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Heavy Metal Toxicity: A Major Driver of Past Biodiversity Crises?

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Abstract

Whether today's heavy metal pollution represents an unprecedented threat to biodiversity, in Earth's history remains an open question. Here, we reassess the state-of-the-art research to evaluate whether heavy metal toxicity played a major role in past extinction events. Although there is evidence to heavy metal loading during several past biotic crises, direct causal links to extinctions are still lacking. Recent studies are beginning to reveal potential connections in terrestrial ecosystems, while geochemical signatures point to heavy metal impacts in marine environments. Nonetheless, it remains unclear whether modern heavy metal toxicity represents a uniquely severe threat to biodiversity in Earth's history.

Keywords: heavy metal toxicity**,** teratology, malformations, mass extinctions, bolide impact, volcanism, anthropogenic activity

1 Introduction

The Industrial Revolution marked a critical turning point in the history of heavy metal pollution, shifting the primary sources of emissions from natural to human-driven activities[1]. Since the 1970s, heavy metals such as mercury (Hg), lead (Pb), and cadmium (Cd), have been acknowledged as a threat to environmental integrity due to their natural abundance, persistence in the environment, and detrimental effects on ecosystems. These inorganic pollutants, characterized by an atomic density greater than 5 g/cm³, or at least five times the density of water, pose severe risks due to their ability to bioaccumulate in organisms and biomagnify through food chains, even at low concentrations (e.g.,[2]). As a result, their toxic effects lead to severe damage to body tissues and organs while also causing long-term ecological disruptions, particularly in apex predators and throughout entire food webs[3,4]. Throughout Earth's history, heavy metal loading was primarily associated with natural processes including volcanic eruptions and the erosion of metal-bearing rocks. Nevertheless, recent research suggests that heavy metal toxicity has played a significant role in past mass extinctions and biodiversity crises, due to the release of vast quantities of heavy metals into the atmosphere associated with Large Igneous Provinces (LIPs)[5]. Some LIPs, such as the Siberian Traps and North Atlantic LIP, have also been linked to contact metamorphism of coal and other carbonaceous sediments that, in addition to carbon dioxide, produces airborne compounds (e.g., coal ash[6]), which contain large quantities of heavy metals that settle or wash out of the atmosphere into oceans, streams and land[7-9]. Evidence of heavy metals into the terrestrial and marine realms has been confirmed by studies in changes in Mercury (Hg) concentrations, normalised Hg concentrations, and isotopes (δ^{202}Hg, Δ^{199}Hg, Δ^{201}Hg) (e.g.,[10-12]). These geochemical proxies serve as a stratigraphical marker and to ground truth the relationship between volcanism and mass extinction events (e.g.,[11,13-14]). Moreover, heavy metal toxicity has also been invoked as being linked to bolide impacts, such as the Chicxulub impact[15-16], which is

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widely regarded as the cause of the end-Cretaceous mass extinction (e.g.,[17]). Given that LIPs and bolide impacts are the most commonly cited triggers of past mass extinction events and biodiversity crises, it is unsurprising that heavy metal toxicity is often hypothesised as a major causal mechanism for a large number of different events from the Early Palaeozoic to the present-day[18-21].

The current prevailing model for heavy metal toxicity during mass extinctions suggests that toxic metal emissions during these biotic crises, reached poisonous levels directly contributing to widespread extinctions[18-20]. Newer models are starting to include the complex interactions of climate change and the methylation of mercury, e.g., through the development of anoxia[21]. However, these models oversimplify the complexity of extinction dynamics, neglecting: **(1)** the bioavailability of these heavy metals, which determines their potential toxicity to the organisms; **(2)** pre-existing environmental stressors such as euxinia, which may have already destabilized/weakened ecosystems resilience prior to metal loading; and **(3)** the knock-on effects of sulphur emissions and climate change, which interact to introduce additional source of heavy metals in the environment (see Fig. 1). This latter point is supported by preliminary study from the Toarcian extinction event (~ 183 Ma) and the Permian-Triassic mass extinction (PTME, ~252 Ma) suggesting that there is evidence of terrestrial Hg being transported to the ocean[10, 22-23], further reinforcing the complex link between LIPs, bolide impacts, climate change and heavy metal mobilization within the biosphere.

