Unraveling Southern Ocean Diatom Diversity Across the Eocene/Oligocene Transition

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Abstract. The Eocene-Oligocene transition (EOT) was a critical interval of global cooling and circulation change that reshaped marine ecosystems. However, current knowledge of diatom diversity and community dynamics during this interval relies mainly on biostratigraphic compilations, which largely document common species and thus likely underestimate true diversity. This study provides a more complete picture of Southern Ocean diatom communities across the EOT by using comprehensive, quantitative surveys from four sites spanning the Atlantic and Indian Ocean sectors. Results reveal a consistent pattern across sites, with two major shifts in community composition around 37–36 Ma and 34 Ma, linked to major environmental change. Following a prolonged interval of diversification without substantial extinction in the late Eocene, we identify a pronounced extinction event approximately 1 Myr after the Eocene/Oligocene Boundary (E/O, ~33.9 Ma). This suggests that significant changes in surface ocean conditions lagged the boundary and varied across the Southern Ocean. These findings highlight the interplay between global climate changes and local environmental factors in shaping diatom communities. By capturing detailed patterns of diatom diversity and extinction, our study improves understanding of past ecological responses.

1 Introduction

Marine diatoms, accounting for up to 25% of total marine productivity, are the main exporters of silica into the deep ocean (Falkowski et al. 1998; Tréguer et al. 2018; Behrenfeld et al., 2021). Dominating both primary productivity and silica export, diatoms link together the carbon and silica cycles while sustaining the vast oceanic biome across seasonal cycles. The position of diatoms at the intersection of the bio- and geospheres makes the geological record of their evolution and abundance particularly significant. Today, diatom communities are being reshaped by broad, overlapping stressors, including warmer surface waters, stronger water column stratification, shifts in upwelling, ocean acidification, and patterns of sea ice and wind (e.g., Marinov et al., 2010; Hinder et al., 2012; Bach and Taucher, 2019; Henson et al., 2021). Understanding how such pressures influence community dynamics is therefore critical. The geological record of diatoms allows us trace past interactions between climate drivers and diatom communities (e.g., Crampton et al., 2016), particularly where changes in ocean circulation, sea surface temperature, and nutrient availability were pronounced. Insights across the Eocene-Oligocene

Boundary (E/O, ~33.9 Ma), when these drivers shifted dramatically, can help predict how modern diatom communities may respond to ongoing environmental change.

The transition from the late Eocene to early Oligocene (EOT) marks a major reorganization in diatom communities, characterized by increased diversity and abundance (Lazarus et al., 2014; Renaudie, 2016). During this interval, opal sedimentation in the Southern high latitudes suggests the development of a modern-like diatom belt, similar to that associated with the present-day Antarctic Circumpolar Current (ACC) (Renaudie, 2016). These changes broadly align with high-latitude cooling and the Eocene/Oligocene boundary (E/O, ~33.9 Ma). This was the largest climatic state-shift of the Cenozoic, a transition to a 'coldhouse' climate with the establishment of the permanent Antarctic ice sheet, likely driven by crossing an atmospheric $p\mathrm{CO}_2$ threshold and changing circulation patterns (DeConto and Pollard, 2003; Kennett, 1977; Pagani et al., 2005; Shackleton and Kennett, 1975). The proto-Antarctic Circumpolar Current (proto-ACC) also developed during this timeand potentially contributed to Antarctic glaciation by enhancinghe thermal isolation of Antarctica (Kennett, 1977; Scher and Martin, 2006; Toumoulin et al., 2020). Stronger circulation system may also have enhanced nutrient upwelling, stimulating diatom productivity, community change and carbon export (e.g., Diester-Haass and Zahn 1996; Salamy and Zachos 1999; Egan et al., 2013; Rodriguez de Faria et al. 2024) Previous studies have suggested that diatoms not only diversified but may have contributed to cooling through CO_2 sequestration (e.g., Egan et al., 2013). Yet the extent of diatom diversity and timing of community composition change across the EOT remains poorly constrained, relying mainly on diversity-incomplete biostratigraphical compilations (Lazarus et al., 2014), underscoring the need for more comprehensive species-level data.

We present a comprehensive record of Southern Ocean diatom diversity across the EOT from approximately 40 to 30 Ma from sites both the Atlantic and Indian sectors. Previous studies have often underestimated diatom diversity in these regions due to reliance on biostratigraphic data, which have mainly focused on stratigraphically important species while not recording full community diversity (e.g., Gombos and Cieselski, 1983; Barron et al., 2014). To address this gap, we conducted an exhaustive survey by counting nearly all preserved species, allowing for a more accurate and detailed understanding of diatom diversity and community evolution. The new data reveal much higher diversity previously unrecognized shifts in diatom assemblages. Our results deepen understanding of diatom response to EOT climate change, refine projections of future adaptability, and fill a key gap in the marine plankton fossil record.

2 Methods

2.1 Site Selection Rationale

We targetted two sub-Antarctic sites, DSDP 511 (Falkland Plateau) and ODP 1090B (Agulhas Ridge), because they retain continuous diatom record across the Eocene-early Oligocene and record large shifts in biogenic opal that track the development of SO fronts and the emerging ACC (Anderson and Delaney 2005; Plancq et al. 2014; Renaudie 2016; see Fig. 1). To contrast these archives, we also focused on ODP Sites 689D (Maud Rise) and 748B (Kerguelen Plateau) that are closer to the Antarctic continent and show low diatom abundance throughout most of the late Eocene, but both record a pronounced shift in biogenic opal deposition near the E/O (e.g., Diester-Haass and Zahn, 1996; Salamy and Zachos, 1999; Fig. 1). These Antarctic-proximal sites allow us to explore how glacial and oceanographic reorganizations near the continent influenced diatom communities. Taken together, the four sites span key latitudinal and environmental gradients, enabling comparison of regional diatom responses to EOT climate change.

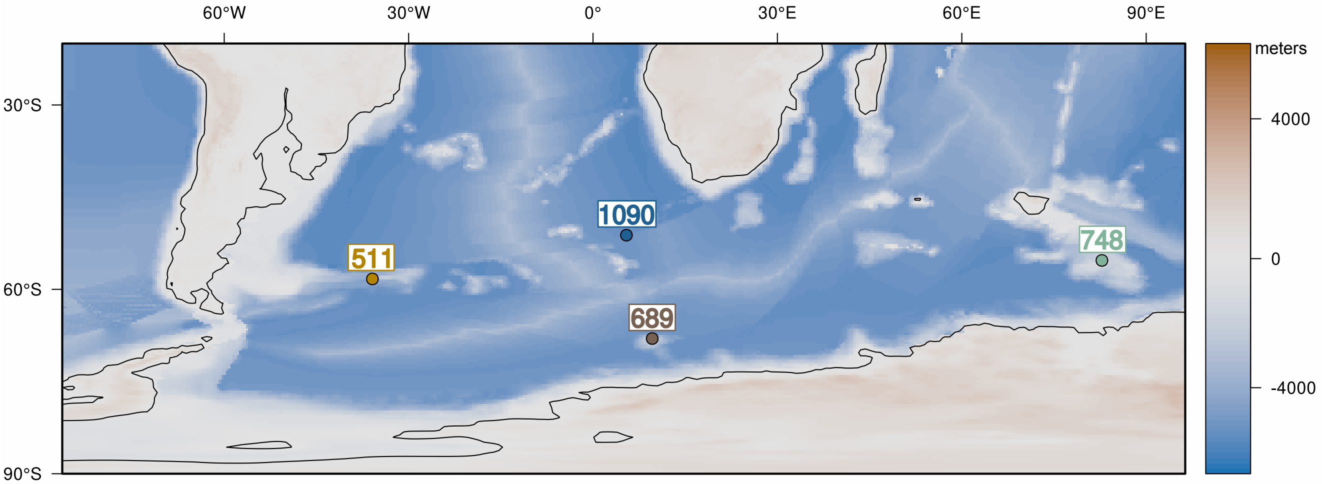

Fig. 1 a) Site map with late Eocene continental configuration in the Southern Ocean. b) Paleodepth and paleolatitude profile of studied sites during the late Eocene. The estimated paleodepths for the studied sites are as follows: Site 1090: ~3000-3300 m (Pusz et al., 2011), DSDP 511: ~2000-2500 m (Basov and Krasheninnikov, 1983), ODP 689: ~1500 m (Diester-Haass and Zahn, 1996), ODP 748: ~ 1200 m (Wright et al., 2018). The paleogeographic and paleobathymetry are derived from the reconstructions of Straume et al. (2024).

