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Plankton resistance and resilience through intervals of extreme Cenozoic climate change

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Abstract. Earth's biosphere has undergone major changes through the last 66 million years, first as terrestrial and marine ecosystems recovered from the devastating Cretaceous/Paleogene (K/Pg; 66 Ma) mass extinction and second as life responded to the profound greenhouse to icehouse climate shift across the Eocene/Oligocene transition (EOT; ~34 Ma). This step change in global climate, saw a switch from warm, high CO_2 greenhouse conditions of the early Paleogene to cooler temperatures, ice sheets and frigid polar water masses of the Oligocene coolhouse. Despite these profound changes we have limited understanding of the relationships between climate and biosphere and in detail how key ecosystem services and functions respond over different timescales of environmental change. Here we use the fossil remains of primary producer ocean plankton (calcareous nannoplankton) to reconstruct community dynamics across this pivotal interval of Earth history. We present a new high-resolution long-time-series middle Eocene to Lower Miocene (45–21 Ma) nannoplankton dataset, combined with complementary published Paleocene to lower Eocene data, to provide a high-fidelity record of biotic response from the base of the marine food web. This 44-million-year record demonstrates a remarkably enduring 'background' state of nannoplankton community stability that emerged around two million years after the K/Pg mass extinction event. This stable state was then only periodically interrupted by short lived excursions of high variance that occurred during geologically rapid warming and cooling events. These ephemeral community perturbations show threshold and scaling relationships, triggered by environmental events broadly equivalent to >~2-3°C of warming or cooling, with volatility of temperature sensitive taxa underpinning the above-background responses regardless of the background climate state (i.e., greenhouse or icehouse). Community stability, resilience and function are likely sustained through high levels of taxonomic redundancy and the long-term dominance of several key species-complexes that have high adaptive genetic potential across vast global populations, which are maintained in their superabundant extant counterparts.

1 Introduction

The most important pre-industrial climate shift of the current geological era was arguably the establishment of large, sustained ice sheets on Antarctica around the Eocene/Oligocene boundary (~34 million years ago [Ma]). This step change moved the

Earth from a warm 'greenhouse' state, in which the biosphere had evolved over 290 million years (Myr), into the current cool 'icehouse' climate mode (Westerhold et al., 2020). Accompanying changes in latitudinal temperature gradients, seasonality, precipitation and ocean circulation have had profound effects on the biosphere, including the restructuring of terrestrial biomes (grasslands, forests, tundra) and initiation of new polar water masses and dynamic thermohaline circulation (Bohaty et al., 2012; Hutchinson et al., 2021; Katz et al., 2011; Lear et al., 2004; Miller et al., 2020). Despite these profound changes, however, we still have only limited understanding of how the Earth's climate and biosphere have co-evolved since the last mass extinction reset (K/Pg; 66 Ma), reducing our ability to predict how key ecosystem services and functions will respond to current and near-future climate change (Norris et al., 2013). Although we expect to see significant responses in ocean primary producer groups, including changes in biogeography, biodiversity, carbon export flux and food chain function, our understanding can be further improved by looking at past examples of environmental perturbation and changing climate over a range of timescales (e.g., Burke et al., 2018; Norris et al., 2013; Tierney et al., 2020).

Coccolithophorid algae (also known as calcareous nannoplankton) are extant marine phytoplankton that have robust calcite exoskeletons that provide an abundant and continuous fossil record stretching back over 240 Myr (Bown et al., 2004; Slater et al., 2025). This fossil archive provides opportunities to document and understand foundational primary producer plankton response across a spectrum of environmental changes in unprecedented detail and resolution. Paleogene nannoplankton research has already revealed long-term trends in diversity and evolutionary turnover (Bown, 2005; Lowery et al., 2020). Catastrophic extinctions at the Cretaceous/Paleogene (K/Pg) mass extinction were followed by rapid recovery of species richness to a Cenozoic peak in the mid-Eocene (~45 Ma), followed by decline through the late Eocene-Oligocene (38-33 Ma), broadly coincident with the onset of the icehouse climate mode (Bown, 2005; Lowery et al., 2020). More recently, research using quantitative census data at higher temporal resolution has targeted shorter intervals of geological time (10^5 a/yrs) that include exceptional environmental change (e.g., hyperthermals) and focused on the ecological impact of these short-lived, near-future-climate analogue events (e.g., Bralower, 2002; Gibbs et al., 2006a, b; Self-Trail et al., 2012). However, to fully assess the impact of these ephemeral events requires an equivalent level of understanding of background states, in particular the range of community variability that occurs across the majority of geological time outside of these anomalous intervals, despite being of less obvious palaeoclimatological or palaeoceanographic interest (Gibbs et al., 2012). The benefits are to contextualize and quantify the 'significance' of biotic responses by constraining levels of background variability and documenting the magnitudes and durations of 'above-background' behaviour (Gibbs et al., 2012). Furthermore, this enables identification of potential threshold behaviour (i.e., tipping points) and scaling of biotic response across different levels of environmental change (Alvarez et al., 2019; Gibbs et al., 2012).

With this goal in mind, long-term, high-resolution Paleocene to lower Eocene (66–56 Ma) community records were generated using efficient counting protocols and applying summed coefficient of variation (Σ_{CV}) analysis, which effectively describes nannoplankton community variance across a wide range of environmental change from mass extinction level to minor hyperthermal warming events (Alvarez et al., 2019; Gibbs et al., 2012). This approach revealed distinct background and above-background response in lower Paleogene nannoplankton communities and showed that event-level response scales with the magnitude of environmental perturbation, as proxied by carbon isotope excursions (CIEs). These records provide a benchmark for nannoplankton diversity, community stability and resilience and here we extend the range of comparable data by 24 Myr, adding new middle Eocene through Lower Miocene records from the North Atlantic Ocean (Integrated Ocean Drilling Program [IODP] Expedition 342). This gives unprecedented coverage of the Paleogene to lower Neogene interval, a record spanning the K/Pg mass extinction through to the establishment of Southern Hemisphere ice sheets (66–21 Ma). These new data enable us to test for changing behaviour (e.g., magnitudes of community variability) and/or resilience (e.g., community recovery times) across a significant proportion of the first 44 Myr of the Cenozoic, and crucially to examine whether plankton communities displayed similar or disparate threshold and scaling responses over a wide range of environmental forcings, including during the contrasting background states of the hot greenhouse and cold icehouse climate modes and through global cooling and glacial onset.

2 Methods

We have analysed nannoplankton diversity and community response across a new 23 Myr interval (45–21 Ma) using a composite record generated from three closely spaced sites in the Northwest Atlantic Ocean (IODP Sites U1406, U1408 and U1411). The clay-rich, drift sediments that characterise these sites provide an expanded stratigraphy with sedimentation rates of ~1.5–3 cm/kyr through certain intervals (Norris et al., 2014) and allowed for a sampling intensity of ~30-80 kyr across both event and background intervals, based on orbitally tuned age models (van Peer et al., 2024) and updated shipboard stratigraphy (see Supplementary Information). As drift sedimentation switched on and off at different times depending on location, the three sites were required to provide continuous or near-continuous stratigraphy in high-sedimentation rate successions, which yield the highest-quality calcareous microfossil preservation (Norris et al., 2014). Intervals of poorer preservation, however, have resulted in several gaps within the record (Fig. 1).

The data collection methods are compatible with the Paleocene-lower Eocene studies of Gibbs et al. (2012) and Alvarez et al. (2019), using directly comparable fossil count, taxonomic and analytical methods (see Supplementary Information). Light microscope (LM) extended count methods were applied that tallied the first 300 nannofossil specimens encountered, followed by an additional 300 count that excluded the most abundant taxa (i.e., those generally contributing >50%). Quantitative nannofossil data are expressed as %relative abundance to evaluate community response and evolution, independent of sedimentological factors such as accumulation rates. Taxonomic equivalency was enabled by direct communication between the nannofossil specialists and through access to extensive shared image collections. Nannofossil preservation was recorded using standard visual assessment categories (Bown and Young, 1998) together with the counting of preservation-sensitive indicators, such as, the disarticulated shields of reticulofenestrids and coccolithaceans (e.g., Blaj et al., 2009).

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These new data were combined with those from Alvarez et al. (2019), however, there is a gap of ~8 Myr between the datasets because drift sedimentation did not start until the middle Eocene at the IODP Exp. 342 sites, and data was not collected in the less well-preserved lower Eocene succession. The two datasets are from different oceanographic settings, with the Alvarez et al. (2019) data coming from the mid-Pacific Shatsky Rise, and the new data coming from the Northwest Atlantic Ocean. Nevertheless, these are both open-ocean locations and given the cosmopolitan nature of Paleogene nannoplankton distributions and connectivity of ocean basins at this time, the community compositions are closely comparable (see Alvarez et al., 2019 for further discussion).

