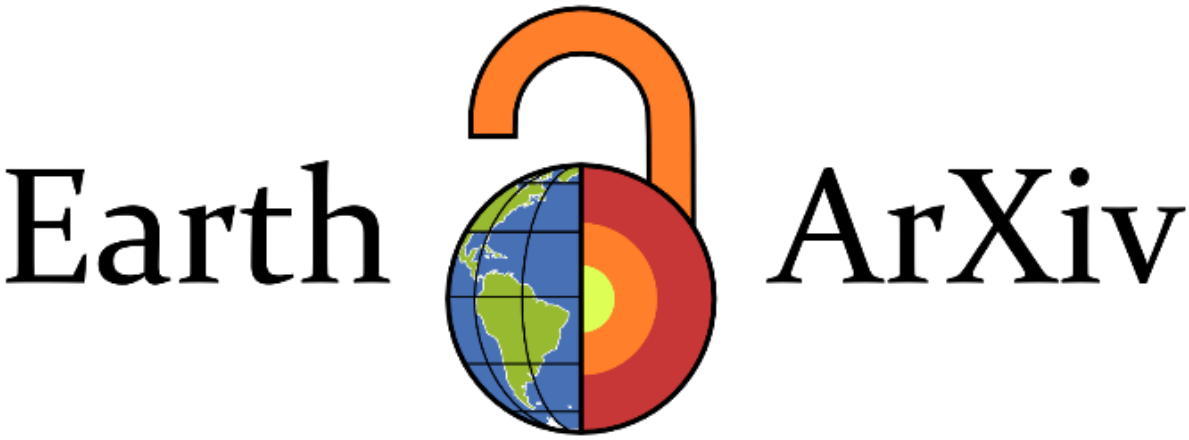

Life After Impact: Paleobathymetric Gradients in Post-K/Pg Nannoplankton Boom-Bust Successions

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Abstract

The Cretaceous/Paleogene (K/Pg) bolide impact ~66 Ma caused the near-demise of calcareous nannoplankton – key primary producers and major components of the biological pump that exports organic and inorganic carbon to the deep sea. Despite their ecological significance, resolving the exact impact of nannoplankton's mass extinction on ecosystem structure and function is complicated by marked global heterogeneity in paleoecological and biogeochemical responses. To explore this further, we generated a ~3.7 Myr nannofossil record from sediment cores at the Global Stratotype Section and Point for the basal Danian near El Kef, Tunisia, representing an outer continental shelf setting in the peri-Tethys Ocean. Our data reveal a series of low-diversity, high-abundance assemblages that persisted throughout the study interval. Although such boom-bust successions typify Northern Hemisphere nannoplankton recovery, statistical comparison with published datasets indicates that their duration – and the sequence of taxa comprising them – were location-specific and predominantly controlled by paleobathymetry, namely a site's position along a shelf-to-open-ocean transect. We hypothesize that this spatial variability reflects faster restoration of biological pump efficiency in open-ocean versus continental shelf settings, which in turn led to a quicker reduction in surface ocean nutrient availability. This would have encouraged the earlier proliferation of specialist, low-nutrient-adapted nannoplankton taxa with larger average cell volumes in open-ocean environments, further boosting pump efficiency via organic matter ballasting. Therefore, future research should prioritize disentangling the causal relationships between carbon cycling and nannoplankton recovery following the K/Pg extinction through rigorous integration of high-resolution biogeochemical time series and abundance-weighted nannofossil cell-volume data.

Plain Language Summary

The mass extinction that killed the dinosaurs ~66 million years ago also nearly wiped out calcareous nannoplankton, tiny algae that live in the surface ocean. These organisms are vital because they support marine food webs and help transport carbon to the deep sea when their shells sink. Understanding how nannoplankton recovered after the extinction is challenging because species

appeared and disappeared at different times across regions, and the marine carbon cycle recovered unevenly. To investigate this, we studied nannofossils from sediments spanning ~3.7 million years after the extinction at El Kef, Tunisia, which preserve an exceptional recovery record. We identified four recovery phases, each dominated by a different nannoplankton species. We suggest these shifts were linked to changes in how efficiently carbon was transported from the surface to the deep ocean. Comparing our results with other Northern Hemisphere sites shows that recovery patterns depended on distance from shore. In deeper open-ocean settings, nannoplankton species increased in size earlier than in shallower coastal areas. As larger shells sink faster and enhance carbon transport, our findings suggest that both nannoplankton communities and the carbon cycle recovered more quickly in the open ocean than nearshore environments.

Key Points

- Nannoplankton boom-bust successions lasted for >~3.7 million years after the Cretaceous/Paleogene mass extinction at El Kef, Tunisia.
- A global comparison reveals that the exact sequence of taxa within boom-bust successions was primarily controlled by paleobathymetry.
- Paleobathymetric variability in boom-bust succession duration and cell size is likely intrinsically tied to biological pump recovery rates.

1. Introduction

The bolide impact at the Cretaceous/Paleogene (K/Pg) boundary ca. 66 million years ago (Ma) – which most famously wiped out all non-avian dinosaurs (e.g., Alvarez et al., 1980; Chiarenza et al., 2020; Hull et al., 2020; Morgan et al., 2022; Schulte et al., 2010) – also led to the largest mass extinction in the evolutionary history of calcifying marine plankton (i.e., calcareous nannoplankton and planktic foraminifera) with >90% species being eliminated (e.g., Bown et al., 2004; Fraass et al., 2015; Lowery et al., 2020; Molina et al., 1998; Perch-Nielsen et al., 1982; Thierstein, 1982). In comparison to marine calcifiers, siliceous and organic-walled plankton groups such as diatoms, radiolarians and dinoflagellates, suffered much lower extinction rates, likely due to the ability of some species to form resting cysts (Lowery et al., 2020; MacRae et al., 1996; Sims et al., 2006). Calcareous organisms living at the seafloor (e.g., benthic foraminifera) also did not experience a mass extinction at this time (e.g., Alegret & Thomas, 2013; Alegret et al., 2012, 2022; Culver, 2003; Thomas, 1990), underscoring that the K/Pg extinction predominantly affected marine calcifiers living in the upper water column (e.g., Lowery et al., 2020). This high level of extinction selectivity suggests that short-lived, impact-induced surface ocean acidification may have been an important kill mechanism (Brugger et al., 2021; Henehan et al., 2019) with impact-winter and decreased light availability caused by the injection of dust and aerosols into the atmosphere also likely playing a major role (e.g., Brugger et al., 2021; Junium et al., 2022; Lyons et al., 2020; Morgan et al., 2022; Senel et al., 2023; Vellekoop et al., 2014).

As the most prolific and diverse phytoplankton group at the end of the Cretaceous (Knoll & Follows 2016; Lowery et al., 2020), the near-demise of calcareous nannoplankton at the K/Pg boundary had a major impact on marine ecosystem structure and function. Although primary productivity did not completely cease as originally proposed in the 'Strangelove Ocean' model (Hsü & McKenzie, 1985) and may have only been reduced by <50 % for less than a few tens of kyr (Henehan et al., 2019), vacated niche space in the photic zone was filled by alternative phytoplankton groups including dinoflagellates, diatoms and cyanobacteria (e.g., Alegret et al., 2022; Bralower et al., 2020; Lowery et al., 2021; Renaudie et al., 2018; Schaefer et al., 2020; Sepúlveda et al., 2009; Vellekoop et al., 2017). The increased relative contribution of organic-walled phytoplankton to surface ocean productivity (e.g.,

Brinkhuis et al., 1998; Vellekoop et al., 2015, 2017) would have produced lower-density marine aggregates than those at the end of the Cretaceous, which were dominated by the heavily-mineralized remains of calcareous nannoplankton and planktic foraminifera. Moreover, because silica-producing diatoms did not become globally prominent until much later in the Cenozoic (~40 Ma), their role in early Paleocene marine carbon cycling was likely far less significant than in the modern ocean (e.g., Cermeño, 2016; Knoll & Follows 2016). This – together with the mass extinction's removal of aggregate-forming organisms at higher tropic levels – severely reduced biological pump efficiency (i.e., the 'Living Ocean' Model; Alvarez et al., 2019; Birch et al., 2016; Coxall et al., 2006; D'Hondt et al., 1998), which we define here as the proportion of carbon fixed during photosynthesis that is subsequently exported from the photic zone (after e.g., Ducklow et al., 2001; Henson et al., 2011; Hilting et al., 2008). In contrast, biological pump strength refers to the absolute flux of organic carbon exported from the surface to the deep ocean (Hilting et al., 2008).

Although the mass extinction exerted a global influence on biological pump strength and efficiency, its effects were geographically and environmentally heterogenous. This variability is reflected in site-to-site differences in both the magnitude and direction of benthic foraminiferal accumulation rates and diversity, which are strongly controlled by the quantity and quality of organic matter exported from the surface ocean to the deep sea (e.g., Alegret & Thomas, 2009, 2013; Alegret et al., 2012, 2022; Hull & Norris, 2011; Sepúlveda et al., 2019). Similarly, export production, as inferred from excess barium, exhibits pronounced geographic variability across the K/Pg boundary (Hull & Norris, 2011). This so-called 'Heterogenous Ocean' (Alegret et al., 2022; Esmeray-Senlet et al., 2015; Henehan et al., 2019) likely reflects taxonomic differences associated with spatially and temporally restricted blooms of non-mineralizing phytoplankton, which may have been unable to efficiently exploit elevated surface ocean nutrients in formerly nutrient-poor regions, although this has not been thoroughly documented (Alegret et al., 2022; Bralower et al., 2020).

The recovery patterns of calcareous nannoplankton communities during the early Danian were similarly complex. In the Southern Hemisphere, nannoplankton extinction rates were somewhat lower than in the Northern Hemisphere and earliest Paleocene communities consisted of previously rare survivor taxa that became regionally incumbent for 300 – 400 kyr post-impact (Jiang et al., 2010; Schueth et al., 2015). In contrast, contemporaneous Northern Hemisphere communities were characterized by a series of low-diversity, high-dominance acmes of newly-evolved taxa, which gave rise to the long-ranging lineages that prevailed throughout much of the Paleogene (Alvarez et al., 2019; Bown, 2005; Bown et al., 2023; Jiang et al., 2010, 2019; Jones et al., 2019; Schueth et al., 2015). Although these early Danian nannoplankton "boom-bust successions" (Jones et al., 2019) have been observed at all previously-studied Northern Hemisphere sites, their duration and the specific taxa that comprised them were geographically variable (Alvarez et al., 2019; Jones et al., 2019; Schueth et al., 2015). For example, boom bust successions ended ca. 1.75 Myr post-impact at Ocean Drilling Program (ODP) Site 1209 (Shatsky Rise) in the pelagic (bathyal) sub-equatorial Pacific Ocean (Alvarez et al., 2019), ca. 2 Myr post-impact at International Ocean Discovery Program (IODP) Site U1407 in the mid-latitude pelagic (abyssal) North Atlantic Ocean (Bown et al., 2023) and ca. 2.5 Myr post-impact at hemipelagic IODP – International Continental Scientific Ocean Drilling (ICDP) Site M0077A in the peak-

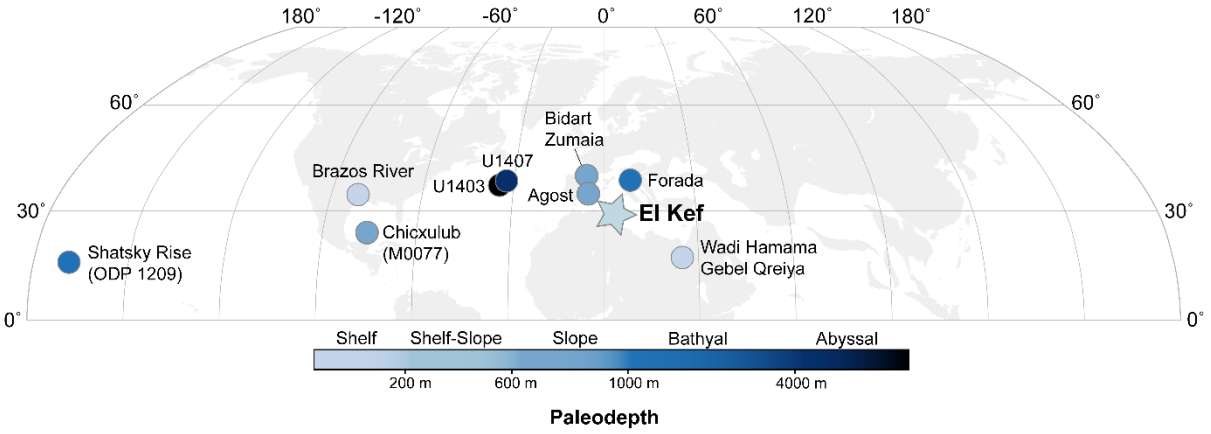

Figure 1. Paleogeographic reconstruction of the Northern Hemisphere at ~66.0 Ma showing the location of El Kef and other sites discussed in this study. Figure was created using pyGPlates (Mather et al. 2024) using the optimized plate model of Müller et al. (2022).

ring of the Chicxulub impact crater (i.e., at "ground-zero" of the mass extinction event; Jones et al., 2019; Lowery et al., 2021; Figure 1).

Although boom-bust successions are a distinctive feature of both calcareous nannoplankton and planktic foraminifera communities during the K/Pg recovery, the mechanisms controlling them are poorly understood (Alvarez et al., 2019; Bown, 2005; Hull, 2015; Hull et al., 2011; Jones et al., 2019). One hypothesis is that these patterns reflect a form of ecological succession analogous to that observed in modern ecosystems, but operating over much longer timescales (tens of thousands to millions of years), in a process referred to as Earth system succession (Hull, 2015). In this framework, a mass extinction event disrupts and destabilizes global biogeochemical cycling through both environmental perturbations and the loss of organisms that play key roles in these cycles (e.g., nannoplankton and planktic foraminifera), driving the Earth system into a state of disequilibrium. Therefore, boom-bust successions were likely a result of the complex biotic and abiotic interactions within the marine ecosystem as it progressively returned to relative equilibrium. These interactions may have included shifts in competitive advantage as environmental conditions and ecosystem function changed (e.g., Alvarez et al. 2019), modifications to feeding strategy (e.g., Gibbs et al. 2020) and changes in biological pump efficiency (Birch et al., 2016; 2021; Jones et al., 2019; Lowery et al., 2021).

Given the pronounced geographic heterogeneity in paleoecological, paleoenvironmental, and biogeochemical responses to the K/Pg mass extinction, global variation in the taxonomic composition and duration of nannoplankton boom-bust successions is hardly surprising. However, these differences and their dominant controls have not been systematically explored. Here we present high-resolution calcareous nannofossil assemblage data from the expanded post-extinction interval in sediment cores recovered near the Global Stratotype Section and Point (GSSP) for the basal Danian at El Kef, Tunisia. This record provides the most complete outer-shelf documentation of post-K/Pg nannoplankton boom-bust successions to date, allowing us to begin identifying the primary controls on these unique assemblages. Furthermore, statistical comparison of these data with those from other Northern Hemisphere sites can better resolve spatial patterns in the taxonomic composition and duration of boom-bust successions, providing new insight into Earth system recovery following the most recent mass extinction event.

2. Materials and Methods

2.1 Study site and Geological Setting

During the El Kef Coring Project, sediment cores were recovered from five closely spaced holes (Holes A-E) drilled near the GSSP outcrop section, ~5 km southwest of the town of El Kef in northwestern Tunisia (Jones et al., 2023). As a result of the drilling process, diagnostic features of the K/Pg boundary observed in the El Kef outcrop (e.g., the 2-3 mm iridium lamina) were not preserved in the cores. Nevertheless, integration of biostratigraphic, geochemical, and X-Ray Fluorescence (XRF) data allowed precise delineation of the boundary and the construction of a composite stratigraphic section ('splice') (Jones et al., 2023).