2.2 Material

We analyzed 61 samples from sites inthe Atlantic and Indian Ocean sectors of the SO (Fig. 1). Sampling density was determined by balancing the need for capturing meaningful diversity trends with the time consuming nature of performing detailed diatom diversity surveys for each sites. We specifically targeted the intervals that offered the best opportunities for meaningful analysis, prioritizing well-preserved sections where available, while also including sections with less optimal preservation to ensure adequate temporal coverage. These intervals span the late Eocene to the earliest Oligocene, as well as the middle- to late Eocene transition, also a critical phase in the history of SO plankton and productivity (e.g., Diester-Haass and Zahn; 1996; Pascher et al., 2015; Rodriguez de Faria et al. 2024). Variations in sedimentation rates, preservation quality, presence of hiatuses, and sample availability, particularly at DSDP 511 and ODP 1090 in the earliest Oligocene, influenced the differing age ranges at each site.

Qualitative preservation assessments were conducted for all samples, accounting for preserved fine morphological features, intact valves, and absence of dissolution relicts. Each sample was classified into one of three categories: poor, fair, or good (see Fig. S1 for individual assessments). We note that Site 511 is the only site in our study not primarily recovered with modern drilling methods (drill string heave compensator, hydraulic piston core and/or XPC), and the initial core descriptions show the typical disturbance of fine scale sediment structure by heave uncompensated rotary drilling. However, at the between-core resolution of our sampling we have not noted any drilling related distortion of the stratigraphic record. The stratigraphic integrity of the studied interval has also been documented in prior detailed biostratigraphic studies of this site (e.g. Gombos and Ciesielski, 1983). Table 1 provides an overview of the sampled intervals, age ranges, and key site-specific details, while stratigraphic sections and sampled horizons for each site are shown in Fig. S1.

Sampled Hole	Sampling Range (depth, mbsf)	Sampling range (age, Ma)	# of Samples	Mean Sampling Pace	Comments
71-511	27.65 – 179.59	32.8 – 37.5	10	0.52 Myr	Sampling primarily driven by recovery and sample availability
113-689D	104.12 – 130.70	30.2 – 36.4	17	0.39 Myr	Hiatus from 30.5 to 31.1 Ma
120-748B	102.17 – 165.69	30.6 – 40.1	17	0.59 Myr	Poor preservation below 36.5 Ma
177-1090B	127.26 – 334.45	33.2 – 38.3	17	0.32 Myr	Hiatus from 29.6 to 33.1 Ma

Table 1. Summary of samples studied here. Mean sampling pace corresponds to the mean age difference between two consecutive samples.

2.2.1 Age models

All age models were updated and revised as part of this research. Detailed descriptions of the updated age models are available in Rodrigues de Faria et al. **(**2024**)** and can also be accessed through the Neptune Database (Renaudie et al. 2020, 2023). Ages are calculated using the 2012 version of the GPTS (Gradstein et al., 2012).

2.3 Sample preparation

Microscope slides were prepared following a version of the procedures described by Moore (1973) and Lazarus (1994) for radiolarian analysis, but modified for diatoms. A measured quantity of dry sediments, approximately 0.5 to 1 gram, was treated with hydrogen peroxide (H_2O_2) and pentasodium triphosphate ($Na_5P_3O_{10}$) over low heat, followed by treatment with hydrochloric acid (HCl). The resulting solution was then sieved through a 10 µm sieve. A measured portion of the residues (was then carefully settled over three coverslips at the bottom of a beaker. Our method ensures the random settling of the residue material over the cover slips preventing the possible biases might arise during the species enumeration phase (see Lazarus 1994 for the detailed procedure).

2.4 Diatom species diversity and its analyses

2.4.1 Species level diversity

In both ecological and evolutionary research, the concept of diversity can have multiple meanings depending on the context of the study. In this paper, we define diversity as total species richness. Evenness, often also used as a component of diversity metrics is here treated as a separate variable. To reconstruct SO diatom diversity across four different SO sites – DSDP 511, ODP Sites 1090B, 748B and 689D– we analyzed 61 samples in which a total of 51,302 individual diatom valves were counted (see Fig. S1). Our methodology follows a simplified version of a previously established protocol (Renaudie and Lazarus, 2013), where specimens were identified and counted at the species level whenever possible. Counting continued until the species accumulation curve began to flatten, typically around 1000 or more specimens, although this threshold varied significantly based on diatom abundance. In cases where the total diatom abundance was too low in a given sample to achieve a flattened species accumulation curve, all specimens were counted exhaustively.

Raw diversity values almost always underestimate the true total diversity due to differences in sampling effort. To address these differences, we calculated Chao1 diversity estimators (Chao 1984) based on raw diversity values, along with 95% confidence intervals for each estimate. This approach allowed us to provide a more accurate representation of diatom diversity at each site, accounting for variations in sample coverage and ensuring a more robust comparison of diversity both spatially and temporally.

2.4.2 Taxonomy

As many of the specimens encountered were not known to have been named, or have published descriptions, informal counting categories were established as needed and documented with images and short keyword differential diagnoses. A full list of the counting groups is available on Zenodo (10.5281/zenodo.14608178, Özen et al., 2025).

2.4.3 Community similarity

Analyzing community similarity can often be a complex task due to the theoretical assumptions and opaque premises that underlie many of the metrics used. While straightforward presence-absence matrices can provide basic comparisons between samples, they often fail to capture the full dynamics of community structure. More complex metrics offer deeper insights, but they come with increased complexity that can obscure interpretations of the results. In the study of diatom communities, understanding the abundance and dominance of specific species over time is crucial for revealing changes in community dynamics.

To capture these nuances, we computed the Morisita-Horn index (Magurran 2004, p. 176) to assess self-similarity among our samples. The Morisita-Horn index is commonly used to measure the similarity between two communities, with values ranging 0 (no similarity) to 1 (complete similarity). This index allows us to track the evolution of diatom communities by analyzing both variations in species diversity and relative abundances over time. The Morisitia-Horn index is particularly suitable for our study because it is minimally affected by sample size (Wolda 1981; Magurran 2004, p. 176), making it reliable metric for examining community similarity across our SO samples.

2.4.4 Diversity Dynamics

Our species-level diversity data provide a unique opportunity to elucidate the diversity dynamics of SO diatoms. However, observed stratigraphic ranges of diatom species often underestimate the actual taxon ranges, complicating the detection of true extinction horizons. To address this evidence-of-absence versus absence-of-evidence dichotomy, we first estimated the possible ranges of species based on gaps in their occurrences. Gaps in taxon occurrences in stratigraphic series have been shown to be a useful source of information to estimate true taxon first and last occurrences (Marshall 1997). Specifically, we calculated the median (50th percentile) of the gaps in each species' range, regardless of whether these gaps were due to sampling limitations or true absences. This median gap was then added to the first appearance datums (FAD) and last appearance datums (LAD) of each species to provide more accurate estimates of their stratigraphic ranges. Although there is no definitive method to eliminate potential biases in detecting true FADs and LADs, decades of micropaleontological research suggest that this straightforward yet effective protocol minimizes potential pitfalls (Marshall, 1997).