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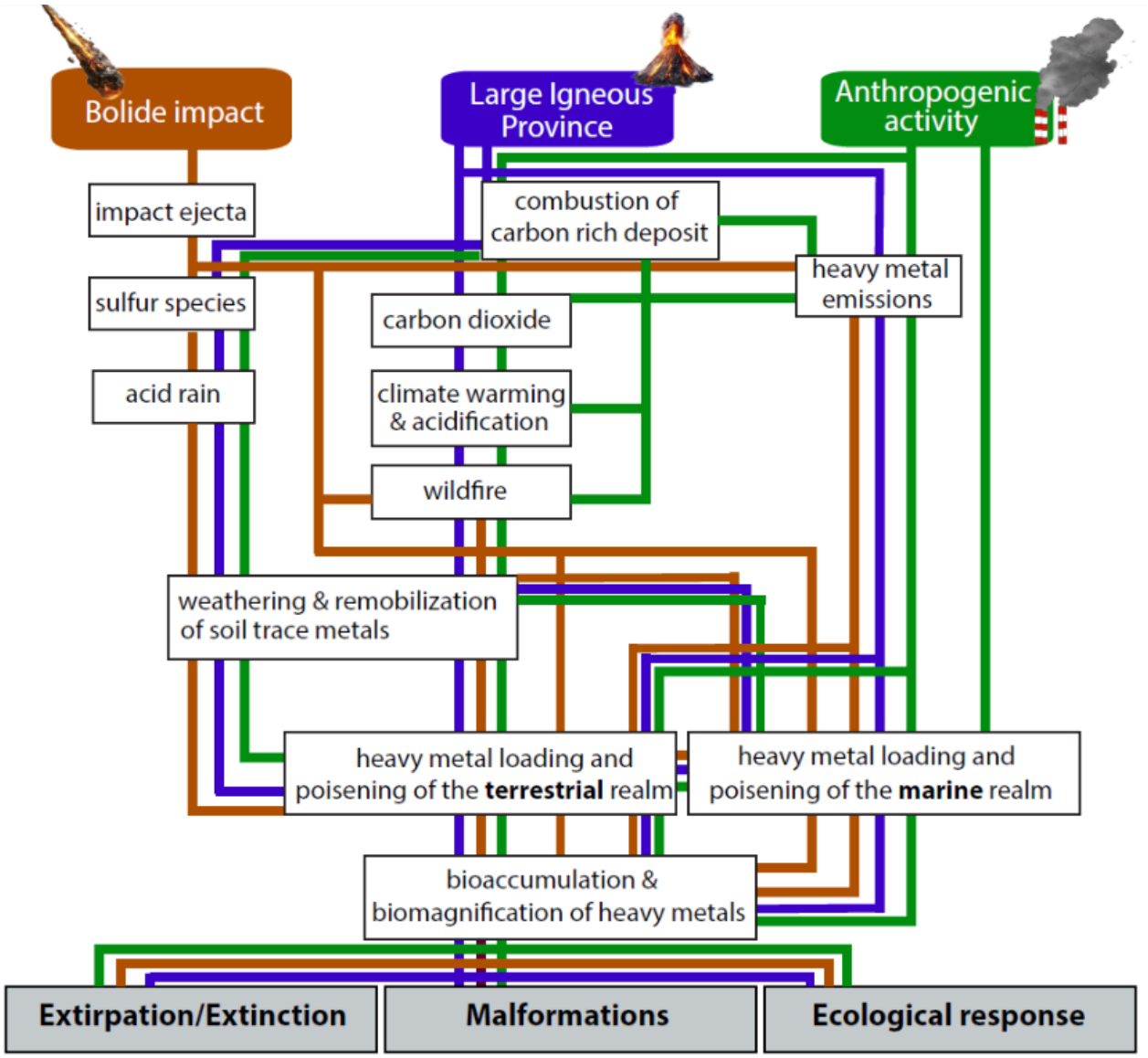


Fig. 1. *Proposed cause-and-effect relationships of bolide impacts, LIPs, and anthropogenic activity with heavy metal toxicity. Despite the different sources of heavy metals, the effects are expected to be similar. Note: Current models do not demonstrate an understanding of this complexity and directly link heavy metal emissions to toxic metal poisoning.*

Here, we review the current state of the literature to test the hypothesis that heavy metal loading of the environment during past mass extinctions and biodiversity crises reached toxic thresholds, potentially contributing to species loss. By doing so, we uncover several key future directions and key outstanding questions for understanding the role of heavy metal toxicity during past biodiversity crises.

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1.1 Bioaccumulation, Biomagnification, and Biological Impact

Heavy metals pose a dual threat to ecosystems due to their ability to bioaccumulate (higher concentrations in organisms than the surrounding environment) and biomagnify (accumulates to higher concentrations with increasing trophic levels). For example, mussels can accumulate heavy metals at concentrations 50-100 times greater than ambient seawater, and both consumer and predators higher in the food chain ingest even greater amount through the consumption of contaminated smaller organisms[24]. The biological effects of heavy metals exposure can vary: some metals affect biological functions and growth, while others accumulate in one or different organs causing many serious diseases[25]. Understanding the role of enriched heavy metals as being toxic or not is also extremely difficult to unravel. This is because certain heavy metals are bioessential elements (aka, physiological metals), meaning they are necessary for biological processes up to a critical threshold before becoming toxic, and this threshold varies between organisms and heavy metals involved. Whereas other heavy metals that are not bioessential (aka xenobiotic), such as Hg and Cd, have unknown biological functions and are toxic even at very small concentrations[26] (Fig. 2).

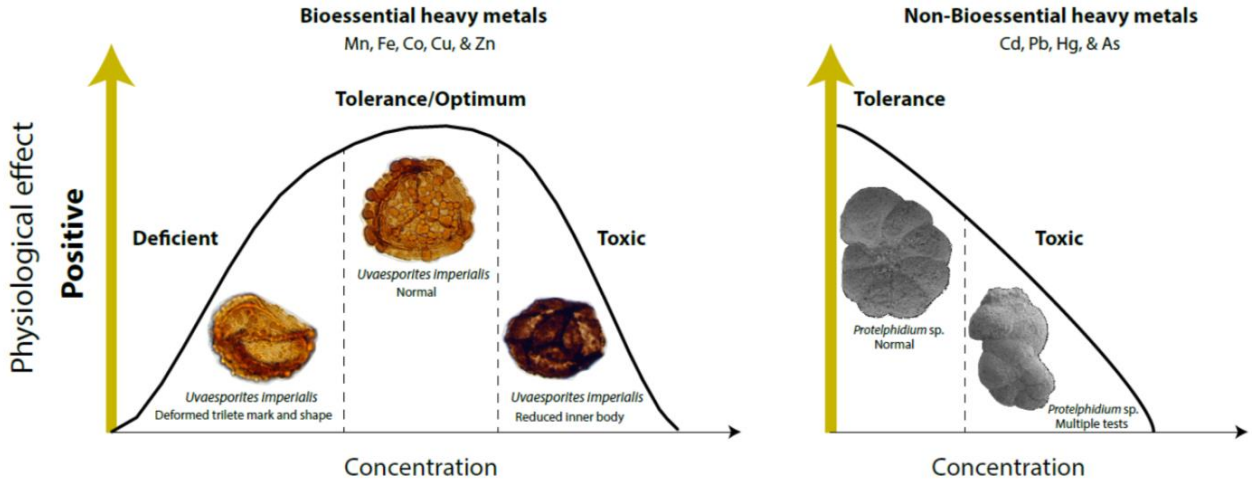


Fig. 2. *Differences in the physiological effects between bioessential and non-bioessential heavy metals in terrestrial sporomorphs and benthic foraminifera: specimens from Hochuli et al.[81] data repository and Ballent and Carignano[100] to show potential morphological responses to elevated heavy metal concentrations.*

