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Increasing opal productivity in the late Eocene Southern Ocean: Evidence for increased carbon export preceding the Eocene-Oligocene glaciation

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Abstract. The Eocene/Oligocene Transition represents a period of profound changes in diatom productivity and evolutionary history within the Cenozoic era. Unraveling how these changes correlate with climatic shifts during this transition is crucial for understanding the potential role of diatoms in the cooling trends observed at the Eocene/Oligocene boundary (~33.9 Ma). Current research predominantly relies on bulk opal accumulation measurements to assess productivity dynamics, which fails to distinguish the contribution of different biosiliceous (e.g., diatom versus radiolarian) plankton to total biogenic silica productivity. Furthermore, despite the fundamental role of community composition and diversity in diatom productivity and carbon sequestration, these factors are often not incorporated in existing studies focusing on the late Paleogene diatom productivity. The main objective of our work is to explore the potential roles of diatom communities in the late Eocene climatic changes by focusing on diatom- and radiolarian-specific productivity across multiple Southern Ocean sites, rather than bulk opal measurements, and by incorporating total diatom abundance into the analysis of diatom diversity evolution throughout the Eocene/Oligocene transition. By quantifying diatom and radiolarian abundances across four Southern Ocean sites in the Atlantic and Indian Ocean sectors, and analyzing diatom productivity through recent reconstructions of diatom diversity from approximately 40-30 Ma interval, our findings reveal a significant increase in diatom abundance coupled with notable shifts in community diversity. These changes suggest a potential ecological shift, likely associated with the development of stronger circum-Antarctic currents in the late Eocene. Such shifts could have influenced the efficiency of the biological carbon pump by enhancing organic carbon export to the deep ocean and thus potentially contributing to reduced atmospheric CO_2 levels. While our findings indicate that the expansion of diatoms may have been a part of the mechanisms underlying the late Eocene cooling, they also highlight the importance of integrating diatom diversity and community evolution into diatom productivity research. Furthermore, our results offer valuable insights into the complex relationship between diatom abundance and diversity in the geological record, reflecting the intricate interplay of environmental and climatic factors.

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1 Introduction

The Eocene/Oligocene boundary (E/O, ~33.9 Ma) marks the end of the Cenozoic Hothouse with high-latitude surface ocean cooling and an abrupt 1.5 per mil increase in global benthic $\delta^{18}O$ values (Shackleton and Kennett, 1975; Zachos et al., 1996, 2001; Coxall et al., 2005; Zachos and Kump, 2005; Coxall and Pearson, 2007; Liu et al., 2009; Westerhold et al., 2020; Hutchinson et al., 2021). It corresponds to the largest cooling shift of the late Paleogene gradual cooling trend and the abrupt emplacement/expansion of the Antarctic ice sheet (Lear et al., 2008) Despite the large volume of research describing the environmental mosaic of the E/O transition, the underlying mechanisms are under dispute. The discussions on the possible causes of the abrupt climatic-state shift have revolved around two main domains (1) gradual thermal isolation of Antarctica with the development of the Antarctic Circumpolar Current (ACC) initiated by the deepening of the Southern Ocean (SO) gateways (Kennett, 1977; Barker, 2001), and (2) the threshold response of the Earth climate to the atmospheric CO_2 decrease in the late Paleogene (DeConto and Pollard, 2003; Ladant et al., 2014).

Proposed mechanisms underlying the E/O transition are not mutually exclusive, and both oceanographic changes and CO_2 as the overriding mechanism have support (Scher and Martin, 2006; Ladant et al., 2014; Elsworth et al., 2017; Toumoulin et al., 2020; Hutchinson et al., 2021; Lauretano et al., 2021). The existing literature on the onset of the ACC is extensive and focuses particularly on the deepening of Southern Ocean gateways (e.g., Kennett, 1977; Stickley et al., 2004; Sijp et al., 2011; Evangelinos et al., 2022). Sufficiently deep gateways would develop a circulation system akin to the ACC, and pave the way for a stronger latitudinal thermal gradient and thermal isolation of the Antarctic continent (Sauermilch et al. 2021).

A significant challenge for the proto-ACC isolation hypothesis lies in the poorly constrained timing of the SO gateway openings. Although the Tasman gateway is thought to have been substantially open by ca 35 Ma (Stickley et al., 2004), the timing of Drake Passage opening remains highly debated, with estimates ranging from mid Eocene to basal Neogene (e.g., Scher and Martin, 2006; Livermore et al., 2007; Barker et al., 2007; Scher et al., 2015; Hodel et al., 2021).

On the other hand, the main difficulty with the CO_2 line of reasoning, as the overriding mechanism, is that, while the CO_2 reconstructions are accepted at face value, the possible mechanism(s) underlying the late Eocene drawdown in CO_2 is not well constrained. It is indeed conceivable that these two domains of possible mechanisms were probably linked: a gradual increase in proto-ACC strength would increase ocean mixing rates and, thus, mixed-layer thickness. Consequently, increasing mixing rates and related upwelling systems would promote SO plankton productivity and thus organic carbon sequestration (via biological carbon pump) into the deep-ocean and sediments, and thus to the atmospheric CO_2 drawdown (e.g., Scher and Martin, 2006; Egan et al., 2013; Rodrigues de Faria et al., 2024).

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The critical point is that a modest decrease in CO_2 may have been sufficient to trigger the threshold response observed at the E/O. Previous studies indicate that CO2 levels in the late Eocene declined significantly, reaching as low as ~800 ppm (Anagnostou et al., 2016), which approaches the model-estimated threshold of ~750 ppm required for E/O cooling and the onset of (primarily East) Antarctic glaciation (DeConto et al., 2008). Therefore, the role of increasing, particularly diatoms, SO productivity (Salamy and Zachos, 1999; Schumacher and Lazarus, 2004; Egan et al., 2013; Rodrigues de Faria et al., 2024) stands out as a critical mechanism that might have contributed to the final increment in CO_2 drawdown, consequently to E/O cooling, although its timing and characteristics remain a matter of contention.

1.1 Opal as a paleoproductivity proxy

Biosiliceous deposition in modern open ocean settings closely correlates with the productivity dynamics of the overlying water column, a pattern observed consistently across diverse regions from the equatorial to high-latitude Pacific and Atlantic Oceans (Baldauf and Barron 1990; Barron et al. 2015). Biogenic silica has significantly higher preservation potential than organic carbon (Tréguer et al., 1995; Ragueneau et al., 2000 and references therein), signifying the potential of biogenic silica deposition and its secular trends in tracking the changing paleoproductivity trends throughout the Cenozoic. However, using opal as a paleoproductivity proxy is complicated by spatial and temporal variations in silica dissolution and preservation, as well as the decoupling of the silica-carbon relationship from surface waters to sediments (Ragueneau et al. 2000). The factors influencing silica dissolution and preservation are not fully constrained and are expected to vary significantly under different oceanographic and climatic conditions throughout the Cenozoic (Ragueneau et al., 2000; Westacott et al., 2021). Although the links between the tempo and mode of opal deposition, and productivity dynamics are complex, it has been shown that the secular trend of opal deposition is closely related with the global oceanographic and climatic changes (Cortese et al., 2004). Additionally, the evolutionary history of biosiliceous plankton underlying opal deposition during the Cenozoic is a critical but often overlooked aspect in paleoproductivity interpretations based on opal accumulation. Most available data are based on bulk opal measurements, which can obscure the contributions of different biosiliceous plankton groups, such as radiolarians (another extremely important siliceous plankton) and marine diatoms. Assessing the relative contributions of different biosiliceous plankton groups to opal sedimentation is essential for accurate paleoproductivity reconstructions (Ragueneau et al., 2000, 2006).