Based on these estimated stratigraphic ranges, we calculated Foote's boundary crosser extinction rates (per lineage-million-years, Foote 2000) by dividing the taxon ranges into equal 0.5 Myr intervals, hereafter referred to as 'time bin(s)'. Binning helps avoid overly noisy signals and maintains a certain level of precision in the case of our SO samples. However, despite our effort to mitigate potential biases, uncertainties in taxon ranges can significantly affect the extinction rates seen in the samples and/or time-bins closer to the observed and estimated ends of taxon ranges. This is often termed as the edge-effect, that extinction and/or origination rates can show artificially high values in the last and first samples respectively.

To achieve a more comprehensive understanding of SO diatom diversity dynamics, we focused on species that are either shared across all studied sites or within specific subsets of sites, such as those common to DSDP 511 and ODP 689D. This approach is particularly valuable given the significant gaps in the early Oligocene sequences at the sub-Antarctic sites DSDP 511 and ODP 1090B, which limit our ability to track diatom community changes across the E/O. In contrast, the Antarctic sites provide a continuous stratigraphic record through the E/O, with samples extending to younger intervals, approximately dated to 30 Ma, thereby enabling a more consistent analysis of diatom diversity throughout this transition. By concentrating on species shared across these different oceanographic settings, we also aim to present broader, SO wide perspective on diatom evolution, reducing the influence of site-specific environmental variabilities in our interpretations.

The metrics and analyses described were calculated using codes written in Python (Python Software Foundation, version 3.11, available at http://www.python.org) and Julia (version 1.10; Bezanson et al., 2012, available at https://julialang.org/). The functions developed for these analyses are publicly available in the GitHub repository: https://github.com/oezenvolkan/Oezenetal2025

2.4.5 Literature-based diversity estimates

For the sake of comparison with prior knowledge on EOT Southern Ocean diatoms, we also computed diversity and extinction rates for diatoms based on what is recorded in the Neptune Database (hereafter NSB; Renaudie et al. 2020, 2023). We selected only the records whose paleolatitude during the time bin of interest fell below 45°S. Sites with poor or very poor age models were discarded. The diversity reported from NSB is the literal number of species encountered per 1Myr bins while the extinction rate was calculated using Foote (2000) metrics on SQS-subsampled data (with a quota of 0.7, over 100 trials; Alroy 2010).

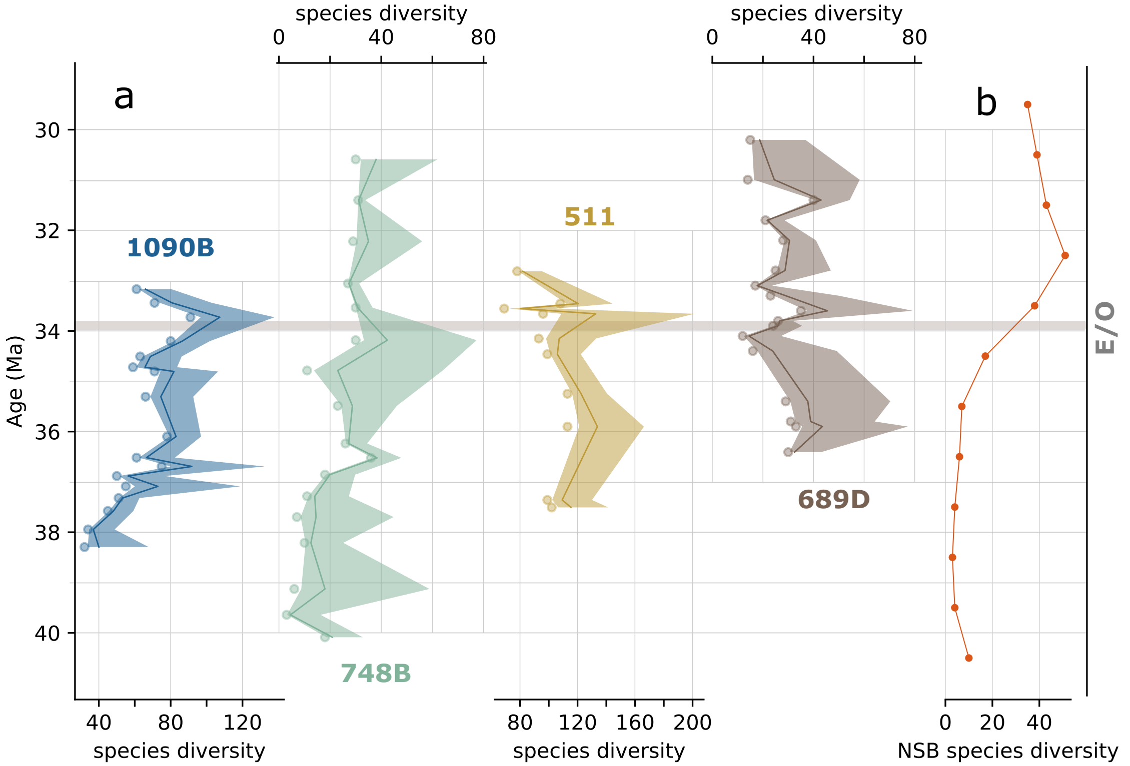

Fig. 2 a) Observed diversity (scatter points) and Chao1 diversity estimates with 95% confidence interval of each site. b) NSB species diversity for the Southern high latitudes. Sites are identified in this and subsequent figures by color: blue for 1090B, green for 748B, yellow for DSDP 511, and brown for 689D. The horizontal gray line marks the Eocene–Oligocene boundary (E/O).

3 Results

3.1 Overall diatom diversity and prior works

Observed and estimated species diversity for each site is summarized in Fig. 2, with approximately 280 diatom species recorded in total. Chao1 estimates (see Section 2.4.1) suggest actual diversity may be even higher (Fig. 2). Our new diversity findings reveal a substantially greater diversity in the Southern high latitudes compared to previous studies. For example, the widely used NSB database, which is often referenced in paleo-micropaleontological studies, documents only around 50 species across the EOT in the SO between 40 and 30 Ma (Fig. 2b).

Our results, focused specifically on the Southern high latitudes, show at least three times higher diversity than previous studies that have discussed and inferred diatom species diversity and turnover rates on a global scale (e.g., Renaudie et al. 2018). This discrepancy highlights the importance of comprehensive species level diversity surveys for reconstructing diatom diversity, rather than relying solely on biostratigraphic work-based diversity compilations.

Furthermore, diversity values clearly differ among our studied sites. Sub-Antarctic Atlantic sites (DSDP 511 and ODP 1090) exhibit significantly higher species diversity compared to the Antarctic sites (ODP 689 and 748;Fig. 2a). Here, we focus on the overall trends in species diversity across each site and on composite species diversity representing those shared by all studied sites (Fig. 3a and 3b), rather than overinterpreting results from individual samples. Exact diversity values and Chao1 estimates are presented in the Supplementary Data 1.

