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Climate of the Past
Discussions

Impact of the Late Miocene Cooling on the loss of coral reefs in the Central Indo-Pacific

Benjamin Petrick[1], Lars Reuning[1], Miriam Pfeiffer[1], Gerald Auer[2], Lorenz Schwark[1]

[1] Institute of Geosciences, Kiel University, Kiel Germany
[2] University of Graz, Graz, Austria

Correspondence to: Benjamin Petrick (benjamin.petrick@ifg.uni-kiel.de)

Abstract. The Late Miocene Cooling (LMC) has been recognized as a global event in the climate record and posited as the start of modern ecosystems. Whereas shifts in modern terrestrial ecosystems around 7.0 - 5.5 Ma occur globally, little is known about changes in aquatic ecosystems. This is especially true of shallow water carbonate ecosystems, such as coral reefs, where few good proxy records exist. A "reef gap" existed during the Pliocene in the area of the Central Indo-Pacific, where reefs that had been present during the Messinian (7 - 5 Ma) drowned by the Early Pliocene (5 - 3 Ma). Here, we present a TEX_{86}^{H}-based sea surface temperature (SST) record for the Coral Sea, suggesting that the LMC was more pronounced than previously thought. During the LMC, the SSTs at ODP Site 811 declined by about 2ºC, and cooling lasted from 7 Ma to possibly as late as 5 Ma. This level of cooling has also been seen in other parts of the Central Indo-Pacific. Previous research showed that coral reefs across the Central Indo-Pacific experienced a major ecosystem change, leading to the collapse of the coral reefs by 5 Ma. This event led to a lack of coral reefs during the Pliocene, an event that has often been described as the "Pliocene reef gap." The timing of the onset of this event matches the cooling in the records. This suggests that the LMC was a final stressor that provided a regional driver for the collapse of reefs and, therefore, a potential cause for the "Pliocene Coral Gap." The relatively rapid and intense change in SST and other stressors associated with the cooling caused coral reef systems to collapse across the Central Indo-Pacific.

1 Introduction

Global climate records have identified the Late Miocene Cooling (LMC) as a worldwide event occurring during the Messinian between 7.2 - 5.5 Ma (Herbert et al., 2016) when SSTs globally decreased by about 6 °C. The LMC has been suggested to be a critical step in developing modern ecosystems and has been seen as a potential precursor to the changes associated with the later onset of the northern hemisphere cooling (Herbert et al., 2016). However, as the LMC does not occur in global benthic $\delta^{18}O$ stacks or splices, it has only recently been identified as a global event (Westerhold et al., 2020; Zachos et al., 1994). Finally, although SSTs are estimated to have changed by 6 °C globally, there is a lot of regional variation in the magnitude and timing of cooling (Herbert et al., 2016). Given these uncertainties, the full impact of the LMC on paleoclimates and paleoecosystems is still unknown.

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It has been hypothesized that the LMC marks the start of "modern ecosystems," (Herbert et al., 2016) and it has been tied to aridification in Asia and Africa due to changes in the monsoonal system (Dupont et al., 2013; Feakins, 2013). Additionally, the LMC has been linked to major shifts from C_3 to C_4 plants, indicating the establishment of grasslands worldwide (Huang et al., 2007; Strömberg and Strömberg, 2011; Steinthorsdottir et al., 2021). Finally, due to the grassland expansion in East Africa, it is thought that some of the earliest hominids first evolved around 7 Ma to take advantage of the changed conditions (Brunet, 2020). In the ocean, it is known that the "biogenic bloom" is marked by an increase in the $\delta^{13}C$ of benthic foraminifera. This has been thought to be due to ocean circulation changes around the same time as the LMC, although the connections are still unclear (Lübbers et al., 2019; Diester-Haass et al., 2004; Drury et al., 2018). Therefore, the LMC had a major impact on numerous terrestrial and aquatic ecosystems. However, almost nothing is known about the impact of the LMC on coral reefs or other tropical shallow carbonate ecosystems. One issue is that for a long time, it was thought that the LMC primarily impacted the Earth's high latitudes. While it is present, initial records showed only muted changes in the tropics (Herbert et al., 2016). However, new low-latitude records show that this is not necessarily the case, and in fact, the cooling in the tropics can be as high as in other parts of the globe (Martinot et al., 2022). This may have important impacts on the development of coral reef ecosystems that are strongly dependent on their physical environment. In particular, there is a strong temperature dependence, with both warm and cold temperature anomalies leading to reef loss (Higuchi et al., 2015; Hoegh-Guldberg and Fine, 2004; Kawahata et al., 2019; McWhorter et al., 2022). Here, we present an SST record based on the TEX_{86}^{H} molecular paleothermometer for the Late Miocene and Pliocene from the Coral Sea to investigate these changes and their effects on coral reefs during the LMC.