1.2 Prior opal records from the Southern Ocean Paleogene and their limitations

Considerable evidence has been accumulated showing that SO productivity increased across the late Eocene (Diester-Haass and Zahn, 1996; Schumacher and Lazarus, 2004; Villa et al., 2014; Rodrigues de Faria et al., 2024). Data suggest that the first pronounced changes in the SO productivity started between 38 and 37 Ma (Diester-Haass and Zahn, 1996; Diekmann et al., 2004; Anderson and Delaney, 2005; Rodrigues de Faria et al., 2024). The concurrent increase in opal productivity, when combined with the key role of modern diatoms in carbon sequestration via biological carbon pump (Tréguer et al., 2018), motivated the hypothesis that increased diatom productivity, and thus the opal sedimentation, might have contributed to the

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CO_2 drawdown across the E/O transition (e.g., Egan et al., 2013). Indeed, the data so far show that the first pronounced increase in Cenozoic diatom abundance occurred at the E/O boundary (Renaudie, 2016). Further, based on diatom Si geochemistry, it has been proposed that SO diatom productivity increased during the late Eocene (Egan et al., 2013). However, a recent diversity survey has suggested that observed changes in silicic acid measurements may reflect shifts in community composition rather than, or in addition to, increased productivity (Özen et al., subm.).

In the Indian Ocean sector, Salamy and Zachos (1999) (ODP Site 744A) showed that opal deposition profoundly increased right before the E/O boundary. A recent data from the same region (ODP Site 748B) show strong agreement in opal accumulation trends, reinforcing the robustness of these records (Bryłka et al., 2024). However, utilizing the opal deposition history to elucidate the diatom productivity across the end-Eocene is problematic because the data so far is based on bulk opal measurements which do not allow to assess the relative contribution of diatoms and other siliceous plankton, especially radiolarians. Although in modern oceans opal sedimentation is dominated by diatoms, data suggest radiolarian dominated communities in the early Paleogene, and the shift to diatom dominance occurring in a poorly constrained interval in the mid to late Paleogene (Renaudie, 2016).

1.3 Links between biodiversity, abundance and productivity

It has been suggested that community diversity in diatoms is important for the overall abundance and productivity, and this for the efficiency of the biological carbon pump (Tréguer et al., 2018). This in accord with the frequently, if not universally, seen pattern of a positive, or 'hump shaped', correlation between diversity and productivity in many groups of organisms, particularly groups of plants on global scales (Mittelbach et al., 2001). Indeed, in paleontological studies, diatom diversity has often been used as a proxy for abundance (e.g., Lazarus et al., 2014). In a work based on benthic diatom communities, it has been shown that there is a positive link between diverse communities and biomass production (Virta et al., 2019). Moreover, it has been shown that diversity might promote stability in community dynamics (Hatton et al., 2024), this in turn, community stability would presumably lead to a sustained periods high level overall productivity. Although a link between diverse communities and abundance/productivity is a fundamental concept in plankton studies, the details of this link are yet poorly understood. For instance, molecular estimates on global diatom distribution and abundance in different oceanic settings suggest that diatom diversity in eutrophic areas are comparable to the numbers seen in oligotrophic settings (Malviya et al., 2016). The presumed link between diatom diversity and abundance in paleo-communities thus needs to be critically investigated. In our study, we combine our diatom abundance data with a recent diversity survey of the late Eocene and early Oligocene SO diatoms (Özen et al., subm.), giving us a ground to provide new insights into diatom-climate interactions at the end-Eocene.

Constraining the SO diatom productivity is one of the central research themes addressing the mechanisms underlying the E/O transition. As diatoms, as primary producers, presumably play a greater role in carbon capture than an equivalent

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cellular mass of other siliceous plankton, discriminating the relative contribution of different siliceous plankton to the total opal sedimentation is therefore an important step to constrain diatom productivity and its possible role at the E/O transition. Here, we present diatom and radiolarian productivity patterns across the E/O transition based on newly generated accumulation rates. We combine our results with previously published opal bulk accumulation rates to assess the relative contribution of these groups to overall siliceous productivity. Recently generated productivity values based on biological barium (bio-Ba) (Rodrigues de Faria et al., 2024), from the same samples we used to generate our data, give us an independent control in interpreting our productivity data. Moreover, we compare the diatom abundances across the E/O transition to discuss the long-presumed link between diatom diversity and abundance.

2 Methods

2.1 Material

We analyzed diatom and radiolarian abundance data from samples collected from the following SO sites: Deep Sea Drilling Project (DSDP) Site 511 (Falkland Plateau) (sampled interval ~27 – 180 meter below sea floor (mbsf)), Ocean Drilling Project (ODP) Site 1090B (Agulhas Ridge) (~188-335 mbsf), ODP Site 748B (Kerguelen Plateau) (~96–171 mbsf), and ODP Site 689D (Maud Rise) (~104-132 mbsf) (Fig. 1). Our study examines 53 samples spanning the temporal interval from the late Eocene to the early Oligocene, approximately between 39 and 30 Ma, with site-specific coverage varying due to differences in sedimentation history at each site.

DSDP Site 511 (Falkland Plateau) and ODP Site 1090 (Agulhas Ridge) contain hiatuses in the earliest Oligocene, limiting the temporal coverage of these sites. At DSDP 511, our samples temporal coverage is ~37.5 – 32.5 Ma. Similarly, at Site 1090, the sampled interval spans ~38 – 33 Ma, with a hiatus restricting samples from extending well into the Oligocene. In contrast, at ODP Site 689 (Maud Rise) and ODP Site 748 (Kerguelen Plateau), sedimentation is relatively continuous, providing a more complete record of the EOT (~36.5 – 30 Ma at Site 689; ~40 – 29 Ma at Site 748). All analyzed samples and corresponding measurements, including diatom and radiolarian abundance data, are detailed in the Supplementary Materials.

