

# A nutrient effect on the TEX<sub>86</sub> paleotemperature proxy

Ronnakrit Rattanasriampaipong<sup>1,2\*</sup>, Jessica E. Tierney<sup>2</sup>, Jordan T. Abell<sup>3</sup>, Lauren D. Gilmore<sup>4</sup>

<sup>1</sup>University Corporation for Atmospheric Research, Boulder, CO 80307

<sup>2</sup>Department of Geosciences, The University of Arizona, Tucson, AZ 85721

<sup>3</sup>Department of Earth and Environmental Sciences, Lehigh University, Bethlehem, PA 18015

<sup>4</sup>Department of Geosciences, Princeton University, Princeton, NJ 08544

## Key Points:

- Nutrient stress alters GDGT distributions in marine sediments, resulting in elevated TEX<sub>86</sub> values beyond those related to thermal effects
- Paleoclimate case studies from the Arabian Sea and Tasman Sea reveal that nutrient levels likely influenced the TEX<sub>86</sub> proxy in the past
- Explicitly accounting for nutrient effects in the proxy system will improve the accuracy of TEX<sub>86</sub>-based temperature estimates

---

\*Current address, Tucson, AZ

Corresponding author: Ronnakrit Rattanasriampaipong, [ronnakritr@arizona.edu](mailto:ronnakritr@arizona.edu), [rrattan@ucar.edu](mailto:rrattan@ucar.edu)

## Abstract

The TEX<sub>86</sub> paleotemperature proxy is widely used to reconstruct ocean surface temperatures over the past 100 million years. However, archaeal culture experiments show that nutrient stress elevates TEX<sub>86</sub> values by increasing glycerol dialkyl glycerol tetraether (GDGT) cyclization. Here, we demonstrate that this “nutrient effect” is also recorded in sedimentary GDGTs. Using an expanded core-top database, we find a significant negative correlation between TEX<sub>86</sub> and nitrate concentrations ( $\rho = -0.31$ ;  $P < .001$ ) once the thermal effect is removed. There are stronger correlations ( $\rho -0.73$  to  $-0.91$ ;  $P < .001$ ) in regions with steep nitrate gradients. Comparisons between TEX<sub>86</sub> and U<sub>37</sub><sup>K'</sup>-based reconstructions from the Arabian Sea and Tasman Sea suggest that nutrient stress influenced GDGT distributions during glacial-interglacial cycles. Our findings underscore the need to account for nutrient effects when applying TEX<sub>86</sub> paleothermometry.

## Plain Language Summary

Marine archaea help regulate the global nitrogen cycle, and their membrane lipids serve as a temperature proxy (TEX<sub>86</sub>) both today and in the past. While temperature is the main driver of lipid changes, lab studies show that nutrient stress also increases lipid cyclization, potentially affecting TEX<sub>86</sub> accuracy. Here, we show that this “nutrient effect” is recorded in marine sediments and can be separated from the temperature signal. This effect may explain discrepancies between TEX<sub>86</sub>-based temperature estimates and other proxies for surface ocean temperature, particularly in regions with strong nutrient variations. Accounting for nutrient effects is essential to improve TEX<sub>86</sub> as a paleotemperature proxy.

## 1 Introduction

Reconstructing ocean temperatures is essential for understanding Earth’s climatic history (Tierney et al., 2020; Judd et al., 2024). The paleotemperature proxy TEX<sub>86</sub> (tetraether index of 86 carbons) is widely applied to reconstruct surface ocean temperatures throughout the Mesozoic–Cenozoic, particularly during greenhouse intervals (Judd et al., 2022). The proxy is based on the degree of cyclization of archaeal membrane lipids preserved in marine sediments. These lipids include isoprenoid glycerol dialkyl glycerol tetraethers (GDGTs) containing 0–3 cyclopentyl moieties (commonly referred as GDGT-*n*, where *n* denotes the number of internal rings), along with crenarchaeol (cren) and its isomer (cren’)—two unique GDGTs with four cyclopentyl and one cyclohexyl moieties (Sinninghe Damsté et al., 2002). Warmer sea surface temperatures (SSTs) generally correspond to a higher proportion of cyclized GDGTs in surface (core-top) marine sediments, resulting in higher TEX<sub>86</sub> values, as defined by Schouten et al. (2002):

$$TEX_{86} = \frac{[GDGT - 2] + [GDGT - 3] + [Cren']}{[GDGT - 1] + [GDGT - 2] + [GDGT - 3] + [Cren']}$$

This relationship reflects homeoviscous adaptation, a physical mechanism where the degree of cyclization in archaeal membrane lipids adjusts to temperature. Experimental evidence, including (hyper)thermophilic (De Rosa et al., 1980; Uda et al., 2001) and mesophilic (Elling et al., 2015) archaeal cultures, as well as seawater mesocosms containing mixed marine archaeal populations (Wuchter et al., 2004; Schouten et al., 2007), strongly supports the use of TEX<sub>86</sub> as a reliable paleothermometer.

Although core-top TEX<sub>86</sub> correlates strongly with ocean surface temperatures, non-thermal factors such as archaeal community structure (Taylor et al., 2013; Villanueva et al., 2015; Hurley et al., 2018; Rattanasriampaipong et al., 2022a; van der Weijst et al., 2022) and biogeochemical conditions that impose energetic stress (Elling et al., 2014; Qin et al., 2015) also influence GDGT distributions. Notably, the role of nutrient availability remains underexplored, despite laboratory evidence showing that archaeal growth under conditions with limited electron donors (i.e., limited substrate availability; Elling et al., 2014; Hurley et al., 2016) or acceptors (i.e., low oxygen conditions; Qin et al., 2015) can enhance GDGT cyclization in archaeal cultures. Observations from both modern water columns (e.g., Hurley et al., 2018) and paleoclimate records (e.g., Junium et al., 2018; Polik et al., 2018) further suggest that nutrient availability may shape TEX<sub>86</sub> signals, potentially through its influence on archaeal metabolism and GDGT production.

Marine archaea are key ammonia oxidizers in today's oceans (Karner et al., 2001; Francis et al., 2005; Wuchter et al., 2006), playing a central role in ocean nitrification by converting ammonia to nitrite, which is subsequently oxidized to nitrate by nitrifying bacteria. The availability of these bioavailable nitrogen species regulates surface ocean productivity (Tyrrell, 1999; Yool et al., 2007) and influences archaeal metabolism (Ward, 2008; Martens-Habbenha et al., 2009; Ward, 2011; Peng et al., 2016; Proctor et al., 2023). While direct indicators of archaeal ammonia oxidation, such as ammonia oxidation rates, ammonia/ammonium concentrations, or nitrite concentrations, would provide the the best constraints on archaeal growth conditions (cf. Wuchter et al., 2006; Beman et al., 2008; Sintes et al., 2013; Smith et al., 2014; Qin et al., 2015), such measurements remain geographically sparse and lack global coverage (cf. Paulot et al., 2015; Tang et al., 2023). In contrast, nitrate—the final product of oceanic nitrification—is widely measured and provides an accessible alternative for assessing ammonia oxidation patterns.

Available data show a moderate yet significant correlation between ammonia oxidation rates and surface ocean nitrate concentrations ( $\rho = 0.34$ ,  $P < .001$ ; see **Figure S1b**), suggesting a general link between ammonia oxidation and nitrate availability in surface oceans. However, this modest correlation reflects the complexity of the marine nitrogen cycle, where physical and biogeochemical factors can decouple ammonia/nitrite from nitrate (Sarmiento & Gruber, 2006). For example, in regions with strong nitrate supply—such as upwelling zones and river-influenced coastal waters—nitrate concentrations may broadly reflect physical transport rather than in situ nitrification, potentially masking low ammonia availability. Given the exploratory nature of our work, we use nitrate concentrations as a practical proxy for ammonia oxidation to investigate how nutrient availability influences marine archaeal TEX<sub>86</sub> at a global scale, while acknowledging the complexity and potential decoupling in nitrate and ammonia/nitrite relationships, particularly near upwelling zones.

## 2 Data and methods

### 2.1 Ocean temperatures and nitrate concentrations

Although marine archaea inhabit the entire water column (Karner et al., 2001), the primary GDGT signals preserved in marine sediments are thought to originate predominantly from above the thermocline due to efficient export mechanisms via the biological pump (cf. Zhang & Liu, 2018; Siegel et al., 2023). The precise export depth range of GDGTs remains an active area of research (e.g., Zhang & Liu, 2018; Hurley et al., 2018), and previous calibration studies have proposed both sea surface and subsurface temperature reconstructions using TEX<sub>86</sub> (e.g., J.-H. Kim et al., 2008, 2010; Tierney & Tingley, 2014, 2015b). To account for the habitat depth range of marine archaea while acknowledging the common application of TEX<sub>86</sub> as a proxy for sea surface and subsurface temperatures, we use thermocline-integrated average temperature and nitrate concentrations.

To compute these values, we use the  $0.25^\circ \times 0.25^\circ$  ocean temperature mean field ( $t_{mn}$ ) from the 1991–2020 decadal average provided by the 2023 World Ocean Atlas (WOA23; Locarnini et al., 2024). The thermocline depth was determined as the depth at which the maximum rate of temperature change occurs in each spatial grid. We then calculated *thermocline-integrated average temperature* (hereafter *thermocline-integrated T* or *thermo-T*) by depth-integrating ocean temperatures down to the thermocline and dividing by the integral depth range. Nitrate concentrations were derived from the Copernicus Marine Environment Monitoring Service (CMEMS) global ocean biogeochemistry hindcast product (Perruche, 2018). Decadal averages of nitrate concentrations were calculated from the  $0.25^\circ \times 0.25^\circ$  monthly mean fields spanning 1993–2022 using the *ncclimo* NetCDF Climatology Generator. We then re-gridded the CMEMS nitrate dataset by interpolating to the spatial coordinates of the WOA23 temperature dataset to ensure coordinate consistency (see **Figure S2**). As with ocean temperatures, we calculated a *thermocline-integrated nitrate* value (hereafter referred to as “*nitrate*”).

## 2.2 Global TEX<sub>86</sub> core-top observations

We update the global core-top dataset previously used in the Bayesian temperature calibration model BAYSPAR ( $n = 1095$ ; Tierney & Tingley, 2014, 2015b). The updated dataset includes 2084 core-top TEX<sub>86</sub> observations, incorporating:

1. Data published in previous compilation efforts (J.-H. Kim et al., 2008, 2010; Tierney & Tingley, 2014, 2015b),
2. Data published in studies since 2015 (Kaiser et al., 2015; J.-H. Kim et al., 2015; Rodrigo-Gámiz et al., 2015; Tierney et al., 2015; J.-H. Kim et al., 2016; Kusch et al., 2016; Pan et al., 2016; Richey & Tierney, 2016; Sinninghe Damsté, 2016; Jaeschke et al., 2017; Ceccopieri et al., 2018; Chen et al., 2018; Lo et al., 2018; Schukies, 2018; Y. Yang et al., 2018; Harning et al., 2019; Wei et al., 2020; Lamping et al., 2021; Sinninghe Damsté et al., 2022; Hagemann et al., 2023; Harning et al., 2023; Varma, Hopmans, van Kemenade, et al., 2024), and
3. New data ( $n = 170$ ) analyzed for this study.