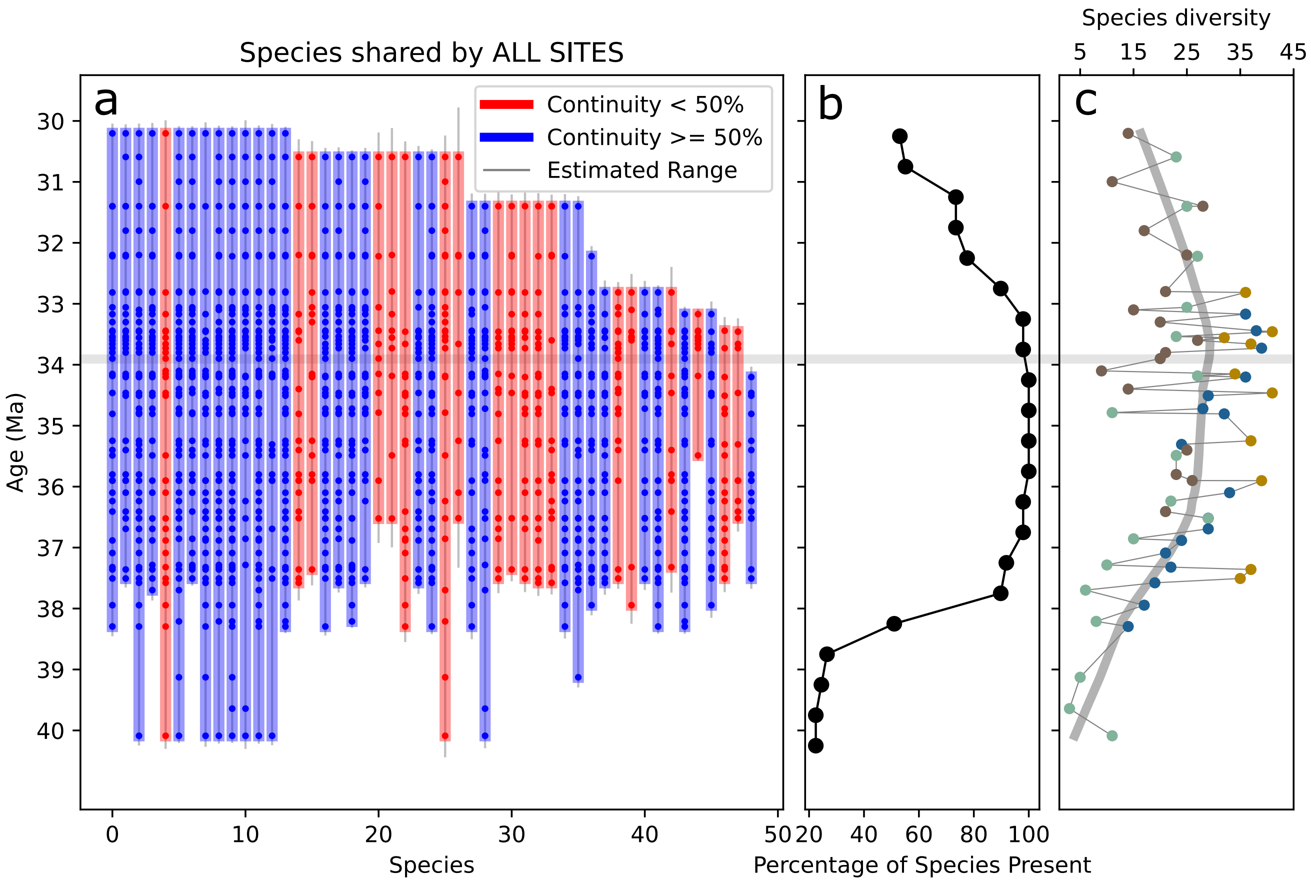

Fig. 3 a) The vertical bars show the stratigraphic ranges of diatom species observed at all four Southern Ocean sites. Each vertical bar (blue or red) represents the observed stratigraphic range of a single species, defined by its first and last occurrences. The thin horizontal blue lines indicate all sampled horizons. A dot is plotted at the intersection of a species' range and a sampled horizon if the species is present in that sample. The color of each vertical bar reflects the proportion of sampled horizons within the species' range in which it is observed. Blue bars represent that if the species occurs in more than 50% of the horizons it spans, and red otherwise. Thin vertical gray lines show gap-corrected range estimates for each species (see Section 2.4.4). The gray horizontal line marks the Eocene/Oligocene Boundary (~33.9 Ma). b) Percentage of species presence in each 0.5 Ma time bin. c) Observed species diversity filtered by species shared by all sites. The colors of each data point represents from which site that specific diversity data come from, and color code follows the Fig. 2, where blue for 1090B, green for 748B, yellow for DSDP 511, and brown for 689D.

3.2 Patterns of species diversity change

Across the four SO sites, we identified about 280 diatom species, but only roughly 50 occur consistently at all sites, highlighting strong regional differentiation. The sub-Antarctic sites DSDP 511 and ODP 1090 exhibit higher diversity, each showing two clear richness peaks at ~36-36.5 Ma and again at ~33.7 Ma, separated by a marked decline. Antarctic sites ODP 689 and ODP 748 have lower diversity throughout the studied interval, especially in late-Eocene samples. At ODP Site 689, diversity falls in the latest Eocene and then rises to a peak at 33.6 Ma, synchronous with the second peaks at sites DSDP 511 and ODP 1090. ODP Site 748 follows a similar pattern, reaching a minimum in the latest Eocene, at 34.7 Ma and show an increase following the E/O. Taken together, the records show a consistent sequence: diversity climbs in the late Eocene

(~36.5-36 Ma) falls between 34.5 and 34 Ma, and rises again around the EOT. Composite species diversity, which combines observations from all sites, reveal broader trends that might otherwise be obscured by site-specific variability (Fig. 3c). This composite record clearly shows an increase in species diversity leading up to the E/O, making a turning point after which diversity begins to decline.