Community variability was documented using Σ_{CV} analysis which enables the quantitative analysis of large amounts of abundance data across long timescales, independent of taxic composition. It has been shown to provide a sensitive measure of community stability/volatility even through intervals of lower-level environmental change and is therefore ideal for the objective of assessing response across a spectrum of known events and through the interstitial background intervals (Alvarez et al., 2019; Gibbs et al., 2012). The combined datasets comprise 1700 samples, typically with 30-35 kyr sampling resolution, and incorporate 400 species and 1.2 million fossil counts. We compare the Σ_{CV} record with carbon and oxygen isotope excursion magnitudes to test for scaling of community variance and environmental change, following Alvarez et al. (2019) and Gibbs et al. (2012). Alvarez et al. (2019) did not include comparison with oxygen isotope excursions (OIEs), but this has been added here as an important additional palaeotemperature proxy, relevant to both the carbon cycle perturbation events of the early Paleogene (hyperthermals) and the climate cooling shifts of the later Paleogene. Crossplots of isotope excursion level and Σ_{CV} (Fig. 2) use published CIE and OIE values for named climatic events and coefficient of variation analysis of the Westerhold et al. (2020) deep-sea benthic isotope compilation as a proxy for isotope excursion (see Supplementary Information).

3 Results and Discussion

3.1 Assemblage variance and environmental perturbation

The new Σ_{CV} record provides a measure of nannoplankton community stability/volatility through the middle Eocene to Lower Miocene (Fig. 1a; Table S2 in the Supplement). Visual assessment of the data reveals a spectrum of varying but low-level values (Σ_{CV} 0.5–2.5) and several statistically distinct intervals with high peak values (Σ_{CV} ~3.5). Ranking the data (Fig. 1b), confirms this continuous spectrum of lower Σ_{CV} values – a background-level range – with an inflection point at Σ_{CV} 2.5, above which a steeper slope is defined by fewer, much higher Σ_{CV} values – an above-background range (Fig 1b). The previously published Paleocene to lower Eocene Σ_{CV} record of Alvarez et al. (2019), separated into pre- and post-64 Ma datasets in Fig. 1b, has Σ_{CV} values ranging from 1.1 to 10.2, but almost all of the highest values (Σ_{CV} >4.5) come from the short (<2 Myr) lowermost Danian post-mass-extinction interval (Fig. 1a, b). Outside of this exceptional Danian interval there is a very similar range of background values (Σ_{CV} 1.0–2.5) across the two time-series, and the ranked data fall on virtually the same line across the background range (Fig. 1b). The inflection point marking the shift to higher, above-background, levels is also almost identical, at around Σ_{CV} 2.5 (Fig. 1b).

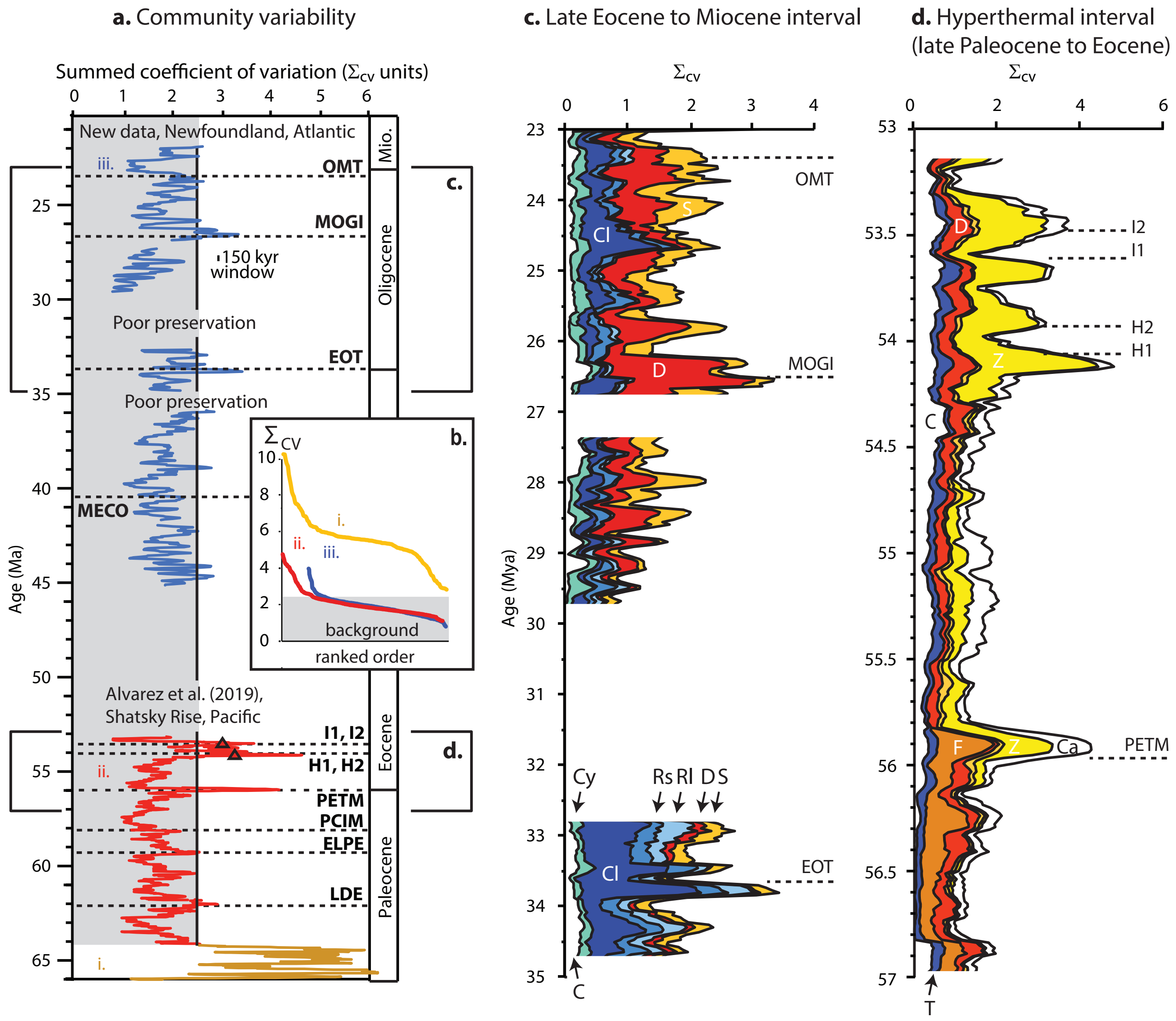

Figure 1: a. K/Pg boundary to Lower Miocene nannoplankton Σ_{CV} using eight (normalised) taxa across 150 kyr moving windows. Blue line is the new middle Eocene to Lower Miocene data, the red (Paleocene to lower Eocene) and dark yellow lines (exceptional lowermost Danian interval) are the Alvarez et al. (2019) data. Grey shaded area represents background level values (Σ_{CV} <2.5) based on the ranked order inflection point shown in b; above-background variability plots outside of the shaded area. Triangles show values for the short Eocene hyperthermals, calculated across the event duration (<150 kyr). **b.** Ranked order plots for all Σ_{CV} data points, separated into lowermost

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Danian (i), Paleocene-lower Eocene (ii) and middle Eocene-Lower Miocene (iii) subsets. **c, d.** Taxon specific contributions to the Σ_{CV} record (c. EOT to Oligocene interval, d. hyperthermals interval) highlighting the sensitivity of warm water oligotrophs (D, *Discoaster*; F, *Fasciculithus*; S, *Sphenolithus*; and Z, *Zygrhablithus*) and cool water eutrophs (Cl, *Clausicoccus*; Rs, small reticulofenestrids, Rl, large reticulofenestrids). Cy, *Cyclicargolithus*; Ca, *Calcidiscus*; C, *Coccolithus*; T, *Toweius*; OMT, Oligocene–Miocene Transition; MOGI, Mid-Oligocene Glacial Interval; EOT, Eocene–Oligocene Transition; MECO, Middle Eocene Climatic Optimum; PETM, Paleocene–Eocene Thermal Maximum; H1, H2, I1, I2, hyperthermal events; ELPE, early late Paleocene event; LDE, Late Danian Event, K/Pg, Cretaceous–Paleogene boundary.