1.2 Heavy metal fractionation and Bioavailability

Heavy metal emissions interact with the surrounding environment, which then transform into different metal species and these different species can be divided into different fractions, with differences in their bioavailability. This involves distinguishing 4 phases: (i) Acid-soluble phase – exchangeable metals bound to carbonates that are able to pass easily into the water column, particularly under acidic conditions. It is the fraction with the most labile bond to the sediment and the most dangerous for the environment; (ii) Reducible phase – metals bound to iron and manganese oxides, that can be released if the sediment changes from oxic to anoxic state, potentially triggered for example, by organisms in the sediments (bioturbation); (iii) Oxidizable phase – associated with organic matter and sulfides, which can became bioavailable under

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oxidizing conditions. Such conditions can occur, for example, if the sediment is resuspended (e.g., by currents and tides) and the sediment participles come into contact with oxygen-rich water; (iv) Residual phase – lithogenic and inert metals that are tightly bound in mineral structures and are virtually non-bioavailable[27]. For example, with Hg, identifiable fractions include (i) Exchangeable (HgADS1), (ii) Bound to organic matter (HgABS) and Hg sulfide (HgS), (iii) Mercury sulfate and oxide (HgADS2), and (iv) Residual (HgRES), where the labile fractions (HgADS1, HgABS, and HgADS2) can be easily released from sediment and readily transformed in the environment, whereas HgS and HgRES are insoluble and incorporated into mineral lattices and not biologically available[28]. Previous studies have also shown that marine organisms can intercept and absorb the labile (easily mobilized) fractions, making them bioavailable and potentially hazardous to food webs[28] . In deep-time studies of heavy metal abundances, the concentration of Hg is often normalised against TOC (Hg/TOC) or sulfur (Hg/S) to account for the variation in organic-matter (OM) and sulfides drawdown (e.g.,[29-31]), while other heavy metals are often normalised against Al. However, these normalisations do not account for changes in metal bioavailability or fractionation, which are crucial for assessing environmental toxicity. Recent research demonstrates that heavy metal fractionationprovides deeper insights into past environmental toxicity. Mercury fractionation, in particular, has been successfully applied to deep-time sedimentary records[32], showing promise for reconstructing the bioavailability and ecological impacts of heavy metals during past hyperthermal events.

2 Heavy metal toxicity and its role environment crises

While mercury has been extensively studied in the context of past environmental crises, largely due to its application as a volcanism proxy, the roles of other detrimental heavy metals like copper (Cu), chromium (Cr), cadmium (Cd), lead (Pb), arsenic (As), cobalt (Co), and nickel (Ni) have received comparatively less attention[33-35]. These heavy metals are typically removed from the water column by binding to organic matter or forming insoluble compounds with sulfides and subsequently incorporated into sediments. As a result, their elevated concentrations in the sedimentary record can, in part, be attributed to fluctuation in the amount of total organic carbon (TOC) or development of euxinic (anoxic and sulfide-rich) conditions[13]. However, such interpretation has led to controversary about whether the elevated heavy metals were a direct driver of past extinctions or simply a byproduct of broader geochemical change (e.g.,[36]). Even when heavy metals are normalized against TOC, aluminium (Al) or titanium (Ti), uncertainties persist due the complex effects of taphonomic processes on geochemical signatures. For example, the development of mercury sulfides in the sediment column or the impact of burial related thermal maturity are poorly understood[31,37]. In marine environments, mercury can be sequestered either within organic matter or as insoluble mercury sulfides, the latter requiring euxinic conditions to develop[38]. In such cases, it is unclear whether Hg toxicity added substantially to ecosystem collapse, or whether euxinia was sufficient to drive extinction events on its own.

This uncertainty underscores the need to re-evaluate how mercury enrichments are interpreted in the sedimentary record—particularly during intervals of extreme environmental change. Due to Hg's strong affinity for organic matter (e.g.,[39-41]), accurate interpretations of Hg anomalies require evaluation of TOC-normalized concentrations[42-43] to avoid misinterpretations 'created' through variations in organic matter. A significant constraint of the Hg/TOC approach lies in its

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sensitivity to samples containing low TOC concentrations (<0.2 wt%), where the analytical uncertainty can undermine the reliability of enrichment calculations[11,44].

