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Opinion

Was the Late Ordovician mass extinction truly exceptional?

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The Late Ordovician mass extinction event is the oldest of the five great extinction events in the fossil record. It has long been regarded as an outlier among mass extinctions, primarily due to its association with a cooling climate. However, recent temporally better resolved fossil biodiversity estimates complicate this view, providing growing evidence for a prolonged but punctuated biodiversity decline modulated by changes in atmospheric composition, ocean chemistry, and viable habitat area. This evolving view invokes extinction drivers similar to those that occurred during other major extinctions; some are even factors in the current human-induced biodiversity crisis. Even this very ancient and, at first glance, exceptional event conveys important lessons about the intensifying 'sixth mass extinction'.

Highlights

Mass extinctions of Earth's deep past are impactful evidence of catastrophic loss of biodiversity.

The Late Ordovician mass extinction (LOME) is the oldest of these events, and one of the largest. A revised timeline for this event implies the need to reconsider its drivers. This is significant, as some may be similar to mechanisms behind current events.

Lessons learned from previous mass extinctions are critical for understanding the current biodiversity crisis; they provide real data on the impact of extreme climate change, repeated perturbations of marine chemistry and redox state, and habitat loss, occurring at varying temporal scales.

These insights support the growing concern about a coming wave of (marine) extinctions. Now driven by humans, and at unprecedented speed, some of the mechanisms we are now concerned about have analogues in deep-time extinctions, including the LOME.

An unusual mass extinction event?

For 50 years, the Late Ordovician Mass Extinction (LOME) has been perceived as a geologically short, glacially induced event confined to the terminal Ordovician **Hirnantian Age** (see Glossary) 445–443 million years ago (Ma) [1,2]. This has placed the LOME as a peculiar outlier compared to the more complex climate histories of most other great Phanerozoic extinction events (Box 1) [3]. However, recent **early Palaeozoic** biodiversity curves complicate this classic and strictly Hirnantian scenario for the LOME as they indicate substantial biodiversity decline millions of years prior to the apparent Katian–Hirnantian and mid-Hirnantian extinction pulses [4–6]. Therefore, although we as authors have very substantial disagreements about the fundamental drivers of the LOME, we do agree that hypotheses centred exclusively on Hirnantian climate events are insufficient to explain the observed pattern of biodiversity loss. In our view, this evidence calls for consideration of a broader range of extinction scenarios, some of which may involve environmental drivers more similar to those implicated in subsequent mass extinction events. These potentially include extreme climate change (not just cooling), heavy-metal pollution of the environment, oceanic anoxia, and large-scale habitat destruction during a protracted survival phase. Invoking such extinction determinants for the LOME is timely as similar factors are believed to control the current anthropogenically driven biodiversity declines [7,8]. This suggest that lessons learned from the LOME may be applicable to understanding some of the mechanisms behind the current biodiversity crisis.

The standard model

The LOME is estimated to have caused the extinction of ~85% of all marine species [9], making it the second largest mass extinction event of the Phanerozoic [10]. The onset of the LOME has generally been viewed as tied to a transition to icehouse conditions near the Katian–Hirnantian boundary [11]. Glacial conditions in the Hirnantian are unambiguously evidenced by **glaciogenic sediments** at high southerly palaeolatitudes [12]. These glacial advances are also well

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Box 1. The 'big five'

Five mass extinction events during the Phanerozoic are generally recognised [3]. There are likely more, but current limits to the resolution of the fossil record hinder a better appreciation of past biodiversity change. Particularly during the Cambrian Era, where fewer and less widespread taxa make biostratigraphical intercontinental correlation difficult, accelerated faunal turnover rates potentially hint at several major extinction phases [28].