The TEX_{86}^{H} record was established using sediments taken from ODP Site 811, located on the Queensland Plateau in the Coral Sea (Fig. 1). The Coral Sea has one of the highest coral reef densities in the world (Bridge et al., 2019), as highlighted by the Great Barrier Reef bordering the East Australian coast in the modern Coral Sea. Our study is near the modern Coral Triangle, an area with a unique density of coral reefs centered on the Indonesian archipelago in the Indo-Pacific (Vernon et al., 2009) (Fig. 1). Today, the Coral Sea is outside of the biologically defined Coral Triangle (Vernon et al., 2009). Instead, the Coral Sea and the Coral Triangle are part of the larger biologically defined Central Indo-Pacific (Crandall et al., 2019; Spalding et al., 2007). This area is actually thought to be the focus of Coral Reef diversity during the Miocene (Renema et al., 2008). Therefore, we will refer to the area as the Central Indo-Pacific in this article.

Most coral reefs that are present in the Coral Sea today are thought to have first developed during the Late Pliocene/Early Pleistocene (Droxler et al., 1993), while the Great Barrier Reef appears to have developed even later during the Mid Pleistocene (Dubois et al., 2008). However, research has shown that across the Central Indo-Pacific, including the Coral Sea, more extensive coral reefs prevailed during the Mid-Miocene (Santodomingo et al., 2016; Harrison et al., 2023; Davies et al., 1989; Petrick et al., 2023; Renema et al., 2008). However, during the Late Miocene, most of these systems seemed to have collapsed (Isern et al., 1996), leading to what has been described as the "Pliocene Reef Gap" (Harrison et al., 2023; Isern et al., 1996) (Fig. 2). A recent study (Harrison et al., 2023) rejected climatic controls on reef loss.

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Harrison et al. (2023) argued, based on a global benthic $\delta^{18}O$ stack (Zachos et al., 2001), that temperatures during the Messinian were similar to preindustrial times and thus were considered unlikely to cause coral collapse. However, it has been shown that benthic $\delta^{18}O$ exhibits a poor relationship with SSTs because of the influence of land-bound ice masses and sea level changes. Consequently, the LMC does not appear in the benthic $\delta^{18}O$ record. Also, it is known that the Miocene reefs differed from modern coral reefs in that the corals were predominantly hypo-calcifying, while modern corals are hyper-calcifiers, even though they belong to the same genera (Brachert et al., 2020). In other words, Miocene corals differed from modern ones by having lower growth and calcification rates (Brachert et al. 2020), which should have influenced the carbonate production of Miocene reefs. This is suggested to be an adaptation to warmer SSTs and may be similar to adaptations seen in modern corals from the Arabian Sea (Smith et al., 2022). Therefore, Miocene corals were adapted to high but stable SST, low aragonite saturation, and stable sea levels (Brachert et al., 2020). Finally, while the LMC may not represent warming, there is abundant evidence that all SST changes can impact coral reefs. This is especially true in the modern ocean, where reefs are starting to migrate to higher latitudes, and cold SSTs may be a limitation to proposed high-latitude refugia for corals (Nakabayashi et al., 2019; Higuchi et al., 2015). Therefore, more work needs to be done to understand the impact of cooling on coral reefs.

