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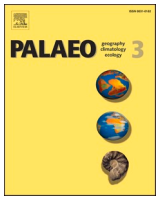

Editorial preface to special issue: Biocalcifier resilience and response during Phanerozoic global climate changes

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ABSTRACT

Through the Phanerozoic, the Earth has experienced several environmental disturbances characterised by varied tempos and modes of ecosystem resilience and response, and organisms that secrete calcium carbonate skeletons (calcifiers) have been especially vulnerable. These events have occasionally reached ecological tipping points, triggering permanent changes in the abundance, biodiversity, ecological range and biomineralization processes of marine calcifiers. Today benthic and planktic marine calcifiers are most impacted by these global perturbations; therefore, it is important to understand how calcifiers responded to global climatic and environmental perturbations in the recent and distant past in order to understand future resilience. This Virtual Special Issue (VSI), entitled *Biocalcifier resilience and response during Phanerozoic global climate changes*, comprises 17 papers that document the adaptative response of marine calcifiers to global stresses, dealing with examples from the geological record and from modern biota. Papers span from the Permian to the Recent, and consider pelagic organisms, benthic organisms, and integrated studies of pelagic and benthic ecosystems. Some of the main findings are as follows: (1) Planktic communities show a greater ecological resilience than benthic ones; (2) Most perturbations trigger ecological shifts rather than complete biotic turnovers, the exceptions being the end-Permian and Triassic-Jurassic boundary crises which led to ecosystem collapse and extinctions; and (3) Benthic ecosystems often respond through reorganization into new community assemblages. It is important to emphasise that each event represents a unique case study, where different duration and environmental stressors are key factors in determining organismal survival and ecosystem restructuring. The papers presented will be of help in detecting the most vulnerable and/or highly tolerant and resilient taxa in order to quantify the most common responses and adaptive strategies to current climate changes.

1. Introduction

The emergence of global climate change as a crucial issue for our society has accelerated our understanding of biotic responses at multiple spatial and temporal scales. Current effects on the biosphere are demonstrated (Walther et al., 2002; Cooley et al., 2022), and comprise changes in abundance, growth rates, predation, competition, dwarfism and vulnerability possibly culminating into extinction. Understanding of the Earth system and of the biotic response to climate change at time scales longer than human observations has become imperative, because anthropogenic activities are likely to telescope by order of magnitude the rates of climatic change that usually result from geologic (i.e. natural) processes. The Phanerozoic geological record indicates that the Earth already experienced extreme environmental conditions, from warmer than the present to much colder climates, on many different timescales, eventually reaching devastating tipping points, with ephemeral or permanent modification in marine calcifiers in pelagic and benthic ecosystems (Erba et al., 2010; Garbelli et al., 2014, 2017; Erba and Parente, 2025).

Life on Earth has survived numerous major (palaeo)environmental disturbances, which caused a wide range of severe stress on the biosphere with evidence of variable resilience. Ecosystem resilience refers to the stability and the capability of recovering from disturbance or endure environmental stress, assessing how well a bionetwork can tolerate environmental stress without collapsing into a different state governed by different processes. Given enough time, a resilient ecosystem may be able to absorb stresses caused by disturbances with little or no sign of degradation and/or to fully recover from perturbations and become as biodiverse and healthy as before the impact. Two conceptual definitions of resilience are widely used in ecology (Todman

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et al., 2016), generally referred to as "ecological resilience" (Holling, 1973) and "engineering resilience" (Pimm, 1984). Ecological resilience considers the capacity of a system to tolerate disturbance without changing to an alternative configuration, whereas engineering resilience is the time taken for a system to return to its pre-disturbed, stable state. Also, there is confusion around what constitutes a disturbance versus a perturbation. Todman et al. (2016, p. 1) define "disturbance as a sudden shock imposed on the system by a change in conditions external to the system (e.g., a sudden increase in ambient temperature) and perturbation as the change in the level of function of a system due to such a disturbance". If the disturbance is of sufficient magnitude or duration, a threshold or tipping point may be reached where the ecosystem undergoes a regime shift, possibly permanently.

In order to cope with the effects of current global changes and to figure out what we have to expect in the next future, it is therefore necessary to assess the resilience and the adaptive capacity of the biota and their ecosystems (Raven et al., 2005).