At 443 Ma, the first of the 'big five', the Late Ordovician mass extinction (LOME), removed ~50% of all marine genera during at least two extinction pulses. An advancing ice age and its ultimate demise and associated oxic–anoxic–euxinic pulses are usually inferred as causes [12]. Next, the late Devonian mass extinctions also removed ~50% of marine genera during a >25 Myr-long extinction phase [5]. The main extinction pulses were the two 90 000–130 000 year-long Kellwasser events at 372 Ma [50] and the end-Devonian 50 000–190 000 year-long Hangenberg Event at 359 Ma [61]. The drivers were climatic shifts from warming to cooling and associated oceanic anoxia, possibly instigated by flood basalts [50,61,62]. The third and largest of the 'big five' is the end-Permian event. More than 80% of all marine genera and 70% of terrestrial vertebrates went extinct. Extinctions started near the end of the Guadalupian Epoch at ~261 Ma and although the scale of this particular extinction pulse is debated, some estimates suggest that a generic loss upwards of 50% occurred [10,63,64]. The main phase, however, occurred 10–12 Myr later during the end-Lopingian Epoch at the close of the Permian at 251 Ma ago where two catastrophic, swift extinction pulses separated by ~50 000 years caused biodiversity loss [5,65]. Massive flood basaltic eruptions are known both during the Guadalupian and Lopingian events so, although probably not related, the main drivers – anoxia and rapidly fluctuating climate induced by greenhouse gas overloading – were similar [64,65]; 50 Myr later, at 201 Ma, >30% of the marine genera went extinct during the latest Triassic in a two-phased, millennia-scale main extinction interval, but richness may have been declining for 8–9 Myr [66,67]. Flood basalts are believed to have triggered repeated global warming, ocean acidification, anoxia and euxinia [68,69]. Lastly, 66 million years ago, the Cretaceous ended with a sudden bolide impact causing instant ecosystem destruction [70], resulting in global catastrophe within days or months [71]. About 40% of marine genera became extinct [10].

Table I. Timing and size of large igneous province (LIP) events associated with the 'big five'

Name	Timing of main LIP pulses (Ma)	Overall duration (Myr)	Area (10^6 km^2)	Volume (10^6 km^3)	Associated mass extinction
Alborz LIP [42]	~450.61 + ~442.5	~45	?	?	Late Ordovician?
Viluy Traps [72]	~362.4–379	~30	>1	>1	Late Devonian
Pripyat–Dnieper–Donets [72]	~364–367	~7	>1	>1.5	Late Devonian
Emeishan Traps [53,73]	~257.6–259.9	<3?	>0.3	>0.3	Late Permian (end-Guadalupian)
Siberian Traps [73]	~251.3–252.3	<6?	>4	>3	End Permian (end-Lopingian)
CAMP [74]	~200.9–201.6	<10	~11	~3	End Triassic
Deccan Traps [73]	~65.6–66.3	<1?	~0.5	~2	End Cretaceous

documented globally in the sedimentary record by rocks indicative of a lower global sea level during the latest Ordovician [13], and further corroborated by palaeontological and geochemical evidence indicating cooler conditions [14–16].

In this Hirnantian crisis model, extinctions are thought to have been primarily driven by the combined effects of equatorward constriction of the tropics, and narrowed habitable space in shelf areas globally, as cooling climate would have triggered rapid, **glacio-eustatically** controlled sea-level falls [11,17,18], and fluctuations in **redox conditions** on shallow shelves would have caused anoxic zones to expand with even **euxinic** oscillations at times [19]. These combined effects particularly impacted the most species-rich marine habitats, which in the Late Ordovician were on the equatorial tropical shelves (as they are today), resulting in substantial extinctions [19–21]. Fossil evidence from several clades – including both mobile and sedentary benthos as well as pelagic groups – outlines two major pulses of extinction: one during the very latest **Katian Age** (or at the Katian–Hirnantian boundary) linked to climate cooling with associated ocean redox changes (including euxinia), and one during the latest Hirnantian linked to subsequent warming and ocean anoxia [12]. Although the duration of the Hirnantian Age remains uncertain, these events are generally viewed as having occurred in less than 2 million years (Myr) [22] – maybe even in as little as 500 thousand years (Kyr) [23].

Emerging evidence for a more protracted extinction interval

Palaeobiodiversity curves are typically constructed with taxa of fossil occurrences counted in time bins of varying resolution. Early global metazoan richness curves that used broad, ~5–11 Myr long, time bins [24,25] suggested a substantial decline in biodiversity well before the Hirnantian crisis, but this decline was not typically considered to be related to the LOME itself, and clade-specific data compilations of (for example) brachiopods [26] and graptolites [27] with much higher temporal resolution showed only the 'classic' two extinction pulses. However, in recent years, an improved global chronostratigraphic stratigraphical framework, and the increasing application of methods for accounting for variation in preservation rates and sampling intensity has led to a new generation of more robust and higher-resolution multiclade Ordovician diversity curves [4–6,28]. These newer curves show a marked early Katian biodiversity decline well before the two classic LOME extinction pulses, similar to that seen in older global datasets (Figure 1). This implies that an 'extended LOME' could be defined as consisting of at least three extinction pulses that occurred during an interval of 8–9 million years, starting during the earliest Katian Age (Figure 1). Such a prolonged extinction interval consisting of multiple distinct phases of biodiversity change cannot be fully reconciled as 'an event' or with the standard Hirnantian 'rapid cooling leads to extinctions' hypothesis [11,12]. Thus, even though the classic Hirnantian glacial 'event' – with associated sediments, sea-level, and redox changes – is well documented, we argue that the long prelude to the Hirnantian glaciation was demonstrably important, in timing and perhaps in magnitude, and that it cannot be ignored in causative scenarios.

