triassic, and end-Cretaceous Periods. Statistical analysis by Raup and Sepkoski [244] and Bambach [22] confirmed Newell's earlier suggestion that these five events represented distinct mass extinctions which form a quantitatively separate class of events to a lower rate of background extinction. These data were all based on biodiversity compilations plotted against the geological timescale. Consequently, they suffer from biases associated with differential sampling intensities for different fossil groups, for geographic localities, and for time periods, as well as biases associated with differential preservation, variation in taxonomic practice, and varying lengths of geological

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[3]Background extinction rates varied significantly over the Phanerozoic; instead of regarding them as 'constant', Bambach (2006) in identifying mass extinctions looked at a 'relative' increase in extinction rates as compared to the specific background rate preceding the event.

time periods analyzed. Since 2000, work by John Alroy and others (e.g. [11]) has focused on developing models and sub-sampling techniques that take these issues into account to produce more accurate global diversity curve estimates.

2.3 Consequences of Mass Extinctions on Macroevolution

Mass extinctions have substantial and observable impacts on macroevolution, although the linkages between pattern and process require further study. At the broadest level, mass extinctions remove species and clades from the global biosphere and substantially sort the morphological and genetic diversity that exists and may continue to evolve. Mass extinctions result in "winners" and "losers" in the evolutionary game that may or may not be the same species and clades that were successful during background (non-mass extinction) intervals. Consequently, the clean slate of ecological and phylogenetic diversity remaining after a mass extinction has led to substantial global ecological reorganizations, as well as modification of the global evolutionary trajectory [99, 106, 141, 211].

The classic example of this, is the demise of non-avian dinosaurs at the end-Cretaceous (K-Pg) mass extinction event. These taxa had dominated terrestrial environments for over 150 Myrs prior to their extinction and demonstrated little sign of ecological or evolutionary decline prior to the K-Pg bolide impact [50] (but see [66] for an alternative viewpoint). And yet, following the K-Pg mass extinction, only small avian dinosaur clades remained to repopulate terrestrial ecosystems, and thus today, the once majestic dinosaur clade is represented by chickens, doves, and emus. Beyond this evolutionary change, ecological turnover associated with the K-Pg event led to the famous replacement of dinosaurs by mammals as the dominant large-bodied terrestrial clade on Earth today [9, 50, 86, 87, 136, 164].

Notably, there has been a long debate regarding whether mass extinctions are a component of a 'normal' macroevolutionary process [242, 326], or whether they are singular events and with no underlying universal components. While the paleontological literature tends to treat each mass extinction events as unique, in particular because of the wide range of suggested triggers, a more systematic view of extinctions (e.g., relating them to perturbations of the CO_2 cycle) makes it possible to reveal generalities among the phenomenon responsible [253, 256, 257]. This suggests a movement away from mass extinction triggers and towards investigations into the nature of mass extinction kill mechanisms. One can hypothesize that it is the kill mechanisms that are universal, not the triggers, so that the broad variety of triggers lead to mass extinctions through a smaller number of well-defined kill mechanisms. This is where linkages between population and community models to regional biome and global environmental models may substantially contribute to our understanding any general "rules" surrounding the biological consequences of major Earth system perturbations. New and existing mathematical models can contribute substantially to this investigation and to the identification of the degree to which mass extinction occurrence, magnitude, and selectivity may be predictable in our modern world.

2.4 ME triggers, kill mechanisms, and pathways

While understanding of extinction triggers and kill mechanisms have substantially improved in recent decades, there have been relatively few attempts to understand how these factors interact to produce mass extinctions. Models will allow us to identify the specific 'pathways of doom' from the initiating triggers, to the kill mechanisms that exterminate individuals and populations, to the accumulated effects of these losses ultimately resulting in substantial decrease in global biodiversity [32, 37, 38, 55, 327]. Models may also provide insight into how mutually non-

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exclusive triggers and often correlated kill mechanisms may work in combination to produce the highest levels of extinction [30, 37, 55, 118].

In light of this, here we focus on the four common kill mechanisms (temperature change, ocean anoxia, acidification, habitat change) identified as drivers of MEs [90]. We attempt to address these issues systematically by identifying specific pathways, i.e. linkages from population-level phenomena to ecosystems to biomes to the global biota. As we believe that mathematical modeling can be helpful in achieving this, a review of mathematical models that can be used to simulate the corresponding process and dynamics is the first necessary step; see Section 4.

3 The state of Mass Extinction science

The study of mass extinctions begins with collection of global taxonomic ranges. These data form the basis of all analyses that may explore topics such as extinction rates through time, relation of extinction rates to origination rates, potential periodicity in large extinction events, and what analytical tools are appropriate to test hypotheses using these data. As described in Section 2.2, the initial collection of global taxon ranges was painstakingly compiled by Jack Sepkoski in the 1980-90s via summary of existing published literature (the most recent Sepkoski compendium increased taxonomic resolution from the family to the generic level [274]). Since that time, paleontological taxonomic ranges have been accrued in large, international databases (e.g., PBDB), however these are still primarily publication-based and therefore can neglect data reposited in museum collections.

3.1 Mass Extinction data

Extinction Rates. – Sepkoski's plot [271] exhibits simple Poissonian statistics that expresses the probability of a given number of mass extinction events occurring in a fixed interval of the geological stage. This assumes that these events occur with a known constant mean rate (extinction rate) and independently of the time since the last event: however it also assumes that extinctions within a single stage are not independent events [218, 219].

The probability that a certain fraction of the extant species will become extinct in a certain time interval (or stage) is likely to be described by a power-law [284]. However, other forms (e.g., exponential) cannot be ruled out, because the width of the error interval appears to be too large, hence impeding the unique, unambiguous identification of the probability distribution. A possible way to get around this difficulty is to use a rank/frequency plot for extinction that is constructed by taking the stratigraphic stages and numbering them in decreasing order of number of species becoming extinct.

Extinction Periodicity. – An insight into the issue of periodicity of extinction can be made by calculating the power spectrum of extinction data. In case the spectrum exhibits clear peaks, the peak corresponding to the lowest frequency defines the extinction period. Attempts to reveal a periodicity in the timing of extinction events date back to mid-1980s [245, 276]. No convincing evidence has been found so far and the issue remains open. Fossil data do exhibit signs of periodicity (suggesting a period of 26 My, e.g. [245, 246]), but there are concerns that this apparent periodicity may be artificial rather than real, e.g., resulting from the technical bias in handling the data [295]. Although it does not seem likely that a simple periodic signal is behind the mass extinction events throughout whole Phanerozoic (in particular, because mass extinctions were associated with events of entirely different origin, such as LIPs and bolide impact), fossil data indicate that some sort of 'regularity' as a mixture of two, or possibly

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more, signals with a different period may be present [200]. There is also certain evidence that the timing of mass extinction events is well described by a combination of a periodic signal with a random process [95]. The hypothetical periodicity (or, more generically, regularity) of mass extinction events inspired a stream of theoretical research attributing the extinction to the fluctuations of the Earth orbit [122] or to a generic macroevolution process (e.g., [133]); however, results remain inconclusive.

The power spectrum of the fossil extinction record can also be used to explore the probability density function of extinction. However, the accuracy of available data appears insufficient to make an unambiguous decision about the type of the probability distribution. While such analysis originally suggested [285] that the spectrum has a $1/f$ form (i.e. a power-law with exponent -1), later studies found that the $1/f$ is superficial rather than real. A better description of the data is provided by a more complex distribution that is consistent with an exponential form at low frequencies crossing over to a $1/f^2$ behavior at high frequencies [156, 219].

Extinction Magnitude. – An alternative approach attempts to reveal a pattern in mass extinctions disregarding their timing and basing only on their magnitude, e.g., see [333] (especially Fig. 7) and further references there. When extinction rates are ranked according to their magnitude, it appears that all mass extinction events including the Big Five form a smooth, continuous distribution without any clear transition or change in the distribution shape. The Big Five do not stand out in any clear way but gradually grade into extinction crises of smaller magnitude. This apparently contradicts the point of view that the Big Five differ from lesser extinctions, as the difference seems to be quantitative rather than qualitative. However, the issue as a whole remains debatable, in particular because of considerable uncertainties related to the analysis and interepretation of the fossil record (see below).

Origination rates vs. extinction rates. – Origination rates of species are related to extinction rates. Whereas there is an alternation of peaks of origination and that of extinction, the correspondence between the two curves is by no means obvious. The distribution of the lifetimes of taxa (frequency of occurrence vs lifetime) follows the power-law distribution, which can be shown theoretically using a stochastic theory [215, 220]. Pseudo-extinction (the apparent extinction of a group of organisms with the survival of modified descendant forms) and paraphyly (a group of organisms including only some of the descendants of their last common ancestor) may drastically change the statistics [243, 275], as power-law distribution of living and fossil species would have different exponent.

Challenges associated with data and statistics. – The accuracy of the extinction dates assigned to a species depends on several factors (see Fig. 2), including the species' preservation potential, habitat type, and abundance and density of individuals. The latter describes the Signor-Lipps effect wherein the chances of finding the 'true' last appearance of a fossil within a sequence of sedimentary rocks dated to coincide with an extinction/interval of environmental change increases with how common/abundant that fossil is within that sequence of rocks [281]. While the chances of finding individuals at the last moment of a species' extinction is very rare, the probability of finding a fossil further decreases with increased species rarity. Consequently, the last occurrence of a given species is likely to be an earlier date than the actual date of extinction; this effect is worse for more rarer taxa, those with poor preservation potential, and those that live in net erosive habitats (e.g., most terrestrial environments). This can be mitigated to some degree by grouping species into higher taxa to decrease the above effects by increasing the number of individuals that could be fossilized. Lazarus taxa [98, 140] represent a different challenge where species have a fossil record prior to and after the extinction event, but disappear during the event itself; likewise, Elvis taxa describe two very similar taxa, one of which exists prior to the extinction and the other after the extinction, however, their similarities
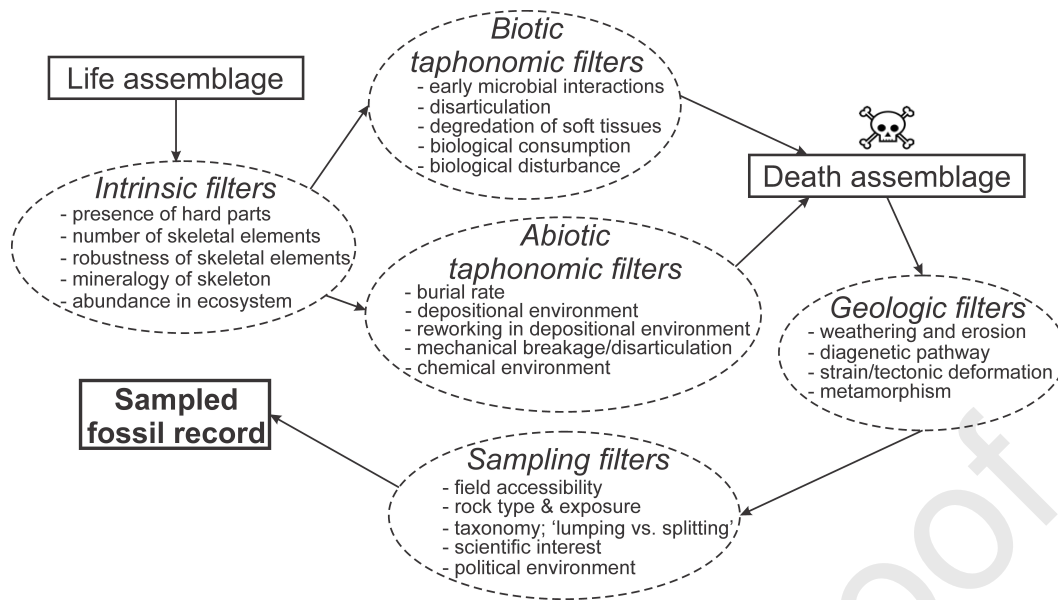
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Figure 2: Schematic 'information flow' showing how the fossil record of an original life assemblage at a given locality in space and time is affected (and can be distorted) by a broad variety of factors of different origins, ranging from the properties of the assemblage itself to social factors that determine the amount of sampling effort.

may make them difficult to distinguish [88].