The spatial distribution of the updated database is shown in **Figure S3**. These data originate from multiple publications and laboratories with different analytical approaches. While protocols for GDGT determination using high performance liquid chromatography (HPLC)–mass spectrometry (MS) have evolved over the years, we specify the method used whenever available. However, previous work suggests that older and newer HPLC-MS methods produce comparable results (cf. Hopmans et al., 2016, see *Supplementary Text S1* for details). We removed samples that are heavily impacted by non-pelagic GDGT sources, based on thresholds of the Branched versus Isoprenoid Tetraether (BIT) index  $> 0.5$  (terrestrial GDGT inputs; Hopmans et al., 2004; Weijers et al., 2006), Methane Index  $> 0.5$  (GDGT inputs from methanotrophs; Zhang et al., 2011; B. Kim & Zhang, 2023), and %GDGT-0  $> 60$  (GDGT inputs from methanogens; Blaga et al., 2009; Sinninghe Damsté et al., 2012; Inglis et al., 2015).

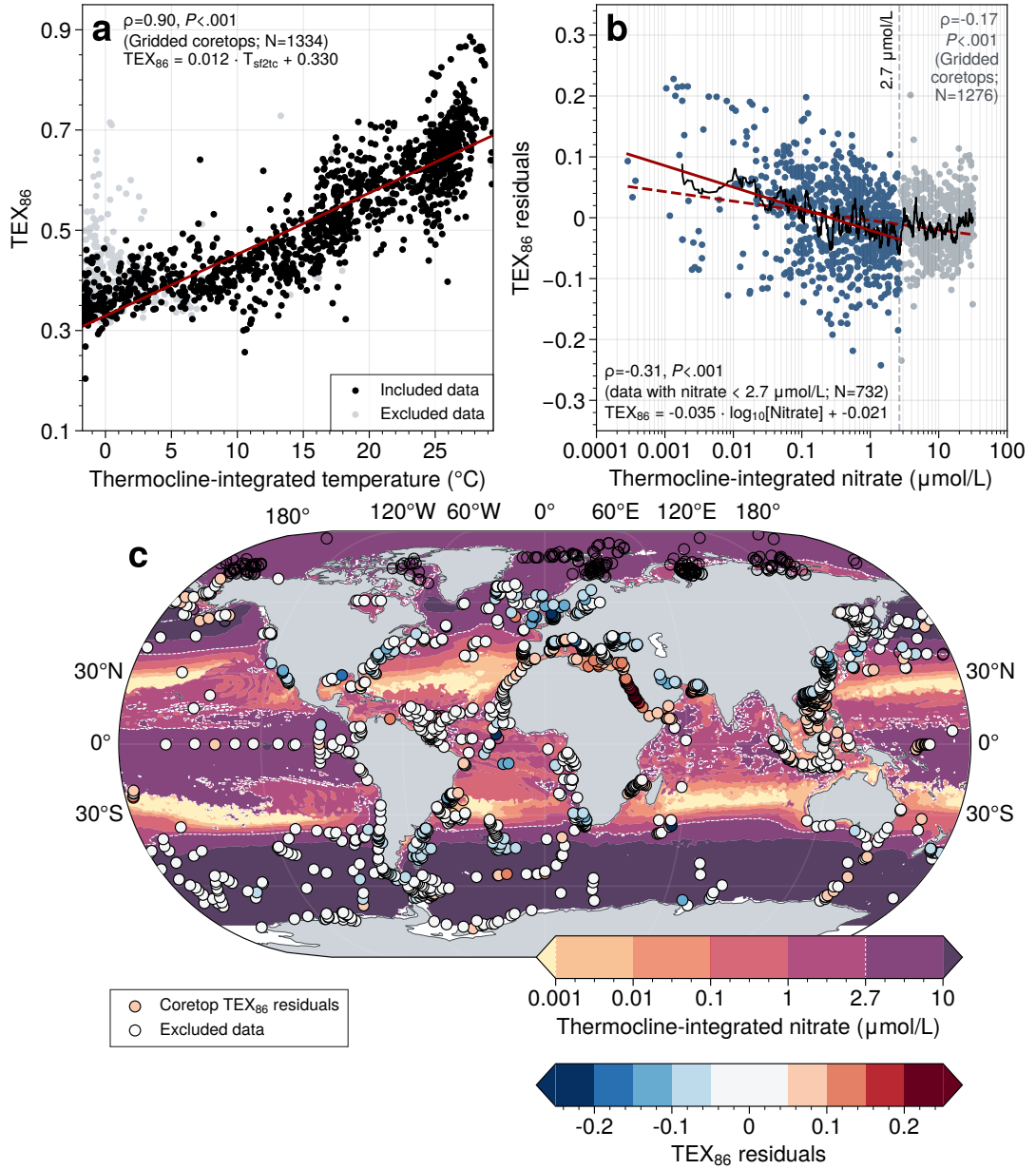
The dominant environmental influence on core-top TEX<sub>86</sub> is ocean temperature (Schouten et al., 2002; J.-H. Kim et al., 2008, 2010; Tierney & Tingley, 2014, 2015b). To ensure spatial consistency, core-top TEX<sub>86</sub> observations were mapped onto a uniform  $0.25^\circ \times 0.25^\circ$  grid, with median values representing grid cells containing multiple observations. A simple linear regression of the updated database indicates that thermocline-integrated temperatures explain 76% ( $r^2=0.76$ ) of the TEX<sub>86</sub> variance (**Figure 1a**). In order to isolate the secondary nutrient effect discussed here, we calculated TEX<sub>86</sub> residuals by subtracting predicted TEX<sub>86</sub> from observed values. Following J.-H. Kim et al. (2010) and Tierney and Tingley (2014, 2015b), core-top TEX<sub>86</sub> from high-latitude sites ( $>70^\circ\text{N}$ ) were excluded from the linear regression, as TEX<sub>86</sub> values from the high Arctic region do not show sensitivity to ocean surface temperatures.

## 3 Results and Discussion

### 3.1 A nutrient effect on marine sedimentary TEX<sub>86</sub>

Core-top TEX<sub>86</sub> residuals exhibit a weak but statistically significant negative correlation with the logarithm of nitrate concentrations (Spearman's  $\rho = -0.17$ ,  $P < .001$ ; **Figure 1b**). This weak global correlation highlights the complexity of sources and sinks of marine nitrogen species, and potentially reflects regions where ammonia and nitrate concentrations are decoupled. A stronger relationship emerges when we restrict the regression to low-nutrient environments, defined as nitrate concentrations below  $2.7 \mu\text{mol/L}$  ( $\rho = -0.33$ ,  $P < .001$ ; **Figure 1b**). The low-nutrient threshold corresponds to the nitrate concentration at which the rolling mean of TEX<sub>86</sub> residuals, calculated using a sliding window of 19 data points, reaches its minimum. We tested different window sizes in the range  $[5, 100]$  and selected the one that yielded the strongest correlation between nitrate and TEX<sub>86</sub> residuals (see **Figure S4**).

While ammonia availability regulates the cellular metabolism of marine archaea (Ward, 2008, 2011; Peng et al., 2016; Proctor et al., 2023), our findings suggest that nitrate is a reasonable proxy



**Figure 1. Positive  $TEX_{86}$  residuals in surface marine sediments correspond to low-nutrient regions.** (a) The correlation between gridded core-top  $TEX_{86}$  values and thermocline-integrated ocean temperature. Data north of  $70^{\circ}\text{N}$  were excluded from the regression following [J.-H. Kim et al. \(2010\)](#) and [Tierney and Tingley \(2014, 2015b\)](#). (b)  $TEX_{86}$  residuals (observed - predicted) from the temperature regression in (a) show a weak but significant negative correlation with nitrate concentrations, suggesting a “nutrient effect.” This effect is more pronounced in low-nutrient regions (highlighted in blue), defined by a threshold of  $2.7 \mu\text{mol/L}$ , where the lowest rolling mean of  $TEX_{86}$  residuals is observed. The solid black line represents the rolling mean, calculated using a sliding window of 19 data points. (c) Spatial distribution of gridded core-top  $TEX_{86}$  residuals, with higher values generally occurring in regions with low nitrate concentrations. Shaded contours indicate nitrate levels, with the low-nutrient threshold contour of  $2.7 \mu\text{mol/L}$  (white dashed line).



for identifying low-nutrient (low-ammonia) locations. The observed relationship between TEX<sub>86</sub> residuals and nitrate indicates that archaeal communities grow more slowly (i.e., exhibit lower ammonia oxidation rates) in regions with low nutrients, and produce GDGTs with more rings, leading to higher TEX<sub>86</sub>. This trend aligns with laboratory experiments showing that archaea decrease membrane permeability by synthesizing GDGTs with higher ring numbers under energy-limiting conditions (Elling et al., 2015; Hurley et al., 2016). The magnitude of elevated TEX<sub>86</sub> of about 0.1 proxy units at the lowest values of nitrate agrees well with experimental evidence (Hurley et al., 2016). Given the logarithmic nature of the regression, the effect of nitrate limitation spans a concentration range of 0.0003–2.7  $\mu\text{mol/L}$ . For context, nitrate levels between 0.5 and 2  $\mu\text{mol/L}$  are considered limiting for primary productivity in the surface ocean (e.g., Henley et al., 2020; Browning & Moore, 2023).

To further investigate this nutrient effect, we analyzed regional-scale patterns, focusing on areas that have strong nutrient gradients and where core-top TEX<sub>86</sub> residuals show a strong negative correlation with nitrate. TEX<sub>86</sub> residuals from these regions show an average negative correlation with nitrate of  $\rho = -0.56$  ( $P < .001$ ; **Figure 2a**), with core-tops near the South Atlantic Subtropical Front exhibiting the strongest relationship ( $\rho = -0.91$ ,  $P < .001$ ; **Figure 2b**). Notably, TEX<sub>86</sub> residuals from the Red Sea show a strong nutrient effect ( $\rho = -0.74$ ,  $P < .001$ ; **Figure 2b**). This contrasts with the original study of sedimentary TEX<sub>86</sub> in the Red Sea, which found no strong correlation between TEX<sub>86</sub> and nitrate concentrations at 100 m depth (Trommer et al., 2009). This discrepancy may stem from the coarse spatial resolution ( $1^\circ \times 1^\circ$ ) of nitrate data in the World Ocean Atlas database used in the original study, which may not adequately capture fine-scale nutrient gradients in restricted basins (see **Figure S5**). While earlier studies attributed anomalously high TEX<sub>86</sub> in the Red Sea to endemic clades of marine archaea (Trommer et al., 2009; J.-H. Kim et al., 2010), our findings suggest a more parsimonious explanation: elevated TEX<sub>86</sub> reflects extreme nutrient stress in this oligotrophic sea.