A Late Ordovician transition driven by increased arc volcanism?

Geochemical proxies, in particular the global **δ^{13}C record,** suggest a step change in the global carbon cycle beginning in the latest **Sandbian Age** with the Gutenberg isotopic carbon excursion (GICE). Whereas the Middle Ordovician **Darriwilian Age** record includes only a single slowly rising ^{13}C excursion – the Middle Darriwilian isotopic carbon excursion (MDICE) – from the GICE onwards, the Upper Ordovician record contains numerous positive ^{13}C excursions culminating in the Hirnantian isotopic carbon excursion (HICE). The drivers of this apparent step change remain unknown, but it is potentially notable that the hitherto overlooked early Katian extinction pulse approximately coincides with ash deposits linked to some of the largest known explosive volcanic eruptions of the Phanerozoic [29,30] (Figure 2). The Deicke and Millbrig eruptive events in **Laurentia**, and the Kinnekulle event in **Baltica**, all occurred close to the Sandbian–Katian transition [29]. These were the most pronounced eruptions in a longer phase characterised by increased **arc volcanism** during the Late Ordovician, as evidenced by a major downturn in global seawater strontium isotopic values [31]. Temperature-sensitive palaeontological [32] and geochemical proxies, such as the **^{18}O-isotope climate record** [16,33], lend some support to the hypothesis of an early Katian transition (Figure 2). Climate events such as the well-documented late Sandbian cooling phase [32], the mid-Katian Boda Warming event [34] – also interrupted by cooling pulses [15,16,35] – and the plunge into the Hirnantian icehouse are evidence of substantial climatic oscillations potentially leading to biodiversity loss and ecosystem volatility.

Potential effects of increased arc volcanism on global biogeochemical cycles and climate

Volcanism has been suggested as a driver for the classic Hirnantian extinction pulses by several studies, often based on mercury records [36–40]. It has also been suggested that the preceding late Katian Boda warming event was instigated either by explosive arc-associated volcanism or

Glossary

Arc volcanism: an arc of volcanoes formed due to the partial melting of the descending crust in subduction zones.
Baltica: early Palaeozoic palaeocontinent composed of present-day Scandinavia, the Baltic regions, and Russia to the Urals, and with its southern border in Ukraine.
Darriwilian Age: spanning from 467.3 to 458.4 Ma, this fourth age of the Ordovician also comprises the main part of the Middle Ordovician Epoch.
δ^{13}C record: in palaeoclimatology and stratigraphy, the measure of the ratio between the two stable isotopes of carbon (^{13}C and ^{12}C) records changes in migration of carbon between reservoirs in sediments. The ^{13}C record is further used as a correlative tool in stratigraphy.
Early Palaeozoic: an informal term for the first half of the Palaeozoic Era spanning the Cambrian, Ordovician, and Silurian periods (~541–419 Ma).
Euxinic: refers to water that is both anoxic and sulfidic.
Flood basalts: synonymous with large igneous provinces (q.v.).
Glacio-eustatic: refers to global changes in sea level due to changing volumes of icecaps and glaciers on land. Fluctuations in sea-levels may be in the order of 100–150 m within less than 20 000 years.
Glaciogenic sediments: sediments deposited in connection with advancing or retreating glaciers. They are used as palaeoclimatic indicators of a cooling climate.
Hirnantian Age: the youngest age of the seven formal geochronological (i.e., time) units of the Ordovician Period.
Iapetus Ocean: large ocean separating Laurentia and Baltica during the early Palaeozoic.
Katian Age: the penultimate age of the Ordovician, spanning the interval 453.0–443.8 Ma.
Large igneous provinces (LIPs): known also as flood basalts, large igneous provinces, or LIPs, are caused by massive volcanic activity of low viscosity basaltic lavas covering major areas (>100 000 km^2) with large volumes (>100 000 km^3) during short time spans (<1.5 Myr). Often occurring in repeated pulses over millions of years.
Laurentia: early Palaeozoic palaeocontinent, predominantly consisting of present-day North America.
^{18}O-isotope climate record: the fractionation of oxygen isotopes – as measured in either fossil shells or bulk