Comparisons of Hg/TOC trends across five major hyperthermal events that coincided with significant biotic crises: the Permian-Triassic transition, Carnian Pluvial Event, Toarcian Event, latest Maastrichtian Warming Event, and the Palaeocene Eocene Thermal Maximum (fig. 3) show broadly similar patterns of elevated Hg/TOC, suggesting a potential link to enhanced volcanic activity and/or widespread ecosystem disruption. In most studies investigating Hg enrichment trends, Hg concentrations are normalized to TOC (see fig. 3). While some studies have taken the threshold of low TOC (<0.2 wt%) into account[12, 45-46], others have placed less emphasis on it[22,33]. For consistency across datasets, and because raw TOC values were not reported in some cases[22], this cutoff was not applied in our comparative analysis (Fig. 3). Beyond organic carbon content, Hg accumulation in sediments is also influenced by additional environmental and depositional factors including variations in lithology, detrital input, and redox conditions—particularly the presence of euxinia (anoxic, sulfide-rich conditions). To disentangle these effects additional normalization of Hg concentrations to detrital tracers such as aluminium (Al), thorium (Th) or titanium (Ti), and indicators for euxinia, such as sulfur (S), is required. Despite the importance of multi-proxy normalization, only[46] reported and applied both Al- and S-normalized Hg data, allowing for a more robust assessment of whether observed Hg enrichments reflect increased Hg flux or are driven by other depositional and/or geochemical conditions. Grasby et al.[33] provided Al and S data, but did not apply these for normalization of Hg, while the studies by Jones et al.[12] Them et al.[22] and Mazaheri-Johari et al.[45] lacked sufficient data to assess detrital or redox influences.

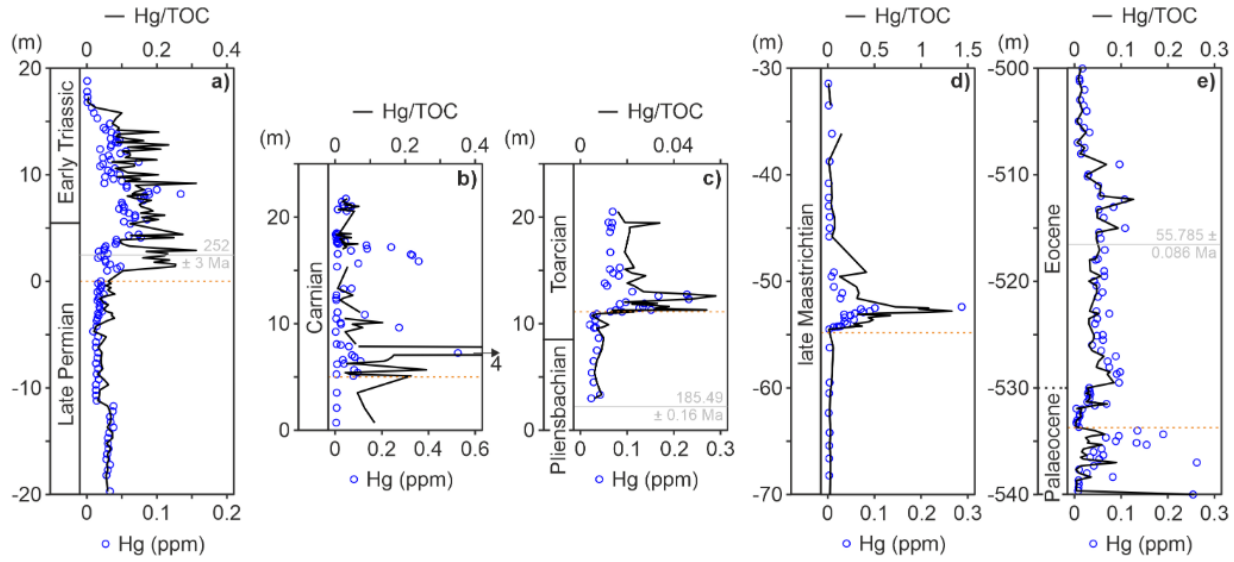


Fig. 3. *Hg concentration (ppm) and Hg/TOC (ppm/wt%) data across* ***a)*** *Permian-Triassic transition, Festningen, Svalbard[33],* ***b)*** *Carnian Pluvial episode, Steinbach and Polzenberg sections, Austira[45],* ***c)*** *Toarcian event, Bighorn Creek, Alberta, Canada[22],* ***d)*** *latest Maastrichtian Warming event, Jiaolai Basin, China[46] and* ***e)*** *Paleocene-Eocene Thermal Maximum, Central Basin, Svalbard[12]. The orange dotted line marks the onset of the carbon isotope excursion in each interval.*

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While mercury leads the discussion of metal toxicity in past biotic crises, this review advances the field by examining the roles of other biologically toxic heavy metals such as As, Pb, and Cd. Through two case studies from different depositional environments during the Permian-Triassic Mass Extinction (PTME), we provide a broader perspective on multi-heavy metal behaviour (Figs. 4 a, b).

Case Study 1: Mercury Enrichment in a Siliciclastic section during the PTME

At the Festningen section (Svalbard), application of sulfur-normalized Hg data significantly alters the interpretation of previously identified Hg enrichments based solely on Hg/TOC[33]. Throughout the Early Triassic, Hg concentrations appear elevated; however, when normalized to S, these enrichments disappear, suggesting Hg accumulation in the sediment corresponding to increased sulfide content (see Fig. 4a). The development of euxinia and associated sulfide formation is further supported by elevated pyrite concentrations reported by Grasby et al.[33], suggesting that the apparent Hg enrichment reflects sequestration of Hg as insoluble mercury sulfides under euxinic conditions, rather than from a true increase in Hg flux. As mercury sulfides are not bioavailable, they are unlikely to have exerted a toxic effect on marine organisms. Instead, the anoxic, hydrogen sulfide-rich conditions would have posed a more immediate threat to marine ecosystems. It is worth noting that both the development of euxinic conditions and mercury enrichments in the sediment occur after the extinction horizon (loss of bioturbated sediment and silica production) at Festningen.