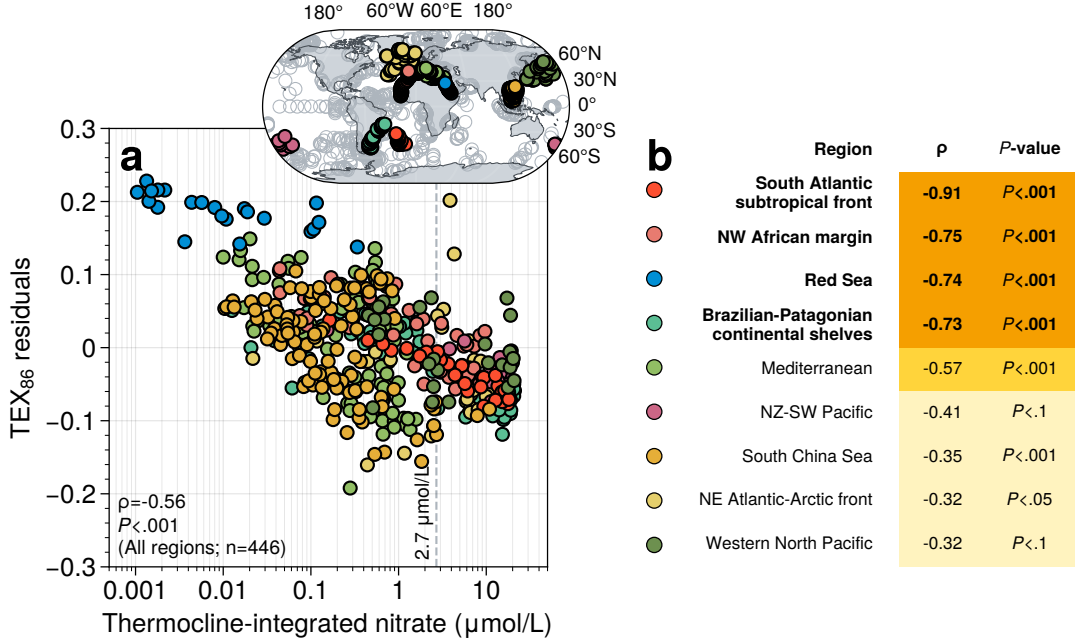
### 3.2 Implications for TEX<sub>86</sub> paleothermometry

TEX<sub>86</sub>-derived ocean temperature estimates occasionally yield anomalously high values that diverge from other proxies and paleoclimate expectations. Here, we explore two paleoclimate scenarios in which nutrient stress may account for the discrepancies between TEX<sub>86</sub>-derived temperatures and SST estimates from the  $U_{37}^{K'}$  proxy—an independent organic paleotemperature proxy based on unsaturated ketones produced by coccolithophores (Brassell et al., 1986; Prahl & Wakeham, 1987). Although multiple calibrations for TEX<sub>86</sub> exist, some of which are non-linear (J.-H. Kim et al., 2010), in these examples we convert TEX<sub>86</sub> to temperatures using the simple linear regression with thermocline-integrated T developed above to highlight deviations from the general linear thermal effect. For the  $U_{37}^{K'}$  data, we use the Bayesian calibration BAYSPLINE (Tierney & Tingley, 2018), which is linear up to temperatures of 25°C, at which point the proxy has a non-linear response as it approaches the maximum possible value of 1.

#### 3.2.1 Denitrification dynamics in the Arabian Sea upwelling zone

Reconstructed ocean temperatures from  $U_{37}^{K'}$  and TEX<sub>86</sub> records in the Arabian Sea capture the overall warming trend since the last deglaciation, marking the transition from the Last Glacial Maximum to the Holocene interglacial (**Figure 3**; Huguet et al., 2006; Tierney et al., 2016). A notable feature, however, is that TEX<sub>86</sub>-derived temperatures are consistently warmer and more variable than  $U_{37}^{K'}$ -based SSTs throughout most of the past 20,000 years (**Figure 3b**). Furthermore, the thermocline-integrated temperatures exceeding 30°C during the Holocene, as suggested by TEX<sub>86</sub>, are likely unrealistic given that modern-day SSTs in this region average approximately 26–27°C in the region. This indicates additional factors contributing to TEX<sub>86</sub> signals on top of seawater temperatures.

A particularly striking feature is the deviation in paleo-temperature proxies found during the Younger Dryas (YD, ca. 12.9–11.7 thousand years ago, ka; Rasmussen et al., 2006) and Heinrich Stadial 1 (HS1, ca. 17.5–14.5 ka; McManus et al., 2004; Broecker & Barker, 2007) events.

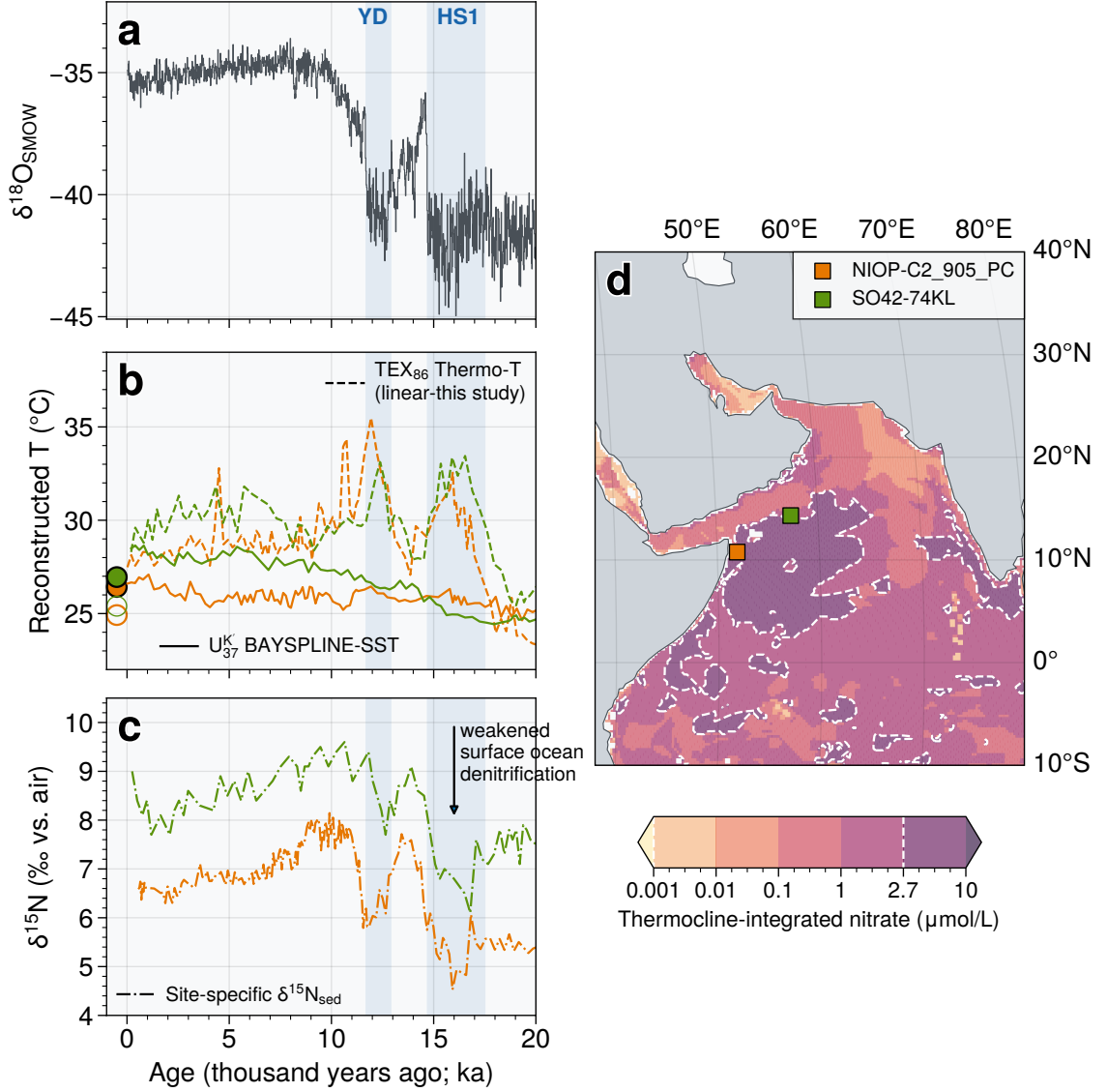


**Figure 2. A pronounced nutrient effect on core-top  $\text{TEX}_{86}$  in regions with strong nutrient gradients.** (a) Scatter plot illustrating the relationship between regional gridded core-top  $\text{TEX}_{86}$  residuals and nitrate concentrations, with an overall Spearman correlation coefficient ( $\rho = -0.56$ ;  $P < .001$ ;  $n = 446$ ). The vertical dash line shows the low-nutrient threshold of  $2.7 \mu\text{mol/L}$ . An inset map showing core-top locations of regions with significant negative correlations between  $\text{TEX}_{86}$  residuals and  $\text{NO}_3^-$  concentrations. (b) Table summarizing Spearman correlation coefficients ( $\rho$ ) and associated  $P$ -values for specific regions.

During these intervals,  $\text{TEX}_{86}$ -derived temperatures increase sharply, whereas  $U_{37}^{K'}$ -based SSTs do not record warming (Figure 3b; Huguet et al., 2006; Tierney et al., 2016). In fact, both the  $U_{37}^{K'}$  records and the TraCE-21ka paleoclimate model simulation—a fully coupled simulation of Transient Climate Evolution over the past 21,000 years—indicate surface cooling during the YD and HS1, reflecting broader Northern Hemisphere climate dynamics (Sonzogni et al., 1998; Schulte & Müller, 2001; Huguet et al., 2006; Tierney et al., 2016). While Tierney et al. (2016) attributed this discrepancy to  $\text{TEX}_{86}$  recording subsurface water warming, the magnitude of the  $\text{TEX}_{86}$  warming anomalies—up to  $7^\circ\text{C}$  from the pre-event baseline (Figure 3b)—is unrealistically large. Together, these observations suggest that  $\text{TEX}_{86}$  is influenced by additional environmental factors beyond temperature alone.

Core sites NIOP-C2.905\_PC and SO42-74KL are located in the Arabian Sea, where nitrate concentrations are generally low. However, these sites lie at the periphery of present-day high-nutrient “blobs” (Figure 3d), making them particularly sensitive to spatial and temporal variations in nutrient dynamics. Under today’s interglacial conditions, the high-nutrient “blobs” persist in this region, potentially supplying nutrients to these sites. However, this feature may have dissipated during past cooling episodes. Weakened monsoon winds during the YD and HS1 (Tierney et al., 2016) likely reduced upwelling, limiting the supply of nutrient-rich waters to the surface. This could have induced relatively stronger nutrient stress in marine archaea, leading to the production of more cyclic GDGTs and higher  $\text{TEX}_{86}$  values.

This interpretation is supported by denitrification proxy records from these two sites. Lower bulk sediment  $\delta^{15}\text{N}$  values during the YD and HS1 indicate reduced denitrification, consistent



**Figure 3. Anomalously warm TEX<sub>86</sub> signals during the Younger Dryas (YD) and Heinrich Stadial 1 (HS1) in the Arabian Sea.** (a) Northern Greenland Ice Project (NGRIP) ice core  $\delta^{18}\text{O}$  record (Seierstad et al., 2014), highlighting cooling during YD (ca. 12.9–11.7 kyr BP; Rasmussen et al., 2006) and HS1 (ca. 17.5–14.5 kyr BP; McManus et al., 2004; Broecker & Barker, 2007). (b) Reconstructed ocean temperatures from sediment cores NIOP-C2.905\_PC and SO42-74KL in the Arabian Sea. U<sub>37</sub><sup>K'</sup>-derived sea surface temperature (SST) records are based on the BAYSPLINE calibration (Tierney & Tingley, 2018), while TEX<sub>86</sub>-derived thermocline-integrated temperatures (thermo-T) are based on the linear regression of the updated core-top dataset (see Figure 1a). Original proxy data were retrieved from Huguot et al. (2006). Modern SST (filled circles) and thermo-T (open circles) are indicated. (c) Bulk sediment  $\delta^{15}\text{N}$  records from NIOP-C2.905\_PC (Ivanochko et al., 2005) and SO42-74KL (Suthhof et al., 2001), serving as a proxy for surface ocean denitrification. The records indicate reduced denitrification during cooling events. Data sourced from the global ocean nitrogen isotope database (Tesdal et al., 2013). (d) A map showing nitrate concentrations with core locations. White dashed contours highlights regions with elevated nitrate concentrations (>2.7 μmol/L surface nitrate) within the overall low-nutrient background of the Arabian Sea.



with weakened upwelling and lower nitrate availability in surface waters (**Figure 3c**; Altabet et al., 1995; Suthhof et al., 2001; Altabet et al., 2002; Ivanochko et al., 2005). Moreover, after interpolating all time series ( $U_{37}^{K'}$ ,  $TEX_{86}$ , and  $\delta^{15}N$ ) onto a common time step, we find that  $TEX_{86}$  T anomalies ( $Thermo-T_{TEX_{86}} - SST_{U_{37}^{K'}}$ ) exhibit a strong negative correlation with bulk sediment  $\delta^{15}N$  during the YD and HS1 (see **Figure S6a–b**). By subtracting the Holocene mean values from the  $TEX_{86}$  records, we de-trend the data and find that temperature anomalies of up to 7°C correspond to increases of up to 0.1 proxy units in  $TEX_{86}$  (see **Figure S6c–d**), which is similar to the magnitude observed in the modern core-top records discussed above.