In the Paleocene to lower Eocene interval (66-53 Ma), the above-background peak values of Σ_{CV} (Fig. 1) have been linked to a series of carbon cycle perturbations (hyperthermal events) that are characterised by rapid global warming and ocean acidification (Alvarez et al., 2019; Gibbs et al., 2013). In the middle Eocene to Lower Miocene part of the record (~45-21 Ma) several short peaks of above-background magnitude occur, with the three most prominent (Σ_{CV} 2.9-3.5) occurring in the Oligocene at 33.8 Ma (Σ_{CV} 3.5), 26.5 (Σ_{CV} 3.2), and 26.3 (Σ_{CV} 2.9) (Fig. 1). These levels coincide with known climate events but in these Oligocene cases, they are associated with cooling, ice sheet growth and glacial/interglacial cycles. The largest peak occurs at the Eocene/Oligocene boundary climate step change ("Step 1" of Hutchinson et al., 2021; 33.8 Ma) and two closely spaced, younger Σ_{CV} peaks fall within the mid-Oligocene glacial interval (MOGI; 26.3 and 26.5 Ma). Like the Eocene hyperthermal examples, these Oligocene Σ_{CV} peaks are of relatively short duration (~<300 kyr), and indicate community resilience, as values return to background on timescales that are similar to, or shorter than, the climate excursions. Several other intervals, at 44.7 (Σ_{CV} 2.8), 38.9 (Σ_{CV} 2.8), 32.9 (Σ_{CV} 2.7) and 23.7 Ma (Σ_{CV} 2.6), have Σ_{CV} values that just cross the above-background threshold (Σ_{CV} 2.5), but only the youngest level (23.7 Ma) is coeval with an identified palaeoclimate event, the Oligocene-Miocene transition (OMT) abrupt cooling and glaciation. Conversely, the middle Eocene climatic optimum (MECO) 'hyperthermal' event at 40 Ma, shows no indication of above-background community response (Σ_{CV} 1.9).

Crossplots of Σ_{CV} and geochemical climate proxy data (Fig. 2) provide a test for the existence of relationships between nannoplankton community response and environmental forcings. The application of carbon and oxygen stable isotope records allows us to test for the influence of both carbon-influx driven forcing, characteristic of the Paleocene–Eocene hyperthermals, and also the multicausal climate cooling events that are a feature of the late Eocene to Early Miocene record (Fig. 2).

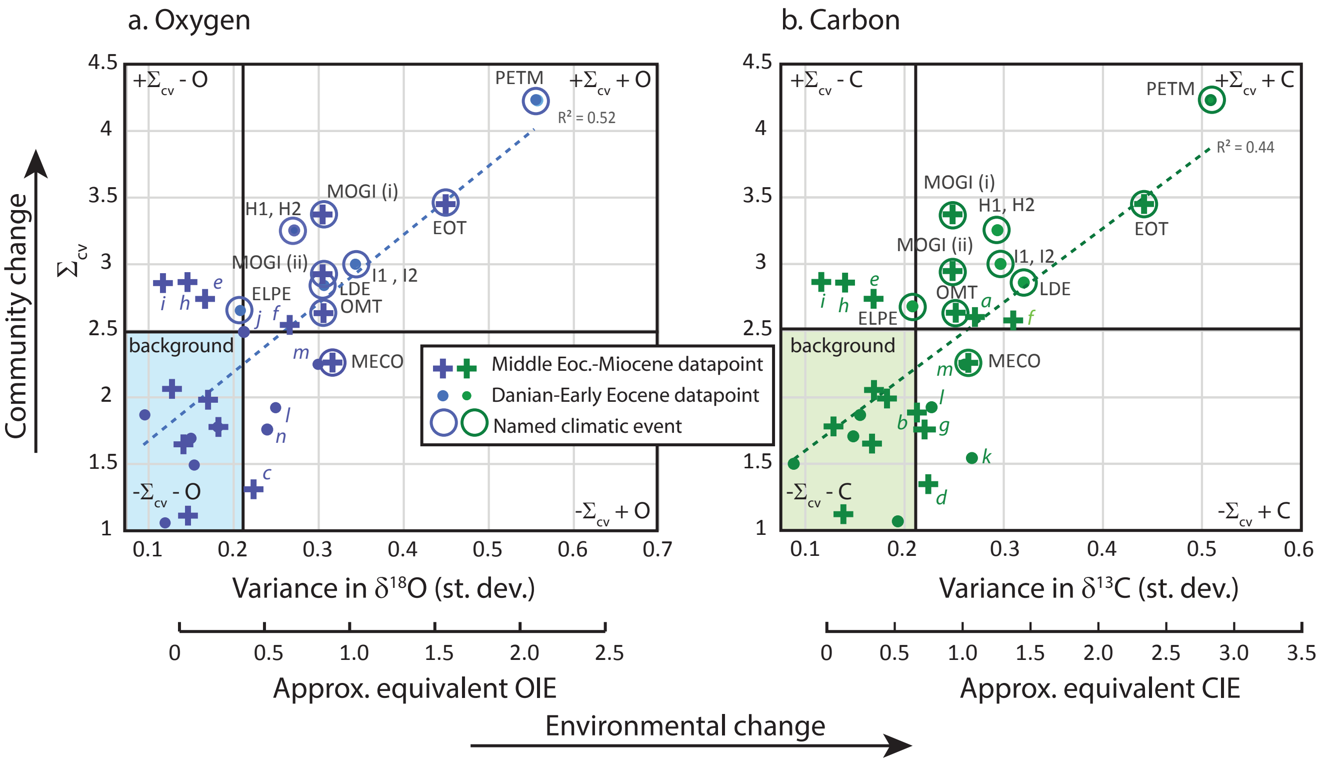

Figure 2: Crossplots of Σ_{CV} and magnitude of environmental perturbation as proxied by **a.** oxygen and **b.** carbon stable isotope variance. Crosses are the new middle Eocene-Lower Miocene datapoints, dots are lower Paleocene-lower Eocene datapoints from Alvarez et al. (2019); outer circles indicate occurrences coincident with named climate events and associated oxygen and carbon isotope excursions (OIE/CIE). Event names abbreviated as Fig. 1. Green and blue shaded areas are the 'background' fields corresponding to <2.5 Σ_{CV} and background isotopic variance, where the majority of data plot. The datapoints shown represent a subset of background values taken approximately every 2 Myr through the intervals between named climatic events (Fig. S1). The dashed line is a line of correlation for all of the datapoints. Datapoints with letters correspond to datapoints in Fig. S1 and Table S3 that fall in the above left and below right quadrants where either above background Σ_{CV} datapoints occur without increased variance in isotopes (+Σ_{CV}-O; +Σ_{CV}-C) or above background variance datapoints in isotopes occur without increased Σ_{CV} (-Σ_{CV}+O; -Σ_{CV}+C). Note, the post-mass-extinction interval data (pre-64 Ma and coloured dark yellow in Fig. 1) are excluded.

Data in both the oxygen and carbon crossplot space fall into four distinct fields (Fig. 2; Table S3). Excluding the exceptionally high values of the first two million years after the K/Pg mass extinction, most datapoints fall in the lower left background sector (shaded blue and green on Figs. 2a and 2b), having low levels of Σ_{CV} (<2.5) and low, background values of stable isotope variance (and CIE/OIE equivalent). The inference here is that the low levels of environmental change through these intervals did not significantly impact the nannoplankton communities (i.e., the communities were resistant to these magnitudes or types of environmental change), and background levels of variance were sustained across most of our stratigraphic record.

Many of the known climate event levels, however, plot in the upper right above-background sector, having high levels of Σ_{CV} (>2.5) and high, above-background stable isotope variance (Fig. 2). This is consistent with the earlier Paleogene threshold and

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scaling behaviour reported by Gibbs et al. (2012), with positive correlation (r^2 ~0.50 and 0.43) between stable isotope excursion magnitude and community variance above a threshold of ~0.21 for both carbon and oxygen records. This relationship is also clear for several of the younger events documented in our new record, most obviously at the EOT and OMT. This indicates that plankton community equilibrium was consistently disrupted above a threshold level of environmental change (i.e., the communities were unable to resist these levels of perturbation). Furthermore, the degree of variance/disruption increases linearly with the magnitude of this environmental change.

A small number of data points fall in either the upper left or lower right sectors of the crossplots (labelled a-m on Fig. 2 and Fig. S1), where either low, but above-background community variance is associated with low stable isotope variance (upper left), or low, background community variance is associated with low, but above-background, stable isotope variance (lower right) (Fig. 2). These levels are exceptions to the threshold and scaling relationships that characterise most of the known climate change events. In most cases these values lie close to the threshold level and indicate that either some aspect of the environmental change was insufficient to push the communities into an above-background variance state or community variance was perturbed by some other forcing, perhaps a biotic driver or an environmental factor not reflected in the stable isotope records. Of these exceptions, only the MECO interval is identified as an important climate change event that records no above background response. The gradual onset of its carbon isotope excursion (over ~300 kyr) and muted carbon influx and associated environmental change, may explain the lack of community disruption (Henehan et al., 2020). Although warming and muted biotic turnover have been identified through this time interval (Toffanin et al., 2011), it is no longer considered a typical hyperthermal event (van Der Ploeg et al., 2018; Henehan et al., 2020).