The resulting preferred age model indicates that the Danian succession is nearly complete in the El Kef cores, with the exception of a single unconformity within planktic foraminiferal biozone P1b. This unconformity is recognized by a sharp lithological contact and abrupt shifts across multiple geochemical records (Jones et al., 2023). Although the duration of the unconformity cannot be tightly constrained due to the absence of within-biozone tie points, sedimentation-rate estimates suggest it was ~500 kyr. As the early Danian at El Kef is characterized by a progressive decrease in sedimentation rates, this unconformity may represent an interval of reduced sediment accumulation or non-deposition, potentially linked to sea-level rise associated with the reactivation of syndepositional faulting. The Danian sediments at El Kef predominantly consist of gray marls (carbonate-rich mudstones) that are darker in color and less heavily bioturbated below the unconformity (Jones et al., 2023). The entire section was deposited at a paleolatitude of 25-30°N on the Tunisian outer continental shelf to upper ramp, at an estimated paleodepth of ~200-600 m (Figure 1; Alegret et al., 2022).

2.2 Age model revision

The current preferred age model for the El Kef cores (Jones et al., 2023) is primarily constrained by planktic foraminiferal biostratigraphic datums and is regarded as robust for the early Danian (biozones P0 through the base of P1b). Above this interval, however, its reliability declines due to challenges in identifying key biozone markers immediately above the unconformity in Hole E, as a result of poor preservation, weathering and reworking. There were also some difficulties in precisely delineating the base of biozone P2 in Hole C, where the defining marker taxon *Praemurica uncinata* is rare and exhibits a discontinuous occurrence (Jones et al., 2023). This issue is likely exacerbated by methodological constraints, as biozone determinations were based solely on the 38–63 µm size fraction due to sampling restrictions during the COVID-19 pandemic. Therefore, the larger specimens that became increasingly more common during the Danian, may not have been observed.

To further improve the reliability of our age model, planktic foraminiferal biostratigraphy was conducted on the >75 µm size fraction for 28 samples from El Kef Hole C and 44 samples from El Kef Hole E. The specific purpose of these additional analyses was to better constrain the base of biozone P2 and the timing of the unconformity, whilst ensuring biostratigraphic consistency between different size fractions during the earlier Danian (i.e., biozones P0 through P1b). Samples were soaked in a solution of peroxide and borax for a minimum of 24 hours and then washed over a 45µm sieve. Between samples, the sieve was soaked in methylene blue to stain any residual material, allowing potential carryover contamination in subsequent samples to be readily identified by its blue coloration. The washed samples were then dried overnight in a 40 °C oven. Each sample was sieved at 75 µm and analyzed under a Zeiss Discovery V8 microscope for presence/absence of biostratigraphic markers

using the biozonation scheme of Wade et al (2011), with ages calibrated to CENOGRID (Westerhold et al. 2020).

2.3 Calcareous nannofossil assemblage counts

Using the El Kef age model and composite section (Jones et al., 2023) as a guide, we chose to use samples from Holes E and C, as combined these represent a nearly stratigraphically continuous K/Pg succession from immediately after the mass extinction event to the base of the *Futyania* acme (planktic foraminiferal biozones P0 to P1c; Hole E), and from the *Futyania* acme to the *Praeprinsius* acme (planktic foraminiferal biozones P1c and P2; Hole C). Nannofossil smear slides were made following the standard procedures outlined in Bown & Young (1998) and examined under cross-polarized light at 1600x magnification using a Zeiss Axio Image A2m microscope. Smear slides were analyzed at a 10 to 20 cm sampling resolution between 54.75 and 61.33 meters composite depth (mcd), a 10 to 20 cm sampling resolution between 35.88 and 54.75 mcd, and a sampling resolution of 60 cm above this (17.47 – 35.88 mcd) (Jones et al., 2023). As the switchovers in dominant taxa within boom-bust successions were geologically rapid events followed by a relatively prolonged interval of quasi-stability, we do not anticipate that the stratigraphic reduction in sampling resolution up-section has drastically altered our results or interpretations. Nannofossil assemblages in the weathered intervals of Holes C and E (above 17.47 mcd and 51.32 mcd respectively) were also examined, but are not included in the subsequent analyses due to clear downhole contamination and poor nannofossil preservation.

At least 300 nannofossil specimens were counted along a random transect in each sample and identified to species-level using the taxonomic concepts of Bown et al. (2023). Replicate counts were also implemented for most samples along a different random transect to improve reliability of the data. Some specimens, including tiny (<2 µm) *Neobiscutum* coccoliths and intermediate, evolutionary morphotypes of all incoming taxa were difficult to identify to species-level, and thus were only assigned a genus. Ultimately, our nannoplankton relative abundance counts resulted in the creation of a large dataset comprising of 186 samples and over 104,000 nannofossil occurrences (Jones et al., 2026 dataset (doi will go here upon publication).

2.4 Statistical analyses

All assemblage-based statistical analyses were conducted on genus-level data, allowing more reliable comparison among nannofossil records generated by different researchers while retaining meaningful paleoecological trends. Genera comprising <2% of an assemblage were excluded to reduce the influence of rare occurrences that may generate outliers and obscure primary paleoecological signals (e.g., Schneider et al. 2013). The resulting assemblage data were Hellinger-transformed using the *vegan* package (Oksanen et al., 2025) in R Version 4.5.1 (R Core Team, 2025). This transformation first converts counts to relative abundances, which accounts for any small differences in the total number of specimens counted per sample. It then takes the square root of these values to maximize the importance of rare taxa. This is vital in teasing apart differences between assemblages that are almost completely dominated by one abundant taxon, as is the case within the early Danian boom-bust successions.

2.4.1 Nonmetric Multidimensional Scaling (NMDS): NMDS was used to examine temporal and spatial variation in nannofossil assemblage composition. Analyses were performed using the metaMDS function in the *vegan* package in R (Oksanen et al., 2025; R Core Team, 2025), with Bray-Curtis dissimilarity used to construct a best-fit rank-distance configuration in reduced-dimensional space.

The number of dimensions (axes) was manually selected by examining the reduction in stress with increasing dimensionality and identifying the point at which further dimensions produced little improvement in model fit. In this study, three dimensions were retained. Following ordination, metaMDS rotates the sample scores using principal components analysis to maximize variation along the first axis. Consequently, NMDS axis 1 captures the greatest variation among samples, with progressively less variation represented by subsequent axes. Each point in the resulting ordination represents the nannofossil assemblage of an individual sample, with closer points indicating greater similarity in assemblage composition. Taxon scores, calculated by weighted averaging using the wascores function, indicate the taxa most strongly associated with different regions of the ordination space. Although the paleoenvironmental and/or paleoecological gradients represented by the ordination axes cannot be determined directly, sample scores can be compared with independent variables such as age, geochemical proxy data, site location and paleobathymetry to investigate potential controls on assemblage composition.

2.4.1.1 El Kef data: Three separate NMDS analyses were performed on the El Kef dataset: one incorporating nannofossil assemblage data from both Holes E and C, one only using assemblage data from Hole E and the last only using data from Hole C. To test whether changes in nannofossil assemblage composition and paleoenvironmental variables were correlated, we performed a linear regression of the available geochemical data (bulk carbonate $\delta^{13}C$ and $\delta^{18}O$, bulk organic $\delta^{13}C$, wt. % TOC, and wt. % $CaCO_3$; Jones et al., 2023) on the NMDS sample scores using the 'envfit' function in the *vegan* package in R (Oksanen et al.2025; R Core Team 2025). As geochemical measurements were not always conducted on the same samples as the nannofossil assemblage counts, we linearly interpolated geochemical values for each nannofossil sample. Specifically, each missing geochemical value was estimated using the two nearest measured points above and below each sample, assuming a linear change between them. The NMDS ordinations and fitted environmental vectors were then plotted together using the *ggplot2* package (Wickham et al., 2016).

2.4.1.2 Northern Hemisphere literature data: To compare changes in nannofossil assemblages at El Kef with those at other Northern Hemisphere sites, we compiled published datasets spanning a range of ocean basins and marine environments (Figure 1). The dataset comprises six Tethyan sites in addition to El Kef (Figure 2): Bidart, France (Jiang et al., 2019); Zumaia, Spain (Jiang et al., 2019); Agost, Spain (Jiang et al., 2010); Forada, Italy (Fornaciari et al., 2007); Wadi Hamama, Egypt (Tantawy, 2003); and Gebel Qreiya, Egypt (Tantawy, 2003). The wider Northern Hemisphere comparison incorporates IODP-ICDP Site M0077A in the peak ring of the Chicxulub impact crater, Mexico (Jones et al., 2019); Brazos River, Texas, USA (Schueth, 2009); ODP Site 1209 on Shatsky Rise in the North Pacific Ocean (Alvarez et al., 2019); and IODP Sites U1403 and U1407 in the North Atlantic Ocean (Bown et al., 2023). Paleobathymetric estimates used in the statistical analyses were taken from published estimates for each site and were generally based on benthic foraminiferal assemblages, where the basis for the estimate was reported. Estimates for El Kef, Bidart, Zumaia, Agost, and Shatsky Rise were compiled from Alegret et al. (2022), with estimates for IODP-ICDP Site M0077A from Lowery et al. (2018), Forada, Wadi Hamama, and Gebel Qreiya from Jiang et al. (2010), Brazos River from Jiang et al. (2019), and IODP Sites U1403 and U1407 from Bown et al. (2023). Due to differences in temporal coverage and the relatively low-resolution age models available for many of the published sites, statistical analyses were restricted to the first ~3.5 Myr of the Danian. The resulting ordination was visualized using *ggplot2* (Oksanen et al., 2025; Wickham et al., 2016).

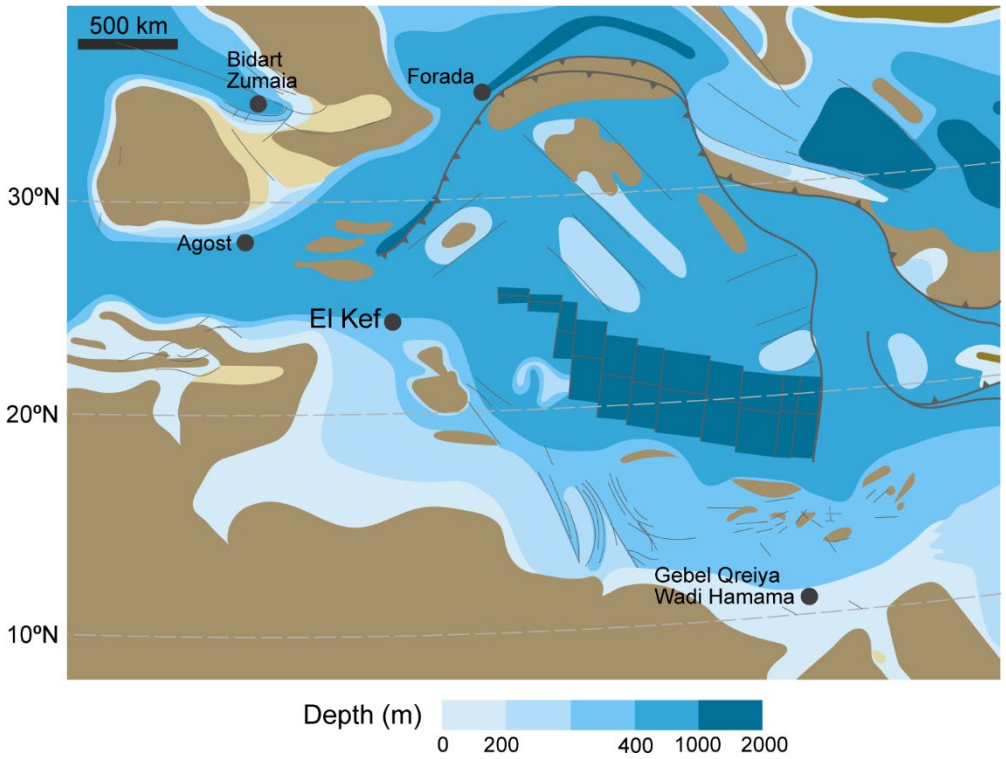

Figure 2. Paleogeographic reconstruction of the peri-Tethys region during the late Maastrichtian, showing the approximate location of El Kef relative to the other Tethyan sites statistically analyzed in this study. Modified from Fornaciari et al., 2007 and Philip & Floquet, 2000.

2.4.2 Spearman's Rank correlation plots: Apparent relationships between nannofossil assemblage changes and geochemical proxy records may arise because both independently covary with time. To assess these relationships and identify the potential influence of shared temporal trends, we calculated pairwise Spearman's rank correlation coefficients among the relative abundances of major nannofossil acme taxa, all available geochemical proxy data, and age (Ma) using our El Kef data. Correlations were calculated using the rcorr function in the Hmisc package in R (Harrell, 2025; R Core Team, 2025), and the resulting correlation matrices were visualized using the corrplot package (Wei & Simko, 2024).

2.4.3 Two-way hierarchical cluster analysis: To determine the extent to which regional paleoceanographic conditions played a role in the recovery of calcareous nannoplankton, we performed a two-way cluster analysis using nannofossil assemblage data from El Kef and the six other Tethyan sites described in Section 2.4.1.2. As in the Northern Hemisphere NMDS analysis, only data spanning the first ~3.5 Myr of the Danian were considered to facilitate comparison among sites with differing temporal coverage and age-model resolution. The two-way cluster analysis was performed using the Bray-Curtis distance measure and Ward's linkage method within the *pheatmap* package in R (Kolde 2025). This creates a dendrogram of genera on the x axis and samples on the y axis, with taxa clustering based on co-occurrence among samples, and samples clustering according to similarities in nannofossil assemblage composition.

3. Results

3.1 Revised El Kef age model

Our revised planktic foraminiferal biostratigraphic framework shows substantial differences in the delineation of the two youngest biozones, P1c and P2, with additional minor adjustments to the bases of P1a and P1b (Table 1; Jones et al. 2023). Delineation of biozones P0 and Pα remains unchanged from the original age model (Jones et al. 2023). However, recently-published ^{3}He isotopic data (Lowery et al., 2026) – including from the El Kef outcrop section – indicate a much shorter duration for P0 (~6.61 kyr) than previously estimated (~30 kyr), requiring revision of the P0-Pα age model (Table 1). These updates imply very high average sedimentation rates during P0 (~12.4 cm/kyr), declining to ~1.7 cm/kyr in Pα and ~0.18-0.22 cm/kyr through P1a-P1b, before increasing slightly in P1c (~0.45 cm/kyr). The very low sedimentation rates in P1b and P1c are consistent with the inferred unconformity, reflecting a possible interval of non-deposition or erosion potentially associated with sea-level fall.

Definitive *Globanomalina compressa* specimens (marker for the base of biozone P1c) and secondary P1c indicators such as *Praemurica inconstans* and *Parasubbotina varianta* were observed within multiple samples at the base of El Kef Hole E Core 4R, 90 to 150 cm (51.32 to 51.92 mcd), which were not previously examined for planktic foraminiferal biostratigraphy (Jones et al. 2023). These samples are from below the heavily weathered/oxidized depth interval that ranges from the top of Hole E to Hole E Core 4R, ~81 cm (46.18 to 51.23 mcd; Jones et al. 2023), indicating that the presence of these taxa is likely a primary signal and not a product of downhole contamination or mixing. These new observations push the depth of base P1c – which was previously placed in a sampling gap between the base of Hole C and top of Hole E Core 5 (~50.63 mcd; Jones et al. 2023) – down to 52.16 mcd (Table 1), which also greatly reduces the error associated with its delineation (from +/- 1.53 m in Jones et al. (2023) to +/- 0.24 m in this study; Table 1). Although this improves the reliability of the El Kef age model, it also means that the unconformity may also include the lowest part of P1c in addition to the upper part of P1b, making it longer than initially estimated (i.e., >500 kyr; Jones et al. 2023). Unfortunately, it is currently unknown exactly how much time is missing from the base of P1c. As only five nannofossil samples were counted above the unconformity in Hole E, this uncertainty will not significantly alter our discussion on recovery dynamics, as the remainder of Holes E and C have relatively reliable age control. However, future studies should aim to constrain the length of this unconformity by conducting further stratigraphic work on El Kef Hole D: the only other hole that preserves the unconformable contact (Jones et al. 2023).