The ocean is the oldest and largest ecosystem on Earth and best records global changes in climate and atmospheric composition. Marine ecosystems are inextricably involved in the physical, chemical, biological and societal processes of global change (Global Ocean Ecosystem Dynamics Project (GLOBEC), 2003) and for these reasons they are the best settings where to study and understand ecosystem resilience. It is impossible to comprehend the Earth system without understanding the ocean and how current global change will affect the abundance, diversity and productivity of marine biota, from plankton to benthos (Global Ocean Ecosystem Dynamics Project (GLOBEC), 2003). Thanks to their abundance through time, the marine calcifying biota may provide important clues regarding the ocean ecosystem resilience and the functioning of our planet.

Studies on recent ecosystems have demonstrated that abrupt global warming and ocean acidification are detrimental for carbonate-secreting organisms (Mostofa et al., 2016; Cooley et al., 2022) and can determine dramatic biotic shifts with the demise of carbonate platforms and coral reefs as well as biocalcification failure of planktic and benthic calcifiers. For instance, the amount of CO_2 in the ocean/atmosphere system exerts a direct control on calcareous nannoplankton. Altered carbonate chemistry may led to the production of smaller and/or malformed coccoliths or incomplete coccospheres (Riebesell et al., 2000; Barcelos e Ramos et al., 2010; Beaufort et al., 2011; Krug et al., 2011; Bach et al., 2012; Lohbeck et al., 2012; Bach et al., 2015), whereas high temperatures may become a stressing factor, reducing the coccolithophore algae metabolic rate (Dedman et al., 2023). Living planktic foraminifera are also sensitive to the effects of ocean acidification and warming, showing reduction of shell thickness, weight, and change in morphology and abundance/diversity (Russell et al., 2004; Moy et al., 2009). In reef environments, scleractinian zooxanthellate corals are most sensitive to changes in seawater conditions associated with rapid anthropogenic climate change and a global severe decline or a total disintegration is expected by the end of the 21st century (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Harborne et al., 2017; Hughes et al., 2017). Smaller corallites, a higher degree of branching and extracalicular budding have been associated with lower stress tolerance and higher extinction risk (Raja et al., 2021). Finally, studies on modern brachiopods and bivalves indicate that biomineralization of marine benthic invertebrates also reacts to environmental perturbations (Watson et al., 2012), modifying calcification and growth (Michaelidis et al., 2005; Fabry, 2008; Beniash et al., 2010; Hiebenthal et al., 2013), even if laboratory observations show that they may be resilient in the short-term (Cross et al., 2015; Jurikova et al., 2019).

Studies on modern biota are crucial for understanding and modelling response and dynamics of ecosystem resilience at (very) short-term, but the Earth's biological systems have been adapting to global change at much longer timescales. Indeed, the geological record has the unique advantage of providing evidence for how species adapt (or not) to environmental conditions different than those of the present day at medium- and long-term.

The aim of this Virtual Special Issue (VSI) is to document the adaptative (or not) response of marine calcifiers from pelagic and benthic ecosystems to global climatic and environmental stresses and the effects on their ability to mineralize, on marine biodiversity and on changes in species distribution during global perturbations. In this VSI are included examples from the geological record that are fundamental to scrutinize the short-, medium- and long-term response of the marine calcifiers prior to human disturbances, as well as those on modern biota, that are vital for measuring ecosystem resilience and response at (very) short-term. This VSI originated as research presented in a thematic session organised during the EGU2023 General Assembly held in April 2023 in Vienna, and it comprises 17 papers, which are arranged as three principal themes: (1) pelagic, (2) benthic and (3) pelagic and benthic ecosystems.

2. Selected time intervals

Papers in this VSI focus on significant geological events associated with environmental and climatic changes (Fig. 1). Each event differs in duration and context, although most are characterised by global warming conditions, occurring at varying rates. Specifically, the studied intervals include the Triassic-Jurassic boundary, the early Pliensbachian, the Aptian-Albian boundary, the Cenomanian-Turonian boundary, the Paleocene-Eocene and Eocene events, and the late Oligocene. The only event related to a cooling phase is the early Wuchiapingian (Late Permian). Finally, some contributions explore the response of modern organisms as a key tool for correlating with the geological record.

2.1. Early Wuchiapingian (Late Permian)

The Permian period witnessed some of the most dramatic environmental and climate changes in the Earth's history which lead-up to the Permian-Triassic mass extinction, the most severe extinction event (e.g., Jin et al., 2000; Benton and Newell, 2014; Stanley, 2016). The general warm climate was punctuated by rapid shift fluctuations in climate which likely played a role in shaping marine and terrestrial ecosystems leading up to the end-Permian mass extinction. One of these is the rapid cooling of 5–8 °C in the early Wuchiapingian (Sun et al., 2022) that lasted from ~259 to ~257.5 Ma, possibly triggered by CO_2 drawdown linked to weathering of the Emeishan LIP in South China (Cheng et al., 2022).