3.2 Temperature controls on nannoplankton populations

The strong positive relationship between nannoplankton community variance (Σ_{CV}) and oxygen isotope variance (Fig. 2) has not been documented before and the threshold and scaling, strongly points to temperature as an important driver of increased volatility, whether the event is characterised by exogenic carbon-injection driven warming, typical of the early Paleogene hyperthermals (e.g., I2, H1 and PETM) or cooling caused by complex interplays of tectonics, ocean circulation, and atmospheric CO_2, as seen during the late Eocene to Oligocene (e.g., EOT, MOGI and OMT).

The highest Σ_{CV} peak in the new middle Eocene to Lower Miocene record occurs at a climate cooling step ("Step 1" of Hutchinson et al., 2021) associated with the onset of sustained Antarctic glaciation at the EOT. Breaking down the EOT Σ_{CV} peak into its constituent parts (Fig. 1c) reveals that the elevated variance is most strongly influenced by the records of several taxa, all of which have strong temperature preferences and/or exhibit opportunistic behaviour (i.e., rapid response to increased productivity). Nannoplankton distributions are primarily controlled by light, temperature and nutrient availability with the group in general characterised by broad environmental tolerances (Baumann et al., 2005; Brand, 1994). A smaller number of modern and fossil taxa, however, show more specialist adaptations (e.g., narrower environmental tolerances or opportunistic behaviour), and therefore provide useful indications of specific surface water conditions (Baumann et al., 2005; Bralower, 2002; Cappelli et al., 2019). At the EOT, the Σ_{CV} peak is predominantly driven by the response of the cool temperate eutroph, *Clausicoccus* (55% of the Σ_{CV}), with subordinate contributions from the large and small reticulofenestrid groups, which are also predominantly cool temperate and opportunistic taxa (Viganò et al., 2023; Villa et al., 2008) (Fig. 1c). The rapidly shifting abundance trends and short acmes of all these taxa are characteristic of global EOT nannofossil records and consistent with other biotic and geochemical proxies that indicate cooling surface waters and higher levels of productivity as the oceans shifted toward a more dynamic, modern-like circulation at this time (Dunkley Jones et al., 2008; Viganò et al., 2023; Villa et al., 2008; Wade and Pearson, 2008). More specifically, the "Step 1" oxygen isotope shift is thought to represent a cooling of both deep and surface ocean waters of around 2°C (Hutchinson et al., 2021).

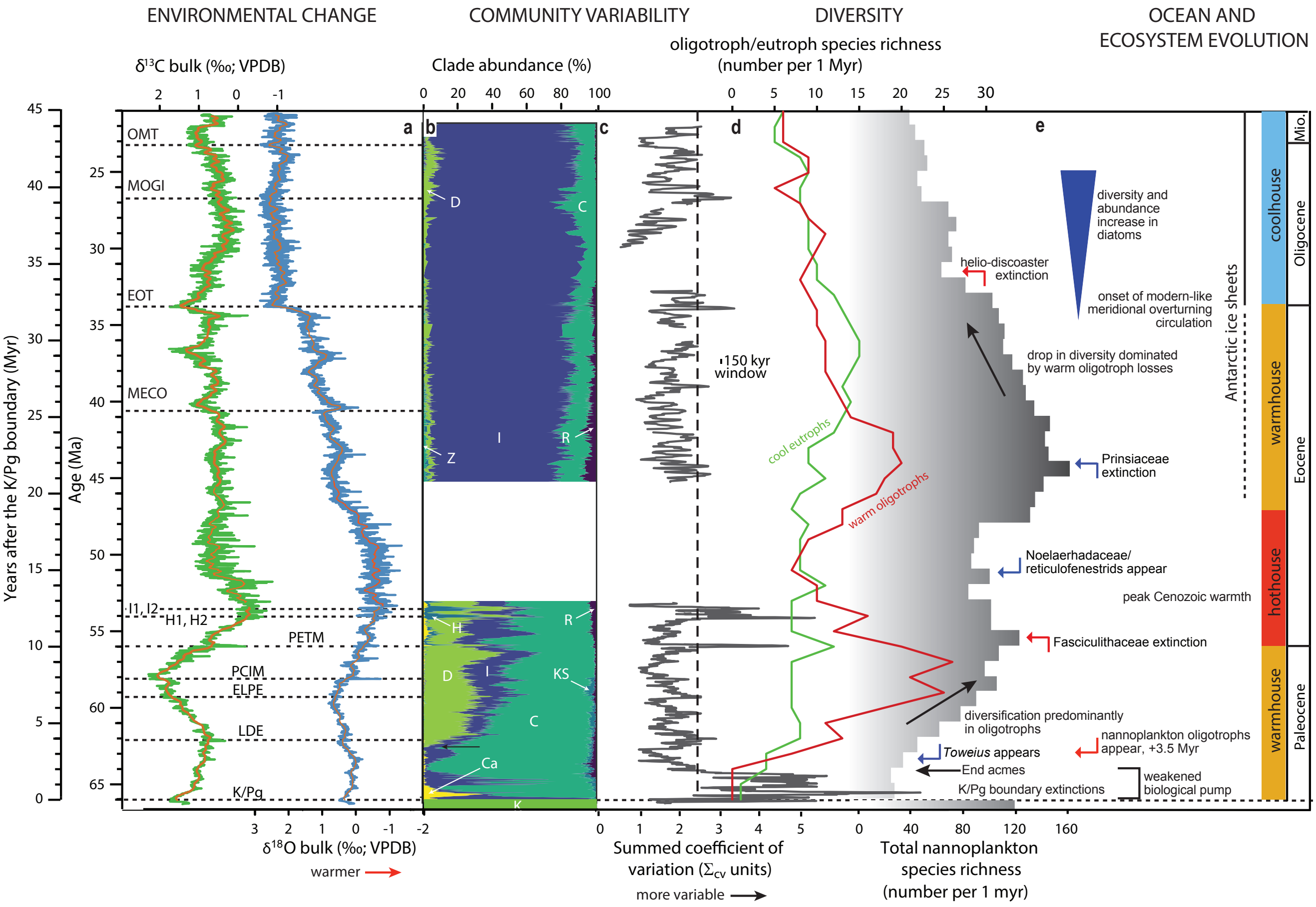

Figure 3. K/Pg boundary to Lower Miocene nannoplankton community data (composition, variability and diversity) and environmental proxies (global reference benthic foraminifer carbon and oxygen isotope dataset). **a.** CENOGRID benthic foraminifer carbon (green line) and oxygen (blue line) isotopes (red lines are 250 kyr running mean) from Westerhold et al. (2020). **b.** Nannoplankton community abundances (%relative abundance) of the main nannoplankton clades/orders from 1700 samples. C, Coccolithales; Ca, calcispheres; D,

Discoasterales; H, holococcoliths (mainly *Zygrhablithus*); Iso, Isochrysidales; K, Cretaceous; KS, Cretaceous survivors. **c.** Σ_{CV} using eight (normalised) taxa across 150 kyr moving windows. Black dashed line represents the above background threshold level (Σ_{CV} <2.5) based on the ranked order inflection point shown in Fig. 1d (see Fig. 1 for further information). **d.** Nannoplankton species richness from Lowery et al. (2020) showing range through data for 1-Myr bins. Diversity of cool water eutrophs (Isochrysidales, including *Toweius* and *Reticulofenestra*) in green and warm water oligotrophs (Discoasterales, including *Discoaster*, *Fasciculithus* and *Sphenolithus*) in red. **e.** Diversity/abundance of oceanic diatoms represented by the broadening blue triangle based on Özen et al. (2025). Additional climate, palaeoceanographic and nannoplankton/ecosystem events are noted to the right of the figure. Event names abbreviated as Fig. 1.

The younger Σ_{CV} maxima, at 26.5 and 26.3 Ma, fall within the mid-Oligocene glacial interval (MOGI) (Liebrand et al., 2017), broadly equivalent to the Oi-2 isotope events of Wade and Palike (2004). This was an extended period (~28-26.3 Ma) of cold and highly unstable climate with orbitally paced, high-amplitude glacial-interglacial cycles (Liebrand et al., 2017; Pälike et al., 2006; Wade and Pälike, 2004). The elevated Σ_{CV} through this interval is driven by volatility in the relative abundance of three taxa which all have strong environmental preferences – *Discoaster*, *Sphenolithus* and *Clausicoccus* (Fig. 1c) – the former two being warm-water-favouring oligotrophs and the latter a cool-water eutroph (see above; Persico and Villa, 2004; Viganò et al., 2023; Villa et al., 2008; Wei and Wise, 1990). *Discoaster* variance dominates both peaks (32% and 57%) with *Sphenolithus* (26%) an important component of the older peak variance and *Clausicoccus* (16%) significant in the younger peak. This record indicates that the above-background community variation is principally modulated by the responses of temperature sensitive taxa, here responding to increased glacial-interglacial intensity, amplified by the persistence of these conditions over a prolonged ~2 Myr interval. This succession of high-amplitude glaciations resulted in a level of disruption not seen during most of the Oligocene, excepting the stepped cooling and onset of Antarctic glaciation during the EOT (discussed above) and the intense OMT (23.7 Ma) glaciation where muted above-background values are recorded alongside an OIE (Mi-1). Variance during the OMT is also driven by the same three temperature sensitive taxa responsible for the MOGI peaks (Fig. 1c).