Collectively, these lines of evidence suggest that  $TEX_{86}$  temperatures in the Arabian Sea are sensitive to nutrient availability in surface waters. Reduced upwelling during the YD and HS1 events likely amplified the nutrient stress on marine archaea, resulting in anomalously high  $TEX_{86}$  values. It is important to note that we do not observe a comparable  $TEX_{86}$  warming anomaly during the Last Glacial Maximum (LGM, ca. 20–19 ka; Clark et al., 2009) in spite of low  $\delta^{15}N$  values. This suggests that surface ocean circulation patterns, monsoonal dynamics, and nutrient availability in this region differed between the nearly steady-state conditions of the LGM and the transient cooling events of the deglacial period.

### 3.2.2 South Pacific Subtropical Gyre poleward expansion

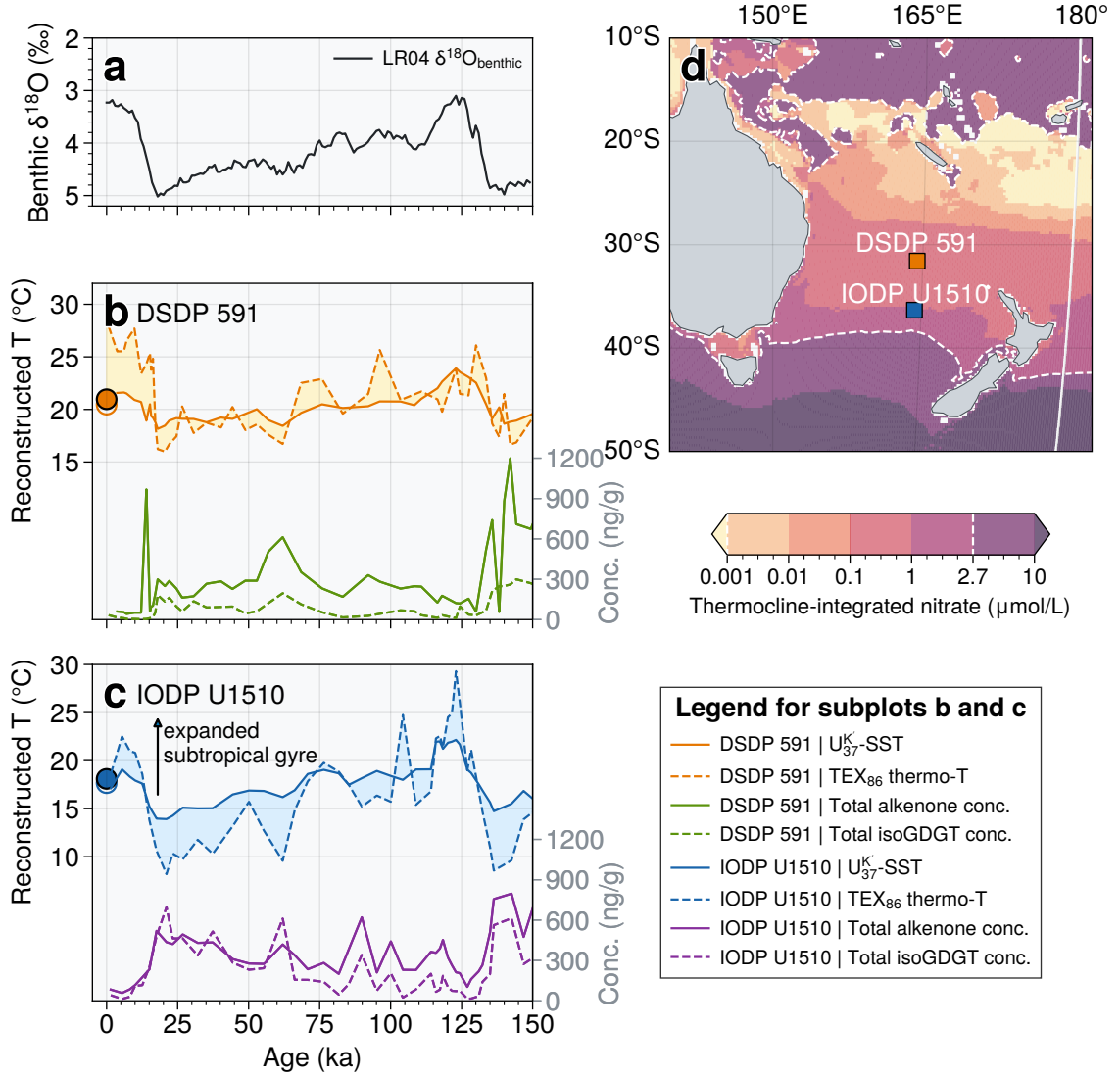
Our second example investigates ocean temperature changes in the Tasman Sea, a region that harbors a strong north-south nutrient gradient in the present day (see **Figure 4d**). Over the past 150,000 years,  $U_{37}^{K'}$  and  $TEX_{86}$  temperatures largely track each other, reflecting the broader global climate history since the penultimate deglaciation (**Figure 4**). However,  $TEX_{86}$ -derived temperatures occasionally exceed 25°C—an implausibly high value given the modern SSTs at these core sites range from 18 to 21°C. This discrepancy suggests that factors beyond temperature influence the proxy.

Today, DSDP Site 591 (31°35.06'S; 164°26.92'E; 2131 m water depth) is located within the Tasman Front, which is a component of the low-nutrient western boundary of the South Pacific Subtropical Gyre (SPSTG). IODP Site U1510 (36°19.7385'S, 164°33.5220'E; 1238 m water depth), while still within the gyre's low-nutrient zone, is positioned approximately 5 degrees further south, where surface waters are more quiescent and impacted primarily by eddies shed from the East Australian Current (Talley et al., 2011; Ganachaud et al., 2014; Sloyan & O'Kane, 2015). Core-top  $TEX_{86}$  residuals from the adjacent southwest Pacific (see the NZ-SW Pacific region in **Figure 2**) also exhibit a pronounced nutrient effect.

Visual inspection reveals episodic warming events in which  $TEX_{86}$ -derived temperatures temporarily exceed  $U_{37}^{K'}$ -based SSTs. These events generally occur during globally-warmer periods (**Figures 4a–c**). Conversely, during colder intervals  $TEX_{86}$  temperatures are typically lower than  $U_{37}^{K'}$ -based SSTs, suggesting that the proxies are either representing different depth habitats (with  $U_{37}^{K'}$  representing the surface and  $TEX_{86}$  the thermocline) or different seasons (e.g.,  $U_{37}^{K'}$  represents the warmer season).

Total  $C_{37}$  alkenone concentrations, indicative of haptophyte productivity, largely follow glacial-interglacial (G-IG) cycles, with elevated concentrations during glacial intervals and lower concentrations during interglacials (see **Figures 4b–c**). Total isoprenoid GDGT (isoGDGT) concentrations follow a similar pattern. Although marine archaea inhabit the entire water column (Karner et al., 2001), we interpret isoGDGT concentrations in our records as reflecting archaeal productivity in the upper water column due to (i) their parallel variations with alkenone concentrations, and (ii) the absence of exogenous GDGT sources (reflected by their low BIT, MI, and %GDGT-0 indices; see *Supplementary Dataset S7*).

We suggest that the extreme warmth in  $TEX_{86}$  temperatures during interglacials reflects changes in surface nutrient availability driven by enhanced upper-ocean stratification, the poleward expansion of the SPSTG, or a combination of both mechanisms. A first-order observation is that biomarker concentrations are generally higher and closely track G-IG cycles at IODP Site



**Figure 4. Nutrient effects on TEX<sub>86</sub> records in the Tasman Sea.** (a) LR04 global benthic foraminiferal  $\delta^{18}\text{O}$  stack (Lisiecki & Raymo, 2005), representing climate variability across glacial-interglacial cycles since the penultimate deglaciation (ca. 138 ka; Govin et al., 2015). (b) Reconstructed ocean temperatures at DSDP 591.  $U_{37}^{K'}$ -derived sea surface temperatures (SST; solid) are based on the BAYSPLINE calibration (Tierney & Tingley, 2018), while TEX<sub>86</sub>-derived thermocline-integrated temperatures (thermo-T; dashed) are based on the linear regression from this study (see **Figure 1a**). Modern SST (filled circle) and thermo-T (open circle) are shown for reference. Total alkenone (solid) and isoGDGT concentrations (dashed) are also plotted. (c) Same as (b), but for IODP U1510. (d) A map showing core locations in the Tasman Sea. Shaded contours represent modern nitrate concentrations. The white dashed contour marks the low-nutrient core (<2.7  $\mu\text{mol/L}$  surface nitrate) of the South Pacific Subtropical Gyre

U1510, whereas at DSDP Site 591, concentrations are overall lower, with episodic spikes of high alkenone concentrations near deglacial periods. Located near the nutrient-depleted core of the subtropical gyre, DSDP Site 591 may have experienced less variability, especially during prolonged interglacial conditions. In contrast IODP Site U1510, located near a dynamic nutrient-rich frontal boundary, likely experienced greater variability in nutrient supply and primary productivity through time. Correlations between temperature anomalies ( $\text{Thermo-T}_{\text{TEX}_{86}} - \text{SST}_{U_{37}^{K'}}$ ) and biomarker concentrations further support these proposed interpretations (see **Figure S7**). Assuming alkenone and isoGDGT concentrations reflect export productivity and in turn nutrient availability, these results suggest that nutrient stress during interglacials results in elevated  $\text{TEX}_{86}$ . Stronger correlations at IODP Site U1510 ( $\rho=-0.68$  for alkenones,  $\rho=-0.82$  for isoGDGTs, both  $P<.001$ ) compared to DSDP Site 591 ( $\rho=-0.31$ ,  $P<.05$  for alkenones and  $\rho=-0.62$ ,  $P<.001$  for isoGDGTs) likely reflects differences in how much the surface nutrient availability is changing through glacial-interglacial cycles at each site. Comparisons between the biomarker concentrations and the benthic foraminiferal  $\delta^{18}\text{O}$  stack also support this; with a stronger correlation at IODP Site U1510 (see **Figure S8**).

Modern observations indicate that warming and weaker winds promote increased stratification in the Tasman Sea's upper ocean layers, a phenomenon evident from satellite ocean color and altimetry data (cf. Tilburg et al., 2002). Paleoclimate reconstructions further suggest poleward migration of the Tasman Front (Martínez, 1994; Kawagata, 2001) and the Subtropical Front in the southwest Pacific (Sikes et al., 2009; Hayward et al., 2012; Bostock et al., 2015) during warmer periods of the late Quaternary. Model simulations also indicate that warming leads to the expansion of subtropical gyres (Polovina et al., 2011; H. Yang et al., 2020), a process that can intensify oligotrophic conditions at these sites. In our view, whether stratification increases primarily due to thermal effects, front migration, or gyre expansion, the outcome is a reduction in nutrient availability at the surface in the Tasman Sea. This nutrient limitation could trigger physiological shifts in marine archaea—altering GDGT production and distribution—and ultimately lead to an overestimation of  $\text{TEX}_{86}$ -based temperatures during warmer intervals of the last 150 kyr.