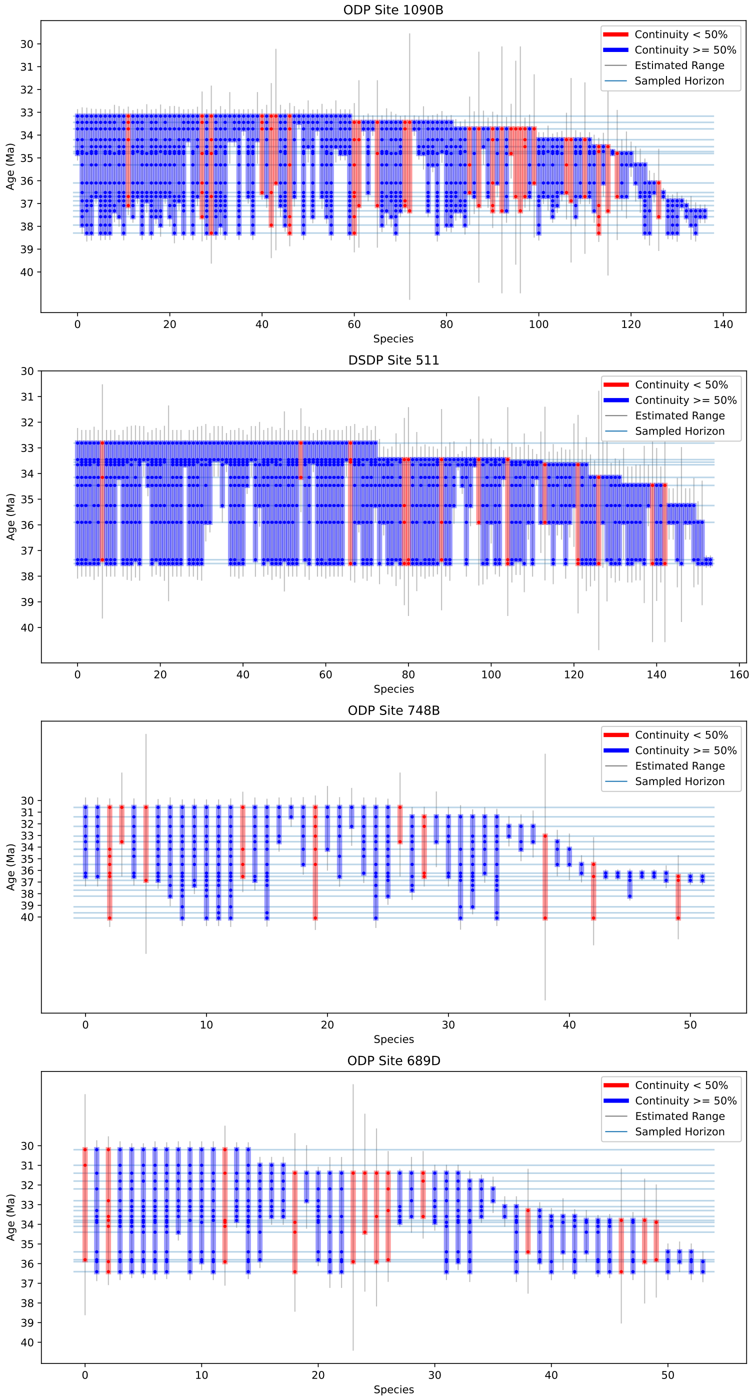

Fig. 4 Stratigraphic ranges of diatom species at each study site. Each vertical bar (blue or red) represents the observed stratigraphic range of a single species, defined by its first and last occurrences at the corresponding site. The thin horizontal blue lines indicate all sampled horizons. A dot is plotted at the intersection of a species' range and a sampled horizon if the species is

present in that sample. The color of each vertical bar reflects the proportion of sampled horizons within the species' range in which it is observed. Blue bars represent that if the species occurs in more than 50% of the horizons it spans, and red otherwise. Thin vertical gray lines show gap-corrected range estimates for each species (see Section 2.4.4). Species recorded in only a single horizon are not shown, as stratigraphic continuity cannot be assessed for single-occurrence taxa.

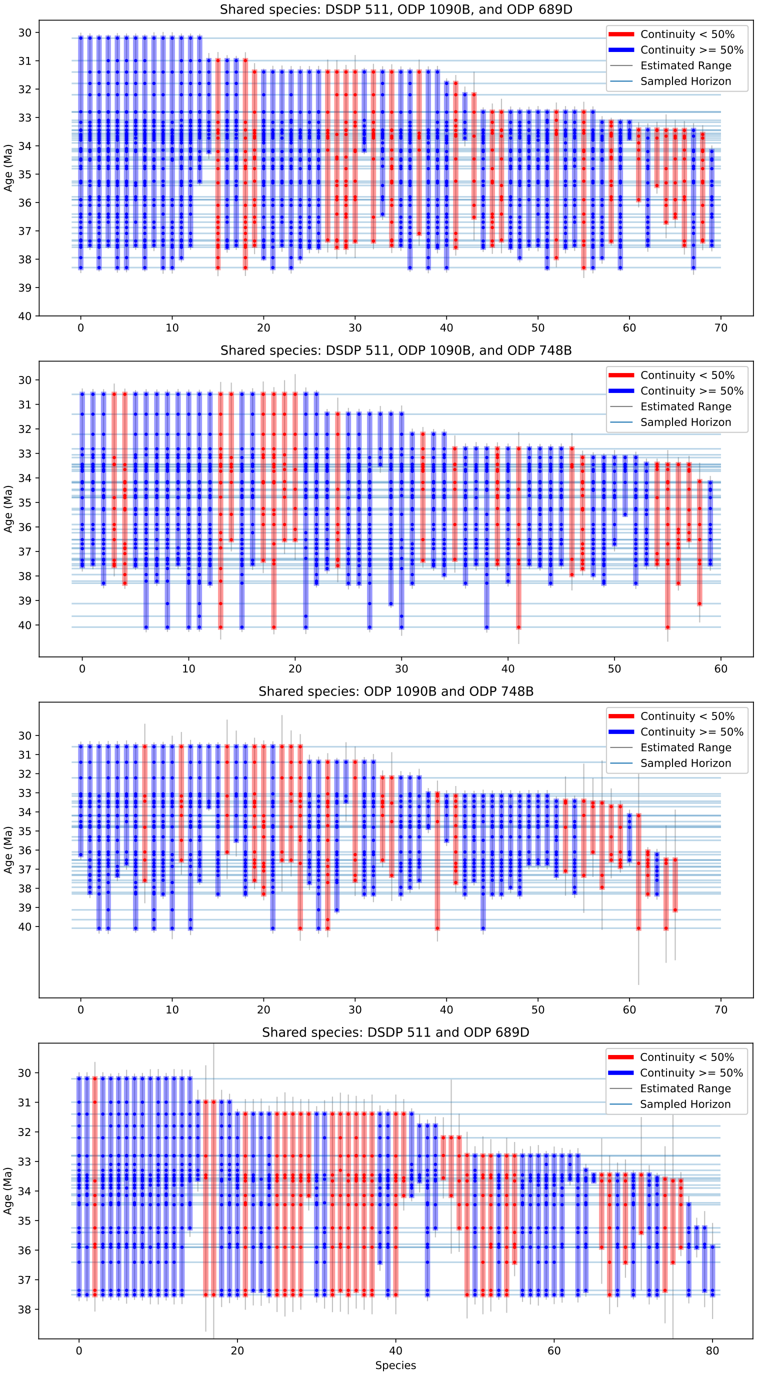

Fig. 5 Stratigraphic ranges of diatom species shared across study sites. This plot follows the same format and visual convention as Fig. 4 but includes only those species that are observed at more than one site. For explanation of bar colors, sampling horizons, continuity calculation refer to the caption of Fig 4.

3.3 Diversity dynamics (extinctions)

Extinction rates calculated from updated stratigraphic ranges (see Section 2.4.4 Diversity Dynamics; Fig. 4 and Fig 5a) show no extinctions during the late Eocene or within the 34-33.5 Ma interval spanning the E/O (Fig. 6a). However, extinction rates consistently increase shortly afterward, peaking within the 33-32.5 Ma interval (Fig. 6a). This peak is evident across all sites combinations analyzed, including the approximately 50 species common to all four sites. The exact values of extinction rates are presented in the Supplementary Data 2.