The older, Paleocene and early Eocene hyperthermal events are characterised by CIEs and OIEs that indicate influxes of exogenic carbon and accompanying rapid warming and in some cases ocean acidification (Babila et al., 2018; Littler et al., 2014; Zachos et al., 2005). The Σ_{CV} peaks associated with these events are predominantly generated by the abundance records of Discoasterales taxa (*Fasciculithus* at the PETM and *Discoaster* during younger hyperthermals) together with *Zygrhablithus* (especially during the younger hyperthermals) (Fig. 1d). *Fasciculithus* and *Discoaster* are warm-water-favouring oligotrophs (Asanbe and Henderiks, 2025; Bralower, 2002; Cappelli et al., 2019) and though there has been some debate over the ecology of *Zygrhablithus*, most studies conclude that it is also a warm water oligotroph (e.g., Asanbe and Henderiks, 2025; Cappelli et al., 2019). The response of these taxa is consistent with global assemblage data that shows abundance volatility in warm-water taxa (e.g., *Fasciculithus* and *Zygrhablithus*) and poleward expansion of tropical taxa (e.g., *Discoaster*) alongside major shifts in dominant taxa through this interval (e.g., Angori et al., 2007; Bralower, 2002; Dunkley Jones et al., 2008; Gibbs et al., 2006b).

Looking at the entire record of community variability highlights the important role of temperature sensitive taxa during these diverse environmental change events. The influence of temperature on nannoplankton communities is reflected in the latitudinally zoned biogeographic distributions of the modern ocean (Winter et al., 1994) and in broad patterns of richness and evolutionary rates through their geological history (Bown et al., 2004; Lowery et al., 2020). However, the importance of temperature in community dynamics during shorter timescale events, such as hyperthermals or glacial/interglacial cycles, is not always clearly evident, especially when temperature and trophic controls are difficult to disentangle, and factors such as productivity or ocean chemistry, are often considered to be the predominant drivers of shifting abundances and extinctions across these intervals (Agnini et al., 2007; Dunkley Jones et al., 2008; Gibbs et al., 2006b; González-Lanchas et al., 2021; Jiang and Wise, 2006). The rapidly shifting variability of temperature sensitive taxa is the common factor through all the peak above-background events in our combined records (Fig. 1). Warm-water groups drive peaks across the hyperthermal intervals and a combination of warm-water oligotrophs and cool-water eutrophs underpin the younger EOT and Oligocene Σ_{CV} maxima, resulting in above-background community perturbations whether the underlying environmental forcing is cooling or warming (Fig. 3). By contrast, the lowermost Danian post-mass-extinction interval differs from the rest of the record with variability that is not linked to climatic perturbations or influenced by temperature sensitive taxa, but which is instead driven by short acmes of incoming anomalous mixotrophic taxa reflecting recovering plankton communities in the unique conditions of the post-mass extinction oceans (Alvarez et al., 2019).

3.3 Evolution and community dynamics

Our combined records of Σ_{CV} from across 37 Myr of Cenozoic nannoplankton history indicate that an equilibrium level of background community variance, once established ~2 Myr after the K/Pg mass extinction, was a consistent feature of the Paleogene through early Neogene communities (Figs. 1 and 3). This result was not expected, given our understanding of the major environmental and biotic regime changes that characterise the Paleogene time interval, and the dynamic diversity trends evident in nannoplankton records (Fig. 3d). The nannoplankton fossil record shows huge changes in diversity and community composition through this time, ranging from ~11 survivor species in the post-mass-extinction early Danian to 146 species in the middle Eocene, declining to 46 species at the onset of the Neogene (Early Miocene) (Lowery et al., 2020). Furthermore, the dominant groups within these communities shifted markedly as important families originated (Noelaerhabdaceae/reticulofenestrids) or were lost (Prinsiaceae, Fasciculithaceae, helio-discoasters) (Fig. 3e; Bown et al., 2004). The patterns of nannoplankton diversity change broadly reflect the overall climate state through the Cenozoic with warm, greenhouse oceans of the early Paleogene supporting rising and higher diversities, driven largely by diversification within warm water oligotroph groups (Bown, 2005; Bown et al., 2004) (Fig. 3). By contrast, the colder, coolhouse to icehouse conditions of the later Paleogene and Neogene (late Eocene to Miocene) saw declining species richness and rise to dominance of cool favouring or eurytopic eutrophs (Bown, 2005; Bown et al., 2004) (Fig. 3). The cooling oceans also saw a major shift in the broader make-up of phytoplankton communities, as oceanic diatoms diversified and rose to dominance, especially in polar oceans and eutrophic settings (Lazarus et al., 2014; Özen et al., 2025) (Fig. 3).

Against this backdrop of changing community composition and diversity, the variance and resilience of nannoplankton, as recorded by Σ_{CV}, is remarkably stable throughout the Paleogene. There is no apparent shift or resetting of the community equilibrium state as climate stepped from greenhouse to icehouse mode through the EOT, even though nannoplankton diversity fell by a third during this time (Bown, 2005; Lowery et al., 2020) (Fig. 3d). Nor is there any obvious effect of the rise of a major competitor group as the diatoms began to dominate in the cold and eutrophic ocean regions (Bown, 2005; Lazarus et al., 2014; Özen et al., 2025). Finally, regardless of whether stability was disrupted by rapid warming or cooling events across greenhouse or icehouse conditions, the magnitudes of event-level variance were similar, and recovery from the perturbed state was rapid with background levels quickly re-established.

3.4 Community stability, resilience and redundancy

Nannoplankton diversity and community data therefore provide contrasting portrayals of Paleogene volatility *versus* stability, respectively (Fig. 3b-d). Given these divergent records, what are the determining factors that sustained continuing function and resilience in these foundational plankton communities? The highest variance values in our records are confined to the initial two million years following the K/Pg mass extinction, when this plankton group was recovering from near eradication (>90% species extinction) and survivorship was facilitated by a switch to mixotrophy, which is not typical of most open ocean species (Gibbs et al., 2020). Danian volatility through this recovery regime was caused by pulses of short-lived species acmes and communities characterised by very low species richness (<26 species) (Alvarez et al., 2019). The emergence of stability coincided with the cessation of these acmes, a shift back to autotrophy, consistently higher species richness levels (~>27 species) and the appearance of long-lived, dominant taxa (e.g., *Toweius*) (Fig. 3). When higher variance did occur after this K/Pg recovery interval, triggered by elevated levels of environmental change (e.g., during Paleocene and Eocene hyperthermal events), Σ_{CV} values rapidly returned to background state indicating an ability to resist and recover from perturbation, i.e., community resilience. This resilience continued even as diversity declined by up to 66 % through the late Eocene and into the Oligocene (Fig. 3), therefore implying high levels of species redundancy within the group.

Long-term stability may also be related to a key feature of calcareous nannoplankton communities which is that they are persistently dominated by a small number of globally abundant long-lived taxa, usually several species from one or two genera (see Isochrysidales in Fig. 3b) (Bown and Dunkley Jones, 2012; Young, 1998). In the modern ocean this dominant group is the genus *Gephyrocapsa* (Noelaerhabdaceae) (and *Emiliania* if considered a separate genus), with dominance of this group under the generic names of *Reticulofenestra* and *Cyclicargolithus* (all collectively known as reticulofenestrids) going back at least to the Eocene (origination at ~51 Ma) and arguably beyond if *Toweius* (origination at 63 Ma) is considered the precursor group (Fig. 3) (Ma et al., 2025; Perch-Nielsen, 1985). Our understanding of this complex modern group has been hampered by taxonomic confusion but this has improved, and we now recognise several extant species complexes that have similar and fluid exoskeletal morphologies, broad ecological preferences, high levels of genetic variability and adaptability, and which are capable of rapid pulses of diversification in response to local fluctuations of the environment (most recently glacial-interglacial cycles) (Bendif et al., 2019; Filatov et al., 2021; Lohbeck et al., 2012). Resolving this level of taxonomic detail and evolutionary turnover in the fossil record is difficult given the lack of distinct morphological characters in the exoskeletal plates (coccoliths), but when morphometric analysis has been applied, we see similar trends over long time-series and the characteristics of these species complexes are likely a conserved feature of most nannoplankton communities through time (Bendif et al., 2019; Matsuoka and Okada, 1989; Young, 1990). These cosmopolitan groups with high adaptive genetic potential in vast populations (estimate for the living *Gephyrocapsa huxleyi* complex is 10^{22} / 10 sextillion cells) are likely to include genotypes that are tolerant to a range of environmental perturbations therefore reducing impacts on the total population and promoting resilience (Lohbeck et al., 2012; Oliver et al., 2015; Peijnenburg and Goetze, 2013). If multiple taxa perform similar functions but have slightly differing responses to environmental perturbations, then resistance and resilience will be even greater, the so called 'insurance effect' of biodiversity (Oliver et al., 2015).