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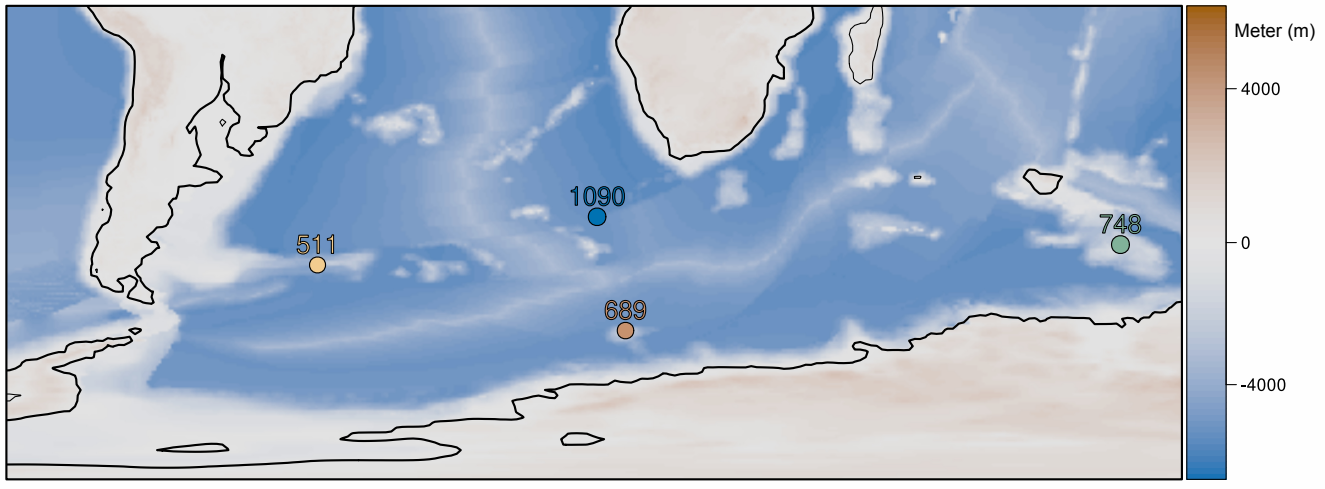

Figure 1: Map showing the locations of the studied sites in the Southern Ocean (paleogeography and paleobathymetry adapted from Straume et al. 2024).

In the southern high latitudes, DSDP Site 511 and ODP Site 1090 are notable for being a major locus of biogenic silica deposition across the Eocene/Oligocene transition (e.g., Diekmann et al., 2004; Anderson and Delaney, 2005; Renaudie, 2016; Wade et al., 2020). While ODP Site 689D and 748B, in general, do not exhibit the same level of opal productivity, significant productivity changes have been documented at these sites across the E/O transition (e.g., Salamy and Zachos, 1999; Bryłka et al., 2024). These findings signify that these sites provide invaluable insights into the SO productivity in the areas proximal to the Antarctic continent. They provide essential insights into how opal productivity varies under different regional settings, offering a broader perspective on productivity changes across the SO.

2.1.1 Sample Preparation

Microscope slides for counting diatom and radiolarian abundances were prepared following a modified version of the methods described by Moore (1973) and Lazarus (1994) and sieved using a 10 µm sieve. About 0.5–1 gram sediment was treated with hydrogen peroxide (H_2O_2) and pentasodium triphosphate ($Na_5P_3O_{10}$) over heat, followed by treatment with hydrochloric acid (HCl). The resulting solution was then sieved through a 10 µm sieve. A controlled amount of the residues was then gently settled over three coverslips at the bottom of a beaker. This approach ensures the material settles randomly across the coverslips, minimizing potential biases might arise during the enumeration phase (for details, see Lazarus, 1994).

2.2 Diatom and radiolarian absolute abundance and accumulation rates

Absolute abundances for diatoms and radiolarians were calculated by counting specimens on a known area of slides, following the equation below:

$$ab = N \times (Ab/Am) \times (Vp/Vu) \times 1/w \quad (1)$$

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with N is being the number of specimens counted, Ab the area of used beaker (6079 mm2), Am the area measured in mm^2, Vp the volume of residue prepared in mL, Vu the volume used in mL and w the weight of the dry sediment in gram.

Accumulation rates of diatoms and radiolarians were calculated by multiplying abundance values with the shipboard measured dry bulk densities and the linear sedimentation rates (LSR). The LSR values applied are based on updated age models for the targeted sites. A comprehensive overview of these revised age models is available in (Rodrigues de Faria et al., 2024). The models can also be accessed via the Neptune Database (Renaudie et al., 2020, 2023).

2.3 Diatom abundance and diversity

Our study also examines the relationship between diatom diversity and total diatom abundance, which is essential for understanding the influence of diversity on overall community productivity in diatoms. Rather than relying on bulk opal accumulation rates, which do not distinguish the relative contribution of different siliceous groups like radiolarians, we focused on diatom-specific abundance values. This approach provides a clearer understanding of the relationship between diversity and abundance within diatom communities.

To explore these interactions, we compared recent diatom diversity reconstructions (Özen et al., subm.) with diatom abundance data obtained in this study across the E/O transition. this approach allowed us to directly examine how variations in diatom diversity correspond to changes in abundance and to explore the potential implications of these interactions for overall diatom productivity. In our comparisons, by focusing on diatom abundances per gram of sediment, we aimed to minimize potential biases associated with accumulation rates, which can be affected by uncertainties in age models. This approach ensures a more accurate representation of the abundance-diversity relationship, offering valuable insights into the ecological and environmental factors that influenced diatom productivity during the E/O transition.

3 Results

Our diatom MARs reveal a prominent latitudinal organization in the late Eocene SO, which is expected as at the DSDP Site 511 (Falkland Plateau) and ODP site 1090 (Agulhas Ridge) sediments, biogenic silica is the main sedimentary component across the study interval (Renaudie, 2016; Wade et al., 2020). In the sub-Antarctic Atlantic, diatom MARs at ODP Site 1090 show an increasing trend from ~38 Ma onward, peaking at ~36.8 Ma, in good agreement with previously published bulk opal MARs (Diekmann et al., 2004; Anderson and Delaney, 2005, see Fig. 2d). Meanwhile, DSDP Site 511 records the highest diatom MARs, with a gradual increase throughout the late Eocene, culminating at around 33.4 Ma (Fig 2d). Our increasing trend across the late Eocene, peaking at ~33.4 Ma (Fig. 2d). Notably, our diatom MAR trend from DSDP Site 511 closely aligns with recently published bulk opal accumulation rates (Bryłka et al., 2024, Fig. 2d)