2.2. Triassic-Jurassic boundary

The end of the Triassic, ~ 202 Ma, was characterised by the emplacement of the Central Atlantic Magmatic Province (CAMP) probably responsible of increased atmospheric pCO_2 and the consequent global warming and ocean acidification (McElwain et al., 1999; Martindale et al., 2012) which strongly contributed to the end-Triassic mass extinction. In the terrestrial domain, these perturbations resulted in the variation of flora composition and distribution patterns (Lindström et al., 2017). In the marine realm, the ocean acidification greatly influenced carbonate-secreting organisms (Hautmann, 2004; Van de Schootbrugge et al., 2007; Kiessling et al., 2009), including nannofossils, which went through stepped extinction paralleled by decline in abundance and size (Clémence et al., 2010; Bottini et al., 2016). The pattern of extinction in the subtropical carbonate platforms, affecting selectively the massive hypercalcifiers, has been taken as a strong evidence of ocean acidification (Kiessling and Simpson, 2011; Hönisch et al., 2012).

2.3. Early Pliensbachian, Early Jurassic

The early Pliensbachian (187–183 Ma) records a global expansion of shallow-water carbonates with proliferation of shallow-water benthic

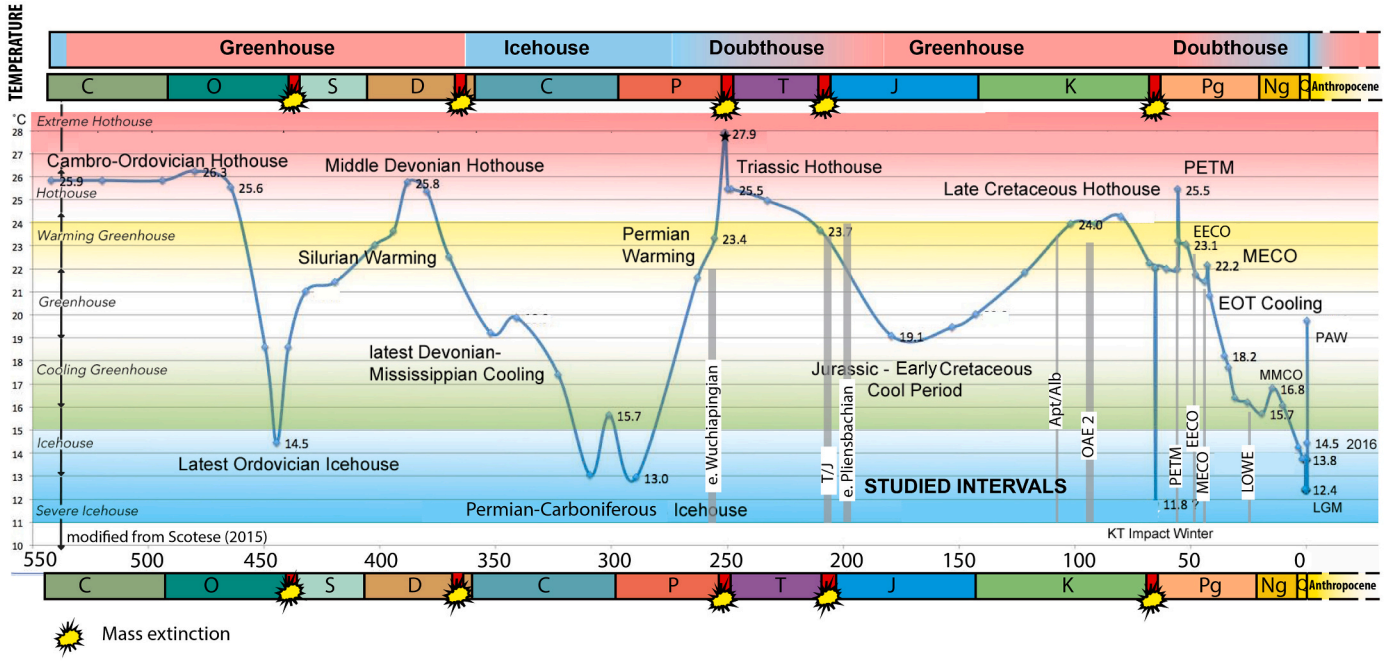

Fig. 1. Studied intervals in this VSI. Figure modified from Scotese (2015).

calcifying organisms and lithiotid bivalves (Posenato and Masetti, 2012). In the southern Alps, this proliferation occurred during a phase of better water oxygenation and meso-oligotrophic conditions, which can be related to a cooling event recorded in basinal setting (e.g., Gómez et al., 2016). The factors that led to the adaptive radiation of these large bivalves remain enigmatic as well as the relation between the large size and photosymbiosis (Fraser et al., 2004; Posenato et al., 2013; Franceschi et al., 2014; Bassi et al., 2015, 2017).