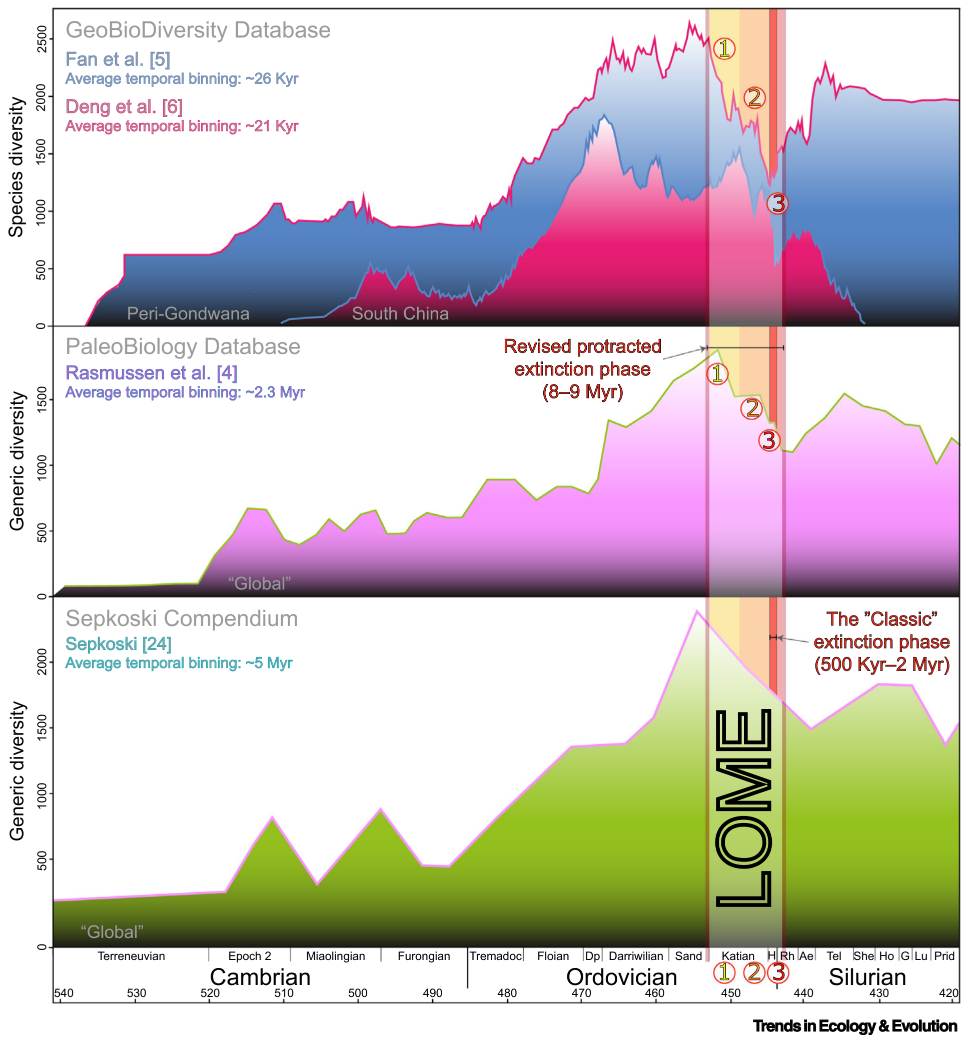
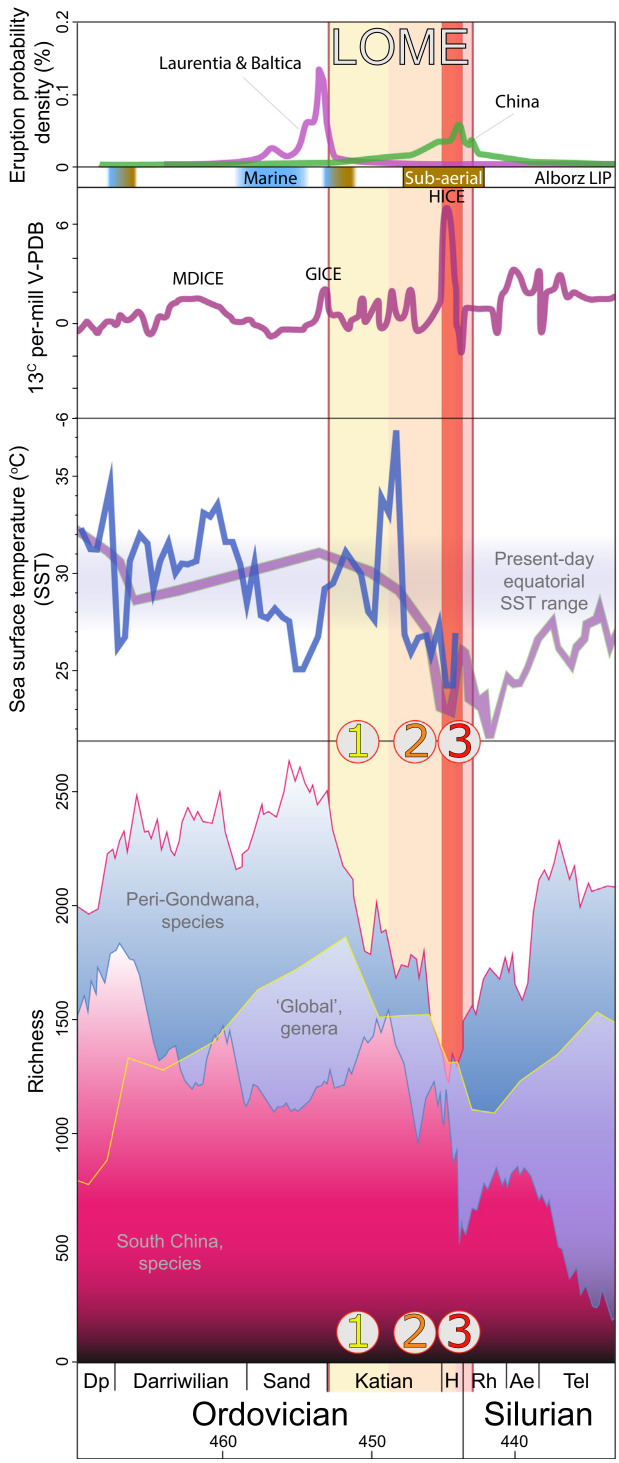