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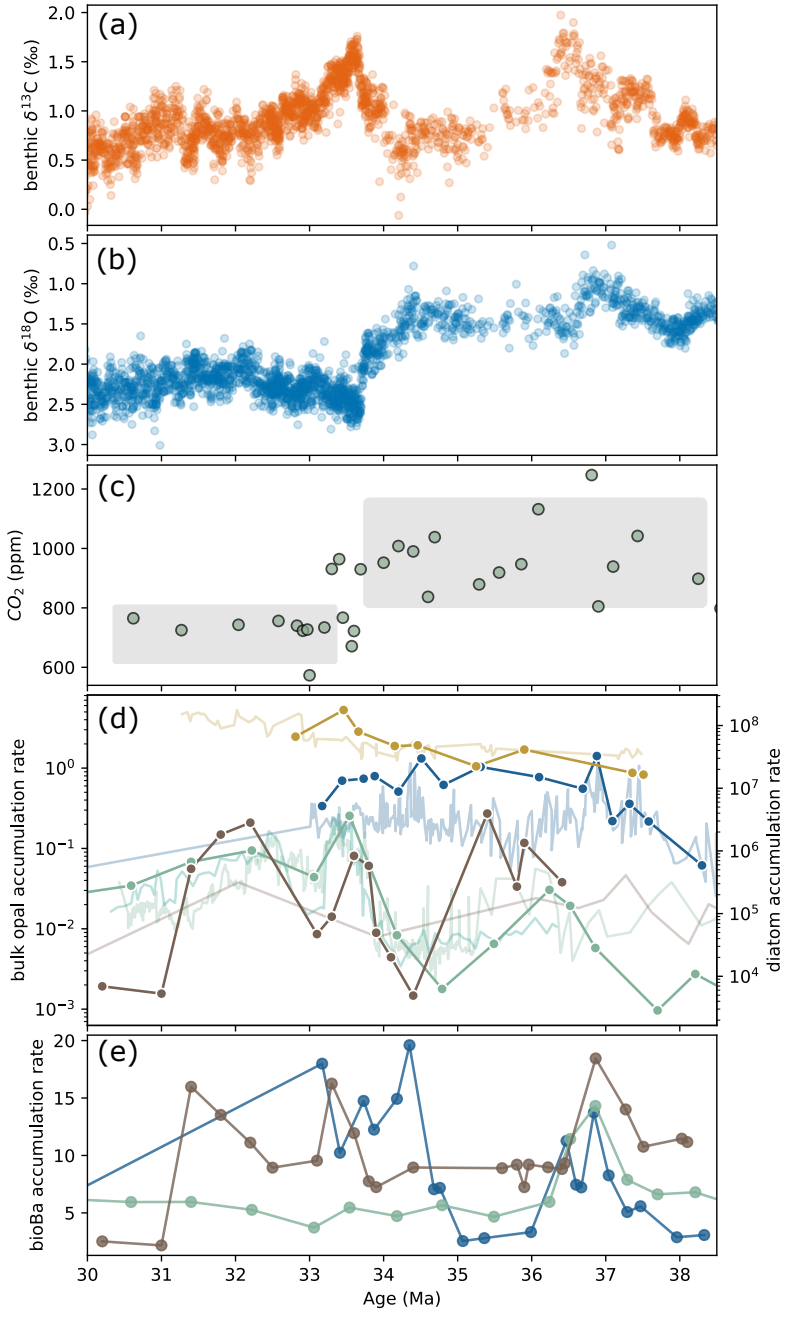

Figure 2. (a) Global composite benthic foraminiferal $\delta^{13}C$ and (b) $\delta^{18}O$ records (from Westerhold et al., 2020). (c) CO_2 compilation (from Zhang et al. 2013; Anagnostou et al. 2020). (d) Diatom mass accumulation rates (MARs) (diatom cm-2 kyr-1; scatter points with solid lines; this study) and bulk opal accumulation rates (gr cm^{-2} kyr^{-1}, solid lines) from DSDP 511 (yellow, Bryłka et al., 2024), ODP 1090 (blue, Diekmann et al. 2004; Anderson and Delaney 2005), Kerguelen Plateau ODP Sites (light green, 744 and 738; dark green 748) (compiled from Ehrmann 1991; Ehrmann and Mackensen 1992; Salamy and Zachos 1999, Bryłka et al.,

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2024), and ODP 689 (Faul and Delaney, 2010). (e) Biogenic barium (bioBa) accumulation rates (µmol cm^{-2} kyr^{-1}) from ODP Sites 1090, 689, and 748 (from Rodrigues de Faria et al. 2024).

In the Antarctic, diatom MARs at ODP Site 689 fluctuate across the E/O transition, with distinctive peaks at ~35.5 Ma, 33.6 Ma, and 32.3 Ma. In the Indian Ocean sector, at ODP Site 748, diatom and bulk opal MARs are in agreement after ~37.5 Ma, suggesting increasing diatom contribution to the total opal productivity towards the E/O boundary. At this site, it has been shown that across the middle Eocene, other siliceous groups, ebridians and radiolarians, dominate the record (Witkowski et al., 2012). Combined with our results, this suggest that diatom dominance in the Kerguelen Plateau region started in towards 37 Ma, which is consistent with our sample surveys that there is a strong presence of ebridians in our samples preceding ~38 Ma.

Our diatom MARs, combined with published bulk opal MAR records, reveal two distinct intervals during the EOT, 36.5-35.5 Ma and 34-33 Ma, when opal productivity at Antarctic sites (ODP 689 and 748) sharply increase, surged to levels approaching those of the sub-Antarctic Atlantic (Fig. 2d). Although sub-Antarctic sites (DSDP 511 and ODP 1090) maintained consistently higher opal productivity throughout the EOT, the Antarctic sites experienced transient but significant increase in diatom MARs during these intervals. These Antarctic productivity peaks temporally narrowed the gap between the two regions.

Crucially, these intervals, of Antarctic and sub-Antarctic diatom MAR convergences, unfolded under distinct climatic conditions. The first (~36.5–35.5 Ma) coincided with the late Eocene warming event, documented at multiple high-latitude Southern Ocean sites (ODP Site 689 (Maud Rise); ODP Sites 738, 744, 748 (Kerguelen Plateau); DSDP Site 277; Diester-Haass and Zahn, 1996; Bohaty and Zachos, 2003; Villa et al., 2008, 2014; Pascher et al., 2015). In contrast, the later interval (~34-33 Ma) corresponds with a sharp increase in global foraminiferal $\delta^{18}O$ in the earliest Oligocene, signalling substantial cooling and the onset of permanent Antarctic glaciation (Fig. 2b and 2d).

This contrast, where diatom MARs at Antarctic sites surged under opposing climatic regimes, highlights that although Antarctic productivity temporally approached sub-Antarctic levels, these shifts occurred during fundamentally different environmental contexts.

Radiolarian MAR patterns are broadly in agreement with diatom MARs across the E/O transition. Our results are summarized in Fig. 3. At ODP Site 1090, our radiolarian MARs reveal two prominent peaks at ~37 and 34.5 Ma. At DSDP Site 511, diatom MAR values do not show any substantial change across the Eocene samples until the E/O boundary. Following the E/O boundary, radiolarian MARs reveal two substantial peaks at ~34.2 and ~33.5 Ma. At ODP Site 748, the major radiolarian MAR peak occurs at ~36.5 Ma, followed by a significant drop. Our results suggest that the radiolarian MAR values, ODP 748, recover back to the pre-E/O values only at around 30.5 Ma. Values for ODP site 689 indicate two

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prominent peaks, between 36-35 Ma, and at ~31.5 Ma. Interestingly, our results reveal that the difference between sub-Antarctic Atlantic and Antarctic sites in radiolarian MARs significantly elevated at approximately 35 Ma onwards.