Biozone	Event	Age estimate (Ma)	Age source	Top sample ID	Top sample depth (mcd)	Bottom sample ID	Bottom sample depth (mcd)	Midpoint depth (mcd)	± (m)
P2	B *Praemurica uncinata*	62.537	Wade et al. (2011); Gradstein et al. (2012); Westerhold et al. (2020)	El Kef C 21R-1, 102-105 cm	45.44	El Kef C 21R-1, 141-144 cm	45.83	45.64	0.20
P1c	B *Globanomalina compressa*	63.978	Wade et al. (2011); Gradstein et al. (2012); Westerhold et al. (2020)	El Kef E 4R-1, 150 cm	51.92	El Kef E 5R-1, 34 cm	52.39	52.16	0.24
P1b	B *Subbotina triloculinoides*	65.184	Wade et al. (2011); Gradstein et al. (2012); Westerhold et al. (2020)	El Kef E 6R-1, 100-101 cm	54.66	El Kef E 6R-1, 120-121 cm	54.86	54.76	0.10
P1a	T *Parvularugoglobigerina eugubina*	65.690	Wade et al. (2011); Gradstein et al. (2012); Westerhold et al. (2020)	El Kef E 7R-1, 30-31 cm	55.60	El Kef E 7R-1, 45-46 cm	55.75	55.68	0.08
Pα	B *Parvularugoglobigerina eugubina*	66.015	Lowery et al. (2026)	El Kef E 10R-1, 70-72 cm	60.99	El Kef E 10R-1, 84-86 cm	61.13	61.06	0.07
P0	T Cretaceous taxa	66.022	Dinares-Turell et al. (2014)	El Kef E 10R-1, 139-140 cm	61.68	El Kef E 11R-1, 1-2.5 cm	62.08	61.88	0.20

Table 1. Updated planktic foraminiferal biostratigraphic zonations for the El Kef composite core section in Holes C and E, with depth in meters composite core depth (mcd).

The base of P2 was also found to be much lower in this study (~45.64 mcd) than in the initial age model (~34.04 mcd), probably due to scarcity of the P2 marker taxon *Praemurica uncinata* within the smaller size fraction (38-63 µm) examined in Jones et al. (2023) compared to the >75 µm size fraction examined here (Table 1). This is supported by the fact that very rare *P. uncinata* specimens were also observed lower in Hole C (~43.75 mcd) within the 38-63 µm size fraction, but were interpreted as downhole contamination due to the continuous absence of this taxon within samples from the ~10 m depth interval above this. However, based on our new data from the >75 µm size fraction, the rare *P.uncinata* specimens observed in the 38-63 µm size fraction were actually likely in situ and representative of the smaller forms typical for a species at the beginning of its stratigraphic range. In this case, the exclusion of *P. uncinata* from the 38-63 µm size fraction samples in the overlying 10 m of sediments may be indicative of their rapid evolution to larger average test sizes, with their reappearance in the smaller size fraction at ~34.04 mcd representing their increased relative abundance in assemblages and/or their diversification to encompass a wider range of test sizes.

The marker for the base of planktic foraminiferal zone P3 (*Morozovella angulata*) was not observed in either the 38-63 µm size fraction (examined up to El Kef Hole C 2R, 46-48 cm; Jones et al. 2023) or the >75 µm size fraction in the highest examined sample (El Kef Hole C 5R, 73-76 cm). Accordingly, the entire interval between ~14.32 and 45.64 mcd is assigned to biozone P2, which spans ~207,000 years (62.33 to 62.54 Ma; Gradstein et al., 2012; Wade et al., 2011; Westerhold et al., 2020). For this study, we assume 14.32 mcd represents the uppermost part of P2 (i.e., 62.33 Ma; the minimum age). This assumption implies unusually high sedimentation rates (~15.1 cm/kyr) within P2, which is unlikely, given the very low rates inferred below. However, because no additional (bio)stratigraphic datums occur within P2, the youngest part of the age model cannot be further constrained, and ages assigned to samples within P2 (i.e., <62.54 Ma) should therefore be treated with caution.

3.2 El Kef nannofossil and geochemical records

Overall, the revised El Kef age model indicates that our new nannofossil assemblage data spans the first ~3.7 Myrs of the Danian (Figure 3). Immediately after the K/Pg impact, nannofossils are almost completely absent, with assemblages comprising reworked Cretaceous specimens and the calcareous resting cysts (calcispheres) of dinoflagellates, assigned to *Cervisiella* spp (previously assigned to *Thoracosphaera* spp.). However, the *Cervisiella* acme lasted only ~11 kyr, before being replaced by *Neobiscutum*: the first of the incoming Paleocene nannoplankton taxa. *Neobiscutum* immediately dominated assemblages, with these communities persisting for 1.88 Myr (Figure 3a).

Within this interval, the relative abundance of the nannolith taxon *Braarudosphaera* peaks at ~65.8 Ma, which coincides with an increase in bulk carbonate $\delta^{13}C$ (Figure 3b) and weight percent (%) calcium carbonate ($CaCO_3$; Figure 3d). The subsequent decrease in the relative abundance of *Braarudosphaera* (Figure 3a) is associated with: (a) the continued decline of *Cervisiella* spp.; (b) the increased abundance of tiny, ancestral *Praeprinsius* spp. (incl. *P.* cf. *vegrandis*; Bown et al. 2023); (c) decreasing trends in both bulk carbonate and bulk organic $\delta^{13}C$ values (Figure 3b; c) and; (d) an overall increase in weight % Total Organic Carbon (TOC; Figure 3d). The remainder of the *Neobiscutum* acme (~64.11 Ma – 65.7 Ma) is characterized by quasi-stable nannofossil assemblages (Figure 3a) and bulk carbonate $\delta^{13}C$ values (Figure 3b), a gradual increase in bulk organic $\delta^{13}C$ (Figure 3c) and a slow decline in both wt. % $CaCO_3$ and TOC (Figure 3d).

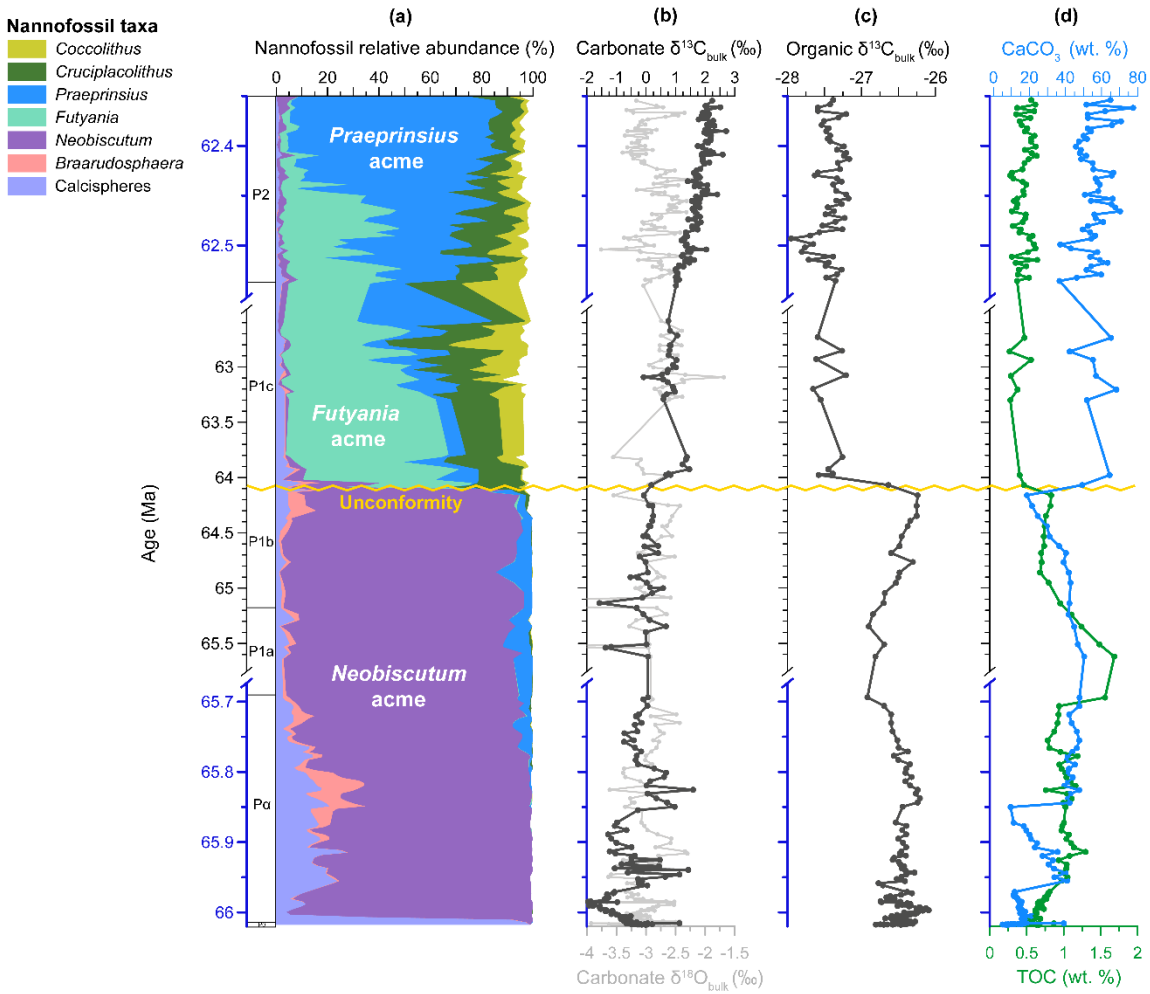

Figure 3. Nannofossil and geochemical records from ~62.35 – 66.02 Ma in sediment cores from El Kef, Tunisia alongside the planktic foraminiferal biozones. Note the two y-axis scale changes (blue), reflecting comparatively high sedimentation rates in P0-Pα and P2. The duration of the unconformity (yellow line) is unconstrained, so sedimentation rates are calculated assuming continuous deposition across the contact, although this likely does not reflect the true depositional history. (a) Cumulative frequency plot showing the relative abundance of the seven most abundant nannofossil genera. (b) Bulk carbonate $\delta^{13}C$ (black) and $\delta^{18}O$ (light gray). (c) Bulk organic $\delta^{13}C$. (d) Coulometric measurements of weight % calcium carbonate ($CaCO_3$; blue) and wt. % Total Organic Carbon (TOC; green).

At ~64.1 Ma, there is a transition from the *Neobiscutum* acme to the *Futyania* acme (Figure 3a). Although this taxonomic shift appears abrupt, it occurred across the unconformity in El Kef Hole E. Given that the hiatus may represent more than 500 kyr, this transition was likely more gradual than it appears. Overall, the *Futyania* acme is associated with the increased relative abundance of long-ranging Paleocene genera *Cruciplacolithus* and *Coccolithus*, a large increase in bulk carbonate $\delta^{13}C$ (~1.5‰) and wt. % $CaCO_3$ (30%) and a decrease in bulk organic $\delta^{13}C$ and wt. % TOC. The next 1.5 Myr (~62.6 – 64.1) marks an interval of quasi-stability both in terms of nannofossil assemblage composition (Figure 3a) and surface ocean paleoenvironmental conditions as indicated by the stable isotope and coulometric data (Figure 3b-d). Beginning at ca. 62.6 Ma, *Praeprinsius* gradually replaced *Futyania* as the dominant genus, with a definitive *Praeprinsius* acme becoming fully established by 62.46 Ma. The transition between the *Futyania* and *Praeprinsius* acmes is associated with: (a) a decline in

Cruciplacolithus and *Coccolithus*, which had previously greatly increased in relative abundance within the *Futyania* acme; (b) a steady ~1.25‰ increase in bulk carbonate $\delta^{13}C$ to the top of the record (~62.35 Ma; Figure 1b); (c) a small negative excursion in bulk organic $\delta^{13}C$; and (d) a sharp decrease from ~65 to 40 wt. % $CaCO_3$ as *Praeprinsius* began to replace *Futyania* as the dominant genus, followed by highly variable values (35 to 75 wt. % $CaCO_3$) to the top of the examined interval (62.35 to 62.55 Ma; Figure 3d).

3.4 El Kef NMDS

The El Kef NMDS results (Figure 4) confirm four distinct generic acmes that define the boom-bust successions observed in the relative abundance data (Figure 3a): (1) the short lived *Cervisiella* acme, (2) the *Neobiscutum* acme, (3) the *Futyania* acme, and (4) the *Praeprinsius* acme. Overall, the largest change in nannofossil assemblages occurred between the *Neobiscutum* and *Futyania* acmes as indicated by increased sample scores along major NMDS axis 1 (Figure 4a). Changes in assemblage

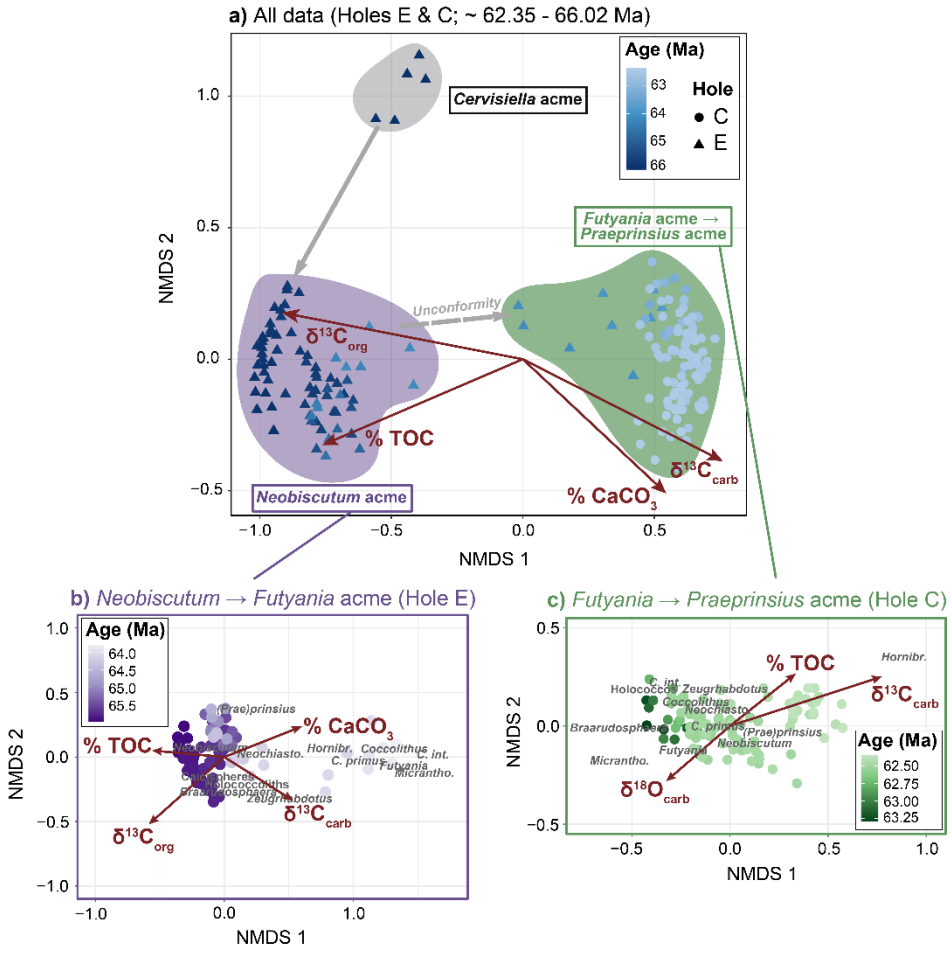

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination plots showing the differences between nannofossil assemblages at El Kef. Points (sample scores) that are closer together in ordination space have more similar nannofossil assemblages that those that are further apart. The red vectors on each ordination show the regression ("environmental fit") of the geochemical data on the NMDS scores. The length of each of the vectors correspond to the strength of each of these correlations, with only statistically significant relationships ($p<0.01$) shown. (a) NMDS results for all nannofossil data (~62.35 – 66.02 Ma). (b) NMDS results for the subset of nannofossil data within Hole E, excluding the oldest five samples (~63.79 – 65.99 Ma). (c) NMDS results for the subset of nannofossil data within Hole C (~62.35 – 63.29 Ma).

composition between the *Futyania* and *Praeprinsius* acme can be observed as a gradual decrease in NMDS axis 2 sample scores (Figure 4c), suggesting a subtler paleoecological transition compared to the *Neobiscutum*→ *Futyania* dominance switchover (Figure 4b). The linear regression (environmental fit) of geochemical/coulometric data on the NMDS sample scores shows a statistically significant positive correlation with bulk carbonate $\delta^{13}C$ (r^2=0.7295, p=0.001) and wt. % $CaCO_3$ (r^2=0.5581, p=0.001), and a negative correlation with bulk organic $\delta^{13}C$ (r^2=0.8709, p=0.001) and wt. % TOC (r^2=0.6874, p=0.001), primarily along NMDS axis 1. Subset analyses of the Hole E data (the *Neobiscutum* acme) reinforces these correlations albeit with lower r^2 values (r^2 = 0.4014, 0.4195, 0.6173 and 0.3181 for bulk carbonate $\delta^{13}C$, wt. % $CaCO_3$, bulk organic $\delta^{13}C$ and wt. % TOC, respectively; Figure 4b), likely because the sediments within this hole contain the unconformable *Neobiscutum* → *Futyania* transition, which represents the largest paleoecological and paleoenvironmental transition within the entire El Kef record (Figure 4a). In contrast, the separate NMDS analysis for the Hole C samples – which contain the *Futyania* and *Praeprinsius* acmes – only shows a strong, statistically significant correlation with bulk carbonate $\delta^{13}C$ (r^2= 0.664, p=0.001) along NMDS axis 1 (Figure 4c). Interestingly, the strength of this correlation is higher than in the subset Hole E NMDS results (r^2= 0.4014, p=0.001; Figure 4b).