It was recently suggested that multiple stressors, including climate, might have led to coral reef collapse on the Queensland Plateau during the Late Miocene (Petrick et al., 2023). There is, however, a dearth of data to understand the factors that led to the Pliocene reef gap because many SST records for the Central Indo-Pacific have not covered the LMC and early Pliocene. Furthermore, because of the variations seen within the LMC, even in near proximity sites, more records are necessary to understand the spatial heterogeneity of the event. Finally, even in the records produced, the relationship to shallow water ecosystem change was not discussed. Therefore, this paper will investigate whether the LMC could have acted as a final stressor leading to the collapse of other reef systems across the Central Indo-Pacific.

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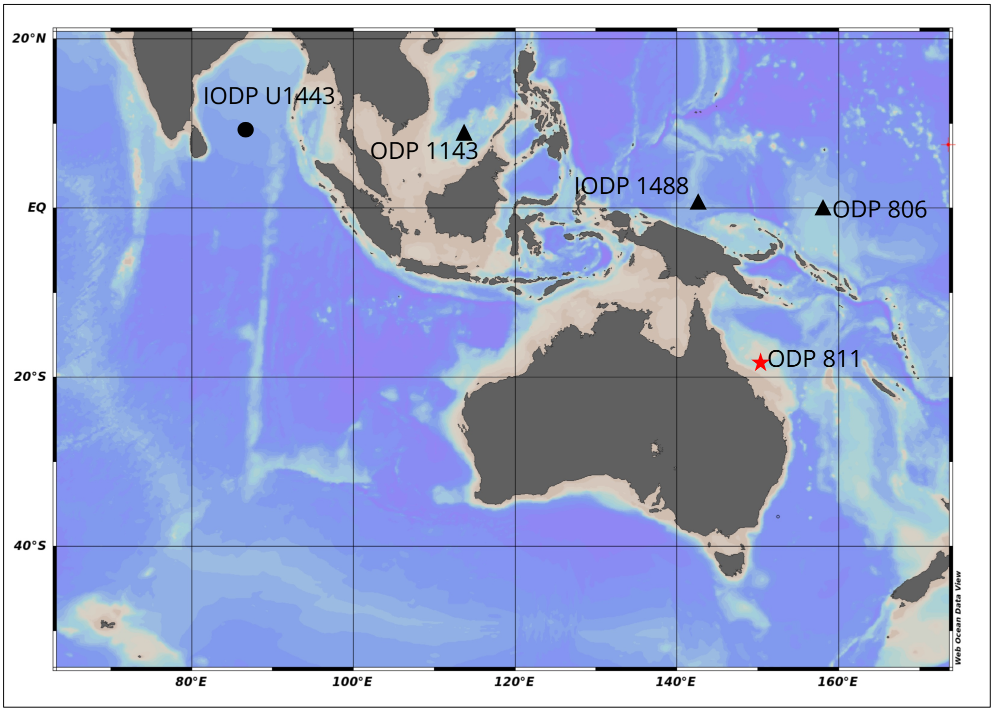

Figure 1: Map showing the Central Indo-Pacific and the location of ODP site 811 studied here (red star). Other sites, including those of the TEX_{86}–derived West Pacific Warm Pool stack (Liu et al., 2022), are indicated with black triangles, and IODP site U1443 (Martinot et al., 2022) is shown by a filled circle. The base map is from (Ocean Data View).

2 Methods

2.1 Biogeochemistry

We extracted 50 cc of sediment for this project, which resulted in between 50 and 60 g of sediment, suitable for extracting sufficient organic material for TEX_{86} determination. Dried and homogenized samples were Soxhlet extracted for 48 h using a solvent mixture of DCM: MeOH (9:1, v/v). The addition of activated copper turnings removed elemental sulfur. A Büchi solvent evaporator reduced excess solvent to a final volume of 2 ml. Samples were then transferred into a 4 ml vial, where the total extract (TE) was taken to dryness under a gentle stream of nitrogen. TEs were fractionated into aliphatic, aromatic, and polar fractions by silica gel-column chromatography (6 ml SPE column, 2.8 g Silica 60 mesh, 25–40 µm) using solvents with increasing polarity in an LC-TECH automated SPE system. NSO (polar) compounds were eluted with 14 ml DCM/ MeOH (1:1, v/v). The polar fraction was reconstituted in hexane/isopropanol (9:1, v/v) and re-chromatographed