3.1 Correlation of opal abundance to other paleoproductivity proxies

Our diatom MARs results reveal a significant overall shift in SO productivity dynamics at approximately around 37 Ma. This is reorganization in SO productivity is a not restricted to diatom and radiolarian MARs. Notably, in a recent study based on bio-Ba proxy, it has been shown that there was a strikingly correlated increase in productivity at the ODP Sites 1090, 748, and 689 (Fig. 2e) (Rodrigues de Faria et al., 2024), aligning with the trends observed in our diatom MAR results at ODP site 1090. Although our diatom MAR values do not show great agreement with those seen in bio-Ba values at ODP 748, prominent change in bio-Ba values clearly marks the beginning of the increasing diatom MARs values, peaking at around 36.2 Ma at this site. It has been also shown that, based on benthic foraminiferal accumulation rates (BFAR), at ODP 689, there was a distinct increase in productivity across the 37-36.5 Ma interval (Fig. S2). This interval also marks a significant change in abundance and diversity of the radiolarian communities in the Southern Pacific (Pascher et al., 2015), and in the Antarctic Atlantic (Funakawa and Nishi, 2008). Moreover, in the Kerguelen Plateau region towards 37 Ma, a reorganization in nannofossil assemblages suggesting a substantial eutrophication was documented (Villa et al., 2014) (Fig. S3). These findings, based on multiple productivity proxies, are strikingly consistent with our diatom and radiolarian and strengthen the evidence for a pronounced productivity change and diatom dominance in the SO towards and onwards ~37 Ma.

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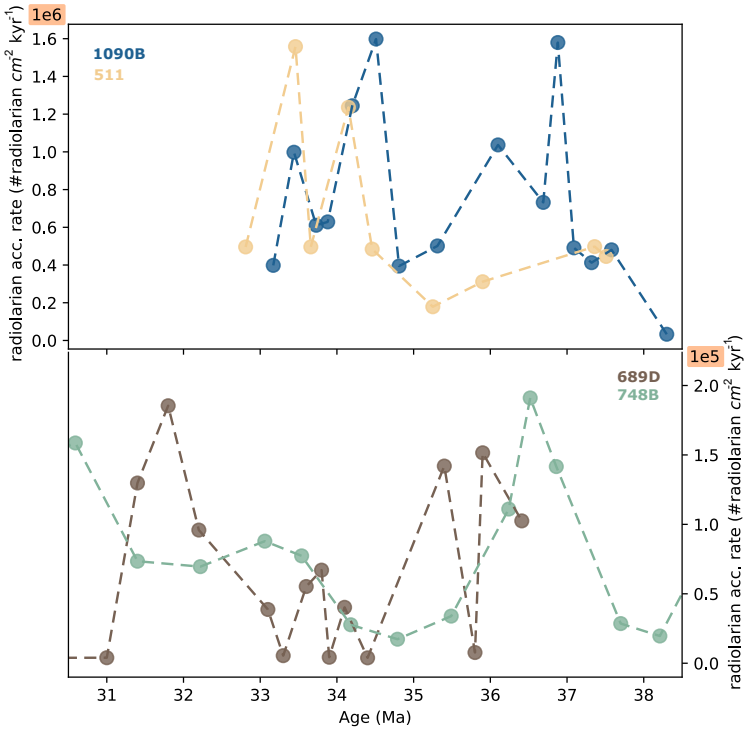

Figure 3. Radiolarian accumulation rates (radiolarian cm^{-2} kyr^{-1}) at the study sites (this study).

3.2 Correlations between diatom diversity and abundance

At DSDP Site 511, exhibiting the highest diversity, diatom abundance and diversity were in great agreement across the E/O transition (Fig. 4c). At ODP Site 1090, diatom abundance and diversity were generally synchronous in trends, except a clear divergence between approximately 37 and 34.5 Ma, during which diversity values stayed relatively low and constant while abundance values showed the highest values. Moreover, the pronounced peaks in diatom abundance around 36.8 and 34.5 Ma did not correspond with similar increase or trend shift in diatom diversity (Fig. 4d). In contrast, at ODP Sites 689 and 748, diatom diversity and abundance values were in agreement (Fig. 4b and 4e). At ODP Site 748, there was a substantial increase in both bulk opal (Bryłka et al. 2024, Fig. 4a) and diatom abundance, reaching values similar to those seen at sun-Antarctic Atlantic sites ODP 1090 and DSDP 511. However, diversity values remained significantly lower compared to those documented at the sub-Antarctic Atlantic sites (Fig. 4e).

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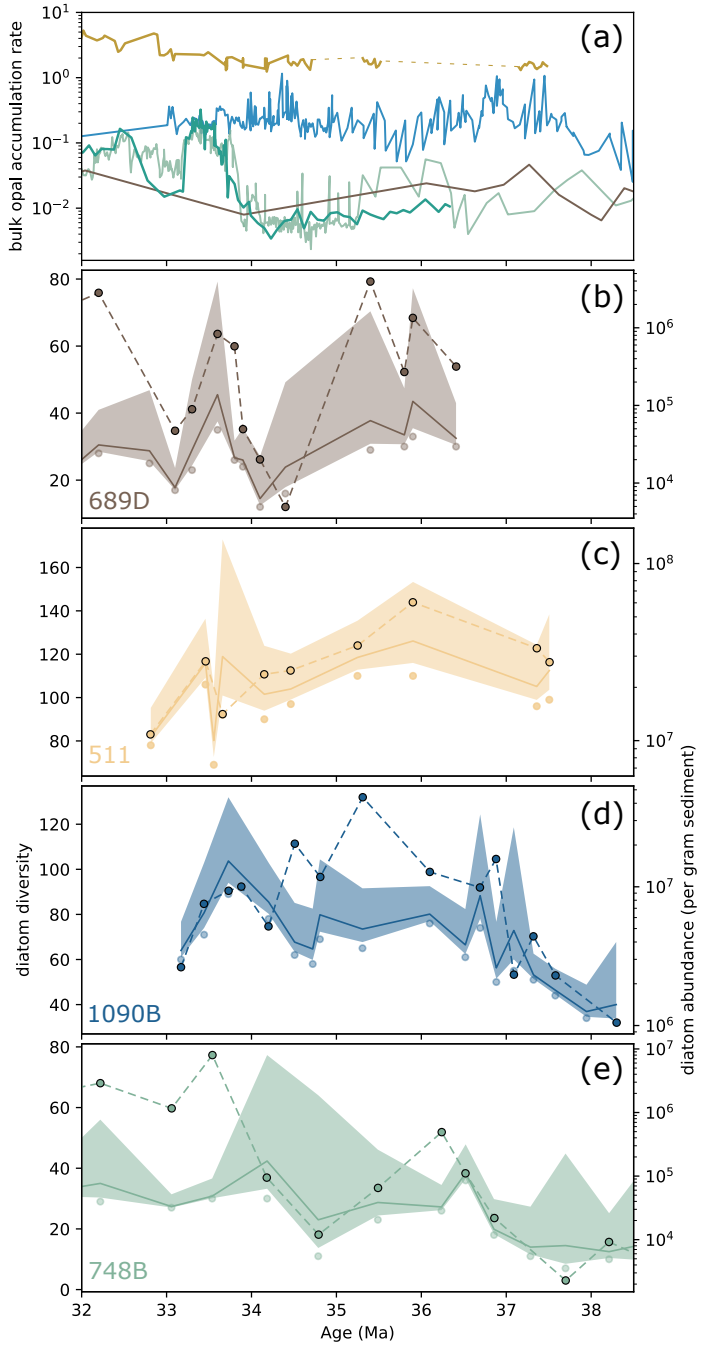