## 4 Conclusions

Our study demonstrates that a “nutrient effect” is recorded in sedimentary  $\text{TEX}_{86}$ , wherein low-nutrient regions of the global ocean are associated with higher  $\text{TEX}_{86}$  values. This observation is consistent with laboratory studies showing that nutrient limitation leads to higher GDGT cyclization (Elling et al., 2014; Hurley et al., 2016), and the magnitude of increased cyclization observed in modern environments aligns well with experimental evidence (Hurley et al., 2016). Furthermore, comparisons between  $\text{TEX}_{86}$  and  $U_{37}^{K'}$  paleotemperature reconstructions in the Arabian Sea and Tasman Sea indicate that nutrient stress likely influenced GDGT distributions during the last glacial-interglacial cycle, albeit with region-specific signatures.

These findings suggest that previous  $\text{TEX}_{86}$ -based temperature reconstructions—especially for warm climate intervals—may require reevaluation. Integrating  $\text{TEX}_{86}$  with independent proxies such as  $\delta^{15}\text{N}$  and paleoproductivity markers could help resolve discrepancies among proxies and between proxy data and climate model simulations—e.g., during the early Eocene (Hollis et al., 2019). Nutrient stress may also explain extreme  $\text{TEX}_{86}$  values in deep-time hyperthermal events such as the Paleocene-Eocene Thermal Maximum (cf. Zachos et al., 2001, 2008) and Ocean Anoxic Events (cf. Kuypers et al., 2001; van Helmond et al., 2014). During these intervals, increased weathering likely supplied nutrients to coastal oceans, but intensified warming and stronger upper-ocean stratification restricted vertical nutrient supply in the open ocean (Erbacher et al., 2001). This could have led to lower concentrations of important nitrogen species, enhanced nutrient stress on marine archaea, and overproduction of cyclic GDGTs, resulting in anomalously high  $\text{TEX}_{86}$  values ( $>0.8$ ) (e.g., Forster, Schouten, Baas, & Sinninghe Damsté, 2007; Forster, Schouten, Moriya, et al., 2007; Sinninghe Damsté et al., 2010). Our findings highlight the importance of considering nutrient stress when interpreting  $\text{TEX}_{86}$  signals in both recent and deep-time climate reconstructions.

Recognizing the dual influence of temperature and nutrient availability on GDGT production is crucial for improving TEX<sub>86</sub>-based paleotemperature reconstructions. Future studies should quantify nutrient effects on GDGT cyclization across diverse archaeal clades via controlled culture experiments—similar to those reported by Hurley et al. (2016)—to further elucidate the mechanisms driving GDGT production. Additional core-top TEX<sub>86</sub> observations in regions with pronounced nutrient gradients will help refine proxy calibrations. However, as nitrate concentrations can become decoupled from ammonia and nitrite—particularly in upwelling regions—future studies would benefit from globally distributed measurements of ammonia and nitrite to better constrain nutrient-driven variations in TEX<sub>86</sub>. Furthermore, we encourage future research to utilize high-resolution ocean data products whenever available, as low-resolution oceanographic datasets may fail to capture fine-scale nutrient gradients. As ongoing warming alters ocean stratification and nutrient distributions, explicitly incorporating nutrient effects into TEX<sub>86</sub> calibrations will improve the accuracy of both past climate reconstructions and future projections, thereby enhancing the reliability of TEX<sub>86</sub> as a paleotemperature proxy.

## Open Research Section

In this study, we update the core-top TEX<sub>86</sub> dataset by integrating previous calibration compilations (J.-H. Kim et al., 2008, 2010; Tierney & Tingley, 2014, 2015b; Rattanasriampaipong et al., 2022a; Hagemann et al., 2023; Varma, Hopmans, van Kemenade, et al., 2024). These datasets are available via NOAA-NCEI (Tierney & Tingley, 2015a), Figshare (Rattanasriampaipong et al., 2022b), and PANGAEA (Hagemann et al., 2023; Varma, Hopmans, van Kemenda, et al., 2024). A full list of original data sources is provided in Table S1.

All geochemical proxy datasets, ocean data products, and analysis codes needed to reproduce our results are publicly accessible on Zenodo (Rattanasriampaipong et al., 2025) and GitHub (<https://github.com/PaleoLipidRR/nutrient-effect-on-TEX>). The analyses were performed using Python 3.10 (Python 3.10, 2010) with key libraries including NumPy (Harris et al., 2020), Pandas (McKinney, 2010), and Xarray (Hoyer & Hamman, 2017). Statistical work utilized SciPy (Virtanen et al., 2020) and scikit-learn (Pedregosa et al., 2011), while figures were generated using Matplotlib (Hunter, 2007) and enhanced with the Proplot wrapper (<https://proplot.readthedocs.io/en/stable/>). A complete list of dependencies is provided in an exported .yml file in the GitHub repository.

We also used data from the EU Copernicus Marine Service Information’s Global Ocean Biogeochemistry Hindcast product (<https://doi.org/10.48670/moi-00019>), ocean temperature data from the 2023 World Ocean Atlas (Locarnini et al., 2024), and datasets from the global nitrification (Tang et al., 2023) and ocean nitrogen isotope databases (Tesdal et al., 2013).

## Acknowledgments

This work was supported by the NOAA Climate and Global Change Postdoctoral Fellowship Program, administered by UCAR’s Cooperative Programs for the Advancement of Earth System Science (CPAESS) under the NOAA Science Collaboration Program award (Grant number #NA21OAR4310383) to R.R. This work was also supported by a National Science Foundation Ocean Sciences (NSF-OCE) Postdoctoral Research Fellowship (PRF) (award number #2126500) to J.T.A. J.E.T. acknowledges support from the David and Lucile Packard Fellowship in Science and Engineering and the Thomas R. Brown Distinguished Chair in Integrative Science.

## References

- Altabet, M. A., Francois, R., Murray, D. W., & Prell, W. L. (1995). Climate-related variations in denitrification in the Arabian Sea from sediment  $15\text{N}/14\text{N}$  ratios. *Nature*, *373*(6514), 506–509. doi: 10.1038/373506a0
- Altabet, M. A., Higginson, M. J., & Murray, D. W. (2002). The effect of millennial-scale changes in Arabian Sea denitrification on atmospheric  $\text{CO}_2$ . *Nature*, *415*(6868), 159–162. doi: 10.1038/415159a
- Beman, J. M., Popp, B. N., & Francis, C. A. (2008). Molecular and biogeochemical evidence for ammonia oxidation by marine Crenarchaeota in the Gulf of California. *The ISME Journal*, *2*(4), 429–441. Retrieved from <https://doi.org/10.1038/ismej.2007.118> doi: 10.1038/ismej.2007.118
- Blaga, C. I., Reichart, G.-J., Heiri, O., & Sinninghe Damsté, J. S. (2009). Tetraether membrane lipid distributions in water-column particulate matter and sediments: a study of 47 European lakes along a north–south transect. *Journal of Paleolimnology*, *41*(3), 523–540.
- Bostock, H. C., Hayward, B. W., Neil, H. L., Sabaa, A. T., & Scott, G. H. (2015). Changes in the position of the Subtropical Front south of New Zealand since the last glacial period. *Paleoceanography*, *30*(7), 824–844. Retrieved from <https://doi.org/10.1002/2014PA002652> doi: <https://doi.org/10.1002/2014PA002652>
- Brassell, S. C., Eglinton, G., Marlowe, I. T., Pflaumann, U., & Sarnthein, M. (1986). Molecular stratigraphy: a new tool for climatic assessment. *Nature*, *320*(6058), 129–133.
- Broecker, W., & Barker, S. (2007). A 190‰ drop in atmosphere’s  $\Delta^{14}\text{C}$  during the “Mystery Interval” (17.5 to 14.5 kyr). *Earth and Planetary Science Letters*, *256*(1), 90–99. doi: <https://doi.org/10.1016/j.epsl.2007.01.015>
- Browning, T. J., & Moore, C. M. (2023). Global analysis of ocean phytoplankton nutrient limitation reveals high prevalence of co-limitation. *Nature Communications*, *14*(1), 5014. Retrieved from <https://doi.org/10.1038/s41467-023-40774-0> doi: 10.1038/s41467-023-40774-0
- Ceccopieri, M., Carreira, R. S., Wagener, A. L. R., Hefter, J. H., & Mollenhauer, G. (2018). On the application of alkenone- and GDGT-based temperature proxies in the south-eastern Brazilian continental margin. *Organic Geochemistry*, *126*, 43–56. doi: 10.1016/j.orggeochem.2018.10.009
- Chen, J., Hu, P., Li, X., Yang, Y., Song, J., Li, X., ... Lü, X. (2018). Impact of water depth on the distribution of iGDGTs in the surface sediments from the northern South China Sea: applicability of TEX86 in marginal seas. *Frontiers of Earth Science*, *12*(1), 95–107. doi: 10.1007/s11707-016-0620-1
- Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., ... McCabe, A. M. (2009). The Last Glacial Maximum. *Science*, *325*(5941), 710–714. Retrieved from <https://doi.org/10.1126/science.1172873> doi: 10.1126/science.1172873
- De Rosa, M., Esposito, E., Gambacorta, A., Nicolaus, B., & Bu’Lock, J. D. (1980). Effects of temperature on ether lipid composition of *jem;Caldariella acidophila;em;Caldariella acidophila*. *Phytochemistry*, *19*(5), 827–831. doi: 10.1016/0031-9422(80)85120-X
- Elling, F. J., Könneke, M., Lipp, J. S., Becker, K. W., Gagen, E. J., & Hinrichs, K.-U. (2014). Effects of growth phase on the membrane lipid composition of the thaumarchaeon *Nitrosopumilus maritimus* and their implications for archaeal lipid distributions in the marine environment. *Geochimica et Cosmochimica Acta*, *141*, 579–597. doi: 10.1016/j.gca.2014.07.005
- Elling, F. J., Könneke, M., Mußmann, M., Greve, A., & Hinrichs, K.-U. (2015). Influence of temperature, pH, and salinity on membrane lipid composition and TEX86 of marine planktonic thaumarchaeal isolates. *Geochimica et Cosmochimica Acta*, *171*, 238–255. doi: 10.1016/j.gca.2015.09.004
- Erbacher, J., Huber, B. T., Norris, R. D., & Markey, M. (2001). Increased thermohaline stratification as a possible cause for an ocean anoxic event in the Cretaceous period. *Nature*, *409*(6818), 325–327. Retrieved from <https://doi.org/10.1038/35053041>