A similar pattern is observed for Cd, which shows in the Early late Triassic a flat trend when normalized to S, further indicating that redox conditions, rather than external inputs, have played a major role for its distribution (Fig. 4a). In contrast, As and Pb remain elevated even after normalization to S near the extinction horizon (±5 m). When further normalized to Al, their enrichments appear independent of a lithological control, implying a potential increase in biologically relevant toxic metal concentrations during the extinction interval. Nevertheless, without direct bioavailability proxies, their ecological significance cannot be determined based on the bulk sediment data alone.

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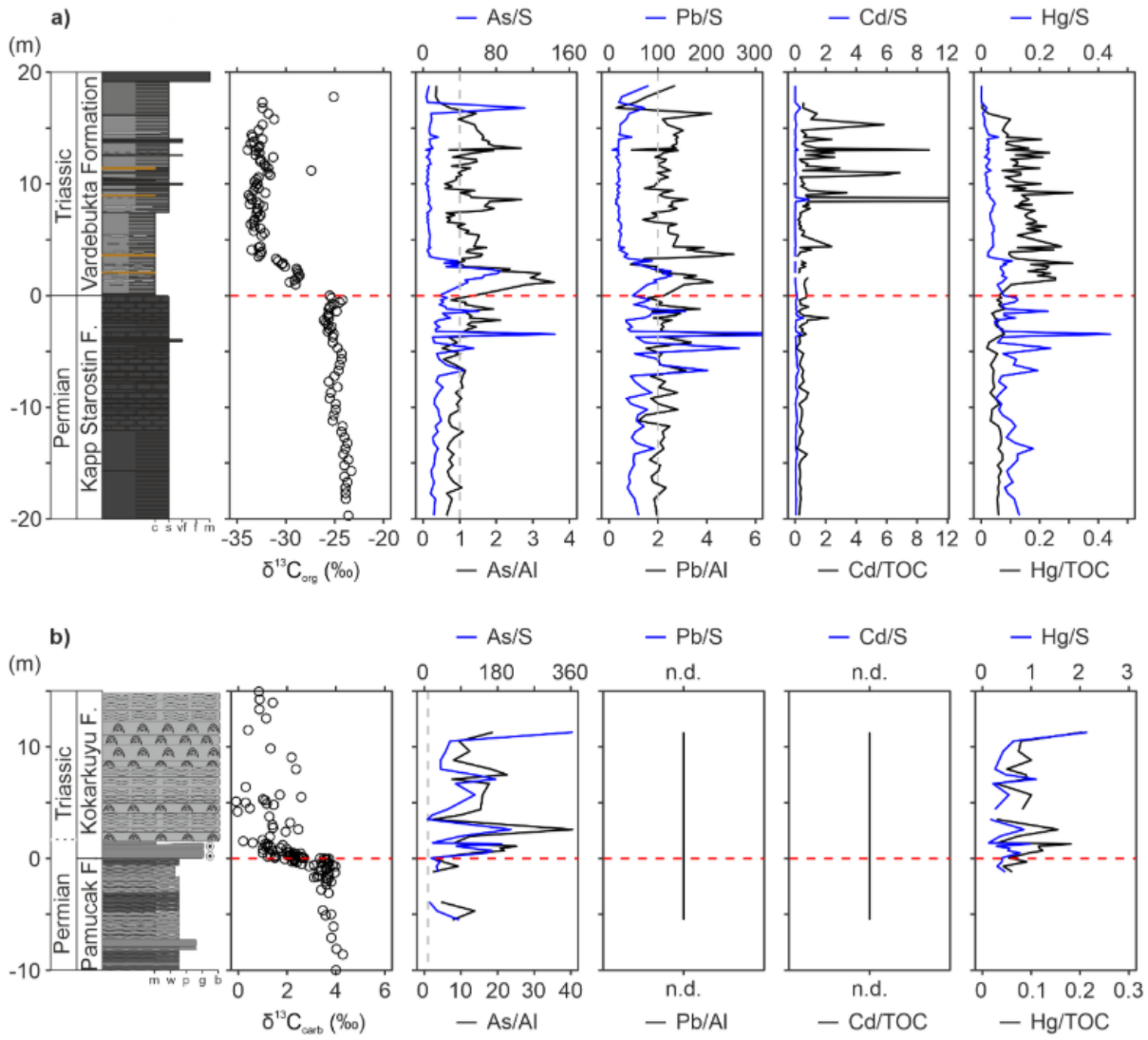


Fig. 4*. δ¹³C and heavy metal trends across the Permian-Triassic mass extinction event at* ***a)*** *the siliciclastic Festningen section, Svalbard[33] and* ***b)*** *carbonate platform section, Çürük Dağ, Türkiye (δ¹³C from Demirtaş[115] and Richoz[116]; major and trace element data from Frank[117]). As and Pb concentrations were normalized to S and Al (ppm/wt%), while Cd and Hg concentrations were normalized to S and TOC (ppm/wt%). The Pb and Cd concentrations from Çürük Dağ were consistently below the detection limit of 3 and 0.3 ppm, respectively. The red dashed line represents the extinction horizon at both sections.*

<u>Case Study 2</u>: Mercury Enrichment in a Carbonate succession during the PTME

In contrast, Çürük Dağ (Türkiye), located within a carbonate platform, shows low or undetectable Pb and Cd concentrations, suggesting no significant increase in sedimentary fluxes for these metals around the extinction horizon (Fig. 4b). However, both As and Hg, show variable trends across the section, regardless of the normalization method. When normalized to Al and S, these

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elements appear significantly enriched compared to Festningen. Yet, this discrepancy is likely a product of differing baseline levels, as the Al and S concentrations at Çürük Dağ are approximately one order of magnitude lower than at Festningen. This highlights a critical methodological challenge as comparisons between sections with differing lithologies—or even within heterogeneous sections—must be approached with caution, since baseline differences can inflate normalized values. One potential solution would be the use of enrichment factors calculated against standard materials or background values. Currently, this approach is readily applied using Al as the baseline, thereby accounting only for lithological variation, but comparable methods using S or TOC are not yet widely adopted.