Figure 4. Comparison of bulk opal accumulation rates (gr cm^{-2} kyr^{-1}) with diatom diversity (number of species) and abundance. (a) from DSDP 511 (yellow, Bryłka et al., 2024), ODP 1090 (blue, Diekmann et al. 2004; Anderson and Delaney 2005), Kerguelen Plateau ODP Sites (light green, 744 and 738; dark green 748) (compiled from Ehrmann 1991; Ehrmann and Mackensen 1992; Salamy and Zachos 1999, Bryłka et al., 2024), and ODP 689 (Faul and Delaney, 2010) (b-e) Diatom diversity (scatter points) with Chao1 diversity estimates (solid line, 95% confidence envelope) (Özen et al. subm.) and diatom abundance per gram sediment (scatter points, dashed lines).

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4 Discussion

4.1 Diatom productivity and opal record across the middle-to-late Eocene transition (~36–38 Ma)

Although the exact timing and mode of opal productivity patterns differ across the studied sites, our results suggest that SO diatom and radiolarian productivity experienced substantial reorganization between ~36–38 Ma. In the sub-Antarctic Atlantic, bulk opal records at ODP Site 1090 show a gradual increase 38 Ma onwards, intensifying by ~37 Ma (Diekmann et al., 2004; Anderson and Delaney, 2005). Our diatom MARs from this site greatly agree with this trend, suggesting increasing diatom dominance in the region.

This shift in SO productivity was not confined to a single site or proxy but reflects a broader reorganization across multiple oceanic sectors during the middle-to-late Eocene transition. In the Southern Pacific, radiolarian communities underwent restructuring (Pascher et al., 2015). In the Indian Ocean sector, nannofossil assemblages also show significant changes (Villa et al., 2014, see Fig. S1), alongside a surge in biological barium (bioBa) accumulation rates (Rodrigues de Faria et al., 2024, Fig. 2e), indicating increased export productivity. Similar productivity reorganizations are evident in the Atlantic sector, where benthic foraminiferal accumulation rates (BFAR) exhibit a substantial increase (Diester-Haass and Zahn, 1996, see Fig. S2). Moreover, comparable opal productivity surges around this time interval have been documented in the equatorial (Nilsen et al., 2003, see Fig. S3), and northern Atlantic (Witkowski et al. 2021), suggesting that the changes across the middle-to-late Eocene transition may have been regionally widespread within the Atlantic basin.

An increase in productivity at ~37 Ma has been documented across SO ODP Sites 1090, 689, and 748 based on bioBa records (Rodrigues de Faria et al., 2024, Fig. 2e). Our diatom MARs at ODP Site 1090 align well with this trend but at Antarctic adjacent sites, ODP 689 and 748, diatom productivity peaks within ~36-35.5 Ma (Fig. 2d), indicating a temporal lag between bioBa and diatom accumulation at these sites. This asynchrony suggest that diatom productivity did not increase uniformly across sub-Antarctic Atlantic and Antarctic adjacent regions and may have been influenced by regional environmental factors and/or differential plankton community composition across the SO regions. Such dominant plankton community variability is consistent with diatoms as *relative newcomers*, gradually expanding their ecological role within an ecosystem previously dominated by other plankton groups, such as calcareous nannoplankton.

Broad changes in plankton productivity (as summarized above) and community composition (e.g., Pascher et al., 2015; Özen et al., subm.) across the middle-to-late Eocene transition (~36–38 Ma) may reflect enhanced nutrient distribution across the Atlantic, hinting at an invigorated cross-latitudinal circulation system, akin to the modern Atlantic Meridional Ocean Circulation (AMOC). Indeed, it has been proposed that ~ 38 Ma onwards this circulation started to strengthen under the effect of increasing circum-Antarctic circulation, often termed as the proto-ACC, which is an integral part of the cross-latitudinal circulation across the Atlantic (Borrelli et al., 2014). This aligns with our diatom accumulation rates, which show

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a substantial reorganization 38 Ma onwards, and as well as with the previous paleoproductivity reconstructions suggesting a substantial productivity increase across the SO sites between 36-38 Ma (e.g., Diester-Haass and Zahn 1996; Pascher et al. 2015; Rodrigues de Faria et al. 2024). However, there are numerous controversies on evolution and steps of the circum-Atlantic circulation patters (Diester-Haass and Zahn, 1996; Mackensen, 2004; Stickley et al., 2004; Scher and Martin, 2006; Livermore et al., 2007; Barker et al., 2007; Hodel et al., 2021; Evangelinos et al., 2024), despite the divergent accounts of the opening and deepening of the SO gateways, the balance of evidence suggest a system of circulation which got started to strengthen in the late Eocene, possibly during the middle-to-late-Eocene transition.

Interestingly, ~37 Ma also marks a suspected ephemeral east Antarctic glaciations, named as the Priabonian Oxygen Maximum event (PrOM) (Scher et al., 2014). This event is marked by a sharp negative excursion in Neodymium (Nd) values, superimposed on a broader positive Nd trend observed throughout the late Eocene (Rodrigues de Faria et al., 2024, after Scher and Martin, 2004, 2006; Scher et al., 2014; Wright et al., 2018). While the overall positive trend in Nd values has been interpreted as evidence for an increasing Pacific influence into the Atlantic sector the SO, likely through Drake Passage widening (Scher and Martin 2004; Rodrigues de Faria et al. 2024), the substantial negative excursion at ~37 Ma, as a stark contrast to the overall positive trend across the late Eocene, has been attributed to glacial weathering discharge into the Kerguelen Plateau region, associated with the PrOM event (Scher et al., 2014).

The PrOM (~ 37 Ma) event coincides with significant changes in productivity in the Kerguelen Plateau region (Villa et al. 2014; Rodrigues de Faria et al., 2024), suggesting enhanced glacial weathering discharge may have supplied key nutrients, fueling productivity in the Indian Ocean sector of the SO. However, our diatom MAR results, and bulk opal data do not indicate a strong link between PrOM event and opal productivity. Notably, the link between negative Nd excursion (data from Scher et al. 2011) and opal productivity is particularly striking in the earliest Oligocene (Fig. S4), where their strong correlation suggests that glacially modulated weathering discharge, as short-lived negative Nd excursions suggest (Scher et al., 2011), may have directly influenced nutrient availability and biological productivity in the region. The link between the PrOM and the late Eocene pulse needs however to be addressed in further studies.