- doi: 10.1038/35053041
- Forster, A., Schouten, S., Baas, M., & Sinninghe Damsté, J. S. (2007). Mid-Cretaceous (Albian–Santonian) sea surface temperature record of the tropical Atlantic Ocean. *Geology*, 35(10), 919–922. Retrieved from <https://doi.org/10.1130/G23874A.1> doi: DOI:10.1130/G23874A.1
- Forster, A., Schouten, S., Moriya, K., Wilson, P. A., & Sinninghe Damsté, J. S. (2007). Tropical warming and intermittent cooling during the Cenomanian/Turonian oceanic anoxic event 2: Sea surface temperature records from the equatorial Atlantic. *Paleoceanography*, 22(1). Retrieved from <https://doi.org/10.1029/2006PA001349> doi: <https://doi.org/10.1029/2006PA001349>
- Francis, C. A., Roberts, K. J., Beman, J. M., Santoro, A. E., & Oakley, B. B. (2005). Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean. *Proceedings of the National Academy of Sciences of the U.S.A.*, 102(41), 14683–14688. doi: 10.1073/pnas.0506625102
- Ganachaud, A., Cravatte, S., Melet, A., Schiller, A., Holbrook, N. J., Sloyan, B. M., ... Send, U. (2014). The Southwest Pacific Ocean circulation and climate experiment (SPICE). *Journal of Geophysical Research: Oceans*, 119(11), 7660–7686. Retrieved from <https://doi.org/10.1002/2013JC009678> doi: <https://doi.org/10.1002/2013JC009678>
- Govin, A., Capron, E., Tzedakis, P. C., Verheyden, S., Ghaleb, B., Hillaire-Marcel, C., ... Zahn, R. (2015). Sequence of events from the onset to the demise of the Last Interglacial: Evaluating strengths and limitations of chronologies used in climatic archives. *Quaternary Science Reviews*, 129, 1–36. doi: <https://doi.org/10.1016/j.quascirev.2015.09.018>
- Hagemann, J. R., Lembke-Jene, L., Lamy, F., Vorrath, M.-E., Kaiser, J., Müller, J., ... Tiedemann, R. (2023). *Collection of GDGT-derived temperatures of 22 new sites at the Chilean margin, supplemented by various previously published sites*. [Dataset]. PANGAEA. doi: 10.1594/PANGAEA.964270
- Harning, D. J., Andrews, J. T., Belt, S. T., Cabedo-Sanz, P., Geirsdottir, A., Dildar, N., ... Sepúlveda, J. (2019). Sea Ice Control on Winter Subsurface Temperatures of the North Iceland Shelf During the Little Ice Age: A TEX86 Calibration Case Study. *Paleoceanography and Paleoclimatology*, 34(6), 1006–1021. doi: 10.1029/2018PA003523
- Harning, D. J., Holman, B., Woelders, L., Jennings, A. E., & Sepúlveda, J. (2023). Biomarker characterization of the North Water Polynya, Baffin Bay: implications for local sea ice and temperature proxies. *Biogeosciences*, 20(1), 229–249. Retrieved from <https://doi.org/10.1594/PANGAEA.956212> <https://bg.copernicus.org/articles/20/229/2023/> doi: 10.5194/bg-20-229-2023
- Harris, C. R., Millman, K. J., van der Walt, S. J., Gommers, R., Virtanen, P., Cournapeau, D., ... others (2020). Array programming with NumPy. *Nature*, 585(7825), 357–362.
- Hayward, B. W., Sabaa, A. T., Kolodziej, A., Crundwell, M. P., Steph, S., Scott, G. H., ... Grenfell, H. R. (2012). Planktic foraminifera-based sea-surface temperature record in the Tasman Sea and history of the Subtropical Front around New Zealand, over the last one million years. *Marine Micropaleontology*, 82–83, 13–27. Retrieved from <https://www.sciencedirect.com/science/article/pii/S0377839811001150> doi: <https://doi.org/10.1016/j.marmicro.2011.10.003>
- Henley, S. F., Porter, M., Hobbs, L., Braun, J., Guillaume-Castel, R., Venables, E. J., ... Cottier, F. (2020). Nitrate supply and uptake in the Atlantic Arctic sea ice zone: seasonal cycle, mechanisms and drivers. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 378(2181), 20190361. Retrieved from <https://doi.org/10.1098/rsta.2019.0361> doi: 10.1098/rsta.2019.0361
- Hollis, C. J., Jones, T. D., Anagnostou, E., Bijl, P. K., Cramwinckel, M. J., Cui, Y., ... Lunt, D. J. (2019). The deepmip contribution to pmip4: methodologies for selection, compilation and analysis of latest paleocene and early eocene climate proxy data, incorporating version 0.1 of the deepmip database. *Geoscientific Model Development*, 12, 3149–3206. doi: 10.5194/gmd-12-3149-2019



- Hopmans, E. C., Schouten, S., & Sinninghe Damsté, J. S. (2016). The effect of improved chromatography on GDGT-based palaeoproxies. *Organic Geochemistry*, 93, 1–6. Retrieved from <https://www.sciencedirect.com/science/article/pii/S0146638015002387> doi: <https://doi.org/10.1016/j.orggeochem.2015.12.006>
- Hopmans, E. C., Weijers, J. W. H., Schefuß, E., Herfort, L., Sinninghe Damsté, J. S., & Schouten, S. (2004). A novel proxy for terrestrial organic matter in sediments based on branched and isoprenoid tetraether lipids. *Earth and Planetary Science Letters*, 224(1), 107–116. doi: 10.1016/j.epsl.2004.05.012
- Hoyer, S., & Hamman, J. (2017). xarray: N-d labeled arrays and datasets in Python. *Journal of Open Research Software*, 5(1), 10.
- Huguet, C., Kim, J.-H., Sinninghe Damsté, J. S., & Schouten, S. (2006). Reconstruction of sea surface temperature variations in the Arabian Sea over the last 23 kyr using organic proxies (TEX86 and U37K<sub>l</sub>). *Paleoceanography*, 21(3). doi: 10.1029/2005pa001215
- Hunter, J. D. (2007). Matplotlib: A 2d graphics environment. *Computing in Science & Engineering*, 9(3), 90–95.
- Hurley, S. J., Elling, F. J., Könneke, M., Buchwald, C., Wankel, S. D., Santoro, A. E., ... Pearson, A. (2016). Influence of ammonia oxidation rate on thaumarchaeal lipid composition and the TEX86 temperature proxy. *Proceedings of the National Academy of Sciences of the U.S.A.*, 113(28), 7762–7767. doi: 10.1073/pnas.1518534113
- Hurley, S. J., Lipp, J. S., Close, H. G., Hinrichs, K.-U., & Pearson, A. (2018). Distribution and export of isoprenoid tetraether lipids in suspended particulate matter from the water column of the Western Atlantic Ocean. *Organic Geochemistry*, 116, 90–102. doi: 10.1016/j.orggeochem.2017.11.010
- Inglis, G. N., Farnsworth, A., Lunt, D., Foster, G. L., Hollis, C. J., Pagani, M., ... Pancost, R. D. (2015). Descent toward the Icehouse: Eocene sea surface cooling inferred from GDGT distributions. *Paleoceanography*, 30(7), 1000–1020. doi: 10.1002/2014pa002723
- Ivanochko, T. S., Ganeshram, R. S., Brummer, G.-J. A., Ganssen, G., Jung, S. J. A., Moreton, S. G., & Kroon, D. (2005). Variations in tropical convection as an amplifier of global climate change at the millennial scale. *Earth and Planetary Science Letters*, 235(1), 302–314. doi: 10.1016/j.epsl.2005.04.002
- Jaeschke, A., Wengler, M., Hefter, J., Ronge, T. A., Geibert, W., Mollenhauer, G., ... Lamy, F. (2017). A biomarker perspective on dust, productivity, and sea surface temperature in the Pacific sector of the Southern Ocean. *Geochimica et Cosmochimica Acta*, 204, 120–139. doi: 10.1016/j.gca.2017.01.045
- Judd, E. J., Tierney, J. E., Huber, B. T., Wing, S. L., Lunt, D. J., Ford, H. L., ... Zhang, Y. G. (2022). The PhanSST global database of Phanerozoic sea surface temperature proxy data. *Scientific Data*, 9(1). doi: 10.1038/s41597-022-01826-0
- Judd, E. J., Tierney, J. E., Lunt, D. J., Montañez, I. P., Huber, B. T., Wing, S. L., & Valdes, P. J. (2024). A 485-million-year history of Earth’s surface temperature. *Science*, 385(6715), eadk3705. doi: 10.1126/science.adk3705
- Junium, C. K., Meyers, S. R., & Arthur, M. A. (2018). Nitrogen cycle dynamics in the Late Cretaceous Greenhouse. *Earth and Planetary Science Letters*, 481, 404–411. doi: 10.1016/j.epsl.2017.10.006
- Kaiser, J., Schouten, S., Kilian, R., Arz, H. W., Lamy, F., & Sinninghe Damsté, J. S. (2015). Isoprenoid and branched GDGT-based proxies for surface sediments from marine, fjord and lake environments in Chile. *Organic Geochemistry*, 89–90, 117–127. doi: 10.1016/j.orggeochem.2015.10.007
- Karner, M. B., DeLong, E. F., & Karl, D. M. (2001). Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature*, 409(6819), 507–510.
- Kawagata, S. (2001). Tasman Front shifts and associated paleoceanographic changes during the last 250,000 years: foraminiferal evidence from the Lord Howe Rise. *Marine Micropaleontology*, 41(3), 167–191. Retrieved from <https://www.sciencedirect.com/science/article/pii/S037783980000058X> doi: <https://doi.org/10.1016/>

- S0377-8398(00)00058-X
- Kim, B., & Zhang, Y. G. (2023). Methane Index: Towards a quantitative archaeal lipid biomarker proxy for reconstructing marine sedimentary methane fluxes. *Geochimica et Cosmochimica Acta*. doi: 10.1016/j.gca.2023.06.008
- Kim, J.-H., Schouten, S., Hopmans, E. C., Donner, B., & Sinninghe Damsté, J. S. (2008). Global sediment core-top calibration of the TEX86 paleothermometer in the ocean. *Geochimica et Cosmochimica Acta*, 72(4), 1154–1173. doi: <https://doi.org/10.1016/j.gca.2007.12.010>
- Kim, J.-H., Schouten, S., Rodrigo-Gámiz, M., Rampen, S., Marino, G., Huguet, C., ... Sinninghe Damsté, J. S. (2015). Influence of deep-water derived isoprenoid tetraether lipids on the TEX86H paleothermometer in the Mediterranean Sea. *Geochimica et Cosmochimica Acta*, 150, 125–141. doi: 10.1016/j.gca.2014.11.017
- Kim, J.-H., van der Meer, J., Schouten, S., Helmke, P., Willmott, V., Sangiorgi, F., ... Sinninghe Damsté, J. S. (2010). New indices and calibrations derived from the distribution of crenarchaeal isoprenoid tetraether lipids: Implications for past sea surface temperature reconstructions. *Geochimica et Cosmochimica Acta*, 74(16), 4639–4654. doi: 10.1016/j.gca.2010.05.027
- Kim, J.-H., Villanueva, L., Zell, C., & Sinninghe Damsté, J. S. (2016). Biological source and provenance of deep-water derived isoprenoid tetraether lipids along the Portuguese continental margin. *Geochimica et Cosmochimica Acta*, 172, 177–204. doi: 10.1016/j.gca.2015.09.010
- Kusch, S., Rethemeyer, J., Hopmans, E. C., Wacker, L., & Mollenhauer, G. (2016). Factors influencing 14C concentrations of algal and archaeal lipids and their associated sea surface temperature proxies in the Black Sea. *Geochimica et Cosmochimica Acta*, 188, 35–57. doi: 10.1016/j.gca.2016.05.025
- Kuypers, M. M. M., Blokker, P., Erbacher, J., Kinkel, H., Pancost, R. D., Schouten, S., & Sinninghe Damsté, J. S. (2001). Massive Expansion of Marine Archaea During a Mid-Cretaceous Oceanic Anoxic Event. *Science*, 293(5527), 92–95. Retrieved from <https://science.sciencemag.org/content/sci/293/5527/92.full.pdf> doi: 10.1126/science.1058424
- Lamping, N., Müller, J., Hefter, J., Mollenhauer, G., Haas, C., Shi, X., ... Hillenbrand, C.-D. (2021). Evaluation of lipid biomarkers as proxies for sea ice and ocean temperatures along the Antarctic continental margin. *Climate of the Past*, 17(5), 2305–2326. doi: 10.5194/cp-17-2305-2021
- Lisiecki, L. E., & Raymo, M. E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}\text{O}$  records. *Paleoceanography*, 20(1). doi: 10.1029/2004pa001071
- Lo, L., Belt, S. T., Lattaud, J., Friedrich, T., Zeeden, C., Schouten, S., ... Hodell, D. A. (2018). Precession and atmospheric CO<sub>2</sub> modulated variability of sea ice in the central Okhotsk Sea since 130,000 years ago. *Earth and Planetary Science Letters*, 488, 36–45. doi: 10.1016/j.epsl.2018.02.005
- Locarnini, R. A., Mishonov, A. V., Baranova, O. K., Reagan, J. R., Boyer, T. P., Seidov, D., ... others (2024). World ocean atlas 2023, volume 1: Temperature.
- Martens-Habbena, W., Berube, P. M., Urakawa, H., de la Torre, J. R., & Stahl, D. A. (2009). Ammonia oxidation kinetics determine niche separation of nitrifying Archaea and Bacteria. *Nature*, 461(7266), 976–979. Retrieved from <http://dx.doi.org/10.1038/nature08465> doi: 10.1038/nature08465
- Martínez, J. (1994). Late Pleistocene palaeoenography of the Tasman Sea: Implications for the dynamics of the warm pool in the western Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 112(1), 19–62. Retrieved from <https://www.sciencedirect.com/science/article/pii/0031018294901333> doi: [https://doi.org/10.1016/0031-0182\(94\)90133-3](https://doi.org/10.1016/0031-0182(94)90133-3)
- McKinney, W. (2010). Data structures for statistical computing in Python. In *Proceedings of the 9th Python in science conference* (Vol. 445).
- McManus, J. F., Francois, R., Gherardi, J.-M., Keigwin, L. D., & Brown-Leger, S. (2004). Collapse and rapid resumption of Atlantic meridional circulation linked to deglacial