This robust community resilience is reflected in our fossil records of dominant groups that are relatively resistant to major taxonomic changes, with higher rates of evolutionary turnover focused in rarer and more specialised groups which have more restricted ecological preferences and geographic distributions, e.g., warm water favouring, tropical oligotrophs (e.g., the Discoasterales; Fig. 3d) (Agnini et al., 2016; Cappelli et al., 2020; Miniati et al., 2021; Young, 1998). Elevated volatility in these temperature sensitive taxa is the principal driver of the above background Σ_{CV} response levels throughout our records (Fig. 1). Nannoplankton resilience is also evident in the overall diversity history of nannoplankton response to environmental perturbation, showing muted or no response to known hyperthermal, ocean acidification or cooling events (e.g., Bown, 2005; Bown et al., 2004; Gibbs et al., 2006a; Lowery et al., 2020), with significant and rapid diversity loss essentially restricted to the last mass extinction interval (66 Ma) which was driven by a singular asteroid impact event (Lowery et al., 2020). Finally, though our records provide a picture of long-term resistance and resilience in these keystone primary producer plankton, it is notable that the tipping point threshold that triggers above-background community perturbations is around 2-3 °C of warming (Fig. 2), a value similar to the magnitudes of warming we are predicting for the coming decades and perhaps already presaged by the migrations and population shifts that we are observing in the warming oceans around us (Chaabane et al., 2024; Ostle et al., 2022).

4 Conclusions

Our high-resolution, long time-series Cenozoic nannoplankton datasets provide a 44 Myr record (K/Pg to Lower Miocene) of keystone community dynamics and diversity, representing the base of the oceanic food web. These data highlight the exceptional nature of the post-mass-extinction Danian ecosystem recovery interval but also the persistence of a stable background state once resistance and resilience were established around 2 Myr after the K/Pg mass extinction. This phytoplankton community steady state was occasionally perturbed, first by carbon-influx driven hyperthermal events in the

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Eocene and later by several major global cooling events at the EOT and through the Oligocene. In each case, the metric of community variability (Σ_{CV}) scales to the magnitude of environmental change (as proxied by carbon and oxygen stable isotopes) and recovery times were rapid, even across contrasting events (warming and cooling) with different baseline ocean conditions (greenhouse and icehouse) and with disparate standing diversities and taxonomic compositions. Perturbation in these communities was primarily driven by the response of temperature sensitive taxa but overall, the persistent resilience and stability of nannoplankton was likely underpinned by the enduring dominance of long-lived reticulofenestrid global species complexes with high adaptive genetic potential and redundancy. The above background community instability was consistently triggered by environmental change associated with oxygen isotope variance of 0.21 equivalent to excursions of >~0.7, roughly equivalent to 2-3 °C of warming and close to the values highlighted by climate scientists today as potentially calamitous for the future oceans and ecosystems.

Supplement link

The link to the supplement will be included by Copernicus, if applicable.

Author contributions

PRB and SG designed the research strategy, all co-authors contributed data, and CMR, PRB and SG prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no competing interests.

Disclaimer

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References

Agnini, C., Fornaciari, E., Raffi, I., Rio, D., Röhl, U., and Westerhold, T.: High-resolution nannofossil biochronology of middle Paleocene to early Eocene at ODP Site 1262: Implications for calcareous nannoplankton evolution, Mar. Micropaleontol., 64, 215–248, https://doi.org/10.1016/j.marmicro.2007.05.003, 2007.

Agnini, C., Spofforth, D. J. A., Dickens, G. R., Rio, D., Pälike, H., Backman, J., Muttoni, G., and Dallanave, E.: Stable isotope and calcareous nannofossil assemblage record of the late Paleocene and early Eocene (Cicogna section), Clim. Past, 12, 883–909, https://doi.org/10.5194/cp-12-883-2016, 2016.

Alvarez, S. A., Gibbs, S. J., Bown, P. R., Kim, H., Sheward, R. M., and Ridgwell, A.: Diversity decoupled from ecosystem function and resilience during mass extinction recovery, Nature, 574, 242–245, https://doi.org/10.1038/s41586-019-1590-8, 2019.

Angori, E., Bernaola, G., and Monechi, S.: Calcareous nannofossil assemblages and their response to the Paleocene-Eocene Thermal Maximum event at different latitudes: ODP Site 690 and Tethyan sections, in: Large Ecosystem Perturbations: Causes and Consequences, vol. 424, edited by: Monechi, S., Coccioni, R., and Rampino, M., Geological Society of America, 0, https://doi.org/10.1130/2007.2424(04), 2007.

Asanbe, J. D. and Henderiks, J.: Major shifts in Equatorial Atlantic and Pacific calcareous mannofossil assemblages across the Early Eocene Climatic Optimum (EECO; ~53–49 Ma), Paleoceanogr. Paleoclimatology, 40, e2024PA005038, https://doi.org/10.1029/2024PA005038, 2025.

Babila, T. L., Penman, D. E., Hönisch, B., Kelly, D. C., Bralower, T. J., Rosenthal, Y., and Zachos, J. C.: Capturing the global signature of surface ocean acidification during the Palaeocene–Eocene Thermal Maximum, Philos. Trans. R. Soc. Math. Phys. Eng. Sci., 376, 20170072, https://doi.org/10.1098/rsta.2017.0072, 2018.

Baumann, K.-H., Andruleit, H., Böckel, B., Geisen, M., and Kinkel, H.: The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity: A review, Paläontol. Z., 79, 93–112, 2005.

Bendif, E. M., Nevado, B., Wong, E. L. Y., Hagino, K., Probert, I., Young, J. R., Rickaby, R. E. M., and Filatov, D. A.: Repeated species radiations in the recent evolution of the key marine phytoplankton lineage *Gephyrocapsa*, Nat. Commun., 10, 4234, https://doi.org/10.1038/s41467-019-12169-7, 2019.

Blaj, T., Backman, J., and Raffi, I.: Late Eocene to Oligocene preservation history and biochronology of calcareous nannofossils from paleo-equatorial Pacific Ocean sediments, Riv. Ital. Paleontol. E Stratigr., 115, 67–85, 2009.

Bohaty, S. M., Zachos, J. C., and Delaney, M. L.: Foraminiferal Mg/Ca evidence for Southern Ocean cooling across the Eocene–Oligocene transition, Earth Planet. Sci. Lett., 317–318, 251–261, https://doi.org/10.1016/j.epsl.2011.11.037, 2012.

Bown, P. R.: Calcareous nannoplankton evolution: A tale of two oceans, Micropaleontology, 51, 299–308, 2005.

Bown, P. R. and Dunkley Jones, T.: Calcareous nannofossils from the Paleogene equatorial Pacific (IODP Expedition 320 Sites U1331-1334), J. Nannoplankton Res., 32, 3–51, 2012.

Bown, P. R. and Young, J. R.: Techniques, in: Calcareous Nannofossil Biostratigraphy, edited by: Bown, P. R., Chapman & Hall, Cambridge, 16–28, 1998.

Bown, P. R., Lees, J. A., and Young, J. R.: Calcareous nannoplankton evolution and diversity through time, in: Coccolithophores, edited by: Thierstein, H. R. and Young, J. R., Springer Berlin Heidelberg, Berlin, Heidelberg, 481–508, https://doi.org/10.1007/978-3-662-06278-4_18, 2004.

Bralower, T. J.: Evidence of surface water oligotrophy during the Paleocene-Eocene thermal maximum: Nannofossil assemblage data from Ocean Drilling Program Site 690, Maud Rise, Weddell Sea, Paleoceanography, 17, 13-1-13–12, https://doi.org/10.1029/2001PA000662, 2002.

Brand, L. E.: Physiological ecology of marine coccolithophores, in: Coccolithophores, edited by: Winter, A. and Siesser, W. G., Cambridge University Press, 39–49, 1994.

Burke, K. D., Williams, J. W., Chandler, M. A., Haywood, A. M., Lunt, D. J., and Otto-Bliesner, B. L.: Pliocene and Eocene provide best analogs for near-future climates, Proc. Natl. Acad. Sci., 115, 13288–13293, https://doi.org/10.1073/pnas.1809600115, 2018.