2.4. Aptian-Albian boundary (mid Cretaceous)

The Aptian-Albian boundary, occurring around 113 million years ago, was marked by a significant global environmental disturbance. This interval is also associated with widespread oceanic anoxia related to Oceanic Anoxic Event 1b and global warming. As a result, weathering and nutrient input into the oceans intensified, stimulating marine productivity and further enhancing oxygen depletion. Marine ecosystems, experienced significant changes, with some groups, such as planktic foraminifera going through major extinction events (Leckie et al., 2002; Huber et al., 2011). Overall, the Aptian-Albian boundary reflects a time of profound climatic and oceanographic upheaval, with lasting impacts on marine life and Earth's geochemical systems.

2.5. Cenomanian-Turonian boundary (Late Cretaceous)

The Oceanic Anoxic Event (OAE) 2 across the Cenomanian-Turonian boundary (94–93 Ma) is arguably regarded as one of the most extreme events of global palaeoenvironmental disturbance in the deep geological past. High concentrations of volcanic CO_2 resulted in the warmest climate of the past 150 Ma, an accelerated hydrological cycle, enhanced production and burial of organic matter, altered structure of the oceans (Jenkyns, 2010). Calcareous plankton changes associated with OAE 2 evidence a general increase in fertility, a turnover and a decrease in abundance and diversity under thermal stress and excess CO_2 (Leckie et al., 2002; Erba, 2004). The widespread drowning of carbonate platforms at the OAE 2 is associated with the flooding of the platform top by nutrient-rich waters, which was also the cause of larger foraminifera extinction (Parente et al., 2008). Compared to the generally carbonate-poor record of deep-water sections, the OAE 2 record of resilient platforms provide a very precious archive of carbonate-associated geochemical proxies of palaeoenvironmental changes (Frijia and Parente, 2008; Owens et al., 2013; Pogge von Strandmann et al., 2013; Zhou et al., 2015; Clarkson et al., 2018; Sweere et al., 2018).

2.6. Paleocene-Eocene

The Paleocene and Eocene epochs were marked by significant global warming episodes, including the hyperthermal Paleocene-Eocene Thermal Maximum (PETM), the Early Eocene Climatic Optimum (EECO), and the Middle Eocene Climatic Optimum (MECO). These events are typified by marked negative shifts in $\delta^{13}C$ curves, suggesting a massive introduction of CO_2 into the atmosphere and oceans that coincided with a reduced saturation state of seawater with respect to $CaCO_3$ (Zachos et al., 2005).

The PETM was a prominent warming event lasting approximately 170,000 years (Zeebe and Lourens, 2019), triggered by a major disturbance in the global carbon cycle around 56 million years ago. During this period, global average temperatures are estimated to have reached about 25.2 °C (Scotese et al., 2021), or possibly as high as 31.6 °C according to Inglis et al. (2020).

The Early Eocene Climatic Optimum EECO (53–49 Ma) is a very long-time interval when Earth surface temperatures and atmospheric pCO_2 reached their Cenozoic maxima (Zachos et al., 2008; Lauretano et al., 2015; Anagnostou et al., 2016). The EECO is characterised by a peak in specific diversity of large benthic foraminifera and by a marked decline of coral reefs (Zamagni et al., 2012). A critical change involved the planktic foraminiferal morozovellids, one of the most important calcifiers of the early Paleogene tropical and subtropical oceans, which declined in abundance, diversity and size (Luciani et al., 2016, 2017a, 2017b) across the carbon isotope excursion known as "J" at the start of the EECO (Luciani et al., 2016).

The Middle Eocene Climatic Optimum MECO (40.5–40.0 Ma) is a global, relatively long-lived warming event centered at ~40 Ma (Bohaty et al., 2009). This event is characterised by remarkable changes in the physical environment testified by a global negative $\delta^{18}O$, a profound perturbation in the carbon cycle and a 500–1500 m shallowing of the carbonate compensation depth (Bohaty et al., 2009; Pälike et al., 2012). This event corresponds to the acme in size and diversity of larger

foraminifera during Shallow Benthic Zone 17. These drastically drop shortly after, in contrast to corals that slowly recover their capacity to form reefs (Pomar et al., 2017).