- climate changes. *Nature*, 428(6985), 834–837. doi: 10.1038/nature02494
- Pan, A., Yang, Q., Zhou, H., Ji, F., Wang, H., & Pancost, R. D. (2016). A diagnostic GDGT signature for the impact of hydrothermal activity on surface deposits at the Southwest Indian Ridge. *Organic Geochemistry*, 99, 90–101.
- Paulot, F., Jacob, D. J., Johnson, M. T., Bell, T. G., Baker, A. R., Keene, W. C., ... Stock, C. A. (2015). Global oceanic emission of ammonia: Constraints from seawater and atmospheric observations. *Global Biogeochemical Cycles*, 29(8), 1165–1178. Retrieved from <https://doi.org/10.1002/2015GB005106> doi: <https://doi.org/10.1002/2015GB005106>
- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., ... others (2011). Scikit-learn: Machine learning in python. *Journal of Machine Learning Research*, 12, 2825–2830.
- Peng, X., Fuchsman, C. A., Jayakumar, A., Warner, M. J., Devol, A. H., & Ward, B. B. (2016). Revisiting nitrification in the Eastern Tropical South Pacific: A focus on controls. *Journal of Geophysical Research: Oceans*, 121(3), 1667–1684. doi: 10.1002/2015JC011455
- Perruche, C. (2018). Product user manual for the global ocean biogeochemistry hindcast global\_reanalysis.bio\_001.029. version 1. *Copernicus Marine Environment Monitoring Service*. doi: <http://dx.doi.org/10.25607/OBP-490>
- Polik, C. A., Elling, F. J., & Pearson, A. (2018). Impacts of Paleoecology on the TEX<sub>86</sub> Sea Surface Temperature Proxy in the Pliocene-Pleistocene Mediterranean Sea. *Paleoceanography and Paleoclimatology*, 33(12), 1472–1489. doi: 10.1029/2018pa003494
- Polovina, J. J., Dunne, J. P., Woodworth, P. A., & Howell, E. A. (2011). Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES Journal of Marine Science*, 68(6), 986–995. doi: 10.1093/icesjms/fsq198
- Prahl, F. G., & Wakeham, S. G. (1987). Calibration of unsaturation patterns in long-chain ketone compositions for palaeotemperature assessment. *Nature*, 330(6146), 367–369.
- Proctor, C., Coupel, P., Casciotti, K., Tremblay, J.-E., Zakem, E., Arrigo, K. R., & Mills, M. M. (2023). Light, ammonium, pH, and phytoplankton competition as environmental factors controlling nitrification. *Limnology and Oceanography*, 68(7), 1490–1503. doi: 10.1002/lno.12359
- Python 3.10*. (2010). <https://www.python.org/>. (Python Software Foundation)
- Qin, W., Carlson, L. T., Armbrust, E. V., Devol, A. H., Moffett, J. W., Stahl, D. A., & Ingalls, A. E. (2015). Confounding effects of oxygen and temperature on the TEX<sub>86</sub> signature of marine Thaumarchaeota. *Proceedings of the National Academy of Sciences of the U.S.A.*, 112(35), 10979–10984.
- Rasmussen, S. O., Andersen, K. K., Svensson, A. M., Steffensen, J. P., Vinther, B. M., Clausen, H. B., ... Ruth, U. (2006, mar). A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research: Atmospheres*, 111(D6). Retrieved from <https://doi.org/10.1029/2005JD006079> doi: <https://doi.org/10.1029/2005JD006079>
- Rattanasriampaipong, R., Tierney, J., & Abell, J. (2025). *Supplementary Data for ‘A nutrient effect on the TEX<sub>86</sub> paleotemperature proxy’*. [Dataset]. Zenodo. doi: 10.5281/zenodo.14806962
- Rattanasriampaipong, R., Zhang, Y. G., Pearson, A., Hedlund, B., & Zhang, S. (2022b). *Expanded compilations of isoprenoidal glycerol dialkyl glycerol tetraethers (GDGTs) in supplement to Rattanasriampaipong et al. “Archaeal lipids trace ecology and evolution of marine ammonia-oxidizing archaea”*. [Dataset]. figshare. doi: 10.6084/m9.figshare.20272866.v3
- Rattanasriampaipong, R., Zhang, Y. G., Pearson, A., Hedlund, B. P., & Zhang, S. (2022a). Archaeal lipids trace ecology and evolution of marine ammonia-oxidizing archaea. *Proceedings of the National Academy of Sciences*, 119(31), e2123193119. doi: 10.1073/pnas.2123193119

- Richey, J. N., & Tierney, J. E. (2016). GDGT and alkenone flux in the northern Gulf of Mexico: Implications for the TEX<sub>86</sub> and UK<sub>37</sub> paleothermometers. *Paleoceanography*, 31(12), 1547–1561. doi: 10.1002/2016pa003032
- Rodrigo-Gámiz, M., Rampen, S. W., de Haas, H., Baas, M., Schouten, S., & Sinninghe Damsté, J. S. (2015). Constraints on the applicability of the organic temperature proxies UK<sub>37</sub>, TEX<sub>86</sub> and LDI in the subpolar region around Iceland. *Biogeosciences*, 12(22), 6573–6590. doi: 10.5194/bg-12-6573-2015
- Sarmiento, J. L., & Gruber, N. (2006, 6). Ocean biogeochemical dynamics. In *Ocean biogeochemical dynamics* (p. 528). Princeton university press.
- Schouten, S., Forster, A., Panoto, F. E., & Sinninghe Damsté, J. S. (2007). Towards calibration of the TEX<sub>86</sub> palaeothermometer for tropical sea surface temperatures in ancient greenhouse worlds. *Organic Geochemistry*, 38(9), 1537–1546. Retrieved from <http://www.sciencedirect.com/science/article/pii/S0146638007001209> doi: <https://doi.org/10.1016/j.orggeochem.2007.05.014>
- Schouten, S., Hopmans, E. C., Schefuss, E., & Sinninghe Damsté, J. S. (2002). Distributional variations in marine crenarchaeotal membrane lipids: a new tool for reconstructing ancient sea water temperatures? *Earth and Planetary Science Letters*, 204(1-2), 265–274.
- Schukies, J. (2018). *Concentrations of glycerol dialkyl glycerol tetraethers (GDGTs) in core top sediments from continental slope off Newfoundland, Orphan Knoll Region*. [Dataset]. PANGAEA. doi: 10.1594/PANGAEA.894305
- Schulte, S., & Müller, P. J. (2001). Variations of sea surface temperature and primary productivity during Heinrich and Dansgaard-Oeschger events in the northeastern Arabian Sea. *Geo-Marine Letters*, 21(3), 168–175. Retrieved from <https://doi.org/10.1007/s003670100080> doi: 10.1007/s003670100080
- Seierstad, I. K., Abbott, P. M., Bigler, M., Blunier, T., Bourne, A. J., Brook, E., ... Vinther, B. M. (2014). Consistently dated records from the Greenland GRIP, GISP2 and NGRIP ice cores for the past 104 ka reveal regional millennial-scale  $\delta^{18}\text{O}$  gradients with possible Heinrich event imprint. *Quaternary Science Reviews*, 106, 29–46. doi: 10.1016/j.quascirev.2014.10.032
- Siegel, D. A., DeVries, T., Cetinić, I., & Bisson, K. M. (2023). Quantifying the ocean’s biological pump and its carbon cycle impacts on global scales. *Annual Review of Marine Science*, 15, 329–356. Retrieved from <https://www.annualreviews.org/content/journals/10.1146/annurev-marine-040722-115226> doi: <https://doi.org/10.1146/annurev-marine-040722-115226>
- Sikes, E. L., Howard, W. R., Samson, C. R., Mahan, T. S., Robertson, L. G., & Volkman, J. K. (2009). Southern Ocean seasonal temperature and Subtropical Front movement on the South Tasman Rise in the late Quaternary. *Paleoceanography*, 24(2). Retrieved from <https://doi.org/10.1029/2008PA001659> doi: <https://doi.org/10.1029/2008PA001659>
- Sinninghe Damsté, J. S., van Bentum, E. C., Reichart, G.-J., Pross, J., & Schouten, S. (2010). A CO<sub>2</sub> decrease-driven cooling and increased latitudinal temperature gradient during the mid-Cretaceous Oceanic Anoxic Event 2. *Earth and Planetary Science Letters*, 293(1), 97–103. Retrieved from <https://www.sciencedirect.com/science/article/pii/S0012821X10001299> doi: <https://doi.org/10.1016/j.epsl.2010.02.027>
- Sinninghe Damsté, J. S. (2016). Spatial heterogeneity of sources of branched tetraethers in shelf systems: The geochemistry of tetraethers in the Berau River delta (Kali-mantan, Indonesia). *Geochimica et Cosmochimica Acta*, 186, 13–31. doi: 10.1016/j.gca.2016.04.033
- Sinninghe Damsté, J. S., Ossebaar, J., Schouten, S., & Verschuren, D. (2012). Distribution of tetraether lipids in the 25-ka sedimentary record of Lake Challa: extracting reliable TEX<sub>86</sub> and MBT/CBT palaeotemperatures from an equatorial African lake. *Quaternary Science Reviews*, 50, 43–54. doi: 10.1016/j.quascirev.2012.07.001
- Sinninghe Damsté, J. S., Schouten, S., Hopmans, E. C., van Duin, A. C. T., & Geenevasen, J. A. J. (2002). Crenarchaeol: the characteristic core glycerol dibiphytanyl glycerol