A species' extinction date often corresponds to a geological boundary (e.g., a boundary between geological Stages, Epochs, or Periods). This is because boundaries in the International Chronostratigraphic Chart are relative and often defined by the taxa that go extinct at those boundaries. As a result, the lengths of geological stages are variable. Numerical ages for geologic boundaries, where they exist, are defined by geochronological analyses, usually radiometric dating of ash beds in the vicinity of the boundary. Since not all boundaries are associated with volcanic ash beds in all places, stratigraphic correlation techniques, based on taxa (biostratigraphy) or sedimentological/geochemical analyses, are required to link numerical ages globally.

Therefore, the computation of extinction rates is complex. Effectively what is needed is a count of the number of species going extinct per unit time (usually estimated at per one Myrs). Fossil counts, compiled from published data, field work, and/or international databases, are conducted at some ranked taxonomic level (e.g., species or genera) for each geological interval (typically the Stage level). Raw counts are often inaccurate due to the spatial and temporal biases in fossil deposition and preservation (see Fig. 2 and also Section 3.2 below). Additionally, thick, heavily mineralized skeletal taxa have higher preservation potential and are therefore overrepresented with respect to thin poorly mineralized or nonmineralized taxa. Large, easily seen taxa are overrepresented relative to small easily overlooked taxa. Common species are overrepresented with respect to rare species. Taxa that have been extensively studied are overrepresented relative to those that are poorly studied (the so called monograph effect). Intervals containing sites of exceptional preservation (known as 'Lagerstätten') tend to be overrepresented because of intense study and the preservation of otherwise poorly preserved taxa. Furthermore, some counted taxa do not represent biological groups because they are paraphyletic or polyphyletic.

Measuring extinction as a fraction of biodiversity may help to decrease uncertainty in these data. However, this method does not provide an extinction rate. There are four extinction

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"metrics": a total number of taxa becoming extinct per stage, percentage of taxa becoming extinct per stage, number per unit time, and a percentage per unit time [220].

3.2 Limitations of the geologic record

Confounding the ambiguity of defining Mass Extinctions are the realities of a limited geologic and fossil record. These limitations impact spatial and temporal resolution of the empirical data, as well as the taxonomic and ecological extent of extinctions. Temporal resolution in the fossil record is uneven and generally coarse (10s to 100s of thousands of years) [154, 161, 266]. Erosional surfaces and sediment bypass surfaces are time-rich, exaggerating the size and rate of taxonomic loss, whereas areas of high sedimentation rate may have more complete temporal archiving, but lower fossil abundances. Because of this, extinction events that are nearly instantaneous, such as those associated with a bolide impact, may show the same relative sharpness as events that occur over ecologic, or even geologic, time. Temporal correlation across large areas can lack precision because correlations are based on fossils that are not globally distributed and/or lateral change in environments that are temporally coeval are difficult to track/recognize..

Similarly, the geographic range of extinction can be limited by lack of outcrop exposure and/or lack of stratigraphic preservation because of erosion and other geological processes. It is further biased by uneven sampling globally and differential sampling density from different stratigraphic horizons (e.g., sampling correlated with distance to the nearest pub and car park in [78]). While it is true that many mass extinction intervals are among the most densely sampled horizons (especially for the Big 5), this is not true for all mass extinctions because of the limits of preserved rock record and accessibility of outcrop areas preserving these rocks.

The ecological context of a ME is limited by the complex interplay of sediment accumulation rate needing to exceed erosional rate, at least locally, to facilitate fossil burial. Consequently, terrestrial ecosystems are difficult to preserve except in basinal settings where there is net accumulation of sediment. In marine settings, most frequently sampled fossils were deposited in shallow settings such as the continental shelf or epicratonic seas. Deeper environments are less likely to be uplifted and, therefore, accessible for study upon continents. This results in the vast majority of fossils occurrences recovered from a relatively narrow environmental (and depositional) setting. Furthermore because of large scale changes in global sea level, some intervals of extremely high sea level such as the Early Cretaceous (145 Ma) are more easily sampled than the times of extremely low sea level such as the Early Silurian (445 Ma).

The challenges outlined here have the consequence that losses in biodiversity may result from any number of underlying causes, some "real" and related to biology, and some that are purely related to fossil preservation (i.e., taphonomy [84]) and researcher sampling. Since biodiversity is essentially composed of the input of new taxa (via speciation) minus the effects of taxon losses (via extinction), biological reasons for large decreases in diversity may reflect: decreases in the speciation rate of new taxa, increases in the extinction rate of existing taxa, or most likely, some combination of both. Attempts to tease apart the contributions of changing speciation versus extinction rates have identified a few large extinctions that seem to primarily reflect decreasing speciation [23]. Bambach et al. [23] point to two of the "Big Five" mass extinctions (end-Devonian and end-Triassic) that fit in this category, which they call "Mass Depletions" (also: Biodiversity Crises [292]) rather than MEs given that the driver of decreased global biodiversity is lack of speciation, not increased extinction (although see [11] for re-analysis of the end-Triassic as a true ME).

Taken together, mass extinctions are the result of a complex suite of environmental and

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evolutionary phenomena, overprinted by an equally complex set of taphonomic, sampling and taxonomic biases. Only so much can be disentangled using raw data derived from the geologic record. Consequently, researchers have relied on statistical modeling techniques to reduce the complexity and attempt to derive both the direction and magnitude of the contribution of particular "causal" factors (described in greater detail below). These models are primarily correlational, and therefore could sorely use validation and increased rigor from more mechanistic mathematical models.

4 Mathematical models, their power and limitations

In the literature on mass extinctions, a mathematical relationship between kill mechanisms and rate of biodiversity decline is not well characterized. Whatever the specific origin of the disturbance that affects the dynamics of a given population, community, or the biosphere as a whole, it is well known that the response is often highly nonlinear [7, 15, 74, 166, 172, 263] [3, 7, 36, 80, 81, 127]. Population dynamics can be resilient to a change in one factor but sensitive to others. The sensitivity of the population or community response to an environmental perturbation, as well as the time scales of the response, can depend on the rate and magnitude of the change in non-trivial ways, e.g., [121, 202, 224]. The biotic response often shows a threshold-type behavior where population dynamics is robust to changes of small or medium magnitude, but extremely sensitive to larger ones. For example, perturbations that bring the population to a tipping point, such that a small change in an environmental variable or factor can result in large changes in the population or community, often lead to sudden extinctions. The threshold-type behavior is widely recognized in ecology, but its relevance to MEs was largely overlooked. Mathematical models provide an efficient research tool to test for and understand nonlinear effects [6, 83, 308]. In particular, nonlinear feedbacks resulting in cascading/accelerating extinctions and/or tipping points have been observed in a variety of population dynamics models (e.g., [263, 264]). In this section, we briefly overview several modeling approaches that have considerable potential to evolve our understanding of mass extinctions.

4.1 Species-Area Relationship models

Habitat loss is recognized as an important kill mechanism (Horseman of the Evolutionary Apocalypse #4) that can lead to mass extinction in the fossil record [37] and is a prime mechanism behind extinctions of modern species [44, 91]. Although paleontological studies of geographic range abound (e.g., [117, 140, 212, 237]), interpretation of the fossil data is difficult given time-averaging and spatial limitations of geological record (cf. Section 3.2). A mathematical framework that may help to account for the limited spatial resolution of this record are Species-Area Relationship (SAR) models [45, 255, 265]: the number of species (say, K) living in a habitat of area A is known to depend on A as a power-law:

$$K = bA^{\alpha}, \tag{1}$$

where b and $0 < \alpha < 1$ are coefficients; numerous empirical studies indicated that usually (albeit not always) $0.15 < \alpha < 0.4$ [334].

Relation (1) quantifies the general tendency that a larger habitat contains, on average, more species than a smaller one, and, more specifically, states that the species increase occurs at a decelerating rate (i.e. slower than linear). Note that the coefficients in (1) are not universal, in

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the sense that they may depend on species traits [102] and also are sensitive to the sampling design (e.g. [225, 265]).

Species-area relationship is one of the best documented models in ecology confirmed and/or used in numerous empirical studies [46, 67, 185, 255]. Theoretical justifications of SAR are predominantly based on either the assumption of an equilibrium between the processes of migration and extinction, cf. [185], or the assumption of random allocation following various probability distributions [64]. A related stream of theoretical research placed SAR into the macro-evolutionary context by linking it to speciation [82]. Interestingly, by considering speciation in a heterogeneous, fluctuating environment, this approach, along with the justification of SAR, also reproduced the power law of extinction times consistent with the fossil record [228].

We mention here that SAR models are often used in the context of island biodiversity, apparently as a follow-up of the hugely influential study by R.H. MacArthur and E.O. Wilson [185]. However, application of SAR is by no means restricted to islands or fragmented habitats and there have been a large number of studies where they were successfully used to quantify biodiversity of continues habitats at a broad range of spatial scales, e.g. [47, 225]; in particular, SAR models were applied to fossil data on the continental scale [46, 180].

Now, consider the case where the area of available habitat shrank, as a result of an extinction triggering event, from the pre-event value A to a new value $\hat{A}$. The corresponding fraction of the species that went extinct is then estimated as

$$\Delta K_{ext} \quad = \quad \frac{K - \hat{K}}{K} = 1 - \left(\frac{\hat{A}}{A}\right)^{\alpha}. \tag{2}$$

Therefore, the effect of habitat shrinking on biodiversity loss occurs not proportionately among taxa but, instead, in a nonlinear and self-accelerating way that is particularly evident when habitat area becomes small. SAR models can provide more accurate estimates of the magnitude of a mass extinction event, e.g. the number of species that became extinct [57]. Further, it has been shown that interpretation of paleodata can be misleading unless SARs are taken into account [24].

Once the response of habitat to a given extinction trigger event is known, Eq. (2) links the number of species extinctions to the magnitude of the environmental disturbance. As an example, consider the change in the habitat size available to marine species caused by a decrease in sea level. Because most of marine life is concentrated in coastal areas and continental shelves (< 200 m water depth), sea level fall is likely to remove shallow marine habitat. It can be shown that the decrease in habitat area is described by a generalized power-law:

$$\frac{\hat{A}}{A} \quad \sim \quad H^{\chi(H)}, \tag{3}$$

where H is the change (decrease) in sea level and exponent χ is scale-dependent exponent, its value being estimated differently for small and large values of H; see Appendix 6.1 for details. Having substituted Eq. (3) to (2), the fraction of extinct species (compared to the pre-change number) is described by the inverse power-law of the height of the sea rise with the exponent $\alpha\chi$.

The utility of SAR models can be tested with case studies in the fossil record with relative ease, especially those investigating the effects of sea level changes on patterns of global biodiversity, e.g. [129, 229]. For example, the Cinncinatti Basin in North America (Late Ordovician $\sim$445-450 Ma) has a well-characterized geologic and fossil record that shows expansion and contraction of marine environments over time in response to sea level oscillation. Decades of detailed fossil collections (e.g. [42, 188]) have documented changes in species diversity in response

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to sea level, and the geologic record allows for an estimation of change in marine basin area. These empirical data could then be compared to predicted species diversity from SAR models, which could either confirm the quality of existing sampling, and/or support additional sampling in this area.

4.2 Habitat fragmentation

Habitat loss is one likely consequence of unfavorable environmental changes but not the only one. Environmental changes of sufficiently large magnitude and duration are also likely to lead to habitat fragmentation. Importantly, the transformation of a continuous habitat into a fragmented one is a threshold phenomenon that occurs when the effect of changes exceeds a certain critical value [309]. During a 'sudden' fragmentation, a single large habitat breaks into several (possibly, many) disconnected fragments or sites. The area of the sites is described by a certain frequency distribution, typically by a power-law [309]):

$$g(A) = \nu A^{-r}, \tag{4}$$

where ν is a coefficient and the value of the exponent is usually $1 < r < 2$. The power-law distribution of fragments size was shown to work well for forests [260], semiarid vegetation (shrublands) [206], and salt marshes [324].