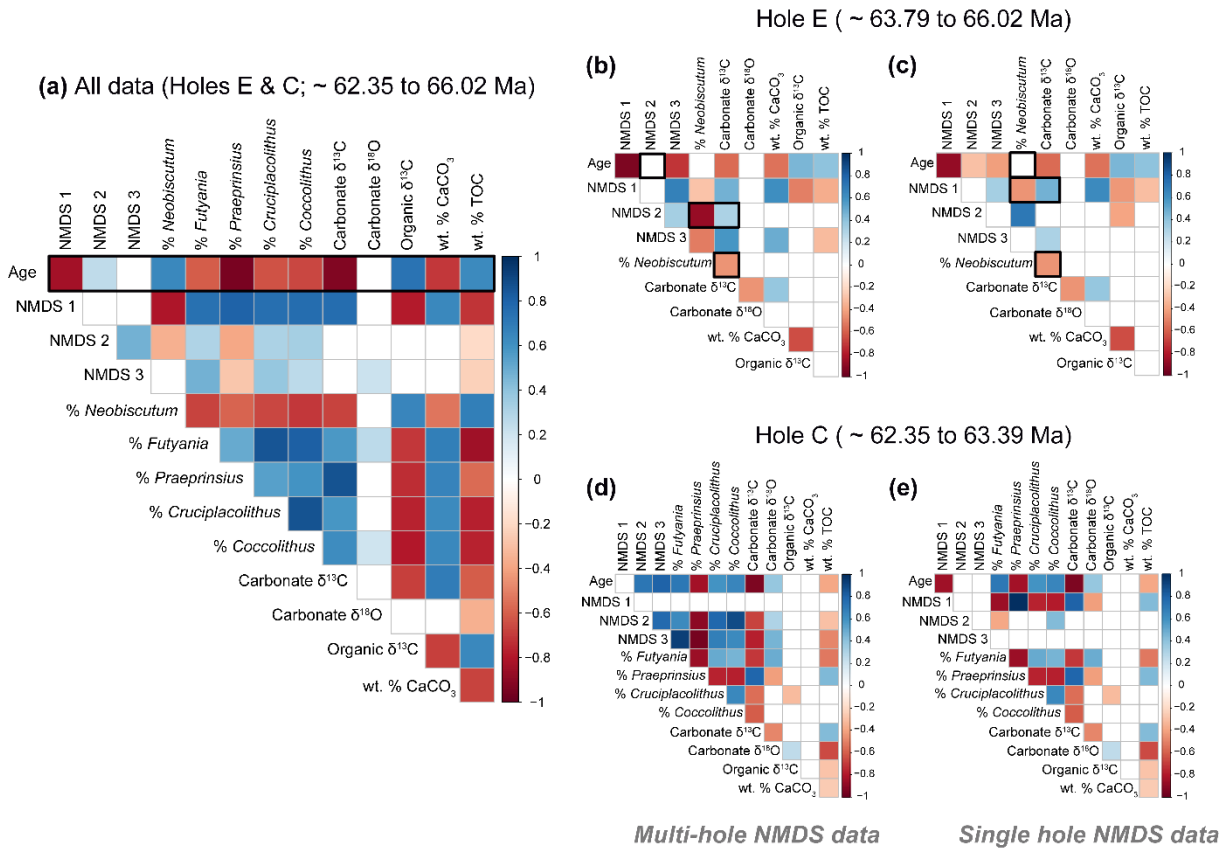

Figure 5. Spearman's rank correlation plots showing the strength of pairwise relationships between multiple variables. Positive relationships (r^2>0) are shown in shades of red, whilst negative relationships (r^2<0) are shown in shades of blue. Empty boxes (white) represent Spearman's rank correlations with a p value of less than 0.01. (a) Combination of all data from Holes E and C (~62.35 – 66.02 Ma). (b) Subset data from Hole E, with NMDS scores taken from the multi-hole analysis (i.e., Figure 4a; (~63.79 – 65.99 Ma)). (c) Subset data from Hole E, with NMDS scores taken from the Hole E single-hole analysis (i.e., Figure 4b; (~63.79 – 65.99 Ma)). (d) Subset data from Hole C, with NMDS scores taken from the multi-hole analysis (i.e., Figure 4a; (~62.35 – 63.29 Ma)). (e) Subset data from Hole C, with NMDS scores taken from the Hole C single-hole analysis (i.e., Figure 4c; (~62.35 – 63.29 Ma)).

Many paleoecological and paleoenvironmental variables are strongly influenced by temporal trends, meaning that apparent correlations between them may not reflect direct relationships. Such associations can instead arise when variables independently covary with time and should therefore not necessarily be interpreted as evidence of causation. To address this, we generated Spearman's rank correlation plots to examine pairwise relationships among multiple variables including estimated ages (Figure 5). As anticipated, the correlation plot based on NMDS axis scores for the complete El Kef dataset (Figure 4a) shows that all considered variables are strongly correlated with time (Figure 5a). This is simply due to the large amount of change that occurred during this volatile study interval, which complicates the interpretation of 'true' correlations between paleoecological and paleoenvironmental variables.

The examination of data from the two separate holes using NMDS axes for the complete El Kef dataset (Figure 5b,d) and those from the appropriate subset analyses (Figure 5c, e) show similar results. The one important exception is the apparent negative correlation between the relative abundance of *Neobiscutum* and bulk carbonate $\delta^{13}C$ (Figure 5b, c). In the case of the multi-hole statistical analysis (Figure 5b), NMDS axis 2 does not show a significant statistical correlation with time, but does with both % *Neobiscutum* and bulk carbonate $\delta^{13}C$. This is supported by the single-hole data (Figure 5c), which suggests that changes in the relative abundance of *Neobiscutum* are not significantly correlated to time but are negatively correlated to bulk carbonate $\delta^{13}C$. Although it is important to note that both of these variables are correlated to NMDS 1 axis values – which is itself strongly correlated to time – these results provide tentative evidence that changes in nannofossil assemblages within the *Neobiscutum* acme and during *the Neobiscutum* → *Futyania* dominance switchover were directly linked to increased bulk carbonate $\delta^{13}C$ values. In contrast, the Hole C multi-site data (Figure 5d) shows that NDMS axis 1 is not significantly correlated to any of the variables, including time. Instead, time is correlated with NMDS axis 2 – and even more so with NMDS axis 3 – which are both in turn correlated with most other considered paleoecological and paleoenvironmental parameters (excluding bulk organic $\delta^{13}C$ and wt. % $CaCO_3$). Although the single hole-analysis for Hole C indicates that time is not significantly correlated to NMDS axes 2 and 3 (Figure 5e), the relative abundance of *Futyania* and *Coccolithus* are the only variables that are significantly correlated with either of these axes. Therefore, it is not possible to make the same speculative link between changes in nannofossil assemblages and bulk carbonate $\delta^{13}C$ within the *Futyania* and *Praeprinsius* acmes as in the earlier *Neobiscutum* acme.

3.4 Regional cluster analysis

The two-way hierarchical cluster analysis conducted on our new El Kef data and additional published records from a range of other Tethyan sites, revealed three major clusters related to distinct nannofossil assemblages (Figure 6). Cluster 1 comprises three sub-clusters of earliest Danian 'disaster' assemblages. Sub-Cluster 1A-I is characterized by the almost complete dominance of calcispheres within samples from Wadi Hamama and Gebel Qreiya (Egypt), as well as the oldest five samples from El Kef. Calcispheres also dominate the sub-Cluster 1A-II samples, but can be distinguished from sub-Cluster 1A-I by the relatively high abundance of Cretaceous survivor taxon *Cyclagelosphaera*. Samples from sub-Cluster 1A-II are predominantly from Bidart (France) and Zumaia (Spain), with one sample from Forada (Italy). Sub-Cluster 1B is characterized by a calcisphere acme with relatively high abundances of *Neobiscutum* and low holococcolith abundance (1B-I) or with a high relative abundance of *Braarudosphaera* (1B-II). Samples from the former are restricted to the Egyptian continental shelf sites Wadi Hamama and Gebel Qrieya, whilst the latter predominantly comprises of samples from

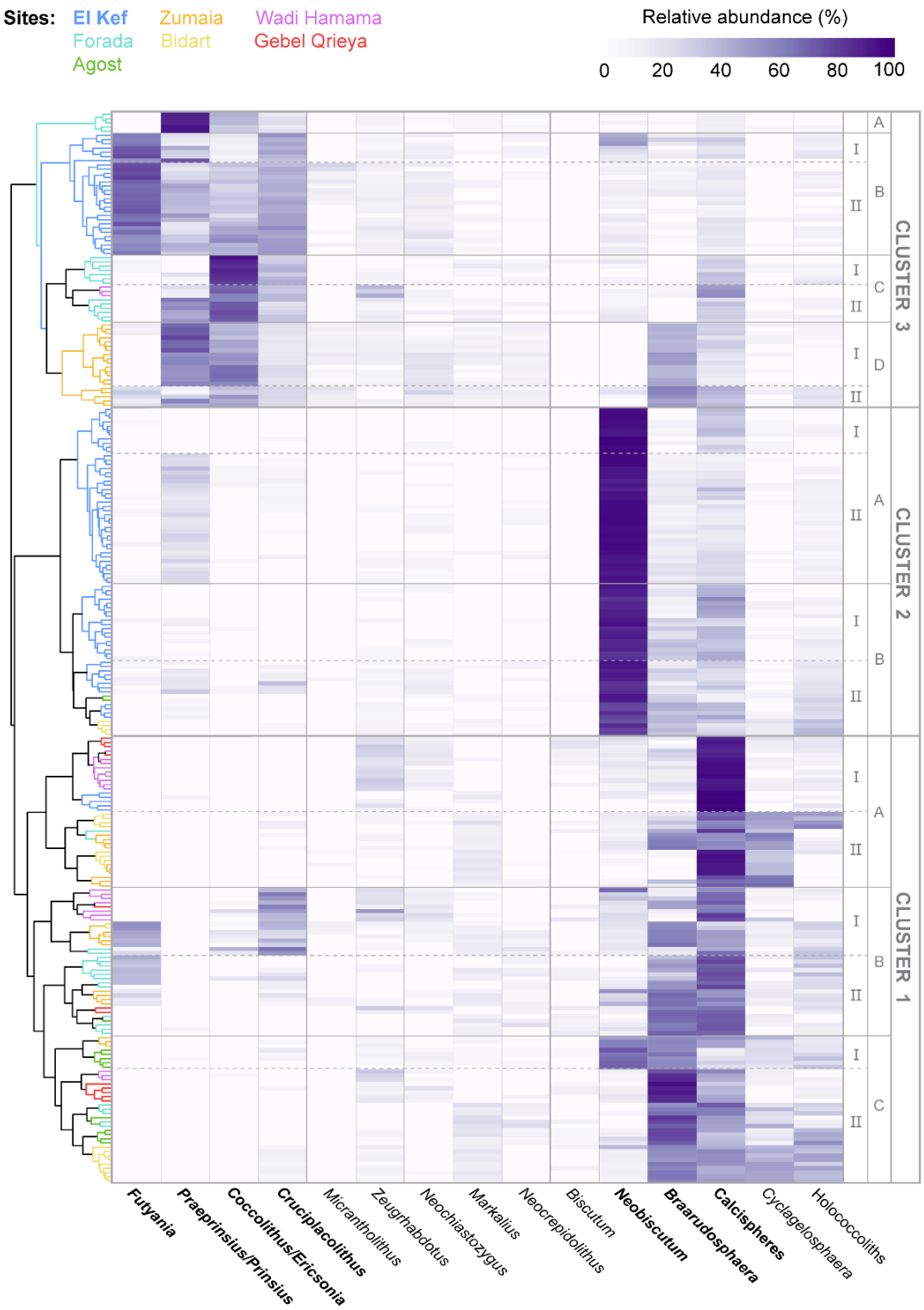

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Figure 6. Dendrogram showing the results of a regional (Tethyan) two-way cluster analysis or 'heatmap' conducted on nannofossil relative abundance data. The horizontal (x-axis) dendrogram shows the clustering of nannofossil genera and the vertical (y-axis dendrogram) shows clustering between samples, with the site that the sample is from distinguished by color: blue = El Kef (this study), teal = Forada (Fornaciari et al. 2007), green = Agost (Jiang et al. 2010), orange = Zumaia (Jiang et al. 2019), yellow = Bidart (Jiang et al. 2019), pink = Wadi Hamama (Tantawy 2003) and red = Gebel Qrieya (Tantawy 2003). The relative abundances of nannofossil taxa are also shown in accordance with the scalebar to the top-right of the figure.

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Forada and Zumaia. The last sub-cluster within Cluster 1 consists of a *Braarudosphaera* acme with relatively high abundances of *Neobiscutum* and low abundances of calcispheres (samples from Zumaia, Agost, Wadi Hamama and Gebel Qrieya; sub-Cluster 1C-I) or a *Braarudosphaera* acme with relatively high abundances of *Cyclagelosphaera,* calcispheres, and/or holococcoliths and low abundances of *Neobiscutum* (samples from Bidart, Agost and Forada; sub-Cluster 1C-II). Samples from El Kef are completely absent from sub-Clusters 1B and 1C. Overall, the sub-clusters within Cluster 1 are dominated by different taxa among sites and regions, with no single taxon dominating across all Tethyan records.

Cluster 2 represents the *Neobiscutum* acme and almost entirely consists of samples from El Kef (Figure 6). Sub-Cluster 2A is characterized by the very high abundance of *Neobiscutum* with a lower abundance of calcispheres (2A-I) or early *Praeprinsius* cf. *vegrandis* (2A-II). In comparison, samples within sub-Cluster 2B have slightly lower relative abundances of *Neobiscutum* with a higher proportion of calcispheres (2B-I) or with increased relative abundances of calcispheres, holococcoliths and *Braarudosphaera* (2B-II). Sub-Cluster 2B-II is the only group to contain samples that are not from El Kef (Agost and Bidart).