The opal pulse across the middle-to-late Eocene is also unique as it marks not simply abundance increase in both diatoms and radiolarians, but also a substantial reorganization in diatom communities. It has been shown that towards 37 Ma there is an accompanying increase in diatom diversity (Özen et al., subm.). Although this apparent diversity increase can be simply a function of the increasing abundance and/or preservation of diatoms, the observation that community composition was dynamically changing with the climate suggest that invigorated circulation system possibly led to increasing nutrient availability in our targeted regions, and this paved the way to increasing carrying capacity and available niches for the more diverse communities. Moreover, within the same timeframe, community changes are not restricted with diatoms, it has been

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shown that radiolarian communities experienced such re-organization too (Funakawa and Nishi, 2008; Pascher et al., 2015). We detail diatom abundance/diversity relation in the Section 4.5 Diatom diversity and productivity: a cause-effect relation?

4.2 Opal pulse at the E/O boundary

It is now well established from a variety of studies, that the E/O boundary marks a substantial increase in opal productivity in the SO. This is the second pulse of productivity across the E/O transition, which is the most pronounced in the Antarctic ODP Sites 689 and 748 where our results suggest approximately 100-fold increase, suggesting a stark dominance of diatoms in the Antarctic sites, where radiolarian abundance particularly low (Fig. 3, see Discussion section 4.4. Environmental implications of radiolarian MARs).

At Antarctic adjacent ODP Sites 689 and 748, the substantial increase in diatom MARs aligns closely with bulk opal accumulation rates (Fig. 2d) and coincides with the largest shift in global $\delta^{18}O$ values, suggesting a link between the emplacement of permanent East Antarctic glaciation, global cooling and opal productivity. Additionally, clay assemblage studies indicate an increase in physical weathering regime in the earliest Oligocene at both Maud Rise (ODP 689) and Kerguelen Plateau (ODP 748) regions (e.g., Robert et al., 2002). This is consistent with the scenario that enhanced weathering influx may have contributed to increase silica availability, fueling opal productivity in Antarctic-adjacent regions (ODP 689 and 748) during the earliest Oligocene. Moreover, the earliest Oligocene Nd excursion shows a strong correlation with opal productivity, reinforcing the link between weathering discharge and silica supply (Scher et al., 2011; see previous section, Discussion Section 4.1).

4.3 Transient geographical shifts in diatom productivity

Our results, together with previously published bulk opal records, reveal a striking pattern in the SO opal record: two extended intervals, 36.5-35.5 Ma and 34-33 Ma, when diatom productivity at Antarctic sites (ODP 689 and 748) increased substantially, approaching levels typically observed in the sub-Antarctic Atlantic (ODP 1090 and DSDP 511; see Fig. 2d). While the mechanisms underlying such transient geographic shifts are beyond the exact focus of our work, the observed fluctuations between sub-Antarctic Atlantic and Antarctic sites reveal a striking pattern.

This apparent latitudinal organization of diatom productivity may reflect the presence of an early frontal system, possibly linked to a developing proto-circum-Antarctic circulation. As Antarctic sites (ODP 689 and 748) show episodic increases in diatom productivity, approaching sub-Antarctic values, this pattern may indicate an early-stage frontal structure influencing nutrient distribution and productivity gradients across the SO. In the modern SO, frontal systems are integral to nutrient distribution and show latitudinal shifts in response to climatic oscillations (e.g., Howard and Prell, 1992; Chapman et al., 2020). This parallel suggests that emerging frontal systems during the late Eocene may have facilitated nutrient

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redistribution in the SO, directly influencing diatom productivity at high latitudes. Therefore, these apparent geographical shifts could represent an early iteration of the nutrient gradients and productivity shifts observed in the modern SO.

4.4 Environmental implications of radiolarian MARs

The late Paleogene Southern Ocean radiolarian communities are an integral part of the silica cycle across the Eocene-Oligocene Transition. Our data indicates a noteworthy latitudinal disparity in radiolarian MARs, particularly evident at the E/O boundary. Sub-Antarctic sites (ODP 1090 and DSDP 511) experienced a significant increase in MAR values, while there was a sharp decline in the Antarctic margin (ODP 689 and 748) (Fig. 3). This latitudinal organization suggest a possible northward shift in locus of maximum radiolarian productivity toward the sub-Antarctic region due to substantial cooling at the Antarctic margin. Alternatively, markedly low radiolarian MARs in the Antarctic margin may reflect the growing dominance of diatom communities in that region, resulting in reducing silica availability for the radiolarian communities.

4.5 Diatom diversity and productivity: A cause/effect relation?

One of the most critical features of SO opal productivity across the E/O transitions is that it is concurrent with the substantial changes in community compositions in both diatom and radiolarian communities (Funakawa and Nishi, 2008; Lazarus et al., 2008; Pascher et al., 2015; Özen et al., subm.). Under the influence of the dynamic climatic and oceanographic features of the SO, and within the precision the fossil data provides, it is a complex task tracking the exact ecological response dynamics of the biosiliceous plankton. The changing diatom community composition and increasing diversity (Özen et al., subm.), is however expected to be positively associated with the range of functional traits within the community (Tréguer et al., 2018), and this to increasing efficiency in the nutrient utilization which is one of the operating terms for the biological carbon pump efficiency (Farmer et al., 2021).

However, the close relationship between observed diversity and diatom MARs and abundance might simply suggest that observed diversity can be a function of increasing abundance, either by ecologic links as above, or in the other direction of causation: by the links between opal flux, sediment opal abundance, skeletal preservation, and diversity of preserved morphologies. Our findings suggest that while there is a notable correlation between diversity and abundance (see Fig. 4b-e), the directionality of their influence is not straightforward, reflecting a more intricate interplay between these two metrics. For instance, at ODP Site 748 during the earliest Oligocene, diatom abundance shows a significant increase (Fig. 4e), yet diversity remains relatively low, barely reaching 30 species. This contrasts with observations at ODP Site 1090, where similar abundance values are associated with much higher diversity, suggesting that abundance alone does not drive diversity. Furthermore, at ODP 1090, a period of consistently high diatom abundance between 36.5 and 34.5 Ma corresponds to relatively low and stable diversity values, indicating community stability rather than a direct abundance-diversity relationship. Notably, this interval at ODP Site 1090 is marked by the dominance of a specific diatom genus, *Pyxilla*, (Özen

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et al., subm.) which is likely contributed to the observed stability in diversity despite high overall abundance. Interestingly, in the second opal pulse at ODP 1090, diversity declines even as abundance remains high, further questioning the assumption that these two metrics, diversity and abundance, are directly linked, or that observed diversity is primarily controlled by preservation.

On the other hand, data from DSDP Site 511 for example reveal a strong alignment between diatom abundance and diversity (Fig. 4c). This can be interpreted in an ecologic context, suggesting that the relationship between diversity and abundance can vary considerably depending on the site-specific conditions, community composition, and the associated functional groups. This variability highlights the critical need to account for local factors and align with previous ecologic studies (e.g., Tréguer et al., 2018), which emphasized the role of community composition in maintaining ecosystem function and the efficiency of the carbon export through the diatomaceous pathway. It is plausible that diversity and abundance are co-dependent, with external environmental conditions playing a pivotal role in shaping their dynamics. Our results suggest that the interplay between diatom diversity and abundance is not merely additive. It is more like a complex feedback loop modulated by external environmental conditions.