Cappelli, C., Bown, P. R., Westerhold, T., Bohaty, S. M., Riu, M., Lobba, V., Yamamoto, Y., and Agnini, C.: The Early to Middle Eocene transition: An integrated calcareous nannofossil and stable isotope record from the Northwest Atlantic Ocean (Integrated Ocean Drilling Program Site U1410), Paleoceanogr. Paleoclimatology, 34, 1913–1930, https://doi.org/10.1029/2019PA003686, 2019.

Cappelli, C., Bown, P. R., De Riu, M., and Agnini, C.: Middle Eocene large coccolithaceans: Biostratigraphic implications and paleoclimatic clues, Mar. Micropaleontol., 154, 101812, https://doi.org/10.1016/j.marmicro.2019.101812, 2020.

Chaabane, S., De Garidel-Thoron, T., Meilland, J., Sulpis, O., Chalk, T. B., Brummer, G.-J. A., Mortyn, P. G., Giraud, X., Howa, H., Casajus, N., Kuroyanagi, A., Beaugrand, G., and Schiebel, R.: Migrating is not enough for modern planktonic foraminifera in a changing ocean, Nature, 636, 390–396, https://doi.org/10.1038/s41586-024-08191-5, 2024.

Dunkley Jones, T., Bown, P. R., Pearson, P. N., Wade, B. S., Coxall, H. K., and Lear, C. H.: Major shifts in calcareous phytoplankton assemblages through the Eocene-Oligocene transition of Tanzania and their implications for low-latitude primary production, Paleoceanography, 23, n/a-n/a, https://doi.org/10.1029/2008PA001640, 2008.

Filatov, D. A., Bendif, E. M., Archontikis, O. A., Hagino, K., and Rickaby, R. E. M.: The mode of speciation during a recent radiation in open-ocean phytoplankton, Curr. Biol., 31, 2021.

Gibbs, S. J., Bown, P. R., Sessa, J. A., Bralower, T. J., and Wilson, P. A.: Nannoplankton extinction and origination across the Paleocene-Eocene Thermal Maximum, Science, 314, 1770–1773, https://doi.org/10.1126/science.1133902, 2006a.

Gibbs, S. J., Bralower, T. J., Bown, P. R., Zachos, J. C., and Bybell, L. M.: Shelf and open-ocean calcareous phytoplankton assemblages across the Paleocene-Eocene Thermal Maximum: Implications for global productivity gradients, Geology, 34, 233, https://doi.org/10.1130/G22381.1, 2006b.

Gibbs, S. J., Bown, P. R., Murphy, B. H., Sluijs, A., Edgar, K. M., Pälike, H., Bolton, C. T., and Zachos, J. C.: Scaled biotic disruption during early Eocene global warming events, Biogeosciences, 9, 4679–4688, https://doi.org/10.5194/bg-9-4679-2012, 2012.

Gibbs, S. J., Poulton, A. J., Bown, P. R., Daniels, C. J., Hopkins, J., Young, J. R., Jones, H. L., Thiemann, G. J., O'Dea, S. A., and Newsam, C.: Species-specific growth response of coccolithophores to Palaeocene–Eocene environmental change, Nat. Geosci., 6, 218–222, https://doi.org/10.1038/ngeo1719, 2013.

Gibbs, S. J., Bown, P. R., Ward, B. A., Alvarez, S. A., Kim, H., Archontikis, O. A., Sauterey, B., Poulton, A. J., Wilson, J., and Ridgwell, A.: Algal plankton turn to hunting to survive and recover from end-Cretaceous impact darkness, Sci. Adv., 6, eabc9123, https://doi.org/10.1126/sciadv.abc9123, 2020.

González-Lanchas, A., Flores, J. -A., Sierro, F. J., Sánchez Goñi, M. F., Rodrigues, T., Ausín, B., Oliveira, D., Naughton, F., Marino, M., Maiorano, P., and Balestra, B.: Control mechanisms of primary productivity revealed by calcareous nannoplankton from Marine Isotope Stages 12 to 9 at the Shackleton Site (IODP Site U1385), Paleoceanogr. Paleoclimatology, 36, https://doi.org/10.1029/2021PA004246, 2021.

Henehan, M. J., Edgar, K. M., Foster, G. L., Penman, D. E., Hull, P. M., Greenop, R., Anagnostou, E., and Pearson, P. N.: Revisiting the Middle Eocene Climatic Optimum “carbon cycle conundrum” with new estimates of atmospheric $p\mathrm{CO_2}$ from boron isotopes, Paleoceanogr. Paleoclimatology, 35, https://doi.org/10.1029/2019PA003713, 2020.

Hutchinson, D. K., Coxall, H. K., Lunt, D. J., Steinthorsdottir, M., de Boer, A. M., Baatsen, M., von der Heydt, A., Huber, M., Kennedy-Asser, A. T., Kunzmann, L., Ladant, J.-B., Lear, C. H., Moraweck, K., Pearson, P. N., Piga, E., Pound, M. J., Salzmann, U., Scher, H. D., Sijp, W. P., Śliwińska, K. K., Wilson, P. A., and Zhang, Z.: The Eocene–Oligocene transition: a review of marine and terrestrial proxy data, models and model–data comparisons, Clim. Past, 17, 269–315, https://doi.org/10.5194/cp-17-269-2021, 2021.

Jiang, S. and Wise, S. W.: Surface-water chemistry and fertility variations in the tropical Atlantic across the Paleocene/Eocene Thermal Maximum as evidenced by calcareous nannoplankton from ODP Leg 207, Hole 1259B, Rev. Micropaléontologie, 49, 227–244, https://doi.org/10.1016/j.revmic.2006.10.002, 2006.

Katz, M. E., Cramer, B. S., Toggweiler, J. R., Esmay, G., Liu, C., Miller, K. G., Rosenthal, Y., Wade, B. S., and Wright, J. D.: Impact of Antarctic Circumpolar Current development on late Paleogene ocean structure, Science, 332, 1076–1079, https://doi.org/10.1126/science.1202122, 2011.

Lazarus, D., Barron, J., Renaudie, J., Diver, P., and Türke, A.: Cenozoic planktonic marine diatom diversity and correlation to climate change, PLoS ONE, 9, e84857, https://doi.org/10.1371/journal.pone.0084857, 2014.

Lear, C. H., Rosenthal, Y., Coxall, H. K., and Wilson, P. A.: Late Eocene to early Miocene ice sheet dynamics and the global carbon cycle, Paleoceanography, 19, n/a-n/a, https://doi.org/10.1029/2004PA001039, 2004.

Liebrand, D., de Bakker, A. T. M., Beddow, H. M., Wilson, P. A., Bohaty, S. M., Ruessink, G., Pälike, H., Batenburg, S. J., Hilgen, F. J., Hodell, D. A., Huck, C. E., Kroon, D., Raffi, I., Saes, M. J. M., van Dijk, A. E., and Lourens, L. J.: Evolution of the early Antarctic ice ages, Proc. Natl. Acad. Sci., 114, 3867–3872, https://doi.org/10.1073/pnas.1615440114, 2017.

Littler, K., Röhl, U., Westerhold, T., and Zachos, J. C.: A high-resolution benthic stable-isotope record for the South Atlantic: Implications for orbital-scale changes in Late Paleocene–Early Eocene climate and carbon cycling, Earth Planet. Sci. Lett., 401, 18–30, https://doi.org/10.1016/j.epsl.2014.05.054, 2014.

Lohbeck, K. T., Riebesell, U., and Reusch, T. B. H.: Adaptive evolution of a key phytoplankton species to ocean acidification, Nat. Geosci., 5, 2012.

Lowery, C. M., Bown, P. R., Fraass, A. J., and Hull, P. M.: Ecological response of plankton to eEnvironmental change: Thresholds for extinction, Annu. Rev. Earth Planet. Sci., 48, 16.1-16.27, https://doi.org/10.1146/annurev-earth-081619-052818, 2020.

Ma, R., Bord, D., Jin, X., and Liu, C.: Morphometric analysis of coccolithophore genus *Reticulofenestra*: Insights into taxonomy and evolution during late Eocene to early Oligocene, Mar. Micropaleontol., 195, 102435, https://doi.org/10.1016/j.marmicro.2024.102435, 2025.

Matsuoka, H. and Okada, H.: Quantitative analysis of quaternary nannoplankton in the subtropical northwestern Pacific Ocean, Mar. Micropaleontol., 14, 97–118, https://doi.org/10.1016/0377-8398(89)90033-9, 1989.