- tetraether membrane lipid of cosmopolitan pelagic crenarchaeota. *Journal of Lipid Research*, 43(10), 1641–1651. doi: 10.1194/jlr.m200148-jlr200
- Sinninghe Damsté, J. S., Warden, L. A., Berg, C., Jürgens, K., & Moros, M. (2022). Evaluation of the distributions of hydroxylated glycerol dibiphytanyl glycerol tetraethers (GDGTs) in Holocene Baltic Sea sediments for reconstruction of sea surface temperature: the effect of changing salinity. *Climate of the Past*, 18(10), 2271–2288. doi: 10.5194/cp-18-2271-2022
- Sintes, E., Bergauer, K., De Corte, D., Yokokawa, T., & Herndl, G. J. (2013). Archaeal amoA gene diversity points to distinct biogeography of ammonia-oxidizing Crenarchaeota in the ocean. *Environmental Microbiology*, 15, 1647–1658.
- Sloyan, B. M., & O’Kane, T. J. (2015). Drivers of decadal variability in the Tasman Sea. *Journal of Geophysical Research: Oceans*, 120(5), 3193–3210. Retrieved from <https://doi.org/10.1002/2014JC010550> doi: <https://doi.org/10.1002/2014JC010550>
- Smith, J. M., Casciotti, K. L., Chavez, F. P., & Francis, C. A. (2014, aug). Differential contributions of archaeal ammonia oxidizer ecotypes to nitrification in coastal surface waters. *The ISME Journal*, 8(8), 1704–1714. Retrieved from <https://doi.org/10.1038/ismej.2014.11> doi: 10.1038/ismej.2014.11
- Sonzogni, C., Bard, E., & Rostek, F. (1998). Tropical sea-surface temperatures during the last glacial period: A view based on alkenones in indian ocean sediments. *Quaternary Science Reviews*, 17(12), 1185–1201. Retrieved from <https://www.sciencedirect.com/science/article/pii/S0277379197000991> doi: [https://doi.org/10.1016/S0277-3791\(97\)00099-1](https://doi.org/10.1016/S0277-3791(97)00099-1)
- Suthhof, A., Ittekkot, V., & Gaye-Haake, B. (2001). Millennial-scale oscillation of denitrification intensity in the Arabian Sea during the Late Quaternary and its potential influence on atmospheric N<sub>2</sub>O and global climate. *Global Biogeochemical Cycles*, 15(3), 637–649. doi: 10.1029/2000GB001337
- Talley, L. D., Pickard, G. L., Emery, W. J., & Swift, J. H. (2011). *Descriptive physical oceanography: an introduction* (6th ed.). Academic press. doi: <https://doi.org/10.1016/C2009-0-24322-4>
- Tang, W., Ward, B. B., Beman, M., Bristow, L., Clark, D., Fawcett, S., ... Zhang, Y. (2023). Database of nitrification and nitrifiers in the global ocean. *Earth System Science Data*, 15(11), 5039–5077. doi: 10.5194/essd-15-5039-2023
- Taylor, K. W. R., Huber, M., Hollis, C. J., Hernandez-Sanchez, M. T., & Pancost, R. D. (2013). Re-evaluating modern and Palaeogene GDGT distributions: Implications for SST reconstructions. *Global and Planetary Change*, 108, 158–174. doi: 10.1016/j.gloplacha.2013.06.011
- Tesdal, J.-E., Galbraith, E. D., & Kienast, M. (2013). Nitrogen isotopes in bulk marine sediment: linking seafloor observations with subseafloor records. *Biogeosciences*, 10(1), 101–118. doi: 10.5194/bg-10-101-2013
- Tierney, J. E., Pausata, F. S. R., & DeMenocal, P. (2016). Deglacial Indian monsoon failure and North Atlantic stadials linked by Indian Ocean surface cooling. *Nature Geoscience*, 9(1), 46–50. doi: 10.1038/ngeo2603
- Tierney, J. E., Poulsen, C. J., Montañez, I. P., Bhattacharya, T., Feng, R., Ford, H. L., ... Zhang, Y. G. (2020). Past climates inform our future. *Science*, 370(6517), eaay3701. doi: 10.1126/science.aay3701
- Tierney, J. E., & Tingley, M. P. (2014). A Bayesian, spatially-varying calibration model for the TEX<sub>86</sub> proxy. *Geochimica et Cosmochimica Acta*, 127, 83–106. doi: 10.1016/j.gca.2013.11.026
- Tierney, J. E., & Tingley, M. P. (2015a). NOAA/WDS Paleoclimatology - Global TEX<sub>86</sub> Surface Sediment Database. [Dataset]. NOAA National Centers for Environmental Information. doi: <https://doi.org/10.25921/wt2r-sc81>
- Tierney, J. E., & Tingley, M. P. (2015b). A TEX<sub>86</sub> surface sediment database and extended Bayesian calibration. *Scientific Data*, 2(1), 1–10.
- Tierney, J. E., & Tingley, M. P. (2018). BAYSPLINE: A New Calibration for the Alkenone Paleothermometer. *Paleoceanography and Paleoclimatology*, 33(3), 281–301. doi: 10

- .1002/2017PA003201
- Tierney, J. E., Ummenhofer, C. C., & DeMenocal, P. B. (2015). Past and future rainfall in the Horn of Africa. *Science Advances*, 1(9), e1500682. doi: 10.1126/sciadv.1500682
- Tilburg, C. E., Subrahmanyam, B., & O'Brien, J. J. (2002, may). Ocean color variability in the Tasman Sea. *Geophysical Research Letters*, 29(10), 124–125. Retrieved from <https://doi.org/10.1029/2001GL014071> doi: <https://doi.org/10.1029/2001GL014071>
- Trommer, G., Siccha, M., van der Meer, M. T. J., Schouten, S., Sinninghe Damsté, J. S., Schulz, H., ... Kucera, M. (2009). Distribution of Crenarchaeota tetraether membrane lipids in surface sediments from the Red Sea. *Organic Geochemistry*, 40(6), 724–731. doi: 10.1016/j.orggeochem.2009.03.001
- Tyrrell, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature*, 400(6744), 525–531. Retrieved from <https://doi.org/10.1038/22941> doi: 10.1038/22941
- Uda, I., Sugai, A., Itoh, Y. H., & Itoh, T. (2001). Variation in molecular species of polar lipids from *Thermoplasma acidophilum* depends on growth temperature. *Lipids*, 36(1), 103–105.
- van der Weijst, C. M. H., van der Laan, K. J., Peterse, F., Reichart, G.-J., Sangiorgi, F., Schouten, S., ... Sluijs, A. (2022). A 15-million-year surface- and subsurface-integrated TEX86 temperature record from the eastern equatorial Atlantic. *Clim. Past*, 18(8), 1947–1962. doi: 10.5194/cp-18-1947-2022
- van Helmond, N. A. G. M., Sluijs, A., Reichart, G.-J., Sinninghe Damsté, J. S., Slomp, C. P., & Brinkhuis, H. (2014). A perturbed hydrological cycle during Oceanic Anoxic Event 2. *Geology*, 42(2), 123–126. Retrieved from <https://doi.org/10.1130/G34929.1> doi: 10.1130/G34929.1
- Varma, D., Hopmans, E. C., van Kemenade, Z. R., Kusch, S., Berg, S., Bale, N. J., ... Schouten, S. (2024). Evaluating isoprenoidal hydroxylated GDGT-based temperature proxies in surface sediments from the global ocean. *Geochimica et Cosmochimica Acta*, 370, 113–127. doi: 10.1016/j.gca.2023.12.019
- Varma, D., Hopmans, E. C., van Kemenda, Z. R., Kusch, S., Berg, S., Bale, N. J., ... Schouten, S. (2024). *OHGDGT global surface sediment data*. [Dataset]. PANGAEA. doi: 10.1594/PANGAEA.964885
- Villanueva, L., Schouten, S., & Sinninghe Damsté, J. S. (2015). Depth-related distribution of a key gene of the tetraether lipid biosynthetic pathway in marine Thaumarchaeota. *Environmental Microbiology*, 17, 3527–3539. doi: 10.1111/1462-2920.12508
- Virtanen, P., Gommers, R., Oliphant, T. E., Haberland, M., Reddy, T., Cournapeau, D., ... others (2020). Scipy 1.0: Fundamental algorithms for scientific computing in python. *Nature Methods*, 17(3), 261–272.
- Ward, B. B. (2008). Chapter 5 - Nitrification in Marine Systems. In D. G. Capone, D. A. Bronk, M. R. Mulholland, & E. J. B. T. N. i. t. M. E. S. E. Carpenter (Eds.), (pp. 199–261). San Diego: Academic Press. doi: 10.1016/B978-0-12-372522-6.00005-0
- Ward, B. B. (2011). Nitrification in the Ocean. In *Nitrification* (pp. 323–345). doi: 10.1128/9781555817145.ch13
- Wei, B., Jia, G., Hefter, J., Kang, M., Park, E., Wang, S., & Mollenhauer, G. (2020). Comparison of the UK<sub>37</sub><sup>'</sup>, LDI, TEX<sub>86</sub><sup>H</sup>, and RI-OH temperature proxies in sediments from the northern shelf of the South China Sea. *Biogeosciences*, 17(17), 4489–4508. doi: 10.5194/bg-17-4489-2020
- Weijers, J. W. H., Schouten, S., Spaargaren, O. C., & Sinninghe Damsté, J. S. (2006). Occurrence and distribution of tetraether membrane lipids in soils: Implications for the use of the TEX86 proxy and the BIT index. *Organic Geochemistry*, 37(12), 1680–1693. doi: 10.1016/j.orggeochem.2006.07.018
- Wuchter, C., Abbas, B., Coolen, M. J. L., Herfort, L., van Bleijswijk, J., Timmers, P., ... Sinninghe Damsté, J. S. (2006). Archaeal nitrification in the ocean. *Proceedings of the National Academy of Sciences of the U.S.A.*, 103, 12317–12322.



- Wuchter, C., Schouten, S., Coolen, M. J. L., & Sinninghe Damsté, J. S. (2004). Temperature-dependent variation in the distribution of tetraether membrane lipids of marine Crenarchaeota: Implications for TEX<sub>86</sub> paleothermometry. *Paleoceanography*, 19(4). doi: 10.1029/2004PA001041
- Yang, H., Lohmann, G., Krebs-Kanzow, U., Ionita, M., Shi, X., Sidorenko, D., . . . Gowan, E. J. (2020). Poleward Shift of the Major Ocean Gyres Detected in a Warming Climate. *Geophysical Research Letters*, 47(5), e2019GL085868. doi: 10.1029/2019GL085868
- Yang, Y., Gao, C., Dang, X., Ruan, X., Lü, X., Xie, S., . . . Yang, H. (2018). Assessing hydroxylated isoprenoid GDGTs as a paleothermometer for the tropical South China Sea. *Organic Geochemistry*, 115, 156–165. doi: 10.1016/j.orggeochem.2017.10.014
- Yool, A., Martin, A. P., Fernández, C., & Clark, D. R. (2007). The significance of nitrification for oceanic new production. *Nature*, 447(7147), 999–1002. doi: 10.1038/nature05885
- Zachos, J., Dickens, G. R., & Zeebe, R. E. (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451, 279. Retrieved from <https://doi.org/10.1038/nature06588> doi: 10.1038/nature06588
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001, apr). Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science*, 292(5517), 686–693. Retrieved from <https://doi.org/10.1126/science.1059412> doi: 10.1126/science.1059412
- Zhang, Y. G., & Liu, X. (2018). Export depth of the tex<sub>86</sub> signal. *Paleoceanography and Paleoclimatology*, 33, 666–671. Retrieved from <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2018PA003337> doi: <https://doi.org/10.1029/2018PA003337>
- Zhang, Y. G., Zhang, C. L., Liu, X.-L., Li, L., Hinrichs, K.-U., & Noakes, J. E. (2011). Methane Index: a tetraether archaeal lipid biomarker indicator for detecting the instability of marine gas hydrates. *Earth and Planetary Science Letters*, 307(3–4), 525–534.