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over aminopropyl-substituted silica gel (3 ml SPE column, 1.0 g aminopropyl-silica, 25–40 µm). The alcohol fraction containing the GDGTs was eluted with 5 ml of hexane/isopropanol (9:1, v/v) and, after drying, was re-dissolved in hexane/isopropanol (99:1, v/v) to a final concentration of 6 mg/ml for injection into the HPLC/MS system.

GDGTs were measured on an AGILENT liquid chromatograph coupled to an AGILENT single quadrupole mass spectrometer following the analytical protocol of Hopmans et al. (2016). The HPLC instrument was equipped with an AGILENT HILIC silica column (2.1 x 150 mm; 1.5 µm particle size) and a guard column maintained at 30°C. Detection of archaeal core lipids was achieved by single ion recording of their protonated molecular ions [M + H$^+$], and compounds were quantified by integration of peak areas using AGILENT Masshunter© software. Calculation of TEX_{86}^H followed (Kim et al., 2010). Reproducibility upon duplicate measurements showed a relative standard error of <2%.

3 Results

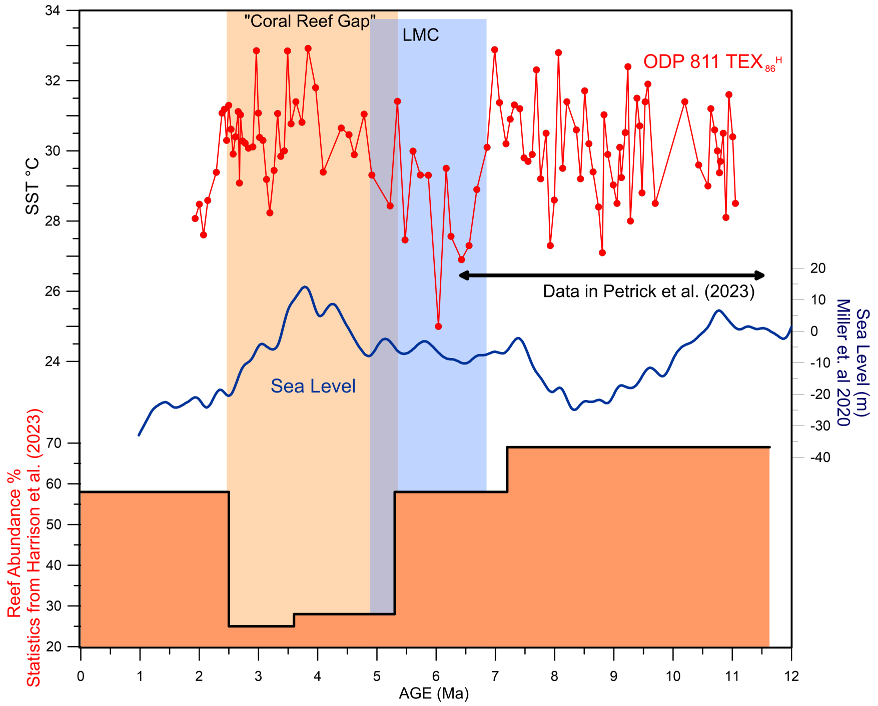

Figure 2: The TEX_{86}^H-derived SST record for site ODP 811 is shown in red, including data from 6 to 12 Ma taken from Petrick et al. (2023). The evolution of sea level is shown in blue after Miller et al. (2020). The relative abundance (%) of areas covered by reefs in the Central Indo-Pacific is shown in orange shading at the bottom, with data taken from Harrison et al. (2023). Shaded boxes indicate the LMC at ODP Site 811 and "Coral Reef Gap."