4.6 Diatom productivity and its possible role in the E/O cooling

Studies to date indicate that, during the late Eocene phase of climatic cooling, SO regions experienced substantial shifts in productivity (e.g., Diester-Haass and Zahn, 1996; Diekmann et al., 2004; Anderson and Delaney, 2005; Egan et al., 2013; Villa et al., 2014; Plancq et al., 2014; Pascher et al., 2015; Rodrigues de Faria et al., 2024). These shifts provide a basis for the hypothesis that increasing productivity may have contributed to declining CO_2 levels at the end of the Eocene through the biological carbon pump (Salamy and Zachos, 1999; Scher and Martin, 2006; Egan et al., 2013). Our findings indicate that increasing diatom accumulation, coupled with the diverse SO diatom communities (Özen et al., subm.), is a notable feature of the SO productivity system during the late Eocene. This observation aligns with earlier studies using the Si isotope proxy of silica utilization (e.g., Egan et al., 2013), which point to diatom-driven and diatom-contributed productivity pulses and associated changes in carbon export into the deep ocean as a potential mechanism contributing to the CO_2 drawdown across the E/O transition.

Criticism of a diatom-driven increase in productivity and its potential role in E/O cooling often focus on the lack of biogenic opal as the dominant sedimentary component outside, for instance, the Agulhas Ridge and Falkland Plateau regions (e.g., Wade et al. 2020). However, this argument is largely shaped by sediment classification systems that emphasize the most abundant component and have historically favored carbonate-rich deposits. Several biases contribute to the underrepresentation of biogenic silica in the deep-sea sediment record: (1) a bias towards carbonate pelagic sedimentation due to substantial carbonate rock weathering on land, (2) pelagic primary sediment names based on the most abundant single sedimentary component, and (3) a historical preference in deep-sea drilling for well-preserved carbonate sections, often

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chosen for geochemical studies. As a result, compilations which rely only on primary sediment names, mostly reflect pelagic carbonates while underestimating the presence of biogenic silica. In contrast, studies that make use of quantitative estimates of biogenic silica in sediments (e.g., smear slide analyses, Renaudie, 2016) are in principle a more accurate, though still incomplete, representation of the history of biogenic silica accumulation. Given these limitations, the absence of opal-dominated sediments in broad sediment classifications does not contradict the evidence for increased biogenic opal deposition. Indeed, our results consistently show a clear rise in biogenic opal across all targeted sites, providing a robust line of evidence for enhanced diatom productivity across the EOT.

However, the mode and magnitude of the opal deposition/preservation vary between the sites, as a natural consequence of the fact that deposition processes in each site is controlled by geologically different settings. Despite these differential geological filters, evidence from previous studies, mentioned above, highlight critical intervals during which productivity across the SO sites exhibited substantial reorganization, in agreement with our results. Moreover, recent studies show that the SO productivity events across the E/O transition are interlinked with taxonomic reorganizations within diatom communities (Özen et al. subm.), which might tune the efficiency of the biological carbon pump (Tréguer et al., 2018).

Over and above these, diatoms are particularly efficient at the carbon export into the deep ocean (Ragueneau et al. 2000; Tréguer et al. 2018). It is known that diatom dominated export buffers particulate organic carbon (POM) much better than e.g. coccolithophore sourced export against microbial decomposition in the mesopelagic zone (e.g., Cabrera-Brufau et al. 2021). The increasing abundance and diversity in diatoms would thus have improved the efficiency of the biological carbon pump, and thus enhanced drawdown of CO_2 even without an increase in productivity. Lastly, the CO_2 values proposed for the late Eocene were already very near the those proposed as threshold values (~750 ppm) for initiating Antarctic icesheets (DeConto and Pollard, 2003). Thus, increasing oceanic productivity, and enhanced, diatom-mediated efficiency of carbon export might have played a role as the final touch in pushing the CO_2 levels below the boundary conditions, and thus contributed to the E/O climate shift.

5 Conclusion

This study focuses on the complex dynamics of diatom productivity and community diversity during the late Eocene, a period in which the final decline of the Cenozoic Hothouse took place and particularly marked in the SO by an opal-pulse around 37 Ma. Our findings reveal that this period saw a pronounced increase in diatom abundance, coinciding with a major reorganization in both diatom (Özen et al., subm.) and radiolarian (Pascher et al., 2015) communities, as well as an overall rise in productivity across the SO (e.g., Diester-Haass and Zahn, 1996; Anderson and Delaney, 2005; Villa et al., 2014; Rodrigues de Faria et al., 2024). This suggests a widespread evolutionary and productivity shift likely driven by major

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changes in ocean circulation, including the early development of the Atlantic Meridional Overturning Circulation (AMOC) (e.g., Borrelli et al., 2014) and the strengthening of the circum-Antarctic currents.

Bulk opal content and its accumulation rates are not fully informative metrics for to understand diatom productivity dynamics and its impact on the biological carbon pump and thus atmospheric *p*CO2. It is because (1) bulk opal accumulation rates fail to differentiate between contributions from diatoms and other biosiliceous plankton, like radiolarians, to the total biogenic silica production and (2) diatom diversity is an important contributor to diatom-mediated carbon sequestration. Our study integrates both the diversity and abundance dynamics of diatoms during the late Eocene, revealing that the increased abundance and diversity of diatoms likely enhanced the efficiency of the biological carbon pump across the late Eocene, 38 Ma onwards. This enhancement is attributed to both increased abundance of diatoms and more effective nutrient utilization with increasing diversity, which together may have facilitated a stronger carbon flux to the ocean interior for a sustained period of time.

Our observations on the synthesis of diatom abundance and increasing diversity are particularly significant given the role diatoms play in carbon cycling and export (e.g., Smetacek, 1999). Changes in both the abundance and composition of diatom communities can influence the efficiency of the biological carbon pump (Tréguer et al., 2018), potentially affecting how carbon is sequestered into the deep ocean over long timescales. However, the strength of this connection in the late Paleogene remains uncertain. Nevertheless, as there is no evidence to suggest otherwise for the late Paleogene oceans, our results support the hypothesis that the expansion of diatoms (both in abundance and diversity) during late Eocene could have contributed to shifts in the efficiency of the biological carbon pump, potentially playing a role in the climate trends (e.g., Sigman and Hain, 2012). That is why the mechanistic link between diatom expansion and cooling across the EOT remains a strong conjecture that deserves further investigation.

Data availability

The supplementary information and raw data are available in the Supplement, and the raw data will be available upon publication on Zenodo (10.5281/zenodo.14826336, Özen et al., 2025).

Supplement

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Author Contribution

VÖ collected and analyzed the data and drafted the manuscript. All authors contributed to revision and editing of the final version.

Competing interests

The contact author has declared that none of the authors has any competing interests.

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