As a result of habitat fragmentation, for a community dominated by species with limited dispersal abilities, a single large community (or population) splits into a number of isolated or only weakly connected subcommunities (subpopulations). Note that the area A_0 of the largest site that emerged from this fragmentation can be significantly smaller than the area of the original habitat; their ratio can be estimated as

$$\frac{A_0}{\bar{A}} \sim (2-r)\delta, \tag{5}$$

where $\bar{A}$ is the area of the habitat before fragmentation occurred and δ is a small factor, $\delta \ll 1$, determined by the geometry of specific system (see Appendix 6.2 for details).

Assuming that the number of species supported by each site is described by the same SAR (1) (i.e., with the same exponent α), the fragmentation will inevitably lead to a corresponding 'sudden' sharp decrease in the biodiversity:

$$\frac{\hat{K}}{K} = [(2-r)\delta]^{\alpha} \ll 1. \tag{6}$$

This can also be directly tested with case studies in the fossil record. On a large scale, there is a long-standing question regarding the influence of tectonic dispersion versus amalgamation on extinction dynamics, where the former increases habitat fragmentation and the latter decreases it on a global scale, e.g. [96, 241]. Paired with the geologic record of shallow shelf habitats, the habitat fragmentation model could be applied to better constrain the contribution of this factor to mass extinctions. On a smaller scale, the habitat fragmentation model could test the potential influence of localized habitat fragmentation associated with expansion of oxygen minimum zones (OMZ). Many periods of elevated extinction in the Phanerozoic are associated with OMZ expansion where anoxic waters move onto shallow continental shelves. This process causes both extinctions in shallow water communities that are now anoxic, as well as habitat fragmentation between shallow and deep water ecosystems, e.g. see [123] and references therein. Changes to the OMZ have been shown to cause some bizarre patterns of extinction with water depth [287]. Application of habitat fragmentation models could help elucidate the degree to which these patterns result from anoxia directly, versus the added effects of habitat fragmentation.

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4.3 Metapopulation models

SAR models, although a reliable tool to describe a decrease in biodiversity resulting from habitat fragmentation, do not provide any information about the time scale over which the decrease may have happened. Insight into this issue can be made by combining the 'geometry' of the discrete (fragmented) habitat with some basic ideas of population dynamics of species that inhabit it. That can be done using the metapopulation concept [112]. The metapopulation theory shows that the number of species supported by a fragmented, 'patchy' habitat consisting of M separate sites (or patches) of area $A_1, \ldots, A_M$, is significantly less than the number of species in a single habitat of the equivalent area $A = A_1 + \ldots + A_M$ [115, 328, 305]. In addition to the approach based on SAR (e.g., see Eq. (6) above), which is largely descriptive, the metapopulation theory shows *how* the decay in biodiversity happens, i.e., what specific processes are responsible for this. Below we briefly outline some relevant mathematical techniques and (some of) the main findings.

In a fragmented habitat, sites are usually assumed to be sufficiently small, so that their inner spatial structure can be neglected. The part (subpopulation) of the population that inhabits the k-th site can then be described by a single variable - say, n_k. The metapopulation dynamics of a given species inhabiting the fragmented habitat consisting of M sites is fully described by M variables, $n_1, \ldots, n_M$. In the classical metapopulation approach, n_k is a binary variable accounting only for species presence-absence but not for their population size, so that either $n_k = 1$ (species present) or $n_k = 0$ (species absent). This is a particularly convenient link to paleontological data where the records may not often be of sufficient precision to estimate the population size.

In the conceptual single species case, the mathematical framework of the metapopulation dynamics is described as follows [114, 115]:

$$\frac{dp_k}{dt} = C_k(1 - p_k) - E_k p_k, \qquad k = 1, \ldots, M, \tag{7}$$

where p_k is the probability of the nth site being occupied, t is time, and C_k and E_k are, respectively, the colonization and extinction rates of site k that account for the geometry of the patchy habitat structure such as the areas of the sites and the distances between them [115].

Alternatively, species abundance in a fragmented habitat can be described by a single 'global' variable such as the fraction of sites that are occupied by the species at time t. In that form, the metapopulation model can be extended to include multiple species. In particular, Tilman et al. [305] considered the following model to study the interplay between interspecific competition and the effect of habitat destruction:

$$\frac{dq_j}{dt} = c_j q_j \left(1 - D - \sum_{i=1}^{J} q_i(t)\right) - q_j \left(m_j + \sum_{i=1 \ (i \neq j)}^{J} c_i q_i\right), \tag{8}$$

where $0 \leq q_j \leq 1$ is the fraction of sites occupied by species j, J is the total number of species ($j = 1, \ldots, J$), D is the proportion of sites being destroyed, and the bilinear (cross-product) terms account for competition[4].

A more advanced variant of the metapopulation approach considers n_k as the size of the kth subpopulation (e.g., [7, 120]). In this formulation, metapopulation models become similar to lattice models, see Section 4.6 below.

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[4]In Tilman's model, the competing species were arranged in the hierarchical order and it was additionally assumed that an inferior competitor always loses to a superior one.

Subpopulations can interact with each other either directly, e.g. through dispersal/migration between sub-habitats (as in models (7) and (8)), or indirectly through a common external factor. As a result of such a coupling, fluctuation in the subpopulation sizes can become synchronized [177]. In particular, spatially-correlated environmental noise (e.g., associated with weather fluctuations) can make local populaiton dynamics synchronized [205, 238, 240]. Since the magnitude of local population oscillations often increases as a result of unfavorable environmental changes [193], for instance when approaching a tipping point [264], synchronized fluctuations can result in a sudden extinction of the whole population as the population size may drop to a dangerously small value simultaneously at all sites.

Another property that makes the metapopulation framework a relevant approach to extinc-
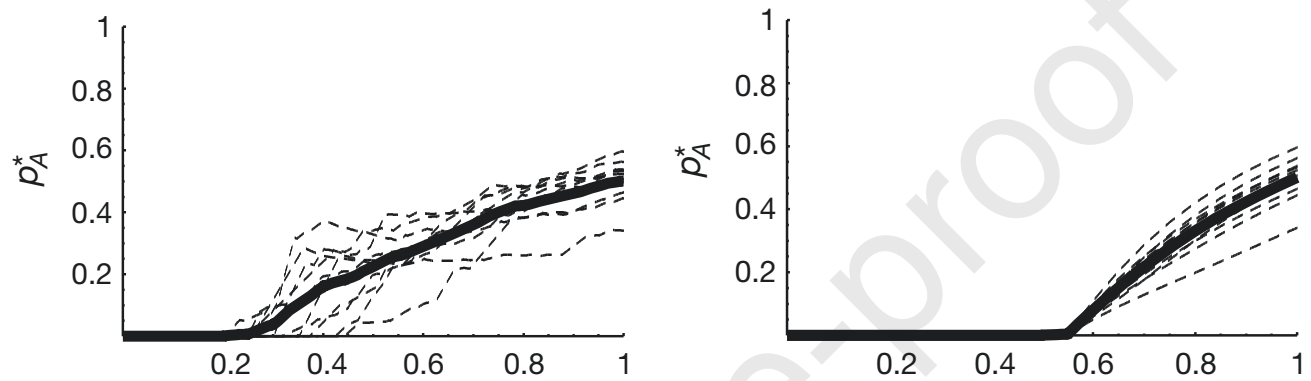

Figure 3: I
disturbance
results in a

Hanski & Ovaskainen   *Extincti*

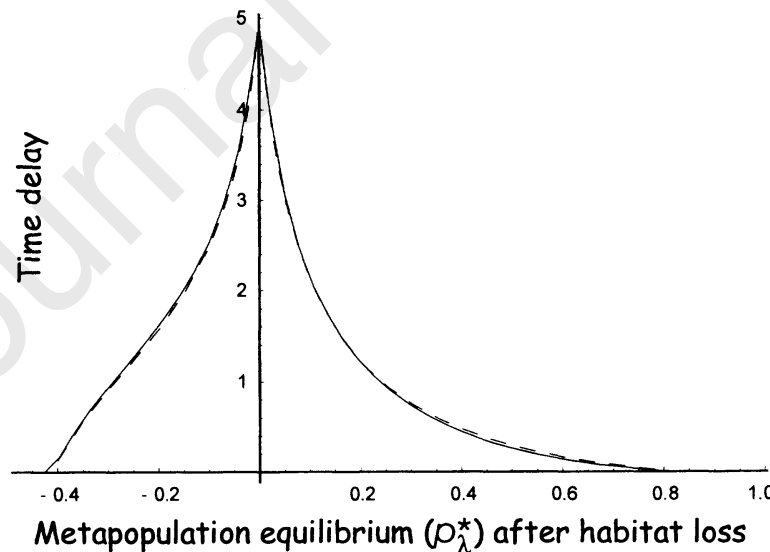Metapopulation equilibrium (p_λ^*) after habitat loss

Figure 4: Dependence of the delay in species response to a disturbance in a metapopulation model. From [116].

Figure 1. Time delay in metapopulation response to habitat loss plotted against the value of the equilibrium fraction of occupied habitat following habitat loss (p_λ^*). The continuous line shows the time delay in the 30-patch landscape, shown in Fig. 2 and predicted by the spatially realistic model. The broken line gives the Levins-model approximation with appropriately interpreted parameters (see text). Values of $p_\lambda^* < 0$ correspond to metapopulation extinction ($p_\lambda^* = 0$), but the
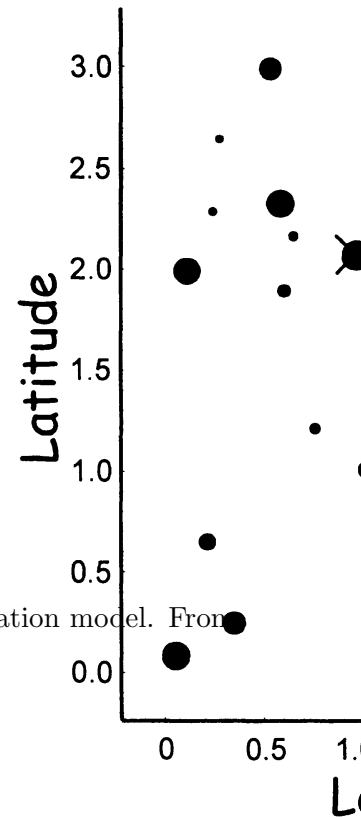
*Figure 2. A hypothetical
areas log-normally distri*

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tion modeling is the existence of long-term transient dynamics [224, 305] (see also [121, 208]). In the context of metapopulations, this is also known as "extinction debt" [305]. A perturbation of the metapopulation's spatial structure, for example, resulting from the destruction of a sufficiently large, supercritical fraction of sites (i.e. exceeding a certain threshold [115]) may lead to the extinction of the whole population. However, the extinction will not happen until after a long period of apparent persistence, its duration being estimated as [224]:

$$T \quad \sim \quad \frac{1}{|\lambda_M - \delta|}, \tag{9}$$

where λ_M is the largest eigenvalue of the matrix describing the strength of inter-site coupling due to the geometry of the environment [115] and δ is the ratio of a site's extinction and colonization rates [115]. In cases where the degree of habitat fragmentation can be linked to the magnitude of the corresponding environmental perturbation (e.g., perturbation of carbon cycle as an extinction trigger [256]), this property provides a framework to investigate the time scales on which extinctions occur.

By way of example, consider the situation where a decrease in the number of available sites results from a change in a certain factor X (for instance, X is the height of decreasing sea level), where X changes as a result of one or more extinction triggers. Let X_0 be the initial, pre-change value. In a rather general case, the fraction of habitat lost P is expected to follow a power-law [216, 220]:

$$P \quad = \quad 1 - a(X - X_0)^{-\gamma}, \tag{10}$$

where a and γ are coefficients that may depend on the specific topography of the sea floor. Since the time required for the population to go extinct, T, is a known function of P, an estimate of the timescale to extinction can be determined from Eq. (10). Note that here we do not aim to provide a detailed study but only outline the way in which the metapopulation framework can be applied for analyzing extinctions.