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3.1 TEX_{86} tests

The TEX_{86}^{H} data generated here for the period of 2-6 Ma complements previous data covering the period 6 to 12 Ma (Petrick et al., 2023). The data both for this study and the previous Petrick et al. (2023) study is found as supplemental data 1. The Methane Index (MI) excludes any data affected by gas-hydrate-related anaerobic oxidation of methane (Zhang et al., 2011). Our MI values are below the 0.5 value for rejection (Fig. 3a). We also used the GDGT0% index to eliminate samples with GDGTs substantially originating from sedimentary archaeal methanogenesis (Weijers et al., 2006; Sinninghe Damsté et al., 2012). The values were well below the 67% cut-off for excessive methanogenesis (Fig. 3b). We used the ring index (RI) to evaluate whether the GDGTs deviate from modern values (Zhang et al., 2016). All of our data fell within the acceptable error envelope of 0.3 (Fig. 3d). Finally, we used the 2/3 index to ensure that the GDGTS were being formed near the surface (Taylor et al., 2013; Hernández-Sánchez et al., 2014). While the appropriate cutoff for this test is still being debated, our data values are low and indicate surface production. This data is shown in supplement 1.

One GDGT index that did not comply in full with recommendations for quality assurance was the BIT index (Fig. 3c). This index was developed to track the amount of terrigenous material that could interfere with the TEX_{86} values via soil-sourced GDGTs (Schouten et al., 2013). The original cutoff point is 0.4, although there is a debate about whether that is a strict cutoff (Schouten et al., 2013) and how to evaluate variations in crenarcheol shown to affect the BIT index (Fietz et al., 2011). Although within the GDGT suite analyzed here, 11 samples exceed a BIT value of 0.5 (Fig 3c). The data shows no covariance with either time, depth, or SST. The highest BIT values neither match the highest nor lowest SST data. Finally, removing the high BIT samples doesn't affect the major trends or conclusions of the paper. Therefore, we have decided to keep all the points in our results because of the uncertainty of the meaning of the BIT index.

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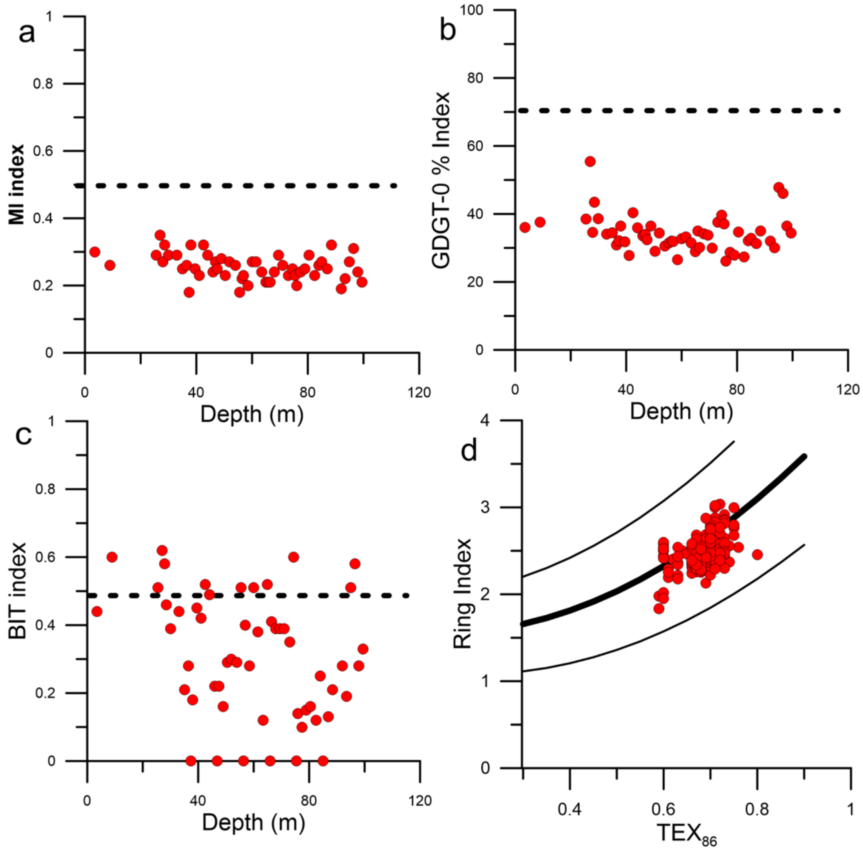