3 Biological response of terrestrial ecosystems

The impact of heavy metals on plant species is complex and varies widely based on factors such as the type of metal involved, concentration, exposure time, chemical form, soil composition, and pH levels[47-49]. While some metals like iron (Fe), copper (Cu), and zinc (Zn), nickel (Ni) or molybdenum (Mo) are bioessential micronutrients required for plant growth and development[50], their availability must be carefully regulated. Excessive concentrations of these metals can surpass the physiological need of plants, leading to toxic effects, including growth inhibition and cellular damage[51-53]. In contrast, heavy metals such as lead (Pb), cadmium (Cd), and mercury (Hg), are non-bioessential and highly toxic, offering no benefits to plants and causing widespread disruption to vital physiological processes[54] (see Fig. 2). These metals interfere with crucial processes such as photosynthesis, nutrient uptake, and reproduction, often resulting in malformed sporomorph and/or reduced growth and survival[52-53].

Despite the different mechanisms by which plants uptake metals, the effects of lead (Pb), mercury (Hg), cadmium (Cd) and arsenic (As) share a common outcome: they induce oxidative stress. This stress is primarily driven by the generation of reactive oxygen species (ROS), which cause significant damage to cellular structures and disrupt essential physiological processes. The accumulation of ROS in plants exposed to these heavy metals leads to oxidative damage in vital components like cell membranes, proteins, lipids, and DNA[55-56]. This oxidative stress impairs vital functions like photosynthesis, nutrient and water uptake, and mitochondrial activity, all of which are crucial for the plant's growth and survival (e.g.,[57]). Additionally, the breakdown of antioxidant defence mechanisms worsens this stress, making it difficult for plants to counterbalance the excess ROS[58-59]. Consequently, plants suffer from stunted growth, chlorosis, reduced biomass, and compromised reproductive processes[52,60-61]. In more severe cases, prolonged oxidative stress caused by heavy metal exposure can lead to genetic mutations, chromosomal abnormalities, and cell death, significantly undermining the plant's ability to grow, reproduce, and maintain overall fitness[62-64]. To mitigate these effects, plants employ both enzymatic and non-enzymatic pathways to scavenge ROS[65-66]. In particular, metals such as Hg and Cd have been shown to interfere with key metabolic pathways by mimicking essential nutrients, thereby replacing them in enzymatic reactions and leading to metabolic dysfunctions[67].

3.1 Malformations in deep time

One of the few direct clues of biological stress preserved in the fossil record during mass extinction events is the significant ecological disruption observed within plant communities. These disruptions are often reflected as morphological changes in palynomorphs and leaf

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structures[35,68-75]. Over the last decade, teratology—extreme morphological change or malformation, in terrestrial biota— has proven to be an excellent proxy for increased environmental perturbations. The strength of the method is that these deformities represent *in vivo* responses to environmental stress, and that they record this response as fossils. A well-documented example of such teratological features have been recorded at the Permian/Triassic boundary where widespread abnormalities in herbaceous lycopsids and *Isoetales* are highlighted by an increased abundance of unseparated *Isoetales*-tetrads and trisaccate pollen. These features have been linked to failures in microsporogenesis, indicative of impaired reproductive process[76-77]. Initially, such morphological variations were attributed to enhanced solar ultraviolet B (UV-B) irradiation,—presumably triggered by stratospheric ozone depletion associated with massive volcanic activity—which can damage plant DNA and interfere with normal cellular activity[76,78-80]. However, emerging geochemical analysis have suggested that elevated concentrations of toxic metals—such as arsenic (As), cobalt (Co), mercury (Hg), and nickel (Ni)—may have contributed to, or acted synergistically with, UV-B exposure in inducing mutagenesis in sporomorphs[10,29-30,33-34,42,71,80-83]. Similar ecological disruptions and significant turnover in ecosystem composition are also well recorded at the Triassic/Jurassic boundary, characterized by a pronounced increase in malformed pollen and spores (e.g.,[69-70,75,84-85]). These morphological changes were interpreted as an acute environmental stress, coinciding with intense volcanogenic activity known as the Central Atlantic Magmatic Province (CAMP).

Geochemical records reveal a positive shift in mercury concentrations across the boundary interval, temporally aligned with the rise in sporomorphs malformation. This correlation supports the hypothesis that the elevated atmospheric mercury emission during the CAMP volcanism may have been a key factor in inducing morphological changes within plant reproductive structure[69-75]. Although less severe than the end-Permian or end-Triassic mass extinctions, the Toarcian event also exerted significant stress on terrestrial vegetation. Sedimentary archives reveal spikes in mercury levels that align with extensive volcanic outgassing from the Karoo–Ferrar Large Igneous Province[13,22,86]. This volcanism likely led to widespread atmospheric deposition of mercury and other heavy metals, contributing to the release of toxic compounds into the environment. Palynological records from this period show evidence of spore dwarfism, malformed spores, and asymmetrical *Classopollis* tetrads, often co-occurring with elevated concentrations of Hg, Cu, Cr, Cd, Pb, and As—indicative of prolonged environmental stress and physiological disruption in terrestrial plant communities[35].

In addition to morphological changes observed in spores and pollen, teratological features are not only confined to terrestrial plant communities but also extended to marine microplankton across extinction intervals, attributed to elevated levels of heavy metal. For instance, during the Late Ordovician extinction event Vandenbroucke et al.[68] and Munnecke et al.[87] documented widespread teratology in chitinozoans and acritarchs accounting for up to 20% of assemblages. These morphological variations were strongly linked to heavy metal enrichment and marine acidification, likely resulting from extensive volcanic emissions.