4.4 Population dynamics and the Allee effect

In the population dynamics of a single species, where the density or size of an isolated population is determined by birth and death events (i.e., neglecting migrations), the population growth rate depends on population density. Mathematically, this can be expressed in a variety of ways [83, 160, 250]; probably the most common is given by the following equation:

$$\frac{du}{dt} \quad = \quad f(u)u, \tag{11}$$

where t is time, u is the population density at a given location, e.g., in a given habitat, and $f(u)$ is the per capita growth rate. Eq. (11) does not explicitly account for possible stochastic factors, instead explicitly, considering their effect 'on average' [6]. Depending on the species' traits (e.g., whether it has overlapping or nonoverlapping generations), Eq. (11) can be replaced by its time-discrete analog such as a difference equation or a map [160, 210]. In the context of species extinction, a relevant property of Eq. (11) is the existence/nonexistence of a nontrivial ($u > 0$) steady state; however such a steady state can disappear as a result of a bifurcation [83, 160, 210] which, in turn, may reflect a change in the environmental conditions.

The single-species model (11) can be generalized to a multispecies case resulting in the following system of equations:

$$\frac{du_j}{dt} \quad = \quad f_j(\mathbf{u})u_j, \qquad j = 1, \ldots, J, \tag{12}$$

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where $\mathbf{u} = (u_1, \ldots, u_J)$. The properties of this system (12) are usually much more complicated compared to the baseline single-species model (11); in particular, its solutions can exhibit population oscllations. Oscillations can be of a large magnitude, such that population densities may periodically fall to very low values. This makes the corresponding species prone to extinction. As one example, a model of type (12) containing only two species, one prey and the other its predator, has been successfully applied to explain species extinction as a result of so called "paradox of enrichment" [105, 192].

The properties of per capita growth rate are determined by species' traits. There can be at least two qualitatively different cases (see Fig. 5). In the first case, $f(u)$ is a monotonously decreasing function (e.g., as a result on increasing intra-specific competition that tends to increase with increasing population density) reaching its maximum at $u = 0$ and becoming negative for large u. In the second case, $f(u)$ is not monotonous: it increases at small u and decreasing for large u, such that the maximum per capita growth rate is reached at some positive value of the population density. The former case is often referred to as logistic growth (sometimes as 'generalized logistic growth') and the latter case as population dynamics with an Allee effect [174, 210]. The Allee effect is increasingly identified as innate in many species [69, 70, 291] which suggests that population growth with the Allee effect is more relevant for the general model (11) than logistic growth.

Given the Allee effect, the growth rate at small population densities can be small and this has important consequences for population survival. The so-called strong Allee effect, where the growth rate becomes negative once the population density falls to a small value, is particularly relevant (cf. curve 4 in Fig. 5). In this case, there exists a survival threshold (β) such that once the population density falls below the threshold ($u < \beta$), an isolated population will inevitably go extinct. In a multi-species community, the existence of the Allee effect can have more subtle effects on population dynamics, with the same general trend of increasing extinction likeliness. As one example, an increase in the predation strength in a predator-prey system may lead to the disappearance of the positive (species coexistence) steady state; this invariably leads to species extinction (Fig. 6).

Importantly, the Allee effect can arise from several biological mechanisms [69, 70, 291].
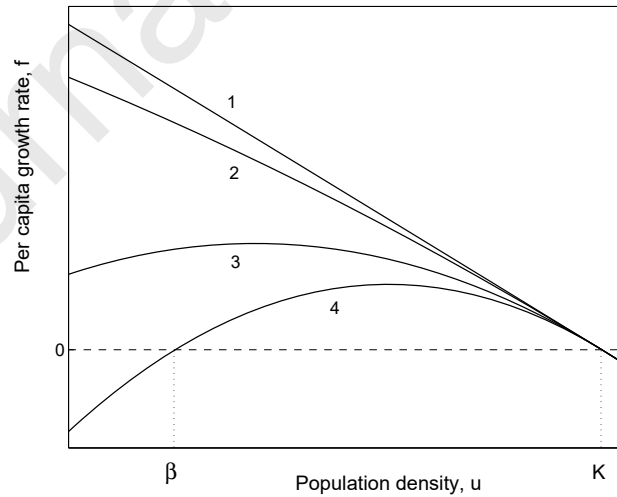

Figure 5: Per capita growth rate in the baseline single-species model (11) for different strengths of the Allee effect: curve 1: no Allee effect, curves 2 and 3: weak Allee effect, curve 4: strong Allee effect. From [174].
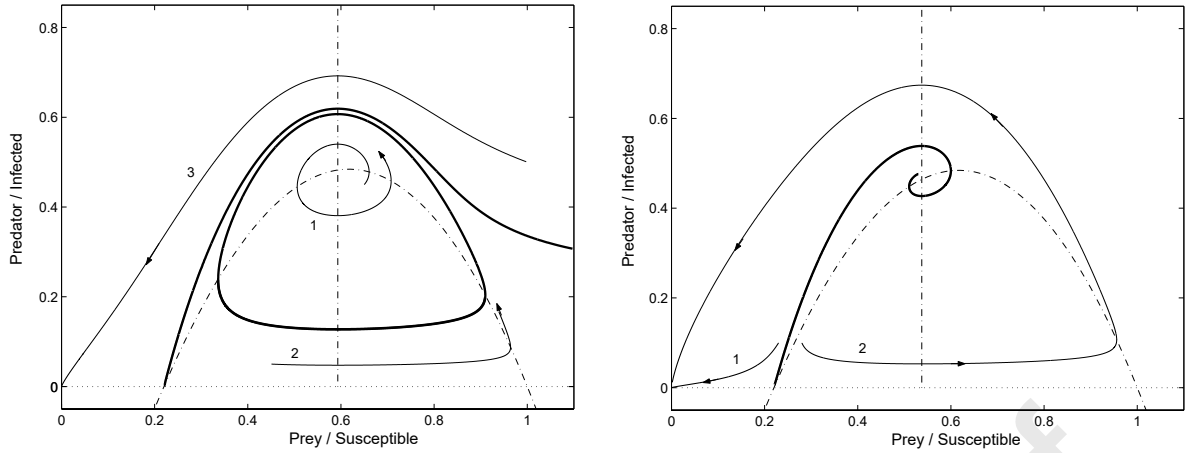
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Figure 6: Dynamics of a predator-prey system with the strong Allee effect for prey and with different predation strengths: (a) intermediate predation, (b) strong predation. From [187].

Perhaps the most common is the difficulty in finding mates at low population densities [15]; this can be exacerbated by a bias in the sex ratio [69]. Another intuitive mechanism is the positive effect of cooperation occurring at small population densities, which can manifest itself in a variety of ways [69, 70, 291]. Many of those mechanisms can be affected by a change in environmental conditions, where an unfavorable change (e.g., habitat degradation) may increase the strength of the Allee effect, hence leading to an increase in the survival threshold and/or to a decrease in the per capita growth rate at small population densities. This increases the population's extinction vulnerability. Placing it into a multi-species context, an increase in the strength of the Allee effect globally is a factor that arguably may result in mass extinction; two hypothetical mechanisms are discussed below. Therefore, models that link environmental changes to an increase in the strength of the Allee effect has immediate application for mass extinctions modeling. The Allee effect is assumed to be an important factor in metapopulation dynamics as well [16].

To demonstrate how the Allee effect can create a 'pathway of doom', consider the effect of global warming (Horseman of the Evolutionary Apocalypse #1, often a consequence of a perturbed carbon cycle [256]). A biased sex ratio is a factor resulting in a strong Allee effect [69]; however, for many species, the sex ratio is environmentally determined, and in particular by temperature [68, 143]. As temperatures rise sex ratios change and strengthen the Allee effect, thus potentially leading to the extinction of whole animal orders and even classes. Notably, this mechanism has been suggested as a factor contributing to the non-avian dinosaur extinction at the end of the Cretaceous [203]. This could be further investigated in the fossil record by testing for correlations between mass extinction selectivity and clades with temperature-dependent sex ratios in modern counterparts. To our knowledge, this type of extinction selectivity has not been previously explored in the fossil record.

As another hypothetical situation, consider the mass extinction trigger of massive volcanic eruptions. These eruptions emit a large volume of noxious gases and volatiles (CO_2, but also methane, mercury, sulfur dioxide and other aerosols, etc.) into the atmosphere [37, 63, 268]. As some of these gases have a distinct smell, their presence may disrupt chemical signaling employed by many species when searching for mating partners. This could then decrease reproductive success and thus total fitness, which increases the strength of the Allee effect, making species extinction more likely. In the case of a LIP-style event, volatile emissions are both high in

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volume and lengthy in timespan of eruption; gas emissions are spread globally, and could then impact the longevity of large numbers of species. A considerable fraction of the emitted gases end up in the ocean, in particular resulting in ocean acidification. In its turn, acidification is known to impair olfactory discrimination and neurotransmitter function in fish [37], which would have similar effect on the corresponding fish species by increasing the strength of Allee effect in their population dynamics.

Note that, although not yet established at the scale of the global biota, interference with pheromone transmission has been shown to produce a strong Allee effect, and consequent decline in population size, in modern populations of agricultural pests [176]. For instance, gypsy moths, known to be affected by the strong Allee effect [176, 321], have been regionally eradicated by the introduction of artificial pheromone sources that disrupt males' search for females [278, 331, 176]. This provides indirect evidence in favor of the above hypothetical mechanism of mass extinction.

A test of this in the fossil record would necessitate strong clade-level information about the importance of pheromone signaling, for example the fishes described above. If pheromone signaling is plausibly a clade-level trait, then testing for extinction selectivity in such clades as associated with LIP deposition would confirm the contribution of this mechanism to mass extinctions.

4.5 Competitive exclusion

Competition is a negative type of ecological interaction that shapes the structure of populations in a community. While the resource-consumer and/or prey-predator interactions couple different trophic levels, competition largely defines how multiple species coexist at the same trophic level, particularly when the species are sufficiently 'similar' to share common resources (including not only food and water but also environmental factors such as habitat space, sunlight, etc.).

In any real-world community, there are usually many species at each trophic level. The number of species is dynamic as populations within the community respond to biotic and abiotic perturbations, in particular to those changing competition strength. Therefore, revealing the environmental conditions and/or their perturbations that lead to a decrease in species richness, e.g. through increased competition, can potentially shed a light on mechanisms of extinction to identify the 'pathways of doom', if these conditions are sufficiently widespread.

The dynamics of a population community consisting of J competing species can be described by the following general system [128]:

$$\frac{du_i(t)}{dt} = \left(f_i(u_i) - \sum_{j=1, j \neq i}^{J} \beta_{ij} u_j \right) u_i, \qquad i = 1 \ldots, J. \tag{13}$$

where the bilinear terms describe the interspecific competition and coefficients β_{ij} quantifies the competition strength. The state of the population community at any given moment of time is described by the vector $\bar{\mathbf{u}} = (u_1, \ldots, u_J)$.

The per capita growth of the ith species $f_i(u_i)$ is determined by the species traits (i.e., logistic growth or affected by the Allee effect). In case the growth rate of each species is logistic, Eqs. (13) take the following form:

$$\frac{du_i(t)}{dt} = \left(r_i - \alpha_i u_i - \sum_{j=1, j \neq i}^{J} \beta_{ij} u_j \right) u_i, \qquad i = 1 \ldots, J, \tag{14}$$

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where coefficients α_{ii} quantify the strength of intra-specific competition and r_i is the difference between the reproduction rate and the mortality rate [160, 210].