The last major cluster (Cluster 3) contains samples from the latest part of the K/Pg recovery interval included in this analysis. Sub-Cluster 3A represents the *Praeprinsius* acme at Forada, which also features lower abundances of *Coccolithus* and *Cruciplacolithus*. In contrast, sub-Cluster 3B – which only comprises samples from El Kef – is characterized by the *Futyania* acme, with relatively high abundances of *Cruciplacolithus*, variable abundances of *Praeprinsius* and either a very low (3B-I) or relatively high (3B-II) proportion of *Coccolithus*. Sub-Cluster 3C predominantly consists of samples from Forada, and is representative of a *Coccolithus* acme with a relatively high proportion of *Cruciplacolithus* and either a low (3C-I) or relatively high (3C-II) abundance of *Praeprinsius*. The last sub-Cluster (3D) only contains samples from Zumaia, and is characterized by a *Coccolithus* acme with a relatively high abundance of *Braarudosphaera* and either a higher proportion of *Praeprinsus* (3D-I) or comparatively higher relative abundances of calcispheres, holococcoliths and *Futyania* (3D-II).

3.5 Northern Hemisphere NMDS analysis

To compare Tethyan nannoplankton recovery patterns for the first ~3.5 Myr of the Danian to those in other Northern Hemisphere ocean basins, we conducted a further NMDS analysis with sample scores coded by both location (site and region; Figure 7a) and estimated paleobathymetry (Figure 7b), based on benthic foraminiferal assemblages from a global compilation of sites (Alegret et al. 2022). Our results reveal that the largest change in nannofossil assemblages – as observed along NMDS axis 1 – is associated with the transition from post-extinction acmes (high NMDS axis 1 scores) to the formation of more diverse communities (low NMDS axis 1 scores). However, it is important to note that within the examined 3.5 Myr time frame, only three open ocean sites – ODP Site 1209 (Shatsky Rise, subtropical Pacific Ocean) and IODP Sites U1403 & U1407 (mid-latitude North Atlantic Ocean) – completed the full transition to stable nannofossil assemblages comprising of long-ranging Paleocene taxa such as *Cruciplacolithus*, *Coccolithus*, *Toweius* and *Fasciculithus*.

The two major pathways leading to the establishment of stable assemblages were dependent on the immediate post-impact community composition (Figure 7a). For almost all of the Tethyan sites and IODP-ICDP Site M0077A (Chicxulub impact crater, Gulf of Mexico), early nannofossil assemblages consist of relatively high abundances of calcispheres, *Braarudosphaera* and/or *Cyclagelosphaera,* with

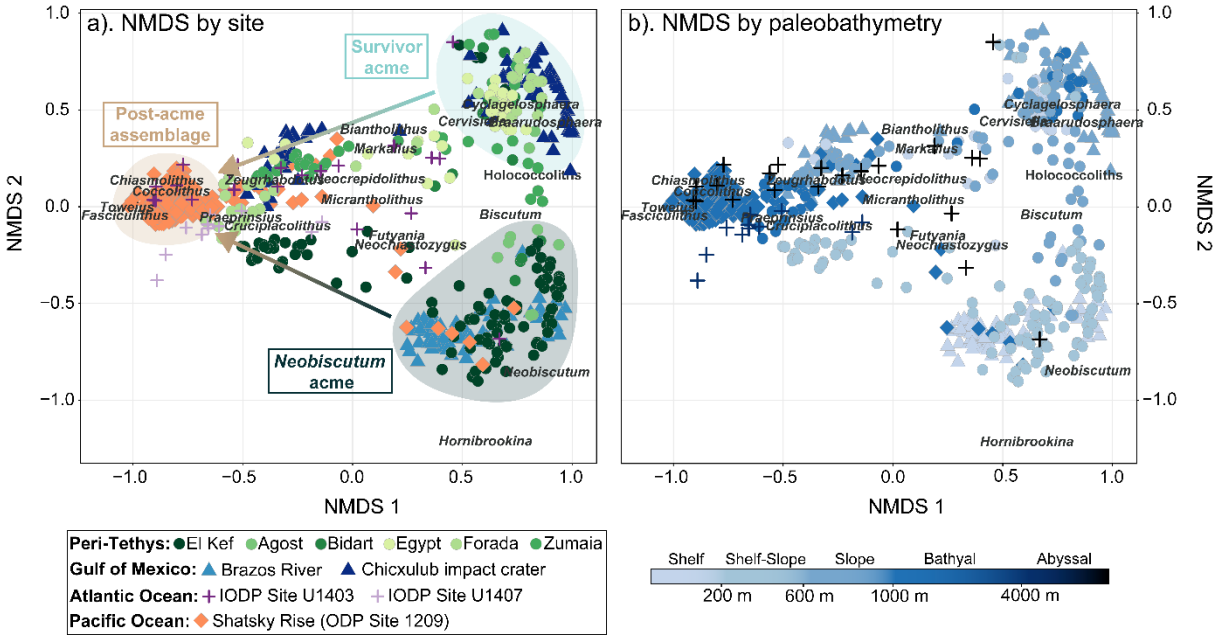

Figure 7. Nonmetric multidimensional scaling (NMDS) ordination plot for the global literature data. (a) Sample scores coded by region (shape) and site (color). Sites from the peri Tethys Ocean (circles) are El Kef (this study), Agost (Jiang et al. 2010), Bidart (Jiang et al. 2019), Egypt (Wadi Hamama & Gebel Qrieya; Tantawy 2003), Forada (Fornaciari et al. 2007) and Zumaia (Jiang et al. 2019). Sites from the Gulf of Mexico (triangles) are Brazos River (Schueth 2009) and IODP-ICDP Site M0077A: Chicxulub impact crater (Jones et al. 2019). Sites from the North Atlantic Ocean (crosses) are IODP Site U1403 and IODP Site U1407 (Bown et al. 2023). Site from the North Pacific Ocean (diamonds) is ODP Site 1209: Shatsky Rise (Alvarez et al. 2019). (b) Sample scores coded by paleobathymetry.

a stratigraphic transition to increased *Cruciplacolithus* and/or *Coccolithus* abundances. Alternatively, earliest Danian assemblages from El Kef, Brazos River (USA), ODP Site 1209 and IODP Site U1403 are characterized by a well-defined *Neobiscutum* acme. Although a few samples from Bidart and Agost also show an increased relative abundance of *Neobiscutum* during the recovery interval, this taxon did not form a true acme as at the aforementioned four sites. The short-lived *Neobiscutum* acme at both ODP Site 1209 and IODP Site U1403 was followed by a succession of dominance switchovers (*Cruciplacolithus* → *Praeprinsius* → *Coccolithus*) prior to the establishment of more permanent, stable Paleocene assemblages. In contrast, at El Kef, the *Neobiscutum* acme was succeeded by the *Futyania* acme (which was also characterized by an increased abundance of *Cruciplacolithus*), whilst assemblages at Brazos River remain within the *Neobiscutum* acme for the entire examined time interval.

3.6 Geographic variation in nannoplankton boom-bust successions

Although the NMDS and cluster analyses reveal geographic variation in early Danian nannofossil assemblages, they cannot directly resolve differences in the timing and duration of individual acmes or the transitions between them. To examine these patterns in more detail, we compared the cumulative abundances of the major acme-forming taxa through time at eight sites with sufficiently well-constrained age models (Figure 8). In addition to El Kef, this included Forada, Italy (Fornaciari et al., 2007), Brazos River, Texas, USA (Schueth, 2009) and Chicxulub, Gulf of Mexico (Jones et al., 2019) – with ages estimated based on linear sedimentation rates between biostratigraphic tie points – and Zumaia, Spain (Jiang et al., 2019), ODP Site 1209, North Pacific (Alvarez et al., 2019) and IODP Sites

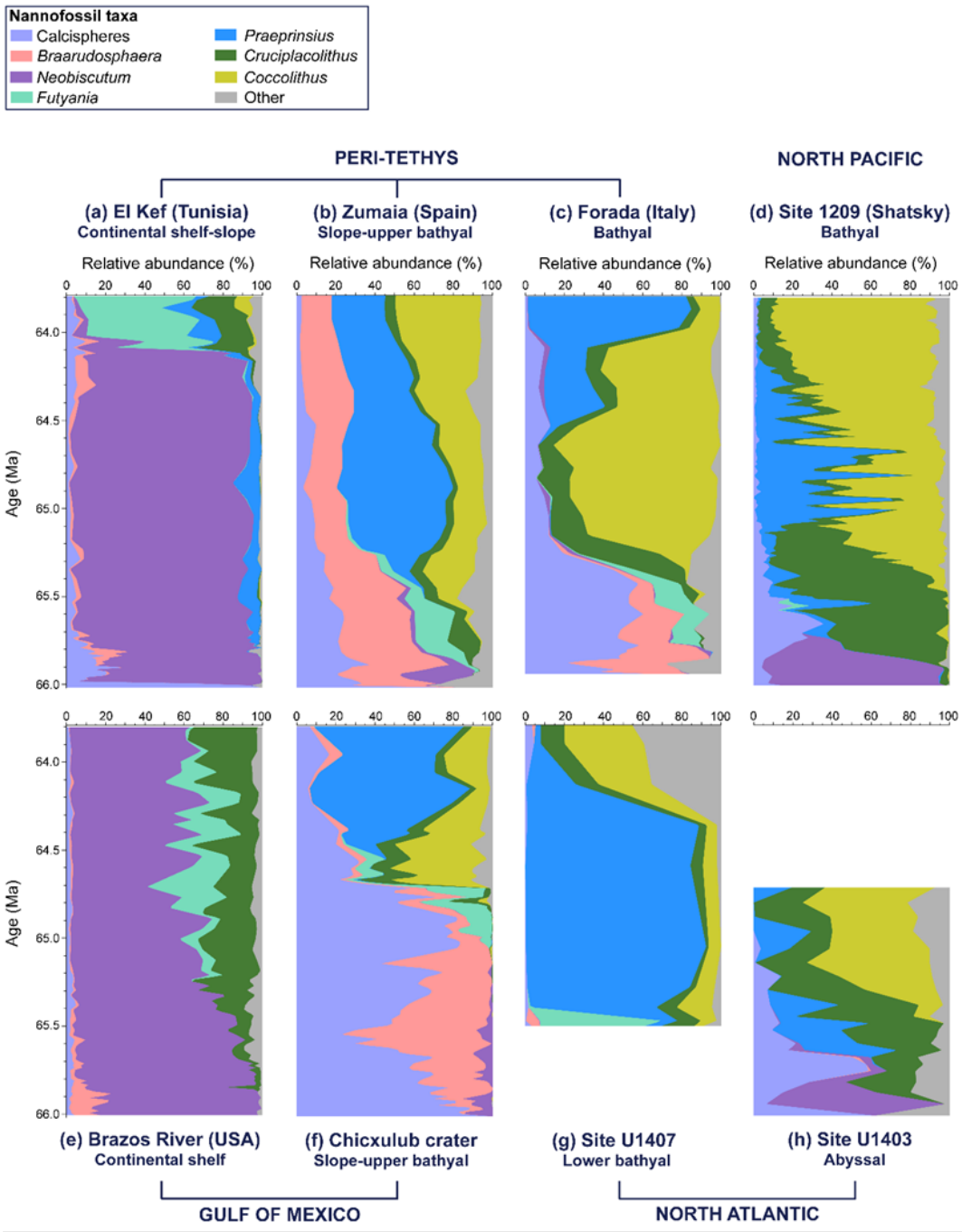

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Figure 8. Cumulative frequency plots showing the relative abundance of the six major acme-forming nannofossil taxa (and calcispheres) between ~63.8 and 66.0 Ma at eight Northern Hemisphere sites. Please note that the traditional duration of P0 (~30 kyr) is used here to facilitate more consistent comparisons of paleoecological patterns between sites that rely on older biostratigraphic age models or employ differing age-modeling methodologies. (a) Nannofossil relative abundances at El Kef, Tunisia (this study). (b) Nannofossil relative abundances at Zumaia, Spain (Jiang et al. 2019). (c) Nannofossil relative abundances at Forada, Italy (Fornaciari et al. 2007). (d) Nannofossil relative abundances at ODP Site 1209: Shatsky Rise, North Pacific Ocean (Alvarez et al. 2019). (e) Nannofossil relative abundances at Brazos River, USA (Schueth 2009). (f) Nannofossil relative abundances at IODP-ICDP Site M0077A: Chicxulub impact crater, Gulf of Mexico (Jones et al. 2019). (g) Nannofossil relative abundances at IODP Site U1407, North Atlantic Ocean (Bown et al. 2023). (h) Nannofossil relative abundances at IODP Site U1403, North Atlantic Ocean (Bown et al. 2023).

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U1403 and U1407, North Atlantic (Bown et al., 2023), which have their own published age models. Due to temporal limitations at some of the sites, we focused our comparison on the ~63.79 - 66.02 Ma stratigraphic interval.

Our results reveal pronounced differences in the timing, duration, and succession of early Danian nannoplankton acmes (Figure 8). The shallow shelf/slope records from El Kef and Brazos River are both characterized by prominent and prolonged *Neobiscutum* acmes. At Brazos River, *Neobiscutum* remained abundant throughout the ~2.2 Myr record, whereas at El Kef its acme extended across much of the examined interval. *Cruciplacolithus* increased in abundance substantially earlier at Brazos River (~65.4 Ma) than at El Kef (~64.1 Ma). In contrast, El Kef contains ancestral *Praeprinsius* cf. *vegrandis* and a distinct *Futyania* acme, neither of which was recognized in the shorter Brazos River record.

The upper bathyal records from Zumaia and Chicxulub also show similar acme successions to each other. Both are characterized by prominent calcisphere/*Braarudosphaera*/Cretaceous-survivor acmes during the earliest Danian, with *Neobiscutum* occurring at considerably lower abundances than at the shallower sites. These early acmes were followed by increased abundances of *Cruciplacolithus* and *Coccolithus*. At Chicxulub, *Coccolithus* formed a short-lived (~250 kyr) acme before being replaced by *Praeprinsius*. A *Praeprinsius* acme is also present at Zumaia but occurred ~1 Myr earlier than at Chicxulub. Boom–bust successions persisted to the top of both records (~2.2 Myr post-impact).

Greater differences are apparent between the two middle bathyal records at Forada and ODP Site 1209. During the first ~1 Myr of the Danian, Forada is characterized by a survivor acme and a *Futyania* pseudo-acme, whereas Site 1209 contains an early *Neobiscutum* acme lasting ~250 kyr, followed by a *Cruciplacolithus* acme. *Coccolithus* became prominent at approximately the same time (~700 kyr post-impact) at both sites. At Site 1209, the *Coccolithus* acme was subsequently interrupted by a *Praeprinsius* acme that terminated ~1.8 Myr post-impact, whereas at Forada the *Praeprinsius* acme did not begin until ~64.5 Ma and persisted to the top of the record (~63.8 Ma).

The deeper North Atlantic sites show closer similarities to the open-ocean Site 1209 record. Although the first ~500 kyr of the Danian are absent at IODP Site U1407, the preserved succession includes a particularly prominent *Praeprinsius* acme beginning at ~65.4 Ma, earlier than at the other bathyal sites examined. Boom–bust successions terminated at approximately the same time at Site U1407 and Site 1209. The shorter abyssal Site U1403 record, which spans only the first ~1.25 Myr of the Danian, shows a broadly similar early succession to Site 1209.

4. Discussion

4.1 Calcareous nannoplankton recovery dynamics at El Kef

The raw nannofossil relative abundance data (Figure 3a) and NMDS results (Figure 4) reveal the existence of four distinct generic acmes at El Kef, with the transitions between them marking major milestones in the nannoplankton recovery. Below we discuss the nannofossil assemblage data and geochemical records for each of these acmes in turn, providing clues as to the potential paleoenvironmental and/or paleoecological conditions during each recovery stage.