Figure 1. Global and regional datasets on multiclade fossil occurrences discussed in the text [4–6,24]. Whereas the classic generic richness curve compiled by Sepkoski relied on an average temporal binning of ~5 million years (Myr) (bottom diagram), the more recent curves above reach considerably higher temporal resolution: 2.3 Myr and <30 thousand years (Kyr), respectively. Note that the two richness curves in the uppermost diagram both represent regional data from two different albeit adjacent regions and further are resolved to the species level. The term 'Global' used for the curves in the two lower diagrams, that are resolved only to the genus level, refers to the data primarily originating from present-day European and North American localities. However, back in the Ordovician these localities were widely distributed across palaeo-latitudes. Yet, despite different temporal, taxonomical and geographical resolutions, all curves show an onset of the Late Ordovician mass extinction (LOME) that predates the traditional Hirnantian Age definition of the LOME as shown by the narrow, red-shaded band. For a description of the methods applied to calculate these richness curves we refer to the original sources [4–6]. The Sepkoski compendium was downloaded from http://strata.geology.wisc.edu/jack/ on 8 July, 2021. Abbreviations: Ae, Aeronian; Dp, Dapingian; G, Gorstian; H, Hirnantian; Ho, Homerian; L, Ludfordian; Prid, Pridoli; Rh, Rhuddanian; Sand, Sandbian; She, Sheinwoodian; Tel, Telychian.

by emplacement of an as-yet unidentified **large igneous province** (LIP) (see Table I in Box 1) [36,40,41]. Until recently, no direct evidence for a Late Ordovician LIP had been reported, but a potential candidate, the Alborz LIP, has recently been described from northern Iran [42]. Emplacement of the Alborz LIP began during the Middle Ordovician and lasted for 45 Myr through seven major eruptive phases. **U/Pb geochronology** constraints of the third phase at 450.61 ± 0.27 Ma and fourth phase at 442.5 ± 2.5 Ma coincide with the explosive arc-related volcanic

rocks – is used to infer marine temperature and ice volume change through geological time.
Peri-Gondwana: island arc settings facing the large palaeocontinent of Gondwana, which stretched from the South Pole to the Equator during the greater parts of the early Palaeozoic. Among other present-day regions, Gondwana encompassed Australia, Africa, Antarctica, South America, and large parts of Asia.
Redox conditions: refers to the state of free oxygen available to organisms in the oceans.
Sandbian Age: this is the fifth age of the Ordovician and first age of the Late Ordovician Epoch. It spans from 458.4 to 453.0 Ma.
Silurian: geological period from 443.8 Ma to 419.2 Ma. It succeeded the Ordovician and preceded the Devonian.
Species pumps: term used to describe a region that actively disperses new species to other regions.
U/Pb geochronology: the radioactive decay of uranium into stable isotopes of lead in certain minerals, such as zircons, is used to date rocks.