Obviously, system (14) always has one trivial, extinction steady state $\bar{\mathbf{u}}_{ext} = (0, \ldots, 0)$, and any non-trivial equilibrium of the system is a solution of the following linear algebraic system:

$$r_i - \alpha_i u_i - \sum_{j=1, j \neq i}^{J} \beta_{ij} u_j = 0, \qquad i = 1, \ldots, J. \tag{15}$$

Steady coexistence of all species corresponds to a stable positive equilibrium $\bar{\mathbf{u}}_{coex} = (\bar{u}_1, \ldots, \bar{u}_J)$ where all components are positive, $\bar{u}_i \neq 0$ for $i = 1, \ldots, J$. The positive steady state, however, only exists under certain restrictions on coefficients α_i, β_i and r_i [280]. Along with the unique positive steady state, there can be multiple states of 'parital extinction' where only some of the species are present, e.g., $\bar{\mathbf{u}}_s = (\bar{u}_1, \ldots, \bar{u}_s, 0, \ldots, 0)$. One simple condition necessary for the stable persistence of the ith species is $\alpha_i > \beta_i$, that is, the strength of the intra-specific competition has to be larger than the strength of the interspecific competition. In a somewhat broader context, this property is often referred to as competitive exclusion – in order to coexist, species should avoid strong interspecific competition: a principle at the foundation of the theory of ecological niches. This is straightforward to see for a system composed of only a few species [160]; notably this result also holds for realistic systems composed of a large number of species with a random competition strength [178]. For given values α_i and β_i (such as $\alpha_i > \beta_i$) the ith species can be driven to extinction by a decrease in r_i [280], e.g., by a decrease in the reproduction rate or an increase in the mortality rate.

This concept is relevant here because environmental perturbations triggering mass extinction events often negatively influence species' suitable habitat. As an example, one consequence of increased pCO$_2$ is ocean acidification and anoxia, both of which have geographic specificity (i.e., increased CO$_2$ does not automatically produce acidification and anoxia globally, but expands from specific regions). Habitat loss, fragmentation, and degradation associated with the spread of ocean acidification and anoxia [59, 163] may locally result in increased interspecific competition as species become concentrated in less altered habitats; this phenomenon has already been observed in modern ecosystems (e.g., [56, 59, 195]). Sufficient, global perturbation of this kind could lead to higher extinction rates related to competitive exclusion worldwide. To the degree that this process also leads to habitat homogenization (see [163]), additional biodiversity loss would be expected (and has been observed in [307]).

4.6 Lattice models

For a species dwelling on a fragmented habitat, for modeling purposes, the individual sites can be regarded as 'nodes' of a certain 'lattice'. The modeling approach combining local population dynamics (e.g., as given by Eq. (11)) with the metapopulation concept leads to lattice models [7, 65, 259]. In a nutshell, lattice models consider local population dynamics coupled with either dispersal/migration between sites or by common abiotic factors, such as weather fluctuations. Note that lattice must not necessarily have a regular geometry. In the more advanced case of irregular shape, lattice models are often called spatial network models [36, 311].

For a single species with overlapping generations, population dynamics on a lattice is defined as:

$$\frac{du_{k,l}(t)}{dt} = F(u_{k,l}) + \sum_{\hat{k}, \hat{l} \in V_{kl}} \left(\frac{\mu}{s_V}\right) F\left(u_{\hat{k}, \hat{l}}\right). \tag{16}$$

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Here $u_{k,l}$ is the population density of a given species at site (k, l) at time t and F is the growth rate. Coefficient μ quantifies the strength of dispersal coupling: it is the rate at which the population leaves a given site (or node in the lattice) during the dispersal stage to migrate to neighboring sites. Thus, the first term and the second term in the right-hand side of (16) describe the migration out of and into a given node, respectively. The whole entity of nodes V coupled by dispersal is called the dispersal stencil; s_V is the number of nodes in the stencil. Depending on species' dispersal properties (e.g., short distance vs long-distance), V can include only immediate neighbors or neighboring nodes as well as more distant nodes. Models similar to (16) are often used to study biological invasions and pattern formation [145, 204, 252, 330].

The baseline model (16) can be extended in a variety of ways to make it more realistic, for instance, to include more species (accounting for predation or intra-specific competition), to include stochastic factors or "noise" (e.g., by adding terms or factors explicitly containing random variables), to add time-delays, etc. Any of these extensions make the properties of the model's solutions more complicated, in particular, often resulting in population oscillations that can be (in a certain parameter range) of considerable magnitude. Interestingly, there is a large amount of empirical evidence that population oscillations at different locations are not independent but are correlated or even synchronized [177]. Local oscillations can be brought to synchrony by either the effect of migration between the sites ('dispersal coupling', as is quantified by parameter μ in model (16)) [142, 145, 144] or by the effect of a common external spatially-correlated stochastic factor [205, 240], e.g. weather conditions. Synchronization of population dynamics across vast spatial areas due to a single large-scale climate system (such as the North Atlantic Oscillation) has been observed in some terrestrial species [236].

Whichever is the specific factor (or combination of factors), synchronization may cause the population density of some species to periodically fall to very low values across the whole array of habitats. Because low density is commonly associated with extinction vulnerability [74, 166], such synchronized population decline may lead to the extinction of entire metapopulations over a large spatial scale and even ultimately species extinction.

Note that the spatial arrangement of habitat sites - the nodes in the lattice - do not have to be regular. In the case where the synchronization occurs due to the Moran effect (i.e., the effect of a common external factor), details of the spatial arrangement, such as the distances between the sites and/or the number of links emanating from each site, do not make much difference as long as the external factor(s) remains spatially correlated. In the case where the synchronization results from inter-site migrations, instead of a lattice the fragmented habitat can be considered as a dispersal network, which can have a broad variety of spatial geometries or 'topologies' (see Fig. 7). Network topology has been shown to determine the so-called "metapopulation mean life time" (MLT) [101]. In a more general case where subpopulations are coupled by both dispersal and a common spatially-correlated external factor, there is theoretical and empirical evidence that the local fluctuations can become synchronized [131, 130]. However, the issue remains controversial and may depend on details of the system geometry, density-dependence of the reproduction rate, and the dispersal mechanism [239]. Synchronization of extinction events (e.g., when the population abundance decreases substantially and simultaneously across space) greatly reduces the metapopulation MLT [119]. Interestingly, the effect of environmental correlation increases sharply when the means and variances of local extinction probabilities become sufficiently high [119]. Since the probability of local extinctions may increase as a result from local habitat degradation, this could be another 'pathway of doom' towards mass extinction provided that local environmental perturbation has a global trigger (cf. Section 4.5).

Fig. 2. Alternative topologies ... (a) ... ('geometrical network' [155]), and (c) 'forest fire' network. From [155].

Table 1. Alternative graphs for comparison (see Fig. 1)

...a collection of coupled nodes (sites) can be modified to account for the directionality ... of the inter-nodes interactions, w_{ij} where such directionality occurs. ... population in a ... habitat ... coupling normally occurs due to the migration/dispersal between different sites, the corresponding network is called a dispersal network, cf. [36, 311]. Dispersal networks become directed if the dispersal is asymmetric [311], i.e., individuals move from site A to site B more frequently than from B to A. If dispersal is due to animal locomotion, the asymmetry (directionality) is relatively rare, because it requires a specific behavioral response (e.g., olfactory, as in chemotaxis), ... and/or ... short timescales (e.g., periods of seasonal migration [196]). However, the directionality becomes common in the cases where the dispersal is assisted by environmental flows; one example being wind-assisted dispersal of airborne species [28].

The directionality of the flows in a network suggests the possibility of a new extinction mechanism and hence can make the corresponding total (meta)population or the community more vulnerable to extinction compared to the population dynamics on the corresponding non-directed network or lattice ... dispersal (e.g., by eliminating the 'stepping stones' [27, 262]), and thus damage overall network connectivity. In turn, substantial node loss may break global connectivity and destroy the global cluster. To this end, the problem of population dispersal on a directed network is similar to a percolation problem, cf. [217, 290, 303]; where global connectivity of the dispersal network is essential for population survival (e.g., ensuring access to breeding grounds), disruptions to network connectivity can lead to extinctions.

Geographical structure is only one possible ecological context where directed networks are important. Food webs provide another and arguably more common network context where the coupling between different species in a community is due to trophic interactions (that may include not only resource-consumer and prey-predator interactions but also interspecific competition) [235]. Similar to dispersal networks, elimination of a node – that is, extinction of a certain species – can affect food web connectivity and result in energy flow bottlenecks [8], which can lead to extinction of additional species. Extinction of 'keystone species' is an example of how global food web connectivity can break down, potentially leading to extinction cascades under certain restrictions on food web geometry [8, 100, 286]. Thus, the extinction of a single

Model name	Description
Erdos-Renyi random	New vertices are added to the graph and 4 times the vertex number created by connecting uniformly randomly chosen vertices (Erdos...)
Complete	Every vertex is connected to every other node (Harary 1969).
Forest fire	Resembles how a forest fire spreads by igniting trees close by. ... sequentially and edges are created with respect to the neighb... (Leskovec et al. 2007).
Barabasi-Albert scale free	One vertex is added in each time step and edges are then crea... with a scale free probability, $P(k) \sim k^{-\gamma}$ (Barabasi & Albert 199...)
Lattice	Based on a regular tree with 2 edges connecting the 'child' ne... Nepusz 2006). The edges created are undirected [8]. A lattice of 2 dimensions is composed of a set of 4 vertices join... replicated for the specified size of the graph (Csardi & Nepusz...)
Geometric (small and large)	First a number of points are dropped on to a unit square, then ... with an undirected edge if they are closer to each other in Euc... radius (Csardi & Nepusz 2006). The small and large Geometric... 0.40 radius values.
...small-world	Derived from a Lagrangian particle model within a wind and...

species may, in principle, lead to extinction of many other species and eventually even to the total community collapse [81] – at least, on a regional spatial scale. The question remains as to how this mechanism may be upscaled to the global level, as a species that is keystone in one community may not necessarily play the same role in another community.

Interestingly, apart from the bottom-up driven cascades of secondary extinctions (e.g., disruption of primary production), there can be also top-down driven extinction cascades. For instance, a top predator may attempt to compensate for the loss of its usual trophic resources by increasing the intensity of alternative trophic interactions [254]. A more intense exploitation of the alternatve resources then may lead to the extinction of the corresponding species.

Placing food web dynamics into broader ecological, environmental and evolutionary contexts, the extinction of keystone species (that can lead to catastrophic changes in the food web and potentially contribute to mass extinction) may occur for a variety of reasons. Apparently, it can take place as a response to unfavorable environmental changes, e.g., because of an increase in the strength of the Allee effect (Section 4.4) or as a result of competitive exclusion (Section 4.5). In turn, unfavorable environmental changes are a typical consequence of an extinction trigger. The corresponding food web alteration and trophic cascades may act as another 'pathway of doom,' a phenomenon investigated previously in the fossil record as a mechanism for mass extinction [254]. These mechanisms, however, remain controversial in part because of insufficient data to reconstruct ancient food webs, and due to theoretical debates regarding food web complexity and its resilience to perturbation [80, 81, 100, 254, 302].

4.8   Coupled climate-population dynamics models

Climate forcing is widely accepted as a major factor that may lead to species extinctions, biodiversity loss and, ultimately, mass extinction. Climate forcing has multifarious downstream effects including temperature change (Horseman of the Evolutionary Apocalypse #1), ocean anoxia and acidification (Horseman #2 and #3, respectively), habitat loss and/or fragmentation (Horseman #4), altering/disrupting food webs, etc. The biosphere is itself a complex adaptive system [172] set within the broader context of the Earth System where changes in atmospheric and oceanographic processes have strong effects on biology. Thus, interactions within the biosphere and between the biosphere and other spheres of the Earth system are often not independent of each other and must be considered in concert [151]. Complex dynamics of food webs in a fragmented environment is one example [175]. For instance, a climate change leading to a decrease in sea level can result in habitat loss for marine species living in coastal waters. Predictions of SAR model would support eventual extinction of some species. In turn, species removal may cause an extinction cascade due to the disruption of the corresponding food web, which if substantially widespread, may facilitate mass extinction. The interplay between different factors is nontrivial and often counter-intuitive: depending on complex interactions between life history, disturbance regime and species distribution pattern, species extinction may be facilitated (as in the above example) or mediated under climate change [151].

As another example, there is frequent discussion regarding the production of widespread oceanic anoxia (Horseman #2) with increased temperature resulting from the fact that warmer water can hold less dissolved gases (e.g., [43, 277]). However, there is also empirical evidence that an increase in water temperature can disrupt photosynthesis [251]. Since about 70% of atmospheric oxygen is produced in the ocean, a substantial decrease of this ilk could have dire consequences for both marine and terrestrial biota, potentially contributing to a marine mass extinction. Although empirical evidence for this possible scenario remains meager (but see [179]), it has been discovered and investigated in detail using mathematical models [269, 270],

including realistic foodweb-type models [232].