4.1.1 Stage 1 – The *Cervisiella* acme (0 - 11.5 kyr post K/Pg; ~66.00 to 66.01 Ma): The oldest five samples examined in the El Kef cores – which represent the first ~11.5 kyr of the Danian – contain only *Cervisiella* calcispheres (calcareous cysts produced by dinoflagellates) and reworked Late Cretaceous

nannofossil species such as *Watznaueria barnesiae*, *Micula* spp. and *Prediscosphaera* spp. This calcisphere "spike" is a global feature driven by the near-total extinction of calcareous nannoplankton (e.g., Lamolda et al., 2016; McLachlan & Pospelova, 2021; Romein, 1977), which opened up niche space that was subsequently filled by plankton groups less severely affected by the K/Pg impact (e.g., Sepúlveda et al., 2019). In addition to calcareous dinoflagellates, this included presumed opportunistic, heterotrophic organic-walled dinoflagellate taxa (Vellekoop et al., 2015), cyanobacteria (Bralower et al., 2020; Schaefer et al., 2020), and other groups of non-calcareous phytoplankton (Sepúlveda et al., 2009), most of which have resting stages that allowed them to escape extreme surface ocean environmental conditions (e.g., global darkness and impact winter) that persisted for the years to decades following the bolide impact (Morgan et al., 2022). Although these environmental effects were geologically short-lived, an increasing body of evidence suggests prolonged surface ocean instability, potentially driven by: (1) pH overshoot following a transient ocean acidification event (up to ~40 kyr post-impact; Henehan et al., 2019), (2) long-term (~100 kyr) global warming due to increased atmospheric CO_2 from wildfires, soil decay and/or impacted target rock (Artemieva et al., 2017; Lyons et al., 2020; MacLeod et al., 2018, 2025; Morgan et al., 2022) and/or, (3) increased upwelling due to cooling-induced vertical mixing, leading to surface ocean nutrient enrichment (eutrophication) for up to 1000-2000 years post-impact (Brugger et al., 2016; Galeotti et al., 2004). Such environmental instability is supported by variability in bulk organic $\delta^{13}C$ values (-26.80 to -26.27 ‰; Figure 2) during the first 20 kyr of the Danian at El Kef, which could reflect fluctuations in terrestrial- vs. marine-derived organic material (Sosa-Montes de Oca et al., 2024), changes in marine productivity and/or non-calcifying phytoplankton community composition (Sepúlveda et al., 2019), or changes in the isotopic fractionation of carbon during photosynthesis due to the aforementioned increase in atmospheric CO_2. Although not possible with our current bulk organic geochemical data, future high-resolution, biomarker and compound-specific $\delta^{13}C$ records from El Kef will help determine which of these options was most likely.

In contrast to the bulk organic $\delta^{13}C$ data, bulk carbonate $\delta^{13}C$ values show a general ~0.7 ‰ decrease during the same interval. This was likely driven by the mass extinction of almost all latest Maastrichtian nannoplankton and planktic foraminifera species, which have relatively high $\delta^{13}C$ signatures compared to the calcareous dinoflagellate cysts (calcispheres) and small, non-symbiotic planktic foraminifera that replaced them (e.g., Alegret et al., 2012, 2022; Birch et al., 2016; Esmeray-Senlet et al., 2015; Sepúlveda et al., 2019). In addition, the absence of relatively dense, heavily calcified calcareous nannoplankton and planktic foraminifera taxa from earliest Danian communities – as well as the extinction of many larger organisms that produced fecal pellets – meant that organic matter was not transported from the surface ocean to the deep sea as effectively as it was during the latest Maastrichtian. This reduction in biological pump efficiency led to increased remineralization in the upper water column, driving down the $\delta^{13}C$ value of the planktic organisms that comprise the majority of bulk carbonate in deep-sea sediments (Figure 9a; Birch et al., 2016; D'Hondt et al., 1998; Henehan et al., 2019). Therefore, the decrease in bulk carbonate $\delta^{13}C$ likely represents the joint effect of the increased dominance of ^{13}C-depleted plankton taxa in surface ocean communities and reduced biological pump efficiency. However, it could also at least partially be explained by the increased abundance of non-biogenic carbonate – including diagenetic dolomite crystals – which are commonly observed in smear slides from both the El Kef sediment cores (Bralower et al., 2020) and outcrop section (Sepúlveda et al., 2019).

4.1.2 Stage 2 – The *Neobiscutum* acme (11.5 kyr – 1.9 Myr post K/Pg; ~64.10 to 66.00 Ma): Approximately 11.5 kyr after the mass extinction event, the earliest Danian disaster assemblages at El Kef were replaced by the *Neobiscutum* acme. This tiny, lightly calcified genus produced coccoliths <2 µm in length and likely evolved immediately after the K/Pg impact (Bown, 2005; Bown et al., 2023; Jiang et al., 2019) or during the latest Maastrichtian (Mai et al., 2003; Schueth et al., 2015). *Neobiscutum* is morphologically similar to the dominant nannoplankton species in the modern ocean – *Gephyrocapsa* (formerly *Emiliania*) *huxleyi* – and is widely considered to have been an opportunistic, generalist taxon that was able to take advantage of high nutrient (eutrophic) surface ocean environments (e.g., Bown, 2005; Jiang et al., 2010; Jiang et al., 2019). Such conditions likely prevailed at El Kef due to reduced biological pump efficiency and increased remineralization within the ocean mixed layer, explaining the exceptionally high dominance of *Neobiscutum* (60-95% of assemblages) at this continental shelf/outer ramp site (Figures 3a; 6; 7).

Approximately 172 kyr post-impact (~65.85 Ma), there was an increase in the relative abundance of both calcispheres and *Braarudosphaera* (Figure 3a), the latter of which reached a maximum of 20% at 65.81 Ma. Interestingly, this paleoecological shift roughly coincides with a transient ~1 ‰ decrease in bulk carbonate $\delta^{18}O$ between ca. 65.90 and 65.82 Ma (Figure 3b), potentially indicating a brief interval of surface ocean warming. Although the bulk carbonate $\delta^{18}O$ record should be interpreted with caution

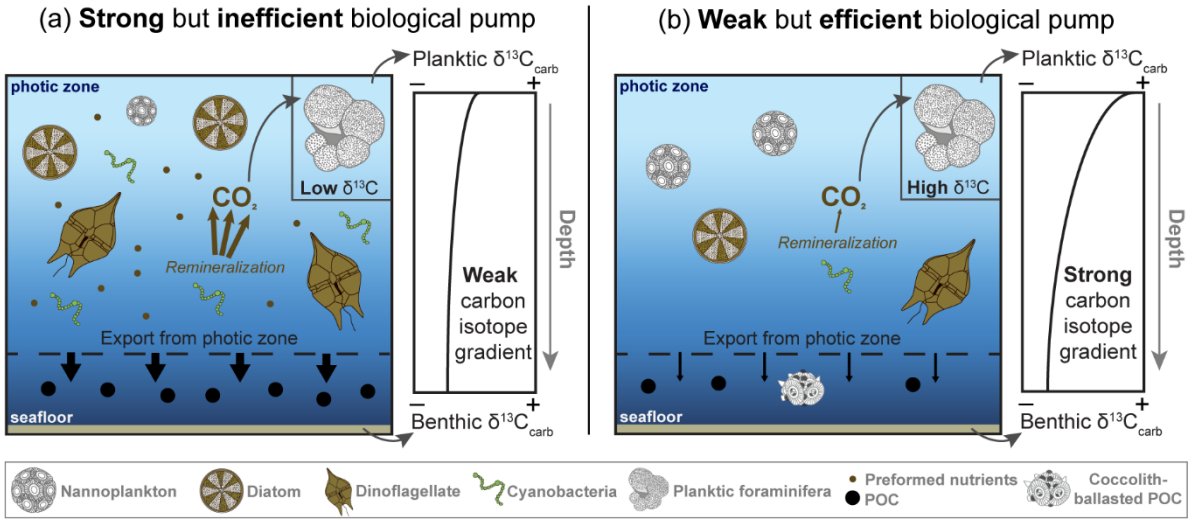

Figure 9. Conceptual model of (a) a strong but inefficient versus (b) a weak but efficient biological pump in the context of this study. (a) An inefficient biological pump may occur when phytoplankton do not fully utilize all available nutrients due to other limiting growth factors such as iron availability, light limitation or grazing pressure. As a result, only a small fraction of the available nutrients is converted into organic matter during photosynthesis and exported to the deep sea. Surface waters remain nutrient-rich (eutrophic), favoring plankton groups such as cyanobacteria, dinoflagellates and opportunistic or generalist nannoplankton taxa (e.g., *Neobiscutum*), as well as those adapted to eutrophic environments (e.g., *Braarudosphaera*). Increased remineralization in the upper water column leads to reduced planktic foraminiferal $\delta^{13}C$ values and a weak planktic-benthic carbon isotope gradient. (b) In contrast, an efficient biological pump develops when nutrients are fully utilized by phytoplankton, converted into organic matter and exported to the deep sea. This process depletes surface nutrients, favoring low-nutrient (oligotrophic)-adapted groups such nannoplankton, especially 'typical' specialized taxa (e.g., *Cruciplacolithus* and *Coccolithus*). Relatively low surface ocean remineralization results in higher planktic foraminiferal $\delta^{13}C$ values and a strong carbon isotope gradient.

due to its low signal-to-noise ratio and potential diagenetic imprint (e.g., Sepúlveda et al., 2019), changes in other geochemical parameters are also apparent, including: (1) a ~2 ‰ decrease in bulk carbonate $\delta^{13}C$ between 65.93 and 65.86 Ma (Figure 3b) followed by a return to pre-excursion values between 65.86 and 65.82 Ma; (2) a decrease in carbonate content from 40 to 10 wt. % between 65.94 and 65.84 Ma (Figure 3d); and (3) a ~0.5% decrease in wt. % TOC between 65.90 and 65.82 Ma (Figure 3d). The timing and nature of these geochemical changes are broadly consistent with the astronomically-paced Dan-C2 hyperthermal event, which occurred ~160 kyr after the K/Pg boundary (i.e., ca. 65.86 Ma) and has been recognized at various Atlantic and Tethyan sites (e.g., Arreguín-Rodríguez et al., 2021; Barnet et al., 2019; Coccioni et al., 2010; Quillévéré et al., 2008). Notably, a *Braarudosphaera* spike also coincided with the onset of Dan-C2 at Gubbio, Italy (Coccioni et al., 2010), providing a further similarity with the El Kef record. Together, these observations suggest that the interval recorded at El Kef could represent Dan-C2, although the available evidence is insufficient to confidently correlate the *Braarudosphaera* spike with this event. If the observed changes do represent the Dan-C2 event, warming may have enhanced upper-water-column stratification and temporarily reduced surface-water salinity, creating conditions favorable for *Braarudosphaera*: a mechanism that has been proposed to explain astronomically paced *Braarudosphaera* blooms in the mid-Oligocene South Atlantic Ocean (Liebrand et al., 2018).

Alternatively, the increase in *Braarudosphaera* may reflect a more local or regional paleoenvironmental perturbation. *Braarudosphaera* is commonly associated with nearshore environments and has frequently been linked to low-salinity and nutrient-rich surface waters, although its precise ecological affinities remain uncertain (e.g., Hagino et al., 2009; Jones et al., 2021; Takano et al., 2006). The *Braarudosphaera* spike at El Kef could therefore record a pulse of increased continental input that introduced cooler, lower-salinity, nutrient-rich waters onto the outer shelf. Such conditions may have temporarily favored *Braarudosphaera* relative to the background *Neobiscutum*-dominated assemblage. Consequently, although the approximate timing and associated geochemical changes are compatible with Dan-C2, we cannot exclude localized changes in continental runoff, surface-water salinity, and nutrient availability as the primary driver of the *Braarudosphaera* spike at El Kef.

Following the *Braarudosphaera* spike, there was a return to almost monospecific *Neobiscutum* assemblages, albeit with a small, sustained increase in ancestral *Praeprinsius* (cf. *vegrandis*). From 260 kyr to 1.9 Myr post-impact (~64.10 - 65.76 Ma), nannofossil assemblages remain relatively stable (Figure 3a). This interval is also associated with a gradual decline in wt. % $CaCO_3$ (following a prior sharp increase, likely driven by the increased abundance of heavily-calcified *Braarudosphaera*), a gradual ~0.75 ‰ increase in bulk organic $\delta^{13}C$ and a sharp decrease in wt. % TOC followed by a steady decrease to the top of the *Neobiscutum* acme (Figure 3c, d). In contrast, there is very little change in the bulk carbonate $\delta^{18}O$ or $\delta^{13}C$ records (Figure 3b), the latter of which fluctuates around an average value of -0.07 ‰. Although the planktic-to-benthic foraminiferal $\delta^{13}C$ gradient (Figure 8) would ideally be used to evaluate changes in biological pump efficiency during the *Neobiscutum* interval, these data are not yet available for the El Kef cores. However, a previous study at Walvis Ridge in the mid-latitude South Atlantic suggests that the increased vertical $\delta^{13}C$ gradient during the early Danian was predominantly driven by increased planktic foraminiferal $\delta^{13}C$ rather than decreased benthic foraminiferal $\delta^{13}C$ (Birch et al., 2016). Assuming that this is the case, the relatively static bulk carbonate $\delta^{13}C$ values indicates continued biological pump inefficiency at El Kef for at least 1.9 Myr post-impact, which is supported by the negative correlation between the relative abundance of *Neobiscutum* and bulk carbonate $\delta^{13}C$ (Figure 5). Biological pump inefficiency was likely driven – at least in part – by the dominance of

Neobiscutum, which had an average cell volume an order of magnitude smaller than the subsequent, long-ranging Paleocene taxa (Alvarez et al., 2019). This would have severely reduced the effectiveness of coccolith calcite in ballasting organic matter, thus maintaining biological pump inefficiency and high-nutrient surface oceans that further bolstered the *Neobiscutum* acme. Therefore, it is likely that the restoration of biological efficiency at El Kef may have not begun properly until *Neobiscutum* was displaced.

4.1.3 Stage 3 – The *Futyania* acme (1.9 - 3.6 Myr post-impact; ~62.46 to 64.10 Ma): The transition between the *Neobiscutum* and *Futyania* acmes occurs across the ~64.10 Ma unconformity (Figures 3a; 4a) and is associated with: (1) a ~1.5 ‰ increase in bulk carbonate $\delta^{13}C$ (Figure 3b), (2) a ~1 ‰ decrease in bulk organic $\delta^{13}C$ (Figure 3c) and, (3) a tripling of wt. % $CaCO_3$ (Figure 3d). As the duration of the unconformity is currently poorly constrained, it is not possible to ascertain how quickly this paleoecological transition occurred. However, the large changes observed in almost all of our geochemical records signal a major regime shift (Figure 4b), with ecosystem function being very different compared to that within the preceding *Neobiscutum* acme. In particular, the concurrent increase in bulk carbonate $\delta^{13}C$ and decrease in bulk organic $\delta^{13}C$, suggests that the *Neobiscutum* → *Futyania* dominance switchover marks the first milestone in the restoration of biological pump efficiency (Figure 8). This meant that a higher proportion of the nutrients in the surface ocean were utilized by phytoplankton, converted into organic matter and exported to the deep sea, lowering mixed layer remineralization and reducing nutrient availability. Lower nutrient (meso/oligotrophic) conditions would have favored the proliferation of typical open-ocean taxa such as *Cruciplacolithus*, as supported by their increased relative abundance in line with the onset of the *Futyania* acme at El Kef (Figure 3b). Although the paleoecological preferences of *Futyania* itself are uncertain, it is likely that it was better adapted to lower nutrient conditions than *Neobiscutum*, making it (at the very least) a mesotrophic taxon (Jones et al., 2019; Lowery et al., 2021).