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provinces reported by Longman *et al.* [43] and thus potentially with the early Katian and early Hirnantian extinction pulses (Figure 2). As the events were primarily subaerial (i.e., terrestrial) they would have contributed to atmospheric outgassing of greenhouse gases and toxins. As such, the Alborz LIP has the potential of having contributed a volcanic component, strongly modulating Late Ordovician climate and environment.

Beyond the intriguing but still speculative potential association of eruptive pulses with specific extinction pulses, a Late Ordovician increase in arc volcanism could have influenced global climate and biogeochemical cycles in numerous ways. Short-term injection of aerosols (such as SO_2) into the atmosphere would have caused transient reductions in insolation with consequent cooling and reduction in photosynthetic activity. On intermediate timescales (<100 years) increased volcanism may have led to elevated atmospheric CO_2 and greenhouse warming with the effects cascading into the marine realm, triggering ocean anoxia and acidification; however, on longer timescales (>10^4 years) this would have been countered by increased silicate weathering and CO_2 drawdown. Increased weathering may also have increased riverine nutrient fluxes, such as phosphorus and nitrogen, to the oceans, stimulating primary productivity and leading to enhanced organic carbon sequestration in marine sediments with further CO_2 drawdown and cooling [43].

In effect, it is the efficiency of CO_2 drawdown, ultimately linked to the plate tectonic configuration and weathering, that seems to regulate whether or not various LIPs through time had a severe impact on the biosphere [3]. Investigating these interrelationships for the Katian is a requirement before we can move from potential correlation to causation.

Potential effects on marine ecosystems

Along with the potential impacts described, enrichments in mercury and other heavy metals suggest toxic metal pollution of the oceans by direct volcanic inputs and secondary weathering inputs [36,37,41]. Metal pollution and its impact on Palaeozoic ecosystems have been demonstrated by malformations in fossil plankton that coincide with enrichments of certain heavy metals in both the depositional environment and the organisms themselves [44]. This has been attributed to hydrothermal system-triggered anoxia and associated heavy metal redox cycling [44–46], but widespread anoxia could also have been stimulated partly by volcanic and weathering inputs, amplified by atmospheric O_2 levels substantially lower than the current ones [21].

Some of the most species-rich regions during the Late Ordovician were located around isolated terranes, such as along the **peri-Gondwana** margin (Figure 1), or at intraoceanic islands arc-settings such as in the **Iapetus Ocean.** These smaller geographic entities may have acted both as steppingstones for species dispersal and as **species pumps** that maintained global biodiversity up through the Middle to early Late Ordovician. However, many of these distinct terranes, particularly peri-Laurentian island arc habitats, were lost by the **Silurian** due to accretion on continental margins [47], contributing significantly to the Late Ordovician biodiversity decline [1,17].

Figure 2. Detail of the Middle Ordovician–early Silurian interval of the recent biodiversity estimates shown in Figure 1. Note that the first wave of extinctions coincides with volcanism, global warming, and a marked step change in the ^{13}C-record: prior to the extinctions, only one slowly progressing positive excursion, the middle Darriwilian isotopic carbon excursion (MDICE), is known from the Darriwilian Age. However, from the latest Sandbian Age onwards, a pattern of oscillating positive excursions began to emerge, with repeated occurrences leading up to the Hirnantian Age Hirnantian isotopic carbon excursion (HICE). Further note the four phases of the Alborz large igneous province (LIP) and the shift from primarily marine (blue) to subaerial (brown) eruptions towards the later part of the Ordovician. Sources: eruption probability [43], Alborz LIP [42], ^{13}C record [75], sea-surface temperature (SSE) [16,33,76] and richness [4–6]. Abbreviations: Ae, Aeronian; Dp, Dapingian; GICE, Gutenberg isotopic carbon excursion; H, Hirnantian; Rh, Rhuddanian; Sand, Sandbian; Tel, Telychian; V-PDB, Vienna Peedee Belemnite reference standard.