The complexity of interactions between the climate and the biosphere is perhaps best captured by the Gaia concept [181, 182]. It states that not only the climate impacts species and communities but also the biosphere may have a feedback on climate to alter it on the global scale. Indeed, dynamic feedbacks are well recognized between the ocean-atmosphere system and the biosphere. Clear examples of this exist in the geologic record as exemplified by the Great Oxygenation Event (2.4 Ga) and evolution of terrestrial land flora. Both of these events significantly modified the Earth system: the former resulted in a three-fold increase in atmospheric oxygen levels resulting from the evolution of photosynthesis; the latter resulting in a dramatic increase in terrestrial weathering kickstarting more rapid biogeochemical cycling (especially of carbon) and allowed for subsequent colonization of land by fauna.

Although the precise formulation of the concept and its implications remain debatable [4, 41, 157, 170, 171], in a few cases the existence of such feedback has been proven unambiguously. In particular, plankton (and vegetation more generally), if present in sufficiently high abundance, was shown to affect the average Earth average temperature by changing the Earth surface albedo and hence shifting the balance between the amount of solar radiation kept by the surface and its fraction that is reflected back to space [60]. Mathematical models have been developed to demonstrate how the broken energy balance may push the global Earth system to a different state (e.g., changing the 'hot Earth' to the 'cold Earth' or visa versa) [313], with the changes in the average Earth temperature to potentially become an extinction trigger through the mechanism discussed above.

Mass extinctions are often associated with significant perturbations to the global carbon cycle as recorded in time-series of the carbon isotopic composition of marine and terrestrial sedimentary rocks. Isotopic compositions are measured either via geochemical analyses of inorganic carbon such as limestones, made up of the remains of carbonate skeletons, or organic matter from plants and microorganisms. Whereas such carbon isotope excursions (CIEs) are commonplace throughout Earth history, those associated with mass extinctions are often large, and when constrained by geochronology, unusually rapid [256]. Although some have attempted to link excursions qualitatively to extinction triggers (e.g., release of CO_2 from a LIP with a depleted isotopic composition [103], would be expected to produce a negative carbon isotope excursion in sediments worldwide), mass balance calculations reveal that these excursions are too large to be explained simplistically and likely represent a complex mixture of processes and carbon fluxes/concentrations from various reservoirs. Consequently, the precise causes of large CIEs remain controversial [3].

Carbon-cycle modeling has contributed significantly to understanding the shuttling of carbon between the atmosphere, biosphere and geosphere over geologic timescales [33] and thereby Earth system dynamics across the Phanerozoic. Recent efforts have focused on applying dynamical systems theory and mathematical modeling to carbon cycle perturbations from extinction and 'background' intervals [257, 258]. These analyses, based around a dynamical-system model of the marine carbon cycle, suggest that CIEs linked to most mass extinctions are quantitatively different to those that occur during background times, both in their rate and size. They therefore identify a critical threshold, crossed when the rate of environmental change/CO_2 flux is sufficiently high, which pushes the system beyond steady state, resulting in a mass extinction event. Under this paradigm, large carbon isotope perturbations in the geological record probably represent the nonlinear amplification of processes that operate within the global carbon cycle [257]. These theoretical studies are an innovative link between geological data and mathematical modeling and have direct relevance to understanding the consequences of forcing of the carbon cycle by present-day anthropogenic activities [132].

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4.9 Stochastic models

Stochastic models are used across a diverse set of fields, in particular, in ecology and environmental sciences, often causing unexpected or counter-intuitive dynamics compared to that of their deterministic counterparts [35, 39, 77, 165, 166]. In population dynamics the presence of noise can change the survival or extinction of competing species [315], cause spatial correlation or anticorrelation between populations [238, 240, 316], modify significatively the characteristics of the Deep Chlorophyll Maximum in a marine ecosystem [317], or increase locally the biomass of some species [168].

The frequency and magnitude of stochastic events are known to depend significantly on the statistical properties of the noise [319]. This is often assumed to be a normal distribution, but finer analysis on complex systems also involves the use of exponential distribution, gamma distribution, Pareto or power law distributions, etc. Once the frequency distribution is identified, these models can provides an insight into the system's properties and dynamics, including the limits of model predictability. In particular, the difference between distributions with a 'thin' tail (exponential decay or faster) and the scale-free distribution with a 'thick' tail (power law, especially with the exponent smaller than three). For a random process described by a thick-tailed probability distribution, the occurrence of rare events (such as mass extinctions) is much more frequent than for a thin-tailed distribution. Perhaps even more important for understanding mass extinctions, the existence of a power law distribution (e.g., $1/f$-noise) may indicate that the processes governing the dynamics of the biosphere are correlated through time.

Unsurprisingly, the properties of extinction frequency distributions attracts considerable attention [220]. It has been shown that the distribution of extinctions in fossil data is well-characterized by a power law [215, 285], although the impact of fossil record bias in data interpolation has questioned this [156]. Recent work supports previous findings that fossil record extinction frequencies follow a fat-tailed distribution within clades, but also exhibits heterogeneity at the taxonomic level of orders, such that the data crossing taxonomic ranks are not scale-free [253].

Simple statistical models are based on the definition of probability. One of the earliest and fundamental models is the so-called "Red Queen hypothesis" proposed by van Valen [318]. If probability per unit time of a particular species becoming extinct is independent of time then the model introduces "stochastically constant" extinction. It means the probability of a species surviving for a certain length of time t decays exponentially with time t:

$$p(t) = e^{-t/\tau}, \tag{17}$$

where τ is in the inverse ratio of the apparently small constant probability per unit time of the species becoming extinct. Based on this definition a survivorship curve can be plotted when one takes a group of species and counts how many of them are still present in the fossil record after time t.

Raup [248] shows that stochastically constant extinction will not allow the survivorship curve for genera be exponential, because it depends not only on the extinction rate but also on the speciation rate. Also, the model does not describe mass extinction events in the fossil record. Raup [247, 249] generalized the model to the case in which extinction is not stochastically constant, giving promising results.

More complex models are based on statistical mechanics, particularly spin glass theory. For example, NKCS models are a class of models of random fitness landscapes called NK models and originally proposed for genes [148, 150, 149] may offer possible connections between the dynamics of evolution and extinction rate. These models are similar in spirit to the spin-glass

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models of statistical mechanics [97], particularly p-spin models [75] and random energy models [76]. The NK model for species fitness maps the states of a model genome onto a scalar fitness mimicking the biological process where the genotype is first mapped onto phenotype and only then onto fitness. The NK model generates a fitness "landscape" which is formed by genotype with higher fitness than all of its nearest neighbors. The extended model [149] called the NKCS model uses two additional quantities. The first is the number of neighboring species with which species interacts and the second is the number of genes in each of those neighboring species which affect the fitness contribution of each gene in species. Extinction appears in the model when a species invades the niche occupied by another. The model discovers the Nash equilibria, phase transitions, and self-organized criticality. Also, there is a connection of the original model to the topology.

The Bak-Sneppen model [20] assumes that the average time taken to mutate across a fitness barrier goes exponentially with the height of the barrier as stated in the Arrhenius law of statistical mechanics. The model shows that a power-law distribution of coevolutionary avalanches might give rise in turn to a power-law distribution of extinction events. Extinction takes place when species have particularly high barriers to mutation.

Another statistical mechanics model [297] addresses quite general, schematic models for several populations coupled to resource supplies, and subject to both systematic and random external forcing. The authors employ stochastic large deviation theory to describe possible extinction scenarios in this generic, albeit coarse-grained, mean-field setup, and illustrate the hysteresis effect in species extinction. The manuscript also states the possible scenarios of extinctions based on an intersection of the attraction of a dynamical system describing the environment state and the boundary (niche) that is defined by the resource supply.

Nonequilibrium statistical mechanics allows for the study of fluctuations in species richness found in fossil records using the method of superstatistics [29]. This approach is based on the idea that nonequilibrium systems can be decomposed into weakly interacting subsystems. Each of the subsystem (e.g., local communities) attains a unique dynamic equilibrium, while the dynamics of the system as a whole may remain transient. Using this approach, Rominger et al. [253] explained fluctuations in Phanerozoic biodiversity.

4.10 Statistical models

Statistical modeling is a powerful tool to analyze fossil data and to bridge, at least partially, the gaps left by the common deficiencies of the geological record (see Sections 3.1-3.2), in particular to obtain information about the spatial aspects of mass extinctions. One form of statistical model that has been applied to studying MEs is Paleo-Ecological Niche Modeling (PaleoENM) [213]. Modern ENM is a widely used technique for estimating abiotic niche attributes (i.e., Grinellian niche [108]) by correlating known species occurrences with spatially explicit environmental characteristics; see Fig. 8. The multivariate statistical model creates an n-dimensional cloud of environments (n is the number of environmental layers) that aims to predict a species' fundamental niche (i.e., the realized niche + some extrapolation) within a "space" defined by environmental variables (e-space). E-space predictions may be projected back onto geography in the same time and place, or different times and/or places to test hypotheses such as the availability and migration of species' predicted suitable habitat. Analysis of e-space predictions can also be used to test hypotheses of niche stability during the lifetime of a species or phylogenetic niche conservation within a clade [231].

Whereas modern ecologists have used ENM to investigate hypotheses surrounding species abiotic niches for the last two decades (e.g., [146, 230, 304, 306, 336]), PaleoENM development
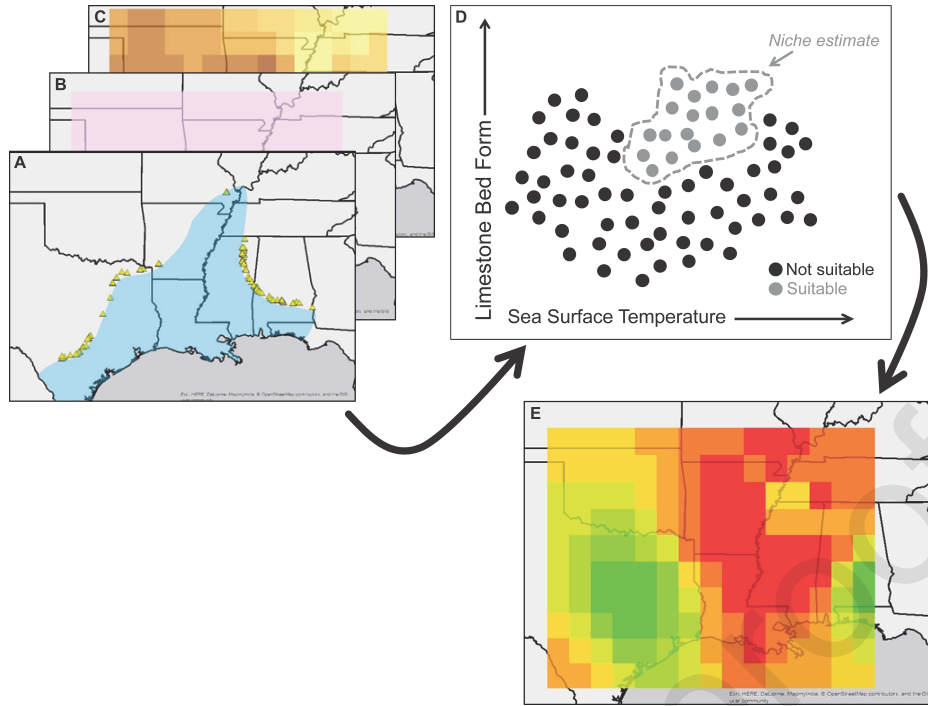
Figure 8: Ecological niche modeling (ENM) processes. (A) Collection of fossil occurrences (yellow triangles) which is then correlated with sedimentology-based environmental layers such as percentage of chalk (B) and percentage of clay (C); ENM algorithms produce a multivariate correlation between the occurrences and paleoenvironments in environmental space (D) where existing environmental space is denoted as dots and the algorithm estimates which dots (gray) in this space are within a species' niche; model output is a map of habitat suitability in geographic space (E) where a value of 1 indicates highly suitable and a value of 0 indicates highly unsuitable habitat. Modified from [213].

is more recent [213, 293, 294]. One unique challenge is the compilation of paleoenvironmental data at high spatial and temporal resolution. Modern ENMs collect these data from freely downloadable global environmental databases (e.g., temperature or sea surface salinity gradients) directly measured and averaged over several decades (e.g., http://www.worldclim.org/). In contrast, these data are not systematically collected or aggregated into an accessible database in the fossil record, nor do they represent direct measurements. Thus, PaleoENM users must construct their own spatially explicit environmental layers for the areas and time periods of interest using geochemical and sedimentological proxies for paleoenvironmental conditions. Myers et al. [213] provides a summary of current best practices in PaleoENM, including choice and reconstruction of environmental layers, modeling algorithms and parameterization, model evaluation, and hypothesis testing.