Miller, K. G., Browning, J. V., Schmelz, W. J., Kopp, R. E., Mountain, G. S., and Wright, J. D.: Cenozoic sea-level and cryospheric evolution from deep-sea geochemical and continental margin records, Sci. Adv., 6, eaaz1346, https://doi.org/10.1126/sciadv.aaz1346, 2020.

Miniati, F., Cappelli, C., and Monechi, S.: Revised taxonomy and early evolution of fasciculiths at the Danian–Selandian transition, J. Micropalaeontology, 40, 101–144, https://doi.org/10.5194/jm-40-101-2021, 2021.

Norris, R. D., Turner, S. K., Hull, P. M., and Ridgwell, A.: Marine ecosystem responses to Cenozoic global change, Science, 341, 492–498, https://doi.org/10.1126/science.1240543, 2013.

Norris, R. D., Wilson, P. A., Blum, P., Fehr, A., Agnini, C., Bornemann, A., Boulila, S., Bown, P. R., Cournede, C., Friedrich, O., Ghosh, A. K., Hollis, C. J., Hull, P. M., Jo, K. nam, Junium, C. K., Kaneko, M., Liebrand, D., Lippert, P. C., Liu, Z., Matsui, H., Moriya, K., Nishi, H., Opdyke, B. N., Penman, D., Romans, B., Scher, H. D., Sexton, P., Takagi, H., Turner, S. K., Whiteside, J. H., Yamaguchi, T., and Yamamoto, Y.: Expedition 342 summary, Proc. Integr. Ocean Drill. Program, 342, 1–149, https://doi.org/10.2204/iodp.proc.342.101.2014, 2014.

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., and Bullock, J. M.: Biodiversity and resilience of ecosystem functions, Trends Ecol. Evol., 30, 673–684, https://doi.org/10.1016/j.tree.2015.08.009, 2015.

Ostle, C., Landschützer, P., Edwards, M., Johnson, M., Schmidtko, S., Schuster, U., Watson, A. J., and Robinson, C.: Multidecadal changes in biology influence the variability of the North Atlantic carbon sink, Environ. Res. Lett., 17, 114056, https://doi.org/10.1088/1748-9326/ac9ecf, 2022.

Özen, V., Lazarus, D., Renaudie, J., and Rodrigues De Faria, G.: Increasing opal productivity in the late Eocene Southern Ocean: Evidence for increased carbon export preceding the Eocene-Oligocene glaciation, Clim. Past, 21, 2283–2297, https://doi.org/10.5194/egusphere-2025-555, 2025.

Pälike, H., Norris, R. D., Herrle, J. O., Wilson, P. A., Coxall, H. K., Lear, C. H., Shackleton, N. J., Tripati, A. K., and Wade, B. S.: The heartbeat of the Oligocene climate system, Science, 314, 1894–1898, https://doi.org/10.1126/science.1133822, 2006.

Peijnenburg, K. T. C. A. and Goetze, E.: High evolutionary potential of marine zooplankton, Ecol. Evol., 3, 2765–2781, https://doi.org/10.1002/ece3.644, 2013.

Perch-Nielsen, K.: Mesozoic and Cenozoic calcareous nannofossils, in: Plankton Stratigraphy: Planktic Foraminifera, Calcareous Nannofossils and Calpionellids, vol. 1, 329–572, 1985.

Persico, D. and Villa, G.: Eocene–Oligocene calcareous nannofossils from Maud Rise and Kerguelen Plateau (Antarctica): paleoecological and paleoceanographic implications, Mar. Micropaleontol., 52, 153–179, https://doi.org/10.1016/j.marmicro.2004.05.002, 2004.

Self-Trail, J. M., Powars, D. S., Watkins, D. K., and Wandless, G. A.: Calcareous nannofossil assemblage changes across the Paleocene–Eocene Thermal Maximum: Evidence from a shelf setting, Mar. Micropaleontol., 92–93, 61–80, https://doi.org/10.1016/j.marmicro.2012.05.003, 2012.

Slater, S. M., Demangel, I., and Richoz, S.: 'Ghost' fossils of early coccolithophores point to a Triassic diversification of marine calcifying organisms, Nat. Commun., 16, 9283, https://doi.org/10.1038/s41467-025-65116-0, 2025.

Tierney, J. E., Poulsen, C. J., Montañez, I. P., Bhattacharya, T., Feng, R., Ford, H. L., Hönisch, B., Inglis, G. N., Petersen, S. V., Sagoo, N., Tabor, C. R., Thirumalai, K., Zhu, J., Burls, N. J., Foster, G. L., Goddéris, Y., Huber, B. T., Ivany, L. C., Kirtland Turner, S., Lunt, D. J., McElwain, J. C., Mills, B. J. W., Otto-Bliesner, B. L., Ridgwell, A., and Zhang, Y. G.: Past climates inform our future, Science, 370, eaay3701, https://doi.org/10.1126/science.aay3701, 2020.

Toffanin, F., Agnini, C., Fornaciari, E., Rio, D., Giusberti, L., Luciani, V., Spofforth, D. J. A., and Pälike, H.: Changes in calcareous nannofossil assemblages during the Middle Eocene Climatic Optimum: Clues from the central-western Tethys (Alano section, NE Italy), Mar. Micropaleontol., 81, 22–31, https://doi.org/10.1016/j.marmicro.2011.07.002, 2011.

van Der Ploeg, R., Selby, D., Cramwinckel, M. J., Li, Y., Bohaty, S. M., Middelburg, J. J., and Sluijs, A.: Middle Eocene greenhouse warming facilitated by diminished weathering feedback, Nat. Commun., 9, 2877, https://doi.org/10.1038/s41467-018-05104-9, 2018.

van Peer, T. E., Liebrand, D., Taylor, V. E., Brzelinski, S., Wolf, I., Bornemann, A., Friedrich, O., Bohaty, S. M., Xuan, C., Lippert, P. C., and Wilson, P. A.: Eccentricity pacing and rapid termination of the early Antarctic ice ages, Nat. Commun., 15, 10600, https://doi.org/10.1038/s41467-024-54186-1, 2024.

Viganò, A., Westerhold, T., Bown, P. R., Jones, T. D., and Agnini, C.: Calcareous nannofossils across the Eocene-Oligocene transition: Preservation signals and biostratigraphic remarks from ODP Site 1209 (NW Pacific, Shatsky Rise) and IODP Hole U1411B (NW Atlantic Ocean, Newfoundland Ridge), Palaeogeogr. Palaeoclimatol. Palaeoecol., 629, 111778, https://doi.org/10.1016/j.palaeo.2023.111778, 2023.

Villa, G., Fioroni, C., Pea, L., Bohaty, S., and Persico, D.: Middle Eocene–late Oligocene climate variability: Calcareous nannofossil response at Kerguelen Plateau, Site 748, Mar. Micropaleontol., 69, 173–192, https://doi.org/10.1016/j.marmicro.2008.07.006, 2008.

Wade, B. S. and Pälike, H.: Oligocene climate dynamics, Paleoceanography, 19, 1–16, https://doi.org/10.1029/2004PA001042, 2004.

Wade, B. S. and Pearson, P. N.: Planktonic foraminiferal turnover, diversity fluctuations and geochemical signals across the Eocene/Oligocene boundary in Tanzania, Mar. Micropaleontol., 68, 244–255, https://doi.org/10.1016/j.marmicro.2008.04.002, 2008.

Wei, W. and Wise, S. W.: Biogeographic gradients of middle Eocene-Oligocene calcareous nannoplankton in the South Atlantic Ocean, Palaeogeogr. Palaeoclimatol. Palaeoecol., 79, 29–61, https://doi.org/10.1016/0031-0182(90)90104-F, 1990.

Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J. S. K., Bohaty, S. M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Lauretano, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A., and Zachos, J. C.: An astronomically dated record of Earth's climate and its predictability over the last 66 million years, Science, 369, 1383–1387, https://doi.org/10.1126/science.aba6853, 2020.

Winter, A., Jordan, R. W., and Roth, P. H.: Biogeography of living coccolithophores in ocean waters, in: Coccolithophores, edited by: Winter, A. and Siesser, W. G., Cambridge University Press, 161–177, 1994.

Young, J. R.: Size variation of Neogene *Reticulofenestra* coccoliths from Indian Ocean DSDP Cores, J. Micropalaeontology, 9, 71–86, 1990.

Young, J. R.: Neogene, in: Calcareous Nannofossil Biostratigraphy, edited by: Bown, P. R., Chapman & Hall, London, 225–265, 1998.

Zachos, J. C., Röhl, U., Schellenberg, S. A., Sluijs, A., Hodell, D. A., Kelly, D. C., Thomas, E., Nicolo, M., Raffi, I., Lourens, L. J., McCarren, H., and Kroon, D.: Rapid acidification of the ocean during the Paleocene-Eocene Thermal Maximum, Science, 308, 1611–1615, https://doi.org/10.1126/science.1109004, 2005.