2.7. Late Oligocene

The Late Oligocene Warming Event (LOWE) (27–26 Ma) is a poorly known warming event, lasting about 1 My (Zachos et al., 2001), which occurred in the late Chattian (Alegret et al., 2008) right after the Oi-2 cooling event and just before the Mi-1 cooling event marking the beginning of the Miocene (Zhang et al., 2013). Pomar et al. (2014) underlined an inverse correlation between large benthic foraminifera (flourishing during warming intervals) and coral reefs (flourishing during cooling intervals). The LOWE roughly corresponds to the Shallow Benthic Zone 23, an interval of flourishing large benthic foraminifera immediately after the early Chattian luxuriant emergence of coral reefs on a global scale (Perrin and Bosellini, 2012).

3. Summary of findings of this VSI

This VSI comprises 17 papers that investigate the tempo and mode of response of marine calcifiers to (palaeo)environmental and (palaeo) climatic perturbations based on multidisciplinary approaches, such as morphometric analysis, species abundance, distribution patterns and biodiversity, sclerochronology and growth rate, biomineralization, geochemistry, stratigraphic palaeontology and palaeoecology. Papers are focused on both pelagic and benthic organisms. Such an integrated analysis of carbonate-secreting pelagic and benthic biota is vital to fully characterise and understand the role of climate change and ocean chemistry in both the pelagic and benthic habitats to better comprehend the response of calcifiers to these changes and assess ecosystem resilience and eventually threshold crossing. Also, integrating pelagic-benthic data is crucial to understand if the same pattern is repeated in both ecosystems during different time intervals of climate and ocean perturbation, their onset and recovery, and during preceding or succeeding stable conditions. This allows the assessment of possibly differential threshold/tipping points and the quantification of resilience. Below we present a short synthesis of the main findings of each manuscript, focusing on pelagic and benthic ecosystems (Table 1).

3.1. Pelagic ecosystems

The response of pelagic organisms to climate and environmental perturbations has been the topic of four papers, spanning from the early

Table 1
Summary of 17 papers that constitute this VSI subdivided into three main themes. For each paper, we describe the topic, the study area, the time interval and the organism(s) analysed.

Papers	Topic	Study area	Time interval	Organisms
Pelagic				
Filippi and Luciani (2025)	Planktic foraminiferal response to the warming of the Early Eocene Climatic Optimum	Indian Ocean and Pacific Ocean	early Eocene	Planktic foraminifera
Filippi et al. (2025)	Planktic foraminiferal response to the warming across the EECO event	Subtropical Pacific Ocean	Eocene	Planktic foraminifera
Sigismondi et al. (2025)	Planktic foraminiferal response to the Middle Eocene Climatic Optimum warming	Atlantic Ocean	Eocene	Planktic foraminifera
Zhu et al. (2025)	Geochemistry of fish otoliths indicative of different environmental conditions	South Shetland Islands, Antarctica	Recent	Fish otoliths
Benthic				
Viaretti et al. (2025)	Brachiopod response to the cooling of the early Wuchiapingian	Julfa and Hambast fms., Iran	early Wuchiapingian (Late Permian)	Brachiopods
Montanaro et al. (2024)	Response of shallow water ecosystem to environmental perturbations in the Triassic-Jurassic Boundary interval	Southern Tethyan carbonate platforms, Greece and Italy	Triassic-Jurassic boundary	Benthic foraminifera, molluscs, algae
Bassi et al. (2024)	Brachiopod response to environmental changes in a relatively instable lagoonal setting	Trento Platform, Southern Alps, Italy	early Pliensbachian (Early Jurassic)	Brachiopods
Posenato et al. (2024)	Response of the *Lithiotis* Facies bivalves to the early Toarcian extinction	Northern Italy	Pliensbachian-early Toarcian (Early Jurassic)	Bivalves
Balestra et al. (2025)	Benthic foraminiferal response across the Aptian-Albian Boundary Interval	Falkland Platau (Southern Atlantic Ocean)	Aptian-Albian boundary (mid Cretaceous)	Benthic foraminifera
Benedetti et al. (2024)	Foraminifera and scleractinian reef corals response to the early Paleogene global warming	Neothetyan circum-Mediterranean area	Paleocene-Eocene	Scleractinian reef corals and shallow-water foraminifera
Bosellini et al. (2024)	Effects on growth of coral buildups in a fandelta system during the Late Oligocene Warming Event	Tertiary Piedmont Basin, NW Italy	late Oligocene	Corals
Brand et al. (2025)	New Li/Ca palaeothermometer for brachiopods	Worldwide	Recent	Brachiopods
Prayudi et al. (2024)	Adaptation of modern biocalcifying shallow-marine benthic organisms to extreme heat exposure	Arabian Gulf	Recent	Benthic foraminifera, ostracods, molluscs
Ye and Bitner (2025)	Influence of temperature on multiple ecomorphological traits in brachiopods	Worldwide	Recent	Brachiopods
Pelagic and benthic				
Petrizzo et al. (2025)	Resilience and extinction of calcareous plankton and shallow-water benthic biocalcifiers at the Cenomanian-Turonian boundary	Worldwide	Cenomanian-Turonian boundary (Late Cretaceous)	Benthic and planktic foraminifera, calcareous algae, rudists and other bivalves, calcareous nannoplankton
Amaglio et al. (2025)	Benthic and planktic foraminiferal response to OAE 2	Offshore SW Australia	Cenomanian-Turonian boundary (Late Cretaceous)	Planktic and benthic foraminifera
Gandolfi et al. (2025)	Benthic and planktic foraminiferal response to the warming of the Middle Eocene Climatic Optimum	Provençal Domain, NW Italy	middle Eocene	Planktic and benthic foraminifera