Alternatively, global climate models (GCMs; e.g., the HadCM3 model from the Hadley Center [314]), are increasingly available for specific times in the distant past (e.g., [92]). GCMs represent coupled oceanographic and atmospheric models that predict different aspects of temperature and precipitation (on land), and sea surface temperature and sea surface salinity (most often) in the ocean. These models attempt to consider a complex array of Earth system conditions, including factors such as: topography/bathymetry, tectonic position, stable isotope records of paleotemperature, paleo-ocean and atmospheric circulation, among others. Some climate models are now also taking explicit account of carbon cycle function and ecosystem

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structure and dynamics in deep time (e.g., application of the cGENIE model [132]).

Whereas GCMs may appear at first blush to provide a more robust record of environmental conditions in deep time (as opposed to sedimentological data), this is not necessarily the case. Dynamic topography (i.e., influence of subduction on the tectonic plate above) makes elevation and bathymetric estimation difficult and accurate reconstruction of plate movements non-trivial. Moreover, conditions describing atmospheric winds and clouds do not have a geologic record and therefore must be inferred during the modeling process. The uncertainly in these factors can have strong effects on the resulting GCM. The classic example of this is the persistent challenge of modeling global latitudinal temperature gradients during the Cretaceous Period where it was sufficiently warm for tropical plants and reptiles to live at the poles, but cool enough to support vibrant ecosystems of flora and fauna at the equator [26, 299].

4.11 Astrophysical models

A number of studies have shown that major atmospheric ionizing radiation events including gamma-ray bursts, supernovae, and extreme solar events [199] inevitably lead to significant reductions in stratospheric ozone, permitting increases in solar UV-B irradiance at Earth's surface and in the top tens of meters of the ocean. It has been hypothesized (e.g., [197, 198]) that ionizing radiation events of sufficient intensity can cause a biological impact sufficient to lead to a mass extinction. This hypothesis has also been used in studies aiming to define environments hospitable to extraterrestrial life, including the concept of a Galactic Habitable Zone [107, 207, 226]. The connection between O_3 depletion and extinction is typically made basing on the well-established damaging effects of UV-B on ocean phytoplankton – the base of the marine food web, responsible for half the global primary production, as well as the main contributor to Earth's oxygen budget. The claim is that major damage to phytoplankton species could cause a crash of the marine food web and lead to mass extinction (cf. Section 4.7), as well as global anoxia. UV-B radiation with a terrestrial cause (e.g. warming and ozone depletion via volatile release from LIP's) has also been proposed as an extinction mechanism quite distinct to the 'extraterrestrial' [34, 191].

Disruption of primary productivity is widely predicted to cause avalanches of secondary extinctions at higher trophic levels, hence making mass extinction much more likely [31, 40, 194, 322]. Evidence supporting such a disruption is present at the end-Permian [31] and end-Cretaceous [335] mass extinctions, and is also associated with extinctions in the Pliocene [301]. While difficult to directly detect, modeling of the response of paleocommunities to disruption of primary productivity strongly supports the conclusion that increased disruption leads to increased secondary extinction in several types of food webs, mainly through loss of primary consumers who suffer from reduced food supplies [254].

In order to connect different factors to mass extinctions, an ecosystem modeling approach can be employed. For example, recent studies [296, 312, 313] used population models of planktonic biodiversity to study mass extinction in a population under varying sets of parameters. This may allow exploration of the level of ionizing radiation sufficient to trigger widespread (mass) extinction. The changing radiation field in this nonlinear system may cause a tipping point in the dynamics of global biota through a variety of mechanisms. For instance, an increase in species mortality resulting from increased radiation can make the Allee effects stronger (Section 4.4) or facilitate species extinction through the competitive exclusion (see Section 4.5).

Arguably, however, it is important to distinguish between extraterrestrial and terrestrial sources of UV-B. There are also likely to be differences between marine and terrestrial realms as to their relative importance. Correspondingly, application of mathematical models to a

specific extinction event needs to be adapted accordingly in order to account for the type of the environment.

The influence of different extraterrestrial phenomena need to be taken into account when building models of kill mechanisms potentially leading to mass extinction. These phenomena may include variations in Earth's orbit [72, 209], solar variability [167], asteroid or comet impacts [13, 19], cosmic rays [279, 282], supernovae and gamma-ray burst [18, 197, 201].

These recent publications show how extraterrestrial influences on Earth biodiversity can be tested using statistical models. Distributions of astronomical characteristics (e.g., available as time-series or frequency spectra) may be associated with the data on global-scale biodiversity changes. For example, the Bayesian inference method can examine how time series of biodiversity change may be correlated with time series of astronomical characteristics reconstructed from models of orbital motion [19]. As one example, Feng and Bailer-Jones [93] developed a model of the orbital motion of the Sun around the Galaxy to explore the influence of the solar orbit variation on biodiversity in the Phanerozoic eon.

5 Discussion and conclusions

Mass extinction is a phenomenon that, during the almost 550 My history of metazoan-dominated life on Earth (the Phanerozoic Eon), has repeatedly altered the course of macroevolution by wiping out a majority of existing biota. Identification of factors and processes (triggers) that led to mass extinction and understanding the specific ways through which they acted (kill mechanisms or 'pathways of doom') is important and has been a major focus of research in paleontology and paleobiology.

Research on mass extinction is ultimately based on analysis of fossil data derived from the geological record. This, however, has severe limitations (cf. Section 3), in particular, because the temporal resolution of fossil data is rarely better than 100 Kyrs, whilst research suggests that mass extinctions have a duration of < 100 Kyrs (e.g., [53]). Low temporal resolution, amongst other biases, make linkages between population- and ecosystem-scale phenomena and the global record of mass extinctions extremely challenging. It is rarely, if ever, possible to estimate the actual duration of extinction for a given species or clade, i.e., the interval between the time when the suggested extinction trigger emerged and the time when the last individual went extinct. The fossil record provides an upper bound for this, but the actual interval may be much shorter. Further, as the quality of fossil preservation depends on the preservation of particular sedimentary environments, the data are inevitably patchy and discontinuous in space. Spatial discontinuities in the geologic record work to blur the ecological processes resulting in extinction patterns.

A model is a mathematical description of a specific process(es) in the context of a specific system. By considering the model properties (or a change in the properties as a result of a change in model's prerequisites), one can investigate the effect of different factors. Mathematical modeling, essentially virtual experimentation, can help to answer outstanding questions and partially close the gaps in understanding mass extinctions. Using models, it appears possible to reveal specific ways in which a given extinction trigger might have affected, through one or more kill mechanisms, the well-being of populations and communities, ultimately driving them to extinction. Since the amount of details included into a model is entirely in the hands of the modeler, one can test different hypotheses and to distinguish between factors of major and minor importance.

The goal of this paper is twofold. Firstly, we revisit factors and processes that have been

recognized as likely causes of mass extinction. We observe that mass extinction is a complex, multi-stage phenomenon that develops through time. Our main focus is on the sequence(s) of simpler phenomena (kill mechanisms) and the corresponding processes ('pathways of doom') initiated by an extinction trigger that eventually results in a mass extinction; see Fig. 9. Extinction pathways have a hierarchical structure where relevant processes can be grouped into a few different levels or stages (shown as the dashed boxes in Fig. 9). We refer to the initiating events (e.g., LIP or bolide impact) as Stage 1 processes. They do not kill species on a global scale directly, but they have some immediate consequences - Stage 2 processes; e.g., LIP emplacement is accompanied by the release of a large amount of volatiles and aerosols into the atmosphere, either directly from the magma or via liberation and degassing of volatiles from buried sedimentary rocks by contact metamorphism [49, 124]. By themselves, they may not cause mass extinctions, but they cause significant changes in the environment globally (signified by the large arrow in Fig. 9) that we combine into Stage 3 processes; e.g., release of aerosols may lead to a decrease in the average global temperature by changing global albedo. Again,
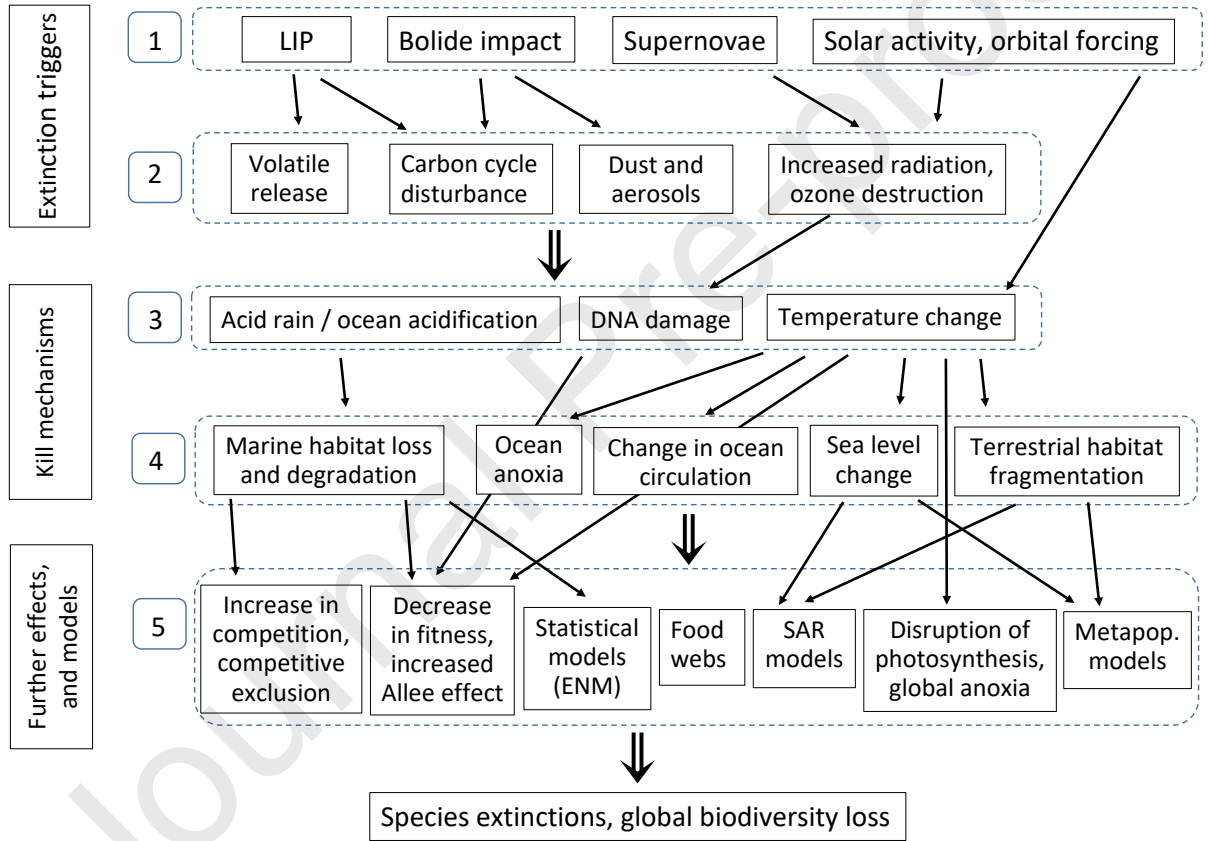
Figure 9: Extinction triggers and kill mechanisms, pathways of doom, and relation between different factors and processes ultimately leading to mass extinction, as derived from the geological and fossil record as well as studies of present-day environments. Dashed-line boxes combine the processes occurring at the same stages of mass extinction development; see details in the text. Large arrows show the generic collective effect of process occurring at a preceding stage to the processes at the following stage. Small arrows indicate the succession of specific events/phenomena. Note that, for ease of visualization, not all processes, patterns, and models discussed in the text are included.

these environmental changes are unlikely to cause mass extinctions by themselves (e.g., although sufficiently decreased temperature would cause organismal deaths by freezing, temperature decrease alone is unlikely to result in 70% or more global species extinction) but they may lead to further environmental changes - Stage 4 processes; e.g., a sufficiently large decrease in temperature would facilitate the growth of polar ice caps and hence a decrease in the sea level, which, in turn, would result in loss and/or fragmentation of shallow water habitats (cf. Section 4.2). Environmental changes in Stage 4 would then affect the biological process combined here in Stage 5, that have a direct effect on species fitness and survival; e.g., because a fragmented habitat has less capacity, the fragmentation will lead to species extinction.