The transition from nannofossil assemblages with dominant *Neobiscutum* (14 μm^3 average cell volume) to those with higher relative abundances of *Futyania* (322 μm^3 average cell volume) and *Cruciplacolithus* (155-475 μm^3 average cell volume) almost certainly contributed to the 3x increase in wt. % $CaCO_3$ that was also observed at this time (Figure 3d, Alvarez et al., 2019). This would have improved the effectiveness of coccolith calcite as organic matter ballasts (Figure 8b), further enhancing biological pump efficiency. However, as the *Neobiscutum* → *Futyania* transition occurred across an unconformity, it is uncertain whether nannofossil assemblage changes drove enhanced biological pump efficiency or vice versa. For example, a paleoenvironmental factor such as surface warming may have increased surface ocean stratification and lowered nutrient availability, driving the observed shifts in nannofossil assemblages that in turn led to increased biological pump efficiency. Conversely, a different parameter such as the faster recovery of planktic foraminifera compared to nannoplankton and/or the reemergence of larger organisms at higher trophic levels, could have led to enhanced biological pump efficiency, lowering surface ocean nutrient availability and driving the transition from eutrophic-to meso/oligotrophic-adapted nannoplankton communities. This causality conundrum highlights the need for multiproxy records that document changes in nannofossil and planktic foraminifera assemblages, the planktic to benthic foraminiferal $\delta^{13}C$ gradient, biomarker records, and temperature proxy data at a high temporal resolution.

The remainder of the *Futyania* acme is characterized by a gradual decline in *Futyania* relative to *Cruciplacolithus* (Figure 3a). *Coccolithus* became an important component of assemblages beginning

at ca. 63.86 Ma (~2.2 Myr post-impact), and gradually increased in relative abundance throughout the *Futyania* acme, whilst *Praeprinsius* maintained a consistently low (~10%) relative abundance until ~62.63 Ma (~3.6 Myr post-impact). The increased proportion of pelagic taxa such as *Cruciplacolithus* and *Coccolithus* with quasi-stability in the geochemical data, suggests a gradual transition to more oligotrophic surface waters between 63.86 and 62.63 Ma (2.2 to 3.6 Myr post-impact), which may have been predominantly ecologically – rather than environmentally – driven (Figures 3-5). At ~62.63 Ma the relative abundance of *Praeprinsius* increased to comprise >50% of assemblages. For the subsequent ca. 200 kyr, there was significant ecological jostling between *Futyania* and *Praeprinsius* at El Kef, with the base of the *Praeprinsius* acme tentatively placed at ~62.46 Ma (3.6 Myr post-impact), when assemblages stabilized and *Praeprinsius* maintained its dominance. This 200 kyr transitional interval coincides with a transient ~2.5 ‰ decrease in bulk carbonate $\delta^{18}O$ (Figure 3b), a gradual 1.5 ‰ increase in bulk carbonate $\delta^{13}C$ (Figure 3b), a transient ~0.75 ‰ decrease in bulk organic $\delta^{13}C$ (Figure 3c) and wildly fluctuating wt. % $CaCO_3$ values (Figure 3d). Aside from the bulk carbonate $\delta^{13}C$, these geochemical trends are similar to those during the earlier interval tentatively assigned to the Dan-C2 event. We therefore speculate that at least some of the paleoecological instability observed in nannofossil assemblages at El Kef was associated with another episode of climatic and environmental perturbation such as the Late Danian Event (LDE; Bornemann et al., 2009). Although our current age model places this potential warming event at El Kef earlier (~62.52 Ma) than the estimated age of the LDE (~62.15 Ma; Harbich et al., 2024), the duration of planktic foraminiferal zone P2 – within which this event occurs – is poorly constrained. If this event does correspond to the LDE, it could therefore provide valuable constraints for refining the El Kef age model in future studies.

4.1.4 Stage 4 – *The Praeprinsius* acme (3.6 – 3.7 Myr post-impact; ~62.35 to 62.46 Ma): The youngest ~100 kyr of the El Kef record is characterized by the high dominance of *Praeprinsius* (generally >70%) with very low relative abundances of *Cruciplacolithus* and *Coccolithus*, especially compared to the *Futyania* acme. The decline in oligotrophic-adapted taxa and the dominance of *Praeprinsius* – a presumed opportunistic, eutrophic-adapted taxon (Jiang et al., 2019) suggests a reversion to higher nutrient surface waters. The part of the *Praeprinsius* acme recorded at El Kef, is associated with only minor changes in the geochemical proxy records suggesting relatively quiescent paleoenvironmental conditions. Overall, the persistence of high dominance, low diversity nannoplankton acmes for at least 3.7 Myr post-impact, suggests that ecosystem function was restored a lot slower at El Kef than at ODP Site 1209, where boom-bust successions ended within ~1.8 Myr (Alvarez et al., 2019).

4.2 Regional variability in Tethyan nannoplankton assemblages and paleoecological controls

The earliest stages of nannoplankton recovery show pronounced differences among Tethyan sites (Figure 6). At El Kef, the initial calcisphere-dominated assemblage was rapidly replaced by an exceptionally strong and sustained *Neobiscutum* acme (Cluster 2). In contrast, during this interval, the other Tethyan sites were characterized by 'disaster' assemblages comprising calcispheres, *Braarudosphaera*, Cretaceous survivors (e.g., *Cyclagelosphaera*, *Markalius*, *Zeugrhabdotus* and *Neocrepidolithus*) and lower relative abundances of newly evolving Paleocene taxa (Cluster 1). Most of these sites represent somewhat deeper outer-shelf to bathyal settings (~600 - 1500 m paleo-water depth) than El Kef (~200 - 600 m; Alegret et al., 2022), suggesting that the unusually prominent *Neobiscutum* acme at El Kef may partly reflect its proximity to the continental shelf. *Neobiscutum* has previously been interpreted as an opportunistic component of early Danian assemblages (Jiang et al., 2010; Jiang et al., 2019; Schueth et al., 2015), suggesting that its exceptional dominance at El Kef may

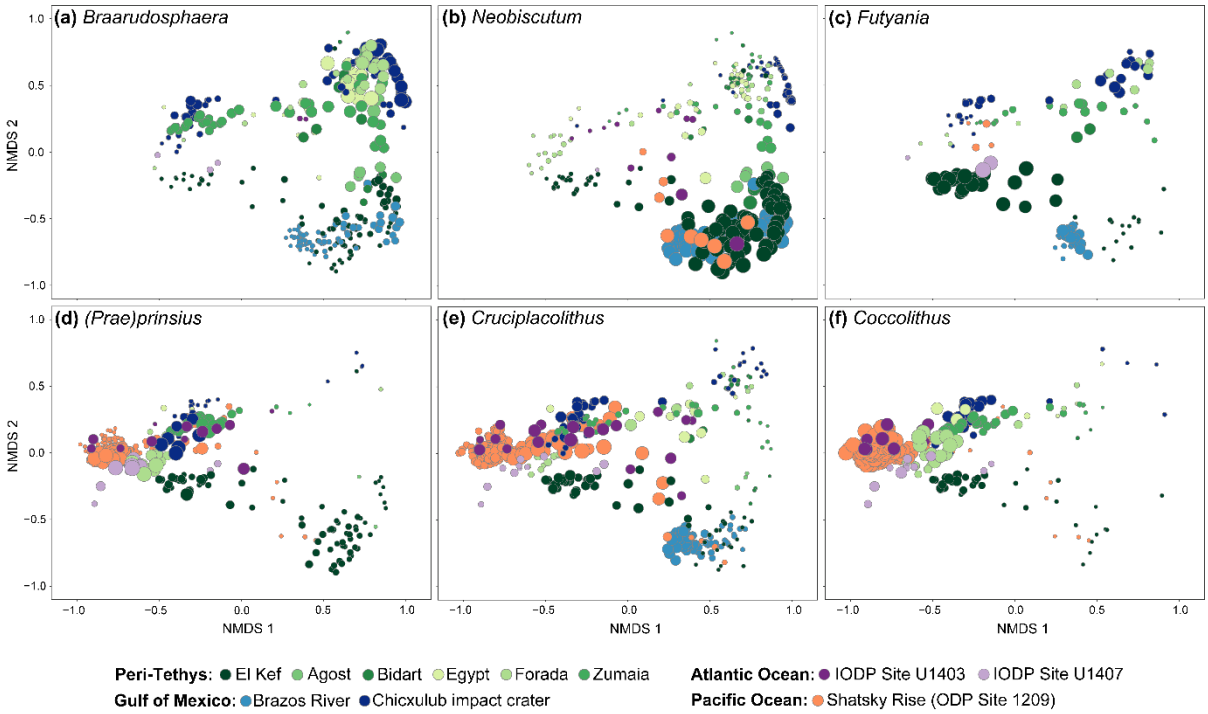

Figure 10. Nonmetric multidimensional scaling (NMDS) ordination plots showing sample scores coded by site. The size of each point (sample score) is scaled by the relative abundance of the six major acme-forming taxa: (a) *Braarudosphaera*, (b) *Neobiscutum,* (c) *Futyania,* (d) *(Prae)prinsius*, (e) *Cruciplacolithus,* (f) *Coccolithus*.

have reflected an ability to tolerate dynamic and highly variable surface-water conditions characteristic of more proximal shelf environments.

A second major difference among the Tethyan records concerns the relative dominance of *Futyania* and *Praeprinsius*. *Futyania* formed a prominent acme only at El Kef (Cluster 3B), where it replaced *Neobiscutum* as the dominant genus (Figure 6). Less well-defined increases in *Futyania* occurred earlier in the recovery succession at the Spanish sites, Zumaia and Agost, where they are represented by sub-cluster 1C-I, whereas other Tethyan sites appeared to largely bypass a *Futyania*-dominated interval and instead transitioned toward assemblages dominated by *Praeprinsius*, *Coccolithus*, and/or *Cruciplacolithus*. This distribution suggests that *Futyania* was particularly well suited to the environmental conditions at El Kef and, to a lesser extent, other outer-shelf to upper-bathyal sites along the western Tethyan margin. Increases in *Futyania* were also generally accompanied by greater abundances of *Cruciplacolithus* and *Coccolithus*, genera that have been interpreted as relatively oligotrophic components of recovering Danian assemblages (Jiang et al., 2010, 2019; Metawally et al., 2024). This association may indicate that *Futyania* was adapted to somewhat lower nutrient conditions than *Neobiscutum*.

However, distinguishing the paleoecological preferences of *Futyania* from those of *Praeprinsius* remains difficult. The two genera belonged to the same evolutionary lineage, and their coccospheres possessed flagellar openings that have been interpreted as evidence for the potential capacity for phagotrophy and mixotrophy (Gibbs et al., 2020), suggesting that they may have shared similar trophic strategies. Despite these similarities, their distributions differed. *Futyania* reached its greatest abundance at El Kef and was more prominent in settings closer to the continental margin in the western Tethys, whereas *Praeprinsius* became abundant across a broader range of Tethyan

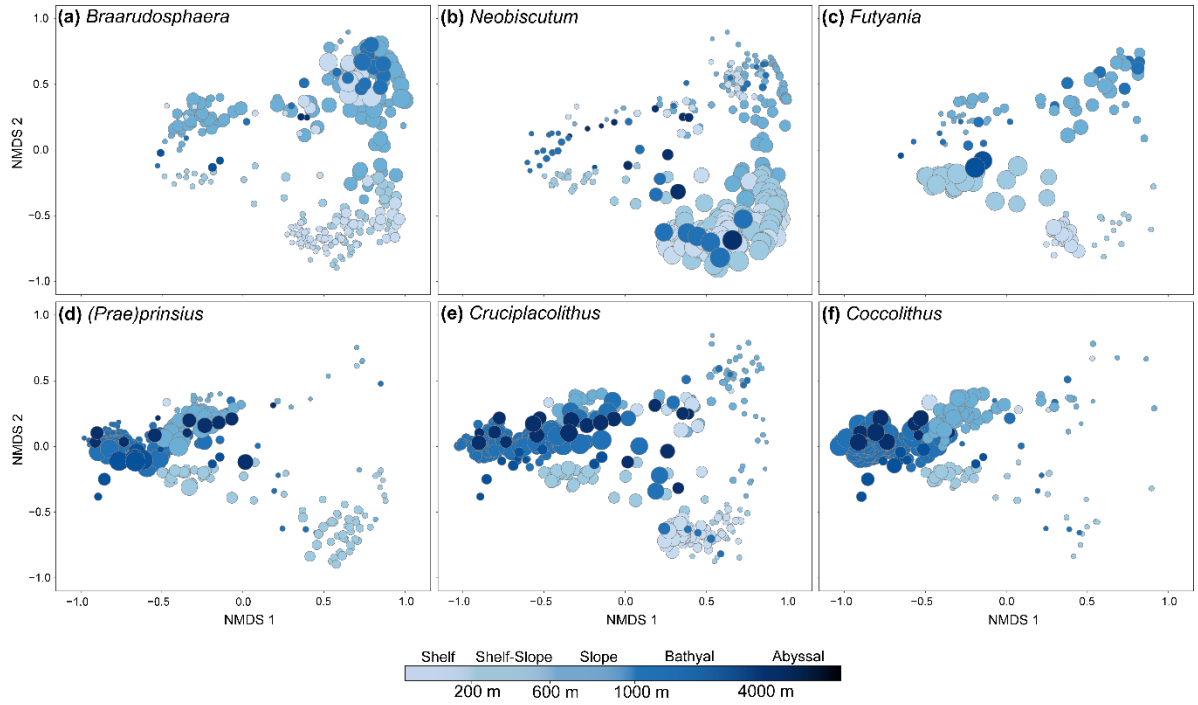

Figure 11. Nonmetric multidimensional scaling (NMDS) ordination plots showing sample scores coded by palebathymetry. The size of each point (sample score) is scaled by the relative abundance of the six major acme-forming taxa: (a) *Braarudosphaera*, (b) *Neobiscutum,* (c) *Futyania,* (d) *(Prae)prinsius*, (e) *Cruciplacolithus,* (f) *Coccolithus*.

environments, in some cases without a preceding distinct *Futyania* acme. The environmental factors underlying these contrasting distributions remain uncertain, although the greater prominence of *Futyania* in proximal paleoenvironmental settings may indicate that it was better adapted to dynamic continental-margin conditions, potentially including greater nutrient availability and variability in surface-water properties. The successive *Futyania* and *Praeprinsius* acmes at El Kef therefore appear to represent one expression of a geographically variable recovery succession rather than a uniform sequence across the Tethys. Additional records from comparable settings are needed to better constrain the environmental controls on the relative success of these closely related genera.

Taken together, the Tethyan records indicate that proximity to the continental margin exerted an important influence on early Danian nannoplankton community composition, particularly along the western Tethyan margin. The shallow Egyptian sites, Wadi Hamama and Gebel Qreiya provide an important exception to this pattern. Despite estimated paleo-water depths of only ~100–200 m (Tantawy, 2003), neither site contains the prominent *Neobiscutum* or *Futyania* acmes observed at El Kef, and both instead cluster with the deeper Tethyan records (Figure 6). This discrepancy suggests an additional regional control between the western and eastern Tethys. Although Tethyan ocean circulation patterns during the Late Cretaceous - early Paleocene remain poorly constrained, neodymium isotope records suggest strengthening of the westward-flowing Tethyan Circumglobal Current during the latest Cretaceous (Soudry et al., 2006). This has been linked to opening of the equatorial Atlantic gateway at the Cenomanian-Turonian boundary (Poulsen et al., 2003) and/or strengthening of the latitudinal temperature gradient following Santonian cooling (Barrera & Savin, 1999), potentially enhancing trade winds, the incursion of Indo-Pacific waters into the eastern Tethys, and upwelling along its southeastern margin (Soudry et al., 2006). Differences in circulation, nutrient supply, and surface-water structure between the eastern and western Tethys could therefore have

contributed to the contrasting recovery assemblages. However, additional early Danian records from intermediate paleolatitudes and paleodepths in the eastern Tethys are required to determine whether this represents a genuine east–west paleoecological gradient rather than differences among individual sites.