Eocene to the Recent.

Filippi and Luciani (2025, this VSI) investigate planktic foraminiferal community changes across the Early Eocene Climatic Optimum (EECO) at southern high-latitude sites (Site U1510 and Hole 762C), showing the dominance and ecological flexibility of *Acarinina* under extreme warmth, contrasting with the decline or disappearance of less adaptable taxa such as *Morozovella* and *Chiloguembelina*. Their results reveal that despite some regional differences, foraminiferal communities globally restructured across the EECO and did not recover their pre-disturbance composition, highlighting limited resilience to sustained warming, nutrient shifts, and oxygenation changes.

Filippi et al. (2025, this VSI) examine the response of planktic foraminifera *Morozovella* and *Acarinina* to extreme climatic conditions during the EECO at ODP Sites 1209–1210 on Shatsky Rise, Pacific Ocean. Findings show that *Morozovella* experienced a temporary increase in test size at the EECO onset, linked to the dominance of larger species, while *Acarinina* displayed a reduction in test size and a shift to a deeper mixed-layer habitat. The $\delta^{13}C$ data suggest that *Acarinina*'s shift to deeper waters and reduced symbiosis helped it to survive the warming, while *Morozovella*'s limited ecological flexibility led to its reduced abundance despite maintaining symbiosis. *Acarinina*'s adaptability, including smaller test size, allowed it to optimize energy use under the EECO's warming and nutrient-limited conditions, making it the more resilient taxon, ultimately replacing *Morozovella* as the dominant mixed-layer dweller.

Sigismondi et al. (2025, this VSI), analyse the impact of the Middle Eocene Climatic Optimum (MECO) on planktic foraminiferal assemblages at Atlantic ODP Sites 1051, 1263, and 702, documenting significant compositional changes linked to increased surface-water temperatures, migration of warm-water taxa, and a decline of the cold-water genus *Subbotina* and ODZ-dwelling *Chiloguembelina*. The results reveal a permanent decrease of warm-index "Large *Acarinina*" and show that post-MECO communities did not recover their pre-disturbance structure, indicating limited resilience to sustained warming and altered nutrient dynamics.

Zhu et al. (2025, this VSI), through chemical analyses and statistical approaches, detect significant differences in otolith nucleus and edge chemical compositions in modern Antarctic fishes, indicative of distinct environmental conditions experienced by fishes inhabiting divergent water masses. With this study the authors demonstrate that the elemental composition of fish otoliths provides a promising tool to elucidate life history and population structure of fishes. This approach may present a window into the response of fishes to the changing climate, potentially documenting the adaptive, or not, response of marine calcifiers to past global stresses.

3.2. Benthic ecosystems

The response of benthic organisms to climate and environmental perturbations has been the topic of ten papers, spanning from the Permian to the Recent.

Viaretti et al. (2025, this VSI) performed sclerochemical analyses ($\delta^{18}O$, $\delta^{13}C$) on brachiopod specimens from Iran to unravel the duration and magnitude of the early Wuchiapingian (Lopingian) cool climate episode and to document its impact on marine biota. The authors concluded that this cooling episode was short lived, lasting about 2 Myr, and that brachiopod assemblages, despite witnessing variations in productivity and food supply, showed a high ecological resilience not undergoing a major change in biodiversity.