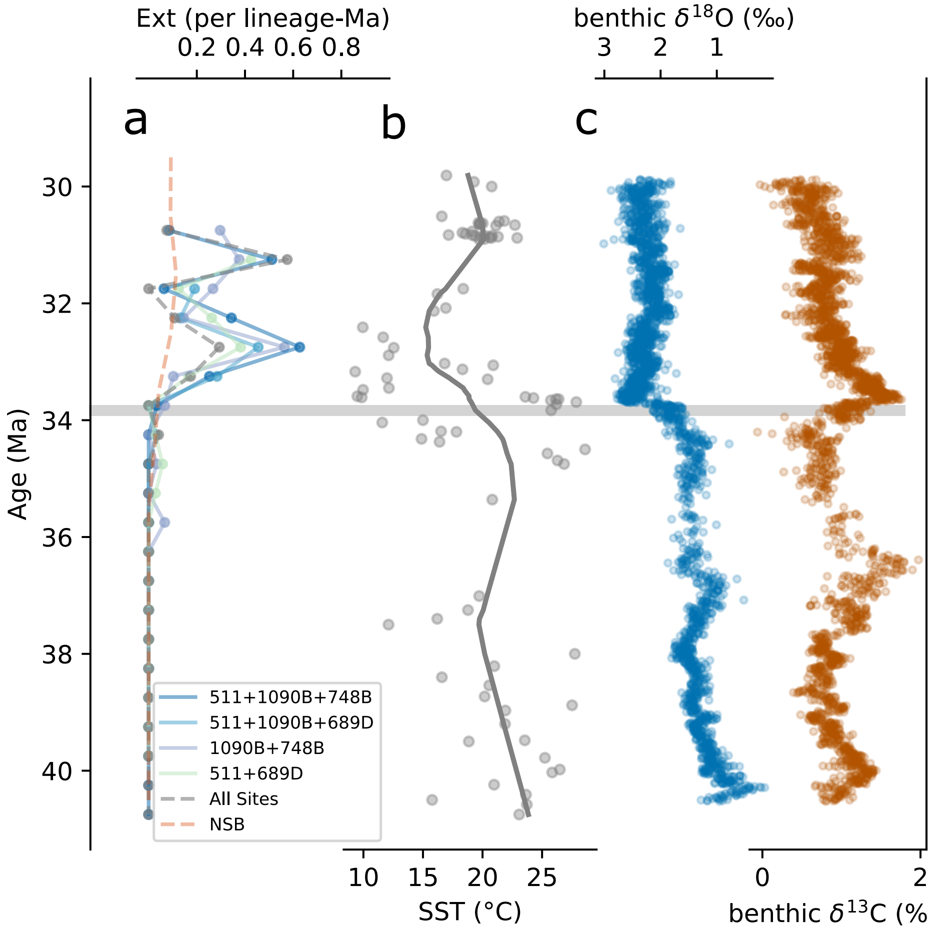

Fig. 6 a) Foote boundary crosser extinction rates b) Southern high-latitude SST compilation from Auderset et al. (2022), with the trend line generated using the Lowess function from Python's statsmodels module (Seabold and Perktold 2010) c) Global

composite benthic $\delta^{18}O$ and $\delta^{13}C$ from Westerhold et al. 2020. The horizontal gray line marks the Eocene–Oligocene (E/O) boundary

Between ODP Sites 1090B and 748B, 14 of the 58 shared species present in the 33-32.5 Ma time bin went extinct by the end of this time-bin. Similarly, between DSDP 511 and ODP 689, 12 out of 69 shared species went extinct within the same interval. Subgroup analyses involving combinations of three sites (DSDP 511–ODP 1090–ODP 689 and DSDP 511–ODP 1090–ODP 748; Fig. 5 and Fig. 6a) reinforce this finding, consistently identifying the 33-32.5 Ma interval as a robust extinction peak. Extinction rates calculated for younger intervals beyond 32.5 Ma may calls caution due to potential edge-effects related to fewer available samples. Overall, there is a consistent extinction event across the SO sites within the 33.32.5 Ma interval, approximately 1 Myr after the E/O.

3.4 Community changes

To identify intervals of community turnover and compositional stability, we calculated Morisita-Horn similarity values for each site (see Section 2.3.4 and Supplementary Data 3). This analysis sheds light on the timings of community transitions, including relative abundances, and their relation to species diversity patterns (Fig. 7). At DSDP Site 511, sample similarities remain above 0.6 throughout most of the studied interval, indicating stable species composition and relative abundances (Fig. 7a). A marked drop in similarity appears around 35 Ma, separating older and younger sample clusters. Following this transition, values remain cyclic but relatively high, and Oligocene samples return to higher self-similarity levels.

At ODP Site 1090, changes in community composition occur more sharply (Fig. 7b). The first pulse of species richness around 36.7 Ma marks a sharp transition, with dominance (near 25%) of the Eocene genus *Pyxilla*. This genus dominated blooms for an extended period between approximately 36.7 and 34.7 Ma (Fig. 7b, see also Fig. S2 for *Pyxilla* relative abundance). Similarity values at ODP 1090 reveal higher self-similarity across this interval. At the end of this self-similar unit, another sharp transition in community composition occurs around 34.7 Ma, where similarity values sharply decrease. At ODP 748, similarity values fluctuate without forming coherent clusters. No sustained intervals of community stability are identified (Fig. 7c). In contrast, ODP Site 689 shows two sharp transitions, including a pronounced decrease in similarity between between 35.9 and 35.8 Ma (Fig. 7d). Both Antarctic sites show cyclic similarity patterns across the studied interval.

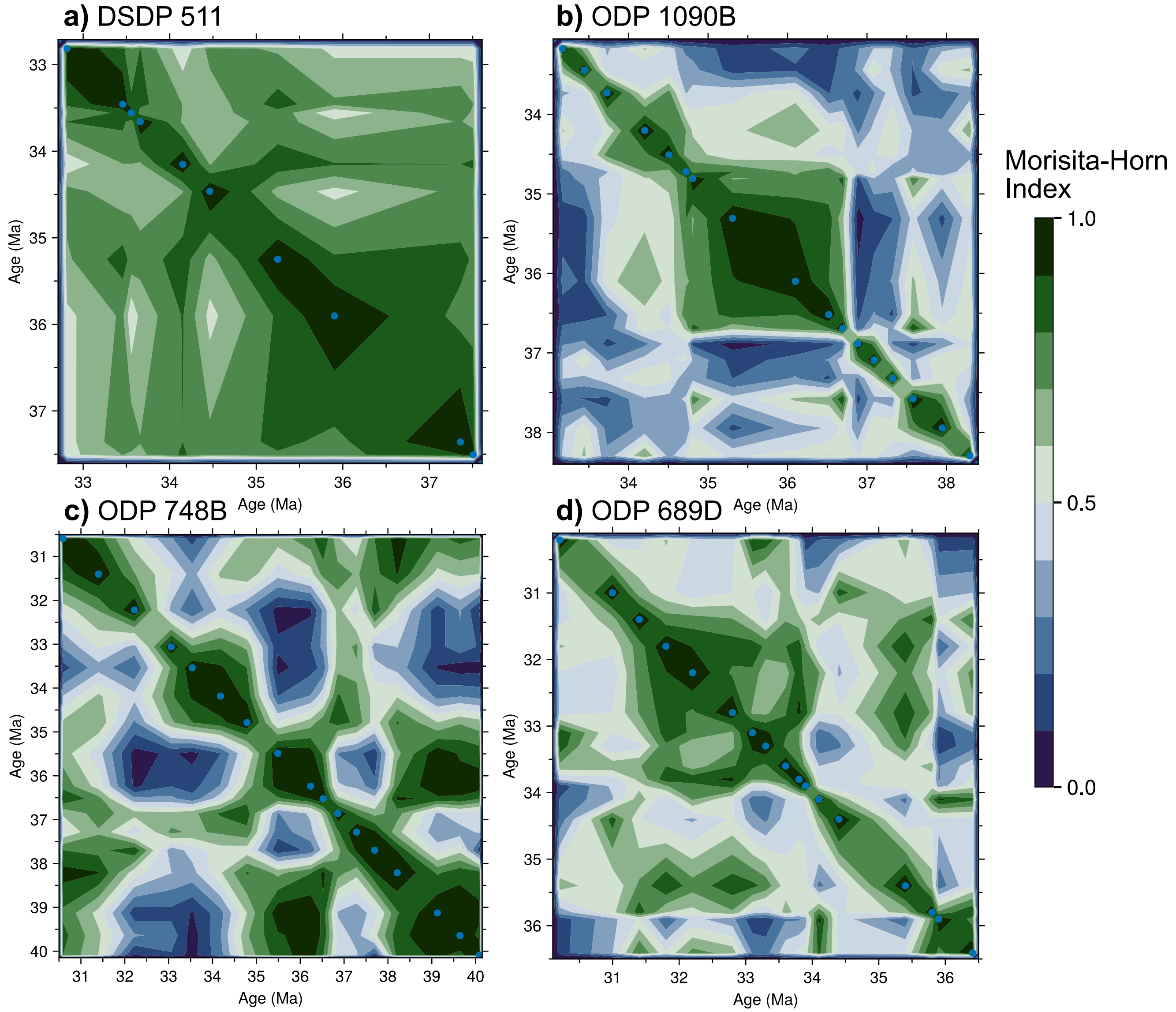

Fig. 7 Temporal self-similarity of diatom assemblages at four SO sites. Contour plots give pair-wise Morisita-Horn similarity values for all sample combinations at each site. In each panel, both axes are sample age (Ma), points on the main diagonal therefore compare a sample with itself (similarity = 1). Color code for similarity values ranges from dark green (high similarity, nearly identical communities) through dark blue (low similarity, distinct communities), as indicated by the scale bar common to all panels. Blue dots mark the positions of the analyzed samples, and the surrounding contours are interpolated between these empirical points. Continuous green zones therefore denote intervals of higher similarity, while abrupt color changes highlight rapid compositional shifts; for example, ODP 1090B exhibits a relatively stable interval between about 37 and 34.5 Ma bounded by sharp transitions. Pair-wise Morisita-Horn similarity values for each site is provided in Supplementary Data 3.