4.3 Global geographic and bathymetric patterns in early Danian nannoplankton assemblages

To investigate the broader controls on early Danian nannoplankton recovery, we scaled the NMDS scores in Figure 7 by the relative abundance of the six major acme-forming genera (*Braarudosphaera*, *Neobiscutum*, *Futyania*, *Praeprinsius*, *Cruciplacolithus* and *Coccolithus*) and coded samples by both geographic region (Figure 10) and estimated paleo-water depth, which we use broadly as an indication of relative distance from the continental margin (Figure 11). These comparisons suggest that, with the exception of *Braarudosphaera* and *Praeprinsius*, global differences in the distribution of acme-forming genera were more closely associated with paleobathymetry than with geographic region. Although *Braarudosphaera* was more abundant in the Tethys and Gulf of Mexico (Figure 10a), its acmes were largely restricted to continental slope-to-middle bathyal paleoenvironments (~600 to 1500 m paleo-water depth), with the exception of the previously identified shallow-water Egyptian sections (Figure 11a). In contrast, sustained *Neobiscutum* acmes were most characteristic of continental shelf to outer-ramp settings (~100 to 600 m paleo-water depth; Figure 11b), whereas its dominance at bathyal sites such as ODP Site 1209 and IODP Site U1403 was restricted to a limited number of samples (Figures 10b; 11b).

Futyania occurred across all examined ocean basins but generally at much lower relative abundances than the other major acme-forming genera and formed a true acme (>40% of the assemblage) only at El Kef (Figures 10c and 11c). Brazos River was the only other site where *Futyania* approached acme-level abundance, further suggesting an association with continental shelf to outer-ramp environments. *Praeprinsius*, by comparison, became abundant across a much broader range of geographic and bathymetric settings (Figures 10d and 11d). Its apparently greater abundance at bathyal and abyssal sites should, however, be interpreted cautiously because the NMDS comparison was restricted to approximately the first 3.5 Myr of the Danian. The later development of the *Praeprinsius* acme at El Kef, and potentially at other shelf and slope sites, therefore, falls partly outside the interval represented in this analysis. Together, these patterns suggest that the early success of *Neobiscutum* and, to a lesser extent, *Futyania* was associated with shallower marine environments, whereas *Praeprinsius* had a substantially broader environmental distribution.

The long-ranging Paleocene taxon *Cruciplacolithus* was similarly widespread but formed a distinct acme only at bathyal ODP Site 1209 (Figure 10e). Elsewhere, it occurred as a secondary component of other acmes, including the *Neobiscutum* acme at Brazos River, the *Futyania* acme at El Kef, and the *Praeprinsius* and/or *Coccolithus* acmes at bathyal-abyssal sites in the Gulf of Mexico, peri-Tethys and North Atlantic Ocean (Figure 10e). Although *Cruciplacolithus* has been associated with relatively oligotrophic environments (Jiang et al., 2010), its broad distribution during the early Danian suggests considerable environmental tolerance. *Cruciplacolithus* has also previously been associated with cooler-water conditions (e.g., Faris et al., 2024), suggesting that temperature may have influenced its distribution. However, its broad geographic distribution in our dataset and occurrence as a subordinate component of several different acme assemblages, make it difficult to separate a temperature control from covarying environmental factors such as nutrient availability and water-column structure. In comparison, *Coccolithus* formed major acmes only at bathyal sites within the analyzed interval (Figures

10f, 11f). Collectively, the NMDS results therefore suggest a broad bathymetric structuring of post-K/Pg nannoplankton assemblages, with the relative success of individual acme-forming genera varying systematically from continental-margin to deeper open-ocean environments, although *Braarudosphaera* may have been subject to an additional regional control.

4.4 Paleoenvironmental controls on Northern Hemisphere boom-bust successions

The succession of nannoplankton acmes provides further evidence that the trajectory and duration of early Danian ecological recovery varied among paleoenvironmental settings (Figure 8). Shallow continental shelf to slope sites were characterized by prolonged boom-bust successions dominated initially by *Neobiscutum*. At El Kef (Figure 8a), this interval was followed by a prominent *Futyania* acme and, later, a *Praeprinsius* acme, whereas at Brazos River (Figure 8e), *Futyania* formed only a pseudo-acme following *Neobiscutum*. The absence of a *Praeprinsius* acme at Brazos River cannot be directly compared with El Kef because the available Brazos record extends only to ~2.2 Myr post-impact, whereas the *Praeprinsius* acme at El Kef developed at ~3.5 Myr post-impact. The possibility that a similar acme developed later at Brazos River is supported by the occurrence of a comparable acme in biozone NP3 assemblages of the Brightseat Formation, another shallow-marine record from the broader Gulf of Mexico-Atlantic Coastal Plain region (Self-Trail et al., 2023). Based primarily on the more complete El Kef record, the characteristic succession in shallow marine settings may therefore be represented as *Neobiscutum* → *Futyania* → *Praeprinsius*, with the important caveat that the magnitude of the *Futyania* increase varied among sites and that the later *Praeprinsius* acme cannot be properly evaluated at Brazos River. The persistence of boom-bust assemblages beyond 2.2 Myr post-impact nevertheless indicates prolonged ecological instability in these relatively shallow environments. Although the available records therefore suggest a broadly similar recovery trajectory, additional well-resolved shelf and slope records are required to determine how consistently this succession occurred across shallow-marine settings.

Upper bathyal sites Zumaia (peri-Tethys; Figure 8b) and Chicxulub (Gulf of Mexico; Figure 8f) followed a somewhat different recovery trajectory from that observed at shallower marine sites. Rather than a *Neobiscutum* acme, their early recovery was characterized by prominent disaster acmes dominated by calcispheres, *Braarudosphaera*, and/or Cretaceous survivors. However, *Neobiscutum* was also present – albeit at much lower abundances than at shallower sites – while *Futyania* was a similarly minor component during the latter part of these acmes. The 'disaster' acmes at both upper bathyal sites were succeeded by increased abundances of *Cruciplacolithus* and – most importantly – *Coccolithus*, which were rare in contemporaneous shelf-slope assemblages. In the Chicxulub impact crater, *Coccolithus* even formed a short-lived (~250 kyr), weakly defined acme before being replaced by *Praeprinsius*. Although present in both upper bathyal records, the *Praeprinsius* acme at Chicxulub occurred ~1 Myr later than at Zumaia, likely reflecting the more severe and unstable environmental conditions at "ground zero" (Jones et al., 2019). Nevertheless, even at Chicxulub, this acme occurred ~2 Myr earlier than at El Kef, suggesting faster nannoplankton recovery in these slightly deeper marine environments. Boom-bust successions continued until the top of both upper bathyal records (~2.2 Myr post-impact), indicating that full ecological recovery had not yet occurred. Overall, the boom-bust successions in lower slope – upper bathyal settings appear to have followed the general sequence: Cretaceous survivor acme → *Coccolithus* (pseudo)acme → *Praeprinsius* acme.

In contrast, despite their broadly comparable paleo-water depths, Forada in the peri-Tethys (Figure 8c) and ODP Site 1209 at Shatsky Rise in the equatorial North Pacific (Figure 8d) display markedly different recovery trajectories. Forada more closely resembled the upper-bathyal peri-Tethyan sites,

particularly Zumaia, with an initial post-impact acme of Cretaceous survivors followed by a *Futyania* pseudo-acme, whereas *Futyania* was rare at Shatsky Rise. In contrast, the early recovery at Shatsky Rise was characterized by successive *Neobiscutum*, *Cruciplacolithus* and *Coccolithus* acmes. Later recovery at Forada more closely resembled that at Chicxulub, with the *Praeprinsius* acme developing and terminating substantially later at both sites than at Shatsky Rise. These differences likely reflect the relatively proximal position of Forada to the continental margin compared with the fully open-ocean setting of Shatsky Rise, making it an important exception to our broader use of paleo-water depth as an indicator of distance from the continental margin. Differences in ocean connectivity and circulation may also have contributed, as the peri-Tethys represented a relatively restricted shallow sea influenced by westward-flowing Indo-Pacific waters transported by the Tethyan Circumglobal Current (Soudry et al., 2006), potentially producing different nutrient regimes and surface-water conditions from those at Shatsky Rise. We therefore distinguish two general middle-bathyal recovery trajectories: *Neobiscutum* → *Cruciplacolithus* → *Coccolithus* → *Praeprinsius* in fully open-ocean settings such as Shatsky Rise, and Cretaceous survivor acme → *Futyania* pseudo-acme → *Coccolithus* → *Praeprinsius* in more restricted settings closer to continental margins, such as the peri-Tethys.

Collectively, these comparisons suggest that post-K/Pg boom-bust successions were strongly structured by paleoenvironmental setting and did not follow a single universal sequence. Shallow settings closer to continental margins experienced particularly prolonged *Neobiscutum*-dominated instability, whereas more distal bathyal and open-ocean settings generally progressed earlier toward the formation of *Coccolithus*, *Cruciplacolithus*, and/or *Praeprinsius* acmes, and, where sufficiently long records are available, toward more stable and diverse Paleocene communities. These patterns suggest that distance from the continental margin was the primary control on global differences in nannoplankton boom-bust successions, with regional oceanographic factors, including ocean connectivity and circulation, exerting a secondary influence.

4.5. Paleoenvironmental controls on early Paleocene nannofossil biostratigraphy

In addition to demonstrating that taxon-specific acmes developed at varying times across paleoenvironments, our results have potentially important implications for the reliability of early Paleocene nannofossil biostratigraphic datums**.** Although the records compiled here are based on relative abundance data and therefore do not precisely constrain the true first occurrences of taxa, they reveal substantial diachroneity in the timing at which biostratigraphically important taxa such as *Cruciplacolithus* and *Coccolithus* became prominent components of nannofossil assemblages. Newly evolved taxa are typically rare during the earliest part of their stratigraphic ranges and may therefore occur well below the level at which they become sufficiently abundant to be consistently detected in assemblage counts. Consequently, the patterns shown in Figure 8 should not be interpreted as evidence for diachronous first occurrences. Nevertheless, the strong paleoenvironmental dependence of *Cruciplacolithus* and *Coccolithus* acmes suggests that their apparent first occurrences in routine assemblage counts may vary among depositional settings, potentially complicating their use as biostratigraphic markers. Such environmentally driven variation in the abundance of marker taxa further supports our use of planktic foraminiferal, rather than nannofossil, biostratigraphy as the primary framework for the age model employed here.

4.6. Implications for biological pump recovery

The causal relationship between nannoplankton recovery and the restoration of biological pump efficiency is still open to debate, due to the various complex mechanisms that connect these two

processes. For example, it remains unknown whether: (Option 1) increased nannoplankton cell volume during the early Danian enhanced the ballasting of organic matter, which drove higher biological pump efficiency; (Option 2) biological pump efficiency recovered through mechanisms independent of nannoplankton recovery, such as the recovery of planktic foraminifera and/or larger organisms at higher trophic levels, producing lower-nutrient surface waters that subsequently favored nannoplankton taxa with larger cell volumes; or (Option 3) nannoplankton recovery and the restoration of biological pump efficiency were largely decoupled. Our El Kef data provides tentative support that nannoplankton recovery and biological pump efficiency were linked – particularly across the *Neobiscutum* → *Futyania* acme transition – making complete decoupling (Option 3) unlikely. However, our current data cannot determine whether nannoplankton recovery led (Option 1) or lagged (Option 2) the restoration of biological pump efficiency.

In contrast to our results, the lack of correlation between early Paleocene nannofossil turnover and changes in benthic foraminiferal $\delta^{13}C$ at ODP Site 1209 has been interpreted as evidence for decoupled nannoplankton and environmental recovery during the first ~1.8 Myr of the Danian (Alvarez et al., 2019), an interval during which these records appear more closely coupled at El Kef. This contrast provides further evidence that the nature and tempo of ecosystem recovery varied across paleoenvironmental settings. Alvarez et al. (2019) further proposed that the termination of nannoplankton acmes and development of more stable communities characterized by larger mean cell volumes coincided with the recovery of biological pump efficiency to pre-extinction levels. This relationship cannot be evaluated at El Kef, where boom–bust successions persist to the top of the studied record. Importantly, however, the interpretation at ODP Site 1209 is based on comparison of the Pacific nannoplankton record with the planktic-benthic $\delta^{13}C$ gradient from ODP Site 1262 on Walvis Ridge in the South Atlantic. These two sites were characterized by markedly different nannofossil assemblages (Jiang et al., 2010; Schueth et al., 2015) and patterns of export productivity (Hull & Norris, 2011), complicating direct assessment of the relationship between nannoplankton community recovery and biological pump efficiency. Resolving whether these processes were consistently coupled during the early Paleocene will therefore require high-resolution records that integrate nannofossil abundances and cell-volume distributions with independent geochemical reconstructions of biological pump efficiency from the same site and within a robust age-model framework.

If increased nannoplankton cell volume contributed directly to enhanced biological pump efficiency (Option 1), the strong dependence of nannoplankton boom-bust successions on distance from the continental margin may help explain spatial heterogeneity in post-K/Pg export productivity (Hull & Norris, 2011). In shallow settings closer to continental margins, very small *Neobiscutum* cells (14 μm^3; Alvarez et al., 2019) dominated assemblages for at least 1.8 Myr post-impact (Figure 8), whereas contemporaneous bathyal sites consisted of more diverse nannofossil assemblages with substantially larger mean cell volumes (~300 μm^3; Alvarez et al., 2019). These large differences in assemblage-level average cell volume suggests, particularly if Option 1 is correct, that the restoration of biological pump efficiency may have occurred slower-to-faster along a continental shelf-to-open ocean transect. However, as relatively rare taxa with larger cell volumes can disproportionately contribute to carbonate production, this hypothesis requires more rigorous testing using nannofossil size-trait models that can estimate changes in community-level calcite production through time (Gibbs et al., 2018; Sheward et al., 2024). The stratigraphically expanded El Kef cores are ideal for this purpose as they contain the common coccospheres (complete nannoplankton cell coverings) required for these analyses, including intermediate morphotypes that offer the exciting opportunity to explore how traits

evolved within individual lineages. Combining such abundance-weighted nannofossil trait data with planktic-benthic $\delta^{13}C$ records will help resolve the causal relationship between nannoplankton recovery and the restoration of biological pump efficiency during the early Danian. More broadly, our study highlights the importance of oceanographic structure in shaping the trajectory of ecosystem recovery following the K/Pg mass extinction. The strong spatial differences in nannoplankton recovery identified here may have contributed to corresponding heterogeneity in biological pump recovery, with feedbacks between plankton community structure, export efficiency, and surface-ocean conditions potentially helping to sustain the prolonged boom-bust dynamics that characterized the recovering post-K/Pg ocean.

5. Conclusions

Our new El Kef nannofossil dataset, from a continental shelf/outer ramp setting in the peri-Tethys Ocean, shows that nannoplankton boom-bust successions persisted for at least 3.7 Myr after the K/Pg mass extinction event: ~1.9 Myr longer than in the pelagic Pacific Ocean. Regional and global comparisons indicate that the composition and duration of these successions were primarily structured by distance from the continental margin, with regional paleoceanographic conditions exerting a secondary influence on the timing and expression of individual acmes. These spatial differences in nannoplankton recovery may also have contributed to heterogeneity in biological pump recovery, as larger-celled communities with potentially greater ballasting capacity developed earlier in open-ocean than continental-margin settings. In the future, this should be tested directly by combining estimates for nannofossil carbonate production with reconstructions of biological pump efficiency at the same site, helping to resolve the causal relationship between these two mechanisms following the most recent mass extinction event in Earth history.

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Conflict of interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The new calcareous nannofossil relative abundance data and updated age model tables are available from PANGAEA (*doi will go here upon publication).

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