Montanaro et al. (2024, this VSI) investigate, through facies analysis and bio- and carbon-isotope stratigraphy, three Southern Tethyan carbonate platform sections across the Triassic-Jurassic boundary to detect the response of shallow-water ecosystem to the perturbations occurred prior to and across the boundary. The authors show that the aragonitic Dachstein-type biota was resilient to the environmental changes associated with the initial negative carbon isotope excursion in Southern Tethys, but failed to survive to the subsequent prolonged stress. Despite this, Southern Tethyan carbonate platforms adapted to environmental disturbances through a shift in the dominant carbonate production style from aragonitic biocalcification to chemical and microbially-mediated $CaCO_3$ precipitation.

Bassi et al. (2024, this VSI) describe and interpret Pliensbachian terebratulide brachiopod accumulations, dominated by the species *Lychnothyris rotzoana*, of the Trento Platform (Southern Alps, Italy) in order to understand their response to changing conditions in an instable tropical lagoonal ecosystem. The authors observed that *L. rotzoana* populations were affected by unpredictable and rapid environmental change, such as water temperature changes, oxygenation and nutrient supply variations and water poisoning, which brought about the demise of the community. The medium-term response of brachiopods to the relatively instable conditions of the tropical lagoon setting shows that they were not able to adapt to continuous perturbations, and that continuing stress severely compromised their survival.

Posenato et al. (2024, this VSI) conduct a detailed microstructural, sclerochronological, and sclerochemical investigation of *Lithiotis* Facies bivalves from the Pliensbachian Rotzo Formation (northern Italy), revealing distinct growth rates and shell architectures correlated with environmental stress during the early Toarcian biocalcifier crisis. The study demonstrates that taxa exhibiting thick, fast-growing aragonitic shells (>15 mm/year) experienced higher extinction rates, whereas more resilient forms with slower growth (<8.3 mm/year), such as *Pachyrisma*, survived, likely due to their tolerance to low-pH and dysaerobic conditions.

Balestra et al. (2025, this VSI) investigate the benthic foraminiferal extinction across the Aptian-Albian Boundary Interval (AABI) using a multiproxy approach, including Mg/Ca ratios and stable isotope analyses. The study suggests a slight cooling of seawater temperatures and/or changes in the carbonate system, potentially contributing to the extinction event. However, diagenetic overprints on the isotopic records complicate the interpretation, making it difficult to definitively link the observed shifts to climatic changes, while also emphasizing the importance of species-specific Mg/Ca relationships for palaeotemperature reconstructions.

Benedetti et al. (2024, this VSI) reconstruct genus- and species-level diversity dynamics of scleractinian reef corals (SRC) and shallow-water foraminifera (SWF) across Paleocene-Eocene hyperthermals in the Neotethyan circum-Mediterranean region, showing that while rapid warming events such as the PETM and EECO triggered pronounced radiations in SWF and reef collapses or transient declines in SRC, the subsequent cooling trend post-MECO reversed these patterns, leading to foraminiferal decline and coral diversification. Their findings highlight the taxon-specific nature of resilience mechanisms, the asynchronous biotic responses of shallow-water versus deep-sea calcifiers to climatic perturbations, and the critical role of the rate and duration of environmental change in structuring evolutionary trajectories.

Bosellini et al. (2024, this VSI) document the effects on growth of coral buildups in a fandelta system of the Tertiary Piedmont Basin (NW Italy) during the Late Oligocene Warming Event (LOWE), a crucial climatic event for coral reefs. In this context, the coral buildups appear to have been intermittently deactivated or smothered by fine-grained terrigenous input during flood phases or shifts in distributary channels until their final suffocation by fluvial sediment input. The authors distinguish four coral facies within the coral buildups, which shifted in time and space during the LOWE, highlighting the adaptability and resilience of Oligocene corals to a complex interplay of environmental stressors such as turbidity, hydrodynamic energy, sediment and nutrient supply within a mesophotic setting.

Brand et al. (2025, this VSI) propose a novel Li/Ca palaeothermometer based on data from modern rhynchonelliformean brachiopod shells from high to low latitudes, shallow to deep and warm to cold seas covering the world's oceans. As brachiopods are important biocalcifiers, being especially abundant during the Palaeozoic, the

proposed Li/Ca thermometer can be an invaluable supplementary tool to the oxygen and clumped isotope thermometers in characterising past seawater and climate history.