Thus, even before the LOME as classically defined, the Late Ordovician world was likely characterised by relatively rapid changes in atmospheric and ocean chemistry, climate, and productivity playing out against a background of long-term habitat loss and reorganisation due to changing paleogeography and ocean circulation patterns. Volcanic activity may have played a role in these processes, but understanding its potential contribution requires further work (see Outstanding questions). Major dispersal and immigration events such as the Laurentian Richmondian Invasion [48] and, on the global scale, the faunal migrations associated with the Boda warming event [34], may be interpreted as faunal responses to some of these changes during a prolonged Katian–Hirnantian biodiversity decline. Dissecting the details of the many Late Ordovician faunal range shifts at the global scale is challenging with currently achievable temporal resolution, but this is a promising area for future research.

The LOME in a Phanerozoic perspective: natural versus anthropogenic extinction causes

The 'extended LOME' model has notable similarities with some other 'big five' mass extinction events, as prolonged intervals of declining biodiversity punctuated by relatively rapid millennia-scale extinction pulses (Box 1). These extended extinction phases often coincide with the emplacement of **flood basalts** [49–53], which have been suggested to be long-term ecological stressors that may set the stage for, or amplify the effects of, other more rapidly operating kill mechanisms (see Table I in Box 1).

The palaeontological record provides insights into the ways in which ecosystems persist, change, or collapse in the face of rapid environmental change. Species are driven to extinction when the rate and magnitude of change exceeds their capacity to locally adapt or disperse, or when they are confronted with entirely novel combinations of environmental conditions. In this context, despite their many differences, past mass extinction events (including the LOME) share notable commonalities with the current anthropogenic biodiversity crisis (Figure 3). Although the timescales of ancient mass extinction events differ radically from the timescale of anthropogenic

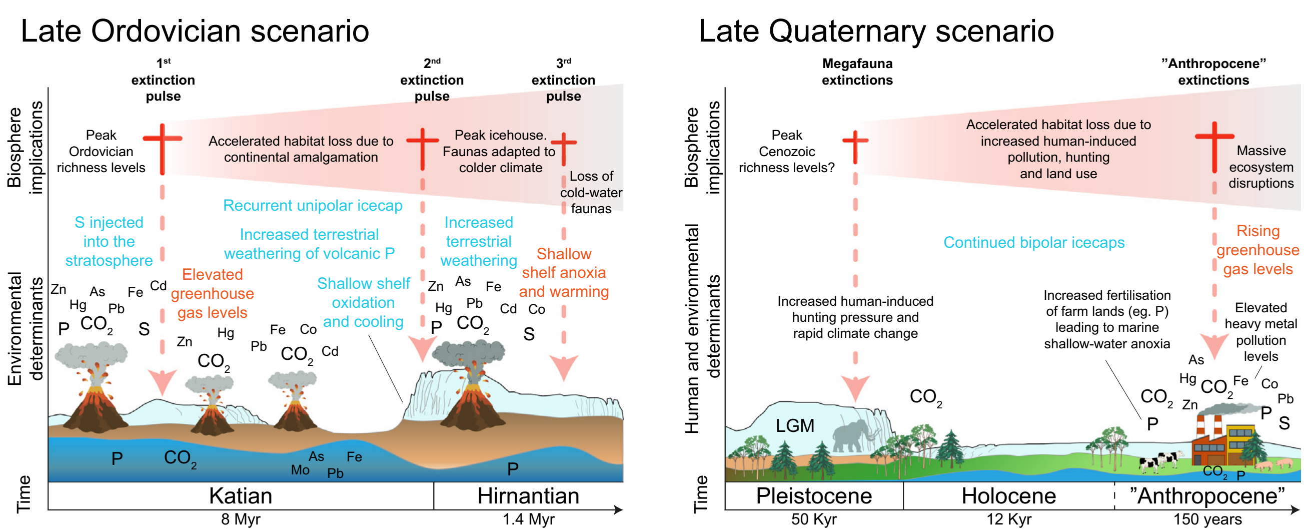

Figure 3. Natural and human-induced environmental determinants in mass extinctions are analogous. Note that the massive volcanic outgassing during the Late Ordovician mass extinctions (LOME) pollutes the ambient environment in a manner similar to that caused by anthropogenic activities, and that habitat was destroyed through natural continent–continent collisions during the survival phase of LOME, while anthropogenic activities are responsible for habitat destruction today. Red font indicates determinants leading to warming, and blue font indicates cooling factors. Abbreviation: LGM, Last Glacial Maximum.