Together, these studies underscore the use of fossil teratology as a sensitive and direct proxy for reconstructing episodes of environmental stress, particularly those involving volcanically driven perturbations in atmospheric and oceanic chemistry. However, teratological studies investigating environmental disturbances driven by non-volcanic sources—such as the Chicxulub impact associated with the end-Cretaceous mass extinction are still unknown.

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4 Biological response of marine ecosystems

Despite the well-known detrimental consequence of elevated heavy metal concentrations in modern marine ecosystems, there are no studies (beyond marine palynology) that directly investigate the role of heavy metal emissions in driving mass extinctions and biodiversity crises in the marine realm. "Direct studies" are meant here as studies that show a link between heavy metal toxicity and extinction beyond a temporal relationship. An exception is the observed asymmetric geographical response of nannoplankton during the end-Cretaceous mass extinction, interpreted as a consequence of heightened heavy metal toxicity in the Northern Hemisphere (Jiang et al., 2010). Studies on the effects of anthropogenic-induced heavy metal pollution have shown that the impacts are recorded in surviving species, in the form of morphological malformations (e.g.,[88]), structural changes in the communities (e.g.,[89]), incorporation of heavy metals into skeletal material (e.g.,[90-91]), and the accumulation of heavy metals into animal tissues (e.g.,[92]).

4.1 Malformations

Morphological abnormalities in marine organisms have been intensely studied in modern environments. It is important to highlight that abnormalities can be divided into two types: deformations/discontinuous abnormalities (i.e., developed following mechanical damage to an organism) and malformations/continuous abnormalities (i.e., developed during the growth of an organism). Evidence based on modern studies, suggest that heavy metal pollution would produce malformations as it affects the growth of organisms rather than physical damage. Examples of heavy metal induced malformations include: bivalves with both posterior and ventral scores, flattening of the posterior shell, changes in height/thickness ratios and asymmetry, with up to 46-87.5% of specimens showing malformations in heavily polluted areas[88,93-94] gastropods with shorter spires, globular shape, smaller relative size, globular malformations on the inner surface[95]; and benthic foraminifera, with reduced chamber size, twisted and distorted chamber arrangement, overdeveloped chambers, aberrant chamber shape, changes in coiling direction, and malformations can even be so extreme that species identification is not possible[96-97]. The intense investigation of benthic foraminiferal malformations in modern ecosystems has also led to the establishment of the Foraminiferal Abnormality Index (FAI), which has shown up to 23% of communities showing malformations in heavily polluted areas[98].

Such morphological malformations are also preserved in the fossil record and have been recorded at the end-Cretaceous mass extinction in foraminifera[99-100], the end-Triassic mass extinction in ammonites[101], end-Permian mass extinction in foraminifera and ammonoids[102-103], and the Frasnian-Famennian extinction in conodonts and brachiopods[104-105]. In addition, certain nannoplankton and planktic foraminifera described from the end-Cretaceous mass extinction and Eocene hyperthermals have also been described as "Excursion taxa", characterized by malformations that deviate significantly from the typical symmetrical structures, often showing features such as weak or excessive calcification (e.g.,[106]). There are even cases where species are defined by their growth malformations and likely represents an extinction survivor of another species, e.g., *Guembelitria irregularis*, a planktic foraminifera from the end-Cretaceous event[99].

Morphological abnormalities have been heavily investigated in modern, coastal marine ecosystems, however because multiple environmental factors can cause malformations, previous

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studies have found it difficult to isolate exactly which environmental changes, or specific heavy metal(s), is the cause of the malformations[96,107]. One key reason why previous studies have not combined malformation development with independent metal fractionation data is because the use of malformations was developed as a cost-effective and efficient biomonitoring tool, especially for developing nations (e.g.,[108-109]). A similar problem exists for deep-time occurrences of malformations, which means that even though malformations have been reported from the fossil record, scientists have indicated that malformations can be associated with heavy metal toxicity but held-back in directly suggesting that heavy metal toxicity played a role in the past (e.g.,[99-100,102]). This means that both in modern and past studies the utility of malformations, without simultaneous tests for the bioavailability of heavy metals from the same samples, makes malformations as a bioindicator of heavy metal toxicity equivocal.

Similar to deep time studies, challenges exist when understanding historical ecological responses to heavy metal pollution, because it often co-occurs with other forms of pollution, such as eutrophication and/or high levels of Polycyclic Aromatic Hydrocarbons (PAHs). Some of the challenges faced in modern environmental studies are similar to those encountered in deep-time, which use geochemistry alone to understand environmental toxicity. Many studies that fail to find a relationship between ecological responses and heavy metals often overlook weather the heavy metals present in the environment were actually biologically available (e.g.,[110]). One example is the influx of Hg and other heavy metals into the Bay of Trieste over the last 300 years, where the lack of an ecological response in foraminifera was interpreted as evidence that the Hg was not biologically available[110], whereas molluscs from the same sediments show a clear ecological response, suggesting that Hg was indeed biologically available to certain taxa[112]. This discrepancy highlights the importance of considering different ecological responses between phyla to heavy metal toxicity as well as the need for independent proxies for heavy metal bioavailability, such as heavy metal fractionation to evaluate the true ecological impact of heavy metal contamination.