Prayudi et al. (2024, this VSI) explore, through field sampling and laboratory heat exposure experiments, the adaptation of modern calcifying shallow-water benthic organisms to extreme heat exposure in the coastal areas of the Arabian Gulf. Although the local biocalcifiers demonstrate high survivability during the thermal exposure, particularly when submerged under water, they are threatened by current and potentially future warming trends, as summer temperatures measured over the 2020–2024 study period already exceed their experimentally-determined thermal limits.

Ye and Bitner (2025, this VSI), by integrating traditional and novel methodologies, provide a framework for exploring complex ecological interactions, offering insights into the resilience of marine ecosystems. The authors observe that temperature had a moderate or weak influence on selected ecomorphological traits of living brachiopods, attributing this to the high temperature tolerance in living brachiopods and to other additional environmental preferences, such as substrate type and ocean currents, which were not significantly related to temperature. They also highlight the significant role of macroevolutionary adaptation history in shaping modern brachiopod biogeographical patterns.

3.3. Pelagic and benthic ecosystems

Three papers analyse the response of both pelagic and benthic organisms to climate and environmental perturbations, spanning from the Cenomanian to the middle Eocene.

Petrizzo et al. (2025, this VSI) present a review of the record of the main biocalcifiers of subtropical carbonate platforms (larger foraminifera, calcareous algae, rudists and other bivalves) and of pelagic basins (planktic foraminifera and calcareous nannoplankton) across the Cenomanian-Turonian OAE 2. The authors observed that the main extinction event, severely affecting the shallow-water benthic biocalcifiers, occurred within and after the Plenus Cold Event; they suggest that fluctuations in surface seawater temperature and extreme warming were probably the main cause of the extinction. Overall, calcareous plankton show a greater resilience than carbonate-platform biocalcifiers to palaeoenvironmental perturbations across OAE 2.

Amaglio et al. (2025, this VSI) investigate the impact of OAE 2 on benthic and planktic foraminiferal assemblages at IODP Sites U1513 and U1516 in the Mentelle Basin, documenting stable eutrophic communities with low diversity during the early OAE 2 and a transient environmental improvement linked to the Plenus Cold Event. The results highlight a phase of extreme eutrophication and suboxic conditions during the low $CaCO_3$ interval, followed by diversification of foraminiferal assemblages, enhanced water-column stratification, and partial environmental recovery, although a turnover toward renewed eutrophic conditions is recorded across the Turonian.

Gandolfi et al. (2025, this VSI) explore foraminiferal community shifts during the MECO in shallow-water settings of the Provençal-Dauphinois Domain, demonstrating that while certain taxa, such as *Cibicidoides, Heterolepa,* and *Subbotina*, showed ecological flexibility and resilience to warming and enhanced runoff, the majority of assemblages experienced significant restructuring. These changes, driven by both climatic perturbations and increased sedimentation, resulted in a permanent alteration of community composition, highlighting the complex interplay between temperature, nutrient availability, and sedimentary dynamics in shaping foraminiferal ecology during the MECO.

4. Conclusions

Understanding the response of marine ecosystems to climatic perturbations of varying intensity and duration is crucial for reconstructing the dynamics of past environmental crises and assessing the potential resilience of modern biota to ongoing and future climate change. The studies presented in this VSI highlight the value of analysing multiple time intervals and of focusing on both benthic and planktic groups to capture the complexity of biotic responses to palaeoenvironmental stress.

This comparative approach reveals that the response of marine organisms to climatic disturbances has not followed a uniform pattern. In general, planktic communities have demonstrated greater ecological resilience than benthic ones, although notable exceptions exist. Importantly, each event examined represents a unique case, underscoring that factors such as the rate of onset, duration, and nature of environmental stressors played decisive roles in determining organismal survival and ecosystem restructuring.

While only a few events, such as the end-Permian and Triassic-Jurassic boundary crises, resulted in widespread ecosystem collapse and major extinctions, most perturbations triggered ecological shifts rather than complete biotic turnovers. Benthic ecosystems, in particular, often responded through reorganization into new community assemblages, indicating adaptive strategies rather than total failure. This highlights the importance of considering ecological plasticity and the capacity for reassembly when evaluating ecosystem resilience in both ancient and modern contexts.

CRediT authorship contribution statement

Cinzia Bottini: Writing – review & editing, Writing – original draft, Conceptualization. **Gaia Crippa:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

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

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Data availability

No data was used for the research described in the article.

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