Secondly, we provide an overview of some of the modeling approaches that, we believe, can be instrumental in facilitating further progress in understand mass extinctions, in particular to reveal and clarify the effect of different links in extinction pathways. Note that processes at different stages of mass extinction, as it develops through time and across spatial scales, require models of different type. Processes occurring in Stages 1-4 are predominantly physical or geophysical or perhaps even astrophysical; we do not consider their modeling much here. Instead, we mostly focus on models describing (some of) the biological processes, i.e., those occurring in Stage 5. In doing that, we revealed a few links that have previously been largely ignored or completely overlooked. One such modeling link shows how mass extinction may occur when a temperature rise increases the strength of the Allee effect for the whole clade (e.g., by breaking species' sex ratio). Another modeling link shows how mass extinction may occur when plankton photosynthesis is disrupted, hence potentially leading to global anoxia, by an increase in average water temperature. We have also provided examples of the types of fossil data that may be collected to test the efficacy of these models on mass extinction science.

A combination of different modeling approaches can be particularly useful for understanding mass extinction mechanisms and scales. For instance, habitat fragmentation leads to species extinction, as described by SAR and fragmentation models (simply because the capacity of fragmented habitat is much lower compared to a continuous habitat of equivalent area, cf. Section 4.2), where the timescale of extinction is predicted by metapopulation models (see Section 4.3). The corresponding decrease in biodiversity, albeit potentially significant, may not necessarily result in mass extinction. However, some of the species that go extinct as a result of fragmentation, may be keystone species, and their elimination will break the connectivity of the corresponding food webs (Section 4.7). That may result in cascading extinctions and, eventually, in mass extinction. The above example shows how application of mathematical modeling can improve linkages between taxonomic scale (individual to population to ecosystem to global biota) that are largely missing in the mass extinction literature.

We appreciate the fact that the full potential of modeling approaches outlined in Section 4 (i.e., to rigorously compare geological data with predictions of the models) requires a level of temporal and spatial accuracy from the fossil record that has so far been rarely, if ever, available. For instance, precise application of SAR and metapopulation models to a specific mass extinction event would require sufficient knowledge about the spatial arrangement of habitats, and the population dynamics models apparently need at least some knowledge about population size or density. However, we mention here that, apart from models application aiming to *quantitatively* describe the data in detail, which may be difficult to achieve at the current state of empirical mass extinction science, mathematical models also and perhaps more importantly provide a powerful *qualitative* description of the corresponding phenomena by revealing hidden and/or counter-intuitive (and hence sometimes overlooked) links between various factors and processes altogether resulting in mass extinction.

Mass extinctions are a complex phenomenon and their comprehensive investigation neces-

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sarily requires application of a very broad variety of approaches, methods and tools. We feel that synthesizing patterns, processes, and modeling methods is a necessary step for a better understanding of the science behind mass extinction events. Although decades of work in siloed research fields have substantially improved our understanding of the component parts, disentangling the great challenges of Earth system science requires an integrated approach [134, 172]. There remains a fundamental disconnect between how we know that organisms, populations, ecosystems experience extinction and our knowledge and data of mass extinctions in the geologic past. In order to understand mass extinctions we have to connect these different biological levels; mathematical modeling provides an efficient and relatively easy way to perform 'virtual experiments' exploring these linkages. We have attempted here to outline some of the models, data, and questions that can be tackled. Consequently, we highlight in particular the need for more mathematical modeling to be applied to mass extinction events and more conversation between mathematical modelers and geoscientists working on mass extinctions.

Acknowledgements

6   Appendices

6.1   Appendix A1. Response of the shallow sea habitat area to a decrease in sea level

A drop in sea level is likely to result in a decrease in the area of the corresponding shallow water habitat. In general, the dependence of lost area on the change in sea level is not simple as it may also depend on the geometry of the shoreline, on the topography of sea bottom and, generally speaking, on the pre-change sea level. It also depends on the spatial scale at which the effect of receding sea is considered. For a shoreline with a simple geometry (e.g., a long straight beach), which usually implies a relatively small size of the area, and in case the difference in sea level (say, H) is not very large, the distance at which the sea moves back (say, R) is proportionate to the sea level decrease [51]:

$$R \;=\; \frac{H}{\tan \phi}, \tag{18}$$

(the Bruun rule) where ϕ is the average slope of the vertical profile. Depending on the slope of the beach, Eq. (18) predicts that the shoreline will move by the distance 10 to 50 times sea change level [169]. In its original form (18), the Bruun rule remains controversial [1, 126]; however, its generalized version using a power law instead of the linear dependence (taking into

account deviations of the vertical profile from the linear function), that is

$$R = aH^\alpha, \tag{19}$$

where exponent α describes the curvature of the vertical profile and a is a coefficient, was shown to be in good agreement with data and works well for a broader range of sea level change [17]. Here, the curvature of vertical profile may depend on the type of sediment that the beach is made of (e.g., rock or sand); in particular, for sandy beaches the exponent is estimated as $\alpha = 3/2$ [17].

Equation (19) readily implies that the relative decrease in the shallow water habitat area is also a function of ΔH:

$$\frac{\hat{A}}{A} = 1 - \left(\frac{aL}{A}\right) H^\alpha, \tag{20}$$

where L is the linear size of the area along the shoreline, $\hat{A}$ and A are the new and the pre-change habitat area, respectively.

On a larger, regional or global scale, the shore line attain fractal properties [189, 190] and its approximation with a straight line becomes irrelevant. In this case, the response of the habitat to the receding sea becomes more complicated. Although the power-law description in most cases remains valid, the exponent is determined by different factors and hence has a different value [139]. Real-world reliefs were shown in many cases to be well approximated by a Brownian surface or, more generally, a fractional Brownian surface [190, 234]. Considering the sea bottom topography as a (fractional) Brownian surface, response of the shallow water habitat to a decreasing sea level – i.e., the fraction of total area that remains under water after sea recedes – can then be estimated using methods of percolation theory [139]. A sufficiently large (exceeding a certain critical value H_c) decrease in sea level breaks a continuous habitat to several disconnected fragments or clusters, including one large (in the mathematical sense regarded as 'infinite') that spans across the whole area. For a sub-critical change where H approaches H_c but does not exceed it, $H < H_c$, the habitat area dependence on H can be approximated as

$$\frac{\hat{A}}{A} = \text{const} \cdot \left(\frac{H_c - H}{\psi_0}\right)^\beta, \tag{21}$$

where ψ_0 is the standard deviation of the sea bottom unevenness height. Once the statistical properties of the height distribution are known, the exponent can be calculated using methods of stochastic theory; for instance, under some additional conditions (that we do not discuss here for the sake of brevity) $\beta = 5/36$, see [139] for details.

In case the effect of receding sea is considered on a sufficiently large spatial scale, and the decrease the sea level is significant enough to bring the habitat close to the percolation threshold, the response of the habitat area can be modeled generically as a crossover between Eqs. (19) and (21), that is

$$\frac{\hat{A}}{A} \sim H^\chi, \tag{22}$$

where the exponent is scale-dependent, $\chi = \alpha$ for $H \ll H_c$ and $\chi = \beta$ for $H \sim H_c$ ($H < H_c$).

A larger, 'overcritical' decrease in the sea level, i.e. for $H > H_c$, can lead to habitat fragmentation through breaking of the largest 'infinite' fragment. Such decrease would results in an abrupt drop in the size of the largest available habitat, with implications for species diversity accordingly; see section 4.2.

6.2 Appendix A2. Effect of habitat fragmentation on available space

The frequency distribution of sites with different area emerging as a result of fragmentation is often described by a power-law [309]:

$$g(A) = \nu A^{-r}, \tag{23}$$

which is also known as Pareto distribution. Here r and κ are certain coefficients; usually, $1 < r < 2$.

Note that, for a real-world system, possible values of A in relation (23) belong to a bounded interval, $A_* < A < A_0 < \bar{A}$, where $\bar{A}$ is the area of the original habitat before breaking, A_0 is the area of the largest site in the hierarchy and A_* is the area of the smallest site that is still capabale to support at least one population (e.g., for forest-dwelling animals, the smallest 'forest' has to include at least one tree). For fragmented habitats like forest or marsh, the range of site areas is known to span over at least two orders of magnitude [260, 324], so that $A_* \ll A_0$.

If the integral of $g(A)$ is scaled to 1 (which is easily achieved by chosing coefficient κ accordingly), then the average area is given as

$$
\begin{aligned}
< A > &= \int_{A_*}^{A_0} Ag(A)da = \nu \int_{A_*}^{A_0} A^{-r+1}dA \\
&= \frac{\nu}{-r+2} A^{-r+2}\Big|_{A_*}^{A_0} = \frac{\nu}{2-r}\left(A_0^{2-r} - A_*^{2-r}\right),
\end{aligned} \tag{24}
$$

and the total area of the fragmented habitat is

$$A_{tot} = M < A >, \tag{25}$$

where M is the total number of sites in the habitat.

We now recall that the fragmentation is a threshold phenomenon that occurs when a controlling factor (e.g. the magnitude of environmental change) exceeds a crtical value. We assume that the transformation from a continuous habitat to a fragmented one occurs on a sufficiently fast timescale, so that shrinking of individual sites can be nglected. The total area of the fragmented habitat as gven by (25) then has to be equal to the habitat area before fragmentation:

$$\bar{A} = A_{tot} = M\nu \int_{A_*}^{A_0} A^{-r+1}dA, \tag{26}$$

from where M can be found.

In order to assess how the fragmentation affects the biodiversity of a given habitat, as described by SAR, we need to assess the area of the larger sites, that is sites with the area $A_0 < A < A_0 - \Delta A$. The fraction of the total area that is occupied by the lagest sites can be readily obtained by calculating the corresponding fraction of the frequency distributon (23):

$$
\begin{aligned}
\frac{A_{large}}{A_{tot}} &= \int_{A_0-\Delta A}^{A_0} Ag(A)dA \cdot \left(\int_{A_*}^{A_0} Ag(A)dA\right)^{-1} \\
&= \left[A_0^{-r+2} - (A_0 - \Delta A)^{-r+2}\right] \cdot \left(A_0^{-r+2} - A_*^{-r+2}\right)^{-1} \\
&= \left[A_0^{2-r} - (A_0 - \Delta A)^{2-r}\right] \cdot \left(A_0^{2-r} - A_*^{2-r}\right)^{-1} \\
&= \left[1 - (1-\delta)^{2-r}\right] \cdot \left(1 - \epsilon^{2-r}\right)^{-1},
\end{aligned} \tag{27}
$$

where $\delta = \Delta A / A_0$ and $\epsilon = A_* / A_0$.

Assuming that ϵ and δ are small, the right-hand side on (27) can be simplified. Taking into account (26) and assuming that the group of larger sites consists of a single site, i.e. the largest one (hence chosing δ accordingly), Eq. (27) turns into the following:

$$\frac{A_0}{\bar{A}} \;=\; (2-r)\delta \left(1 + \epsilon^{2-r}\right) \;\approx\; (2-r)\delta, \tag{28}$$

where $\epsilon \ll 1$ can ultimately be neglected.

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Declaration of Interest

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

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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The corresponding author, on behalf of all coauthors