4.2 Ecological responses beyond malformations

Ecological changes beyond malformations that could be associated with heavy metal toxicity for marine organisms have not been investigated for deep time events, with one exception (see[16]). Expected community structural changes would vary related to the different vital effects between species, where certain marine organisms are known to be more resilient to heavy metal toxicity than others, but also because heavy metals both bioaccumulate and biomagnify through the food chain. Hence, you may expect the selectivity of certain groups of organisms and organisms at higher trophic levels (Fig. 5). Another approach has been to investigate the incorporation of heavy metals in skeletal elements and animal tissues (e.g.,[113]). Whilst it is obvious that animal tissues cannot be studied for past biodiversity crises, the incorporation of heavy metals into skeletal material could be informative. Caution, however, must be taken as the incorporation of heavy metals into the skeletal elements is physiologically controlled and not homogenous across an organism, and therefore the absence of heavy metals does not mean that the organism was not affected by heavy metal toxicity[113-114].

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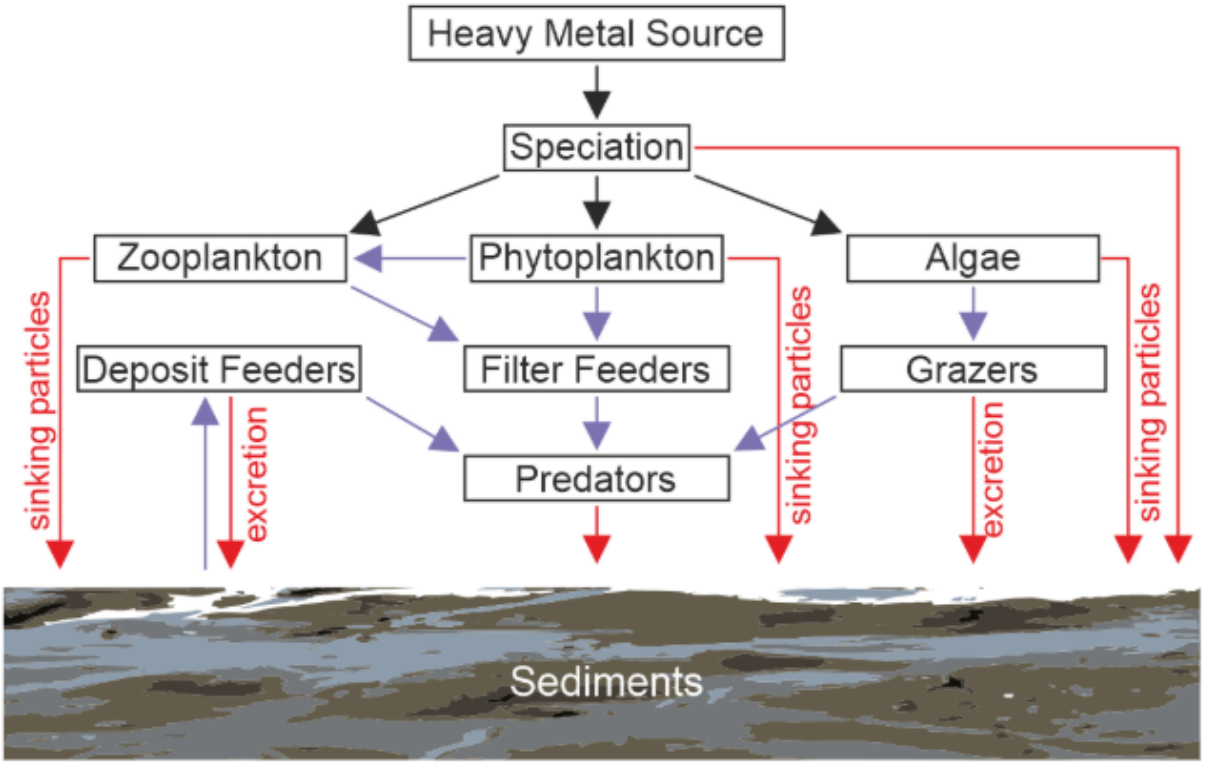


Fig. 5. *The transfer and bioaccumulation (purple arrows) of heavy metals through a marine ecosystem and how that relates to the ecology of different organisms. Note: bioturbation, erosion and water column conditions can remobilize heavy metals from the sediment but are not included in the diagram.*

5 Future directions/ Key outstanding questions

The hypothesis that heavy metal toxicity played a major role in deep-time biodiversity and mass extinction events is still largely an underexplored hypothesis that clearly requires further testing from multiple geoscientific perspectives.

In this review, we used the PTME to highlight the complexities involved in evaluating heavy metal enrichments during hyperthermal events. First, the simple normalization of metal concentrations to a single baseline, such as TOC, may obscure the true environmental signal, as multiple geochemical processes can influence sedimentary metal accumulation. Second, lithological comparisons are challenged with potential misinterpretation, as differences in normalized values may reflect baseline variability rather than actual disparities in metal concentrations. Furthermore, even when metal enrichments are robustly identified, they do not automatically imply biological toxicity without assessing their bioavailability.

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Key outstanding scientific questions include:

- Can heavy metal fractionation provide novel insights into the bioavailability of heavy metals during related extinctions?
- Were heavy metals biologically available at sufficiently high enough concentrations to be toxic and contribute to extinction during past biodiversity crises and mass extinction events?
- Are monstrosities and malformations in both the terrestrial and marine ecosystems related to metal toxicity or other environmental changes?
- Is heavy metal pollution at toxic levels a phenomenon exclusive to modern-day ecosystems or did it also contribute to extinction earlier in the Phanerozoic?

The questions outlined in this review paper highlight critical gaps in our understanding and addressing these will be essential for disentangling the complex environmental dynamics of Earth's deep-time history. By further investigating the bioavailability of heavy metals, their isotopic signatures, and their broader ecological impacts, we can gain invaluable insights into both past and present environmental challenges. We hope that the methods and models summarized herein will motivate further research and testing of these and other related questions.

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