4. Discussion

4.1 Spatial and temporal trends in SO diatom diversity

Our updated record documents approximately 280 diatom species from the SO across the late Eocene – early Oligocene (~40-30 Ma), significantly exceeding previous estimates. For comparison, the Neptune database (Renaudie et al., 2020, 2023), essentially a compilation of biostratigraphic studies, extensively used in plankton evolution studies (e.g., Allen et al., 2006; Liow and Stenseth, 2007; Cermeño & Falkowski, 2009; Lazarus et al., 2014; Rineau et al., 2022), records approximately 50 species (including open nomenclature) for the same interval. The full species richness of SO diatoms from this interval is approximately six times higher than previously compiled diversity, with an estimated range most plausibly between 300 and 470, revealing far greater complexity and richness than previoulsy recognised. We acknowledge that species boundaries in some groups remain challenging, and while our identifications follow consistent light microscopy criteria, future SEM-base revisions may refine or combine some of these morphospecies.

Despite overall high diversity, considerable variation exists among the studied sites. This regional diversity contrasts likely reflect a combination of local settings and paleo-circulation. Each site differs in water depth and distance from the continent, factors that can modulate nutrient supply and preservation. Additionally, the distinct late-Eocene oceanographic regime, characterized by partially open Drake Passage and Tasmanian gateways (e.g., Hodel et al., 2021; Evangelios et al., 2022, 2024), would have produced strong regional hydrographic contrasts. During this time, the SO circulation likely consisted of large sub-polar gyres, such as the Ross and Weddell Gyres, recirculating water within individual basins rather than circulating around Antarctica (Sauermilch et al., 2021). In modern SO, ACC and its fronts, mixing surface-water around Antarctica and smooths east-west gradients in temperature, nutrients, and plankton composition (e.g., Freeman et al., 2019). The absence of such a continuous current during the late Eocene would have fostered sharp regional gradients, influencing diatom assemblage compositions.

Indeed, dominant species compositions differ significantly among sites (see Fig. S3), indicating local environmental control. For example, at sub-Antarctic ODP Site 1090, Genus *Pyxilla* dominates, forming nearly one-third of the assemblage (Fig. S2 and S3). Conversely, *Pyxilla* is almost absent at Antarctic-proximal sites ODP 689 and 748. At DSDP Site 511, it exhibits high morphological variability (Gombos and Ciesielski, 1983), further underscoring regional differences. Towards the latest Eocene and early Oligocene, *Cestodiscus* species increased markedly at all sites, becoming particularly dominant at Antarctic-adjacent sites. This widespread rise suggests an emerging common ecological response across the SO, although regional differences in dominant species composition remain prominent. Although *Cestodiscus* has been associated with surface cooling (e.g., Fenner, 1986), similar increase in abundance occur in equatorial Atlantic (Fenner, 1981; 1986) lacking evidence of sea-surface cooling (Pearson et al., 2007; Liu et al., 2009; Cramwinckel et al., 2018), suggesting that other factors, such as changes in silica supply and/or nutrient stoichiometry, may also be at play. Importantly, this coherent rise in

Cestodiscus is not mirrored by productivity trends inferred from recent paleoproductivity studies, which highlight divergent trajectories among SO sites during the E/O (Bryłka et al., 2024; Rodrigues de Faria et al., 2024). Taken together, these contrasting assemblage patterns point to a dynamic interplay: local hydrographic regimes shaped site-specific assemblages, while superimposed, possibly geochemical, SO wide forcing produced coherent taxonomic signal. This dual structure, spatial heterogeneity and temporal synchrony, parallels the temporal diversity shifts (below) and extinction dynamics (discussed in Section 4.2), where both regional and SO-scale processes appear to have shaped diatom evolution across the EOT.

Despite these regional differences, a common temporal pattern emerges across all sites, suggesting broad-scale oceanographic reorganization. Diatom diversity increased notably between ~36.5-36 Ma, declined toward the E/O (~34-34.5 Ma), and rose again around the boundary itself. This consistent temporal trend aligns closely with known episodes of environmental and productivity shifts documented throughout the SO (Anderson and Delaney, 2005; Diekmann et al., 2004; Diester-Haass and Zahn, 1996; Rodrigues de Faria et al., 2024). At ODP Site 1090, a two-pulse pattern in opal productivity at ~37 and ~34 Ma corresponds closely with our diversity results, reinforcing the hypothesis of significant oceanographic reorganization linked to the proto-ACC development (Rodrigues de Faria et al., 2024), stimulating apparent siliceous plankton productivity (e.g., Anderson & Delaney, 2005; Diekmann et al., 2004; Pascher et al., 2015), and leading to observed increases in diatom diversity across the SO.

Importantly, these diversity shifts were not limited to diatom communities alone. Similar temporal patterns have been observed in radiolarian communities from the southwest Pacific SO (Pascher et al. 2015), reflecting a broader ecological and evolutionary response among siliceous plankton to substantial reorganizations in ocean circulation across the EOT. Our findings suggest the establishment and episodic intensification of the proto-ACC likely played a central role in shaping diversity trends across the SO, imprinting a common signal despite regional variations in assemblage composition and environmental settings. Thus, diatom diversity during the EOT appears to have been driven by both local environmental factors and large-scale oceanographic changes, highlighting they dynamic interplay between regional conditions and SO-wide processes.

While spatial patterns in assemblage composition provide ecological context, interpreting diversity trends across the EOT also requires careful consideration of preservation. Water depth is often considered a key factor in biogenic opal preservation, as biogenic silica remains exposed to silica-undersaturated water column. Despite this, DSDP 511 and ODP 1090, which record significantly greater paleo-water depths relative to the shallower ODP Sites 689 and 748 (Fig. 1), show better diatom preservation, particularly in the late Eocene (Fig. S1). This inverse relationship between diatom preservation and paleodepth points to sedimentation rate as the more influential actor in biogenic opal preservation in these sites during the EOT, rather than water depth alone. The variability in diatom preservation across the studied sites, influenced by differing oceanographic conditions, reflects the inherent dynamics of diatom preservation, where physical oceanographic factors are critical (e.g., Ragueneau et al. 2000; Warnock and Scherer 2016). Diatom productivity and community abundance also play significant roles, as communities must reach a threshold density to form aggregates, initiating effective sequestration (Kiørboe, 1993; Jackson, 2001).

4.2 Changes in community compositions and its implications across the EOT

Our quantitative abundance data allow us to directly compare diversity trends with changes in community composition. Fig. 7 shows the contour map of the similarity values within sites. The most striking shifts occur at ODP Site 1090 (Fig. 7a), where samples between ~37 and 34.5 Ma display high self-similarity, suggesting a community stability. This stability is mirrored in the diversity values, which remain constant across this interval (see Fig 2a). Note that at ODP Site 1090, the intervals around 37 Ma and 34.5 Ma marks bursts in opal accumulation (Anderson and Delaney, 2005; Diekmann et al., 2004), which coincide with the observed increase in diatom diversity (Fig. 2a). Yet our similarity analysis reveals that the underlying diatom community was changing, despite stable diversity values, indicating that the rise in diversity was not simply a consequence of increased productivity, but also reflected shifting species composition in response to environmental change.