impacts, there is emerging evidence that some of the same mechanisms potentially leading to biodiversity decline are involved: rapid changes in ocean chemistry, the distribution and intensity of oxygen minimum zones and widespread anoxia, heavy metal toxicity, and rapid changes in habitat area and distribution driven by temperature and sea-level fluctuations. These processes have driven catastrophic extinction in the geological past and are now operating in concert with novel stressors such as intense human harvesting and defaunation of marine ecosystems [54–57]. Currently, the magnitude of past extinctions seems to be greater than those observed in the past 500 years, while the current rate of extinctions is faster than that shown by the fossil record [55]. Nonetheless, if past extinctions happened in pulses of only a few thousand years, the current rate of extinction could potentially resemble some of the 'big five', affirming the potential severity of the ongoing global biodiversity crisis.

Humans have initiated a cascade of environmental changes resembling previous naturally triggered cascades that ended in major mass extinctions. Like past extinction events, the anthropogenic biodiversity crisis is characterised by sharp punctuations and long decline occurring against a background of rapidly changing boundary conditions. Discernible human impacts on the biosphere began at least with the onset of megafaunal extinctions ~50 000 years ago [58], and have intensified rapidly with overexploitation of natural resources [59,60] driven by the Industrial Revolution, colonialism, and the 20th century 'great acceleration'. Past extinction events, even ones as superficially unusual as the LOME, offer invaluable empirical insights into mechanisms that may define the potential futures that may await.

Concluding remarks

We call for a reassessment of the LOME as the culmination of a prolonged interval encompassing at least three severe millennia-scale extinction pulses. An earlier, Katian, start of declining biodiversity implies different or additional triggers from the hitherto widely endorsed Hirnantian glacial maximum scenario. This 'extended LOME' view also brings the timescale of Late Ordovician biodiversity declines into closer alignment with some of the other 'big five' Phanerozoic extinctions, with multiple extinction pulses occurring over similar temporal intervals in the end-Devonian, end-Permian, and end-Triassic extinctions. In comparison, the end-Cretaceous event was likely instigated within hours, and the present-day extinctions on the scale of centuries to millennia.

Although as yet far from compelling, there is growing evidence that increased arc volcanism and emplacement of a LIP may have played some role in the Late Ordovician biodiversity decline. As such (and while) the 'extended LOME' still has its unique features, it may have more commonalities with other Phanerozoic extinction events than previously suspected. Despite the remaining differences between these extinction events, they appear to share some fundamental drivers in common with each other and with the modern biodiversity crisis. That these drivers are now impacting ecosystems at rates potentially far exceeding those associated with past mass extinction events is cause for deep concern. Future research integrating data on fossil occurrences and geochemical proxies with high temporal resolution will help to provide a much-improved understanding of extinctions dynamics on scales of relevance to the current anthropogenic crisis (see Outstanding questions).

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Declaration of interests

No interests are declared.

Outstanding questions

Are short, catastrophic intervals of biodiversity loss typically nested within longer events through geological time? Highly resolved biodiversity estimates are crucial to identify such events and should be accompanied by geochemical proxy data at sufficiently resolved temporal scales to elucidate the mechanisms driving past biodiversity change. Whereas such biodiversity data – resolved down to the scale of millennia – is now emerging for parts of the Palaeozoic, even surpassing the temporal resolution characterising some younger periods, the ambition should be to resolve datasets at similar timescales throughout geological time.

Can the effects of causal extinction mechanisms be untangled? While the temporal resolution is key, separating causation from correlation remains equally important. Process-based models resolving the discrete links in the cause-and-effect chain of events triggering environmental perturbations in both the marine and terrestrial realms would greatly improve our understanding of the causes of ecosystem instability. Including the role of volcanoes and large igneous provinces in systemic change models may further establish its role as a natural analogue to the current man-made environmental disruptions.

In addition, we need to increase our understanding of the fidelity of geochemical proxies: how rigorously do they represent actual palaeoenvironments and their perturbations? An example of such an approach can be found in studies of fossil teratology, linking direct evidence of *in vivo* abnormal organismal growth with heavy metal pollution of the marine palaeoenvironment.

How relevant is the palaeontological record? Analysis of such better-resolved taxon richness data combined with that of better-understood proxies will – if conducted on a millennia scale through other Phanerozoic mass extinction events – provide much-needed insights into extinction mechanisms at temporal scales of relevance to the present-day biodiversity crisis.

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