A central empirical evidence underlying the hypothesis that diatoms contributed to EOT cooling through enhanced productivity and carbon sequestration (Salamy and Zachos, 1999; Scher and Martin, 2006; Rabosky and Sorhannus, 2009) is the shifts in diatom-based silicon isotope values at ODP 1090. These shifts have been interpreted as evidence of increased silicic acid utilization, suggesting greater diatom-driven export production, and by extension, intensified CO_2 drawdown (Egan et al., 2013). However, our results call for caution. It has been demonstrated that silicon isotope values can be highly species-specific, with up to 70 percent of total variation in isotope measurements being attributed to species composition alone (Sutton et al., 2013). The close correspondence between shifts in isotopic values and changes in diatom community structure raises the possibility that the observed isotopic signal reflects ecological turnover rather than increased nutrient utilization per se.

Within-site community similarity patterns exposecontrasting environmental responses across the SO. DSDP Site 511 exhibits a stable community composition with consistently high similarity values, matching uniform evenness and consistently good preservation (Fig. 7b and Fig. S4). In contrast, Antarctic-proximal ODP Sites 689D and 748B show much broader variability (Fig. 7c and 7d). Part of this variation reflects taphonomy, horizons with few specimens show lower similarity to other levels, inflating apparent turnover. However, substantial fluctuations also occur among well-preserved, high-count samples, demonstrating that the observed variability is not solely a taphonomic artifact, but instead reflects community response.

Diatom evolutionary dynamics and community composition at ODP Sites 689D and 748B are particularly interesting. The most pronounced changes in opal productivity at these sites occur at the E/O , where the opal accumulation values approached values seen in the sub-Antarctic sites (e.g., ODP Site 748, Bryłka et al., 2024). Despite this, diversity values do not show any substantial increase in accordance with the increasing opal accumulation rates. In contrast, diversity at ODP Site 748B remains remarkably stable, matching the levels observed in the late Eocene samples. Despite variability in the early Oligocene, diversity values at ODP Site 689 remain broadly consistent with those from the Eocene. This suggests that diversity values and community composition observed at these sites across the Eocene are not primarily driven by changing rates of opal accumulation or preservation.

4.3 Diatom extinction in the early Oligocene

Despite the variations observed across the studied sites, there is a unifying event within the time-bin 33-32.5 Ma where all subsets of the shared species show a persistent extinction event (Fig. 6a). This event is particularly robust against the edge-effect, a common challenge in the fossil record where the true last occurrences of species may be obscured by sampling limitations. In our case, the subsequent five time bins of nearly two dozen samples following the 33-32.5 Ma interval, and the use of only geographically widespread species provide a solid control. The continued absence of these species over a 2.5 Myr span, till ~30 Ma, reinforces the conclusion that 33-32.5 Ma interval marks an extinction event. Although extinction rates remain high in our records following the E/O, the values after the 33-32.5 Ma bin may be affected by edge effect. We therefore treat these post- 33-32.5 Ma values with caution and exclude them from further analyses and interpretations.

Diatom extinction rates remain low across the E/O itself (Fig. 6a), consistent with limited SST drop in the regions such as the Falkland Plateau and Maud Rise (~1 °C from Tibbett et al., 2023) and with southern high-latitude SST compilations indicating relatively stable conditions across the boundary (Fig. 6b; Auderset et al., 2022). This SST stability aligns with our extinction patterns, suggesting that SO diatoms did not experience a major extinction pulse at the E/O. This is consistent with previous studies showing that high turnover typically requires more substantial environmental disruption in radiolarians (e.g., a ~6 °C threshold is observed by Trubovitz et al., 2020). In contrast, extinction rates rise sharply in the following 33-32.5 Ma interval, coinciding with the lowest SST values of the studied interval and a ~6 °C decline from late Eocene conditions (~21±1 °C to ~15 °C, see Fig 6b). This close correspondence between sustained cooling and elevated extinction rates (see Fig. 6a and 6b) suggests that diatom communities struggled to adapt to the changing surface ocean conditions. Because these extinction rates are based on species shared across multiple sites (see Methods Section 2.4.4 Diversity Dynamics), the disruption in diatom communities may have been even more pronounced than the data suggest, as widespread species generally exhibit higher resistance to extinction (e.g., McKinney, 1997). These patterns underscore the role of temperature in shaping community persistence and support broader view, as also shown by Crampton et al. (2016), that SO diatom communities are resilient to short-term climate variability but are vulnerable to large-scale shifts in mean climate state. The early Oligocene extinction pulse thus appears to reflect a threshold response to large-scale environmental reorganization in the SO, with proxy data pointing to SST decline as the likely driving mechanism.

An extinction pattern comparable to our results might be expected if there had been a sharp drop in opal productivity during the earliest Oligocene, particularly at Antarctic ODP Sites 689D and 748B, which provide majority of the Oligocene samples. However, previous studies indicate that these regions did not experience such a decline; instead, they show evidence of substantial increase in opal productivity during this period (e.g., Salamy & Zachos, 1999; Bryłka et al., 2024; Rodriguez de Faria et al., 2024). This absence of productivity drop suggests that the extinction patterns observed in the 33-32.5 Ma time bin are unlikely to be a result of reduced opal deposition. Rather, these patterns likely reflect diatom community responses to environmental and/or ecological perturbations with cooling SSTs, and were independent of nutrient availability or productivity declines.

5 Conclusions

Our study presents a comprehensive analysis of diatom diversity and community evolution across the Atlantic and Indian Ocean sectors of the SO during the late Eocene to early Oligocene interval. Using newly generated species-level diversity data, we explore the previously undocumented diversity of SO diatoms, offering new insights into late Paleogene diatom ecosystems. Despite representing distinct oceanographic settings and depositional characteristics, all studied sites exhibit a shared pattern in diatom community composition shifts with notable intervals around 37-36 Ma and 34 Ma, suggesting the influence of large-scale environmental changes affecting siliceous planktoWhile a unifying trend in diatom diversity emerges across the SO, the distinct variations in community composition and diversity levels across sites reveal the intricate interplay between global shifts in sea surface temperature and ocean circulation, and regional environmental forces such as upwelling intensity, nutrient availability, and preservation conditions. These findings remind us that even global patterns in Earth's history are woven from finely tuned regional dynamics and ecological responses.n communities across the SO.

The data reveal a significant extinction pulse among SO diatom communities approximately 1 Myr after the E/O. This event coincides with the lowest SSTs recorded in the southern high-latitude compilations during the EOT, marked by a cooling of ~6 °C compared to the preceding late Eocene average. A shift of similar magnitude has been linked to extinction response in Neogene radiolarian communities (Trubovitz et al., 2020), suggesting a broadly applicable thermal threshold for marine plankton. While diatoms initially persisted through the relatively stable conditions at the E/O, this subsequent cooling appears to have suppressed the thermal tolerance of even widespread and previously resilient taxa. The absence of a notable decline in opal productivity during the earliest Oligocene further supports the interpretation that thermal stress, rather than nutrient limitation or preservational bias, was the primary driver of extinction. Our findings thus highlight the critical role of changing SSTs in shaping plankton fitness, showing that boundary conditions for biodiversity are intimately tied to the physical constraints of the climate system.

Code and Data Availability

All raw data and associated taxonomical appendix are readily available on Zenodo repository (Özen et al., 2025;). The functions developed for all analyses are publicly available on GitHub repository (https://github.com/oezenvolkan/Oezenetal2025) and Zenodo (10.5281/zenodo.14605789).

Supplement

The supplement related to this article is available online at:

Author contributions

VÖ collected and analyzed the diversity data and drafted the manuscript. All authors contributed to revising and editing the manuscript.

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