Figure 3: Graphic illustration of the new ODP Site 811 data for various GDGT indices used for quality assurance, for previously published data see Petrick et al. (2023). Quality criteria shown are a. Methane Index (MI, after Zhang et al., (2011)), b. %GDGT-0-index (after Sinninghe Damsté et al., (2012)), c. Branched *vs.* isoprenoid Index (BIT, proposed by Schouten et al., (2002)), d. Ring Index (RI, proposed by Zhang et al., (2016)). Quality assurance tests indicate that GDGT data are suitable for SST reconstruction and are not compromised by other environmental drivers.

3.2 SST trends

For this study, we follow the age model of Petrick et al. (2023), which updated the original shipboard (Davies et al., 1991) and previously published age model (Isern et al., 1996, 1993) for the entire ODP Site 811 record. A part of the record presented in this study (6-12 Ma) was previously published in Petrick et al. (2023) (Fig. 2). Please see the original publication for a more detailed description of that data. Despite some variability, SSTs were stable overall between 11.0 and

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6.9 Ma (Fig. 2), averaging an SST of 30.0 °C, which is 3-4 °C warmer than the modern SST. The LMC has a complex signal at ODP Site 811 with a rapid cooling between 6.9-6.6 Ma, followed by relatively cool SSTs until ~5.0 Ma. However, it is hard to define the exact boundaries of the end of the LMC at our site because there is an initial cooling and then a recovery that seems to last as late as 3.5 Ma. The Messinian (originally defined as the boundaries of the LMC (Herbert et al., 2016)) has an average SST of 28.2 °C, about 2 degrees cooler than the previous Late Miocene SSTs. Using the definitions used by Martinot et al. (2022) for the pre-LMC and the coldest part of the LMC in the nearby tropical Indian Ocean, the pre-LMC SSTs (8 Ma +/- 0.5) are 29.9 °C, and the coldest part of LMC SSTs (6 Ma +/-5) is 27.9 °C. This, again, is about 2 degrees. Finally, if we just look at the coldest period at ODP 811 (6.7-5.9 Ma), it is 27.8 °C during the LMC. This average cooling is about 2 °C, with SSTs possibly getting as low as 25 °C. After the LMC, SSTs reach an average of 30 °C in the Mid-Pliocene, followed by a cooling starting at around 2.5 Ma. There then appears to be a cooling starting around 2.5 Ma. However, because of a condensed sediment interval and coarse-grained material in the core around 2 Ma, the full details of the cooling are unknown.

4 Discussion

4.1 Degree and Rate of Cooling in the Central Indo-Pacific

ODP site 811 was located further south during the Late Miocene (20°S at most) (Van Hinsbergen et al., 2015). The cooling in the record matches the cooling seen in the Bengal Sea using Mg/Ca (Fig 4). Originally, only a moderate cooling of SSTs was described Herbert et al., (2016) (Fig 5) for the LMC within the tropics (defined as lower than 30 degrees latitude and therefore including the location of ODP site 811).. Even though they identified the LMC in all the tropical records, the change was <1°C and was often not as longlived as in other parts of the globe (Fig. 5). More recently, a TEX_{86} stack from the West Pacific Warm Pool (WPWP), showed a 2 °C cooling trend from 7 - 4 Ma during the LMC but no sudden cooling at 7 Ma (Liu et al., 2022) (Fig. 5). Therefore, the patterns from these records seem to show a gradual 1-2 °C cooling during the LMC as a part of a long-term cooling trend in the WPWP that continues to the modern day. These trends differ from the 2-3 °C cooling and slow but full recovery from ODP site 811 between 7-4 Ma (Figs 2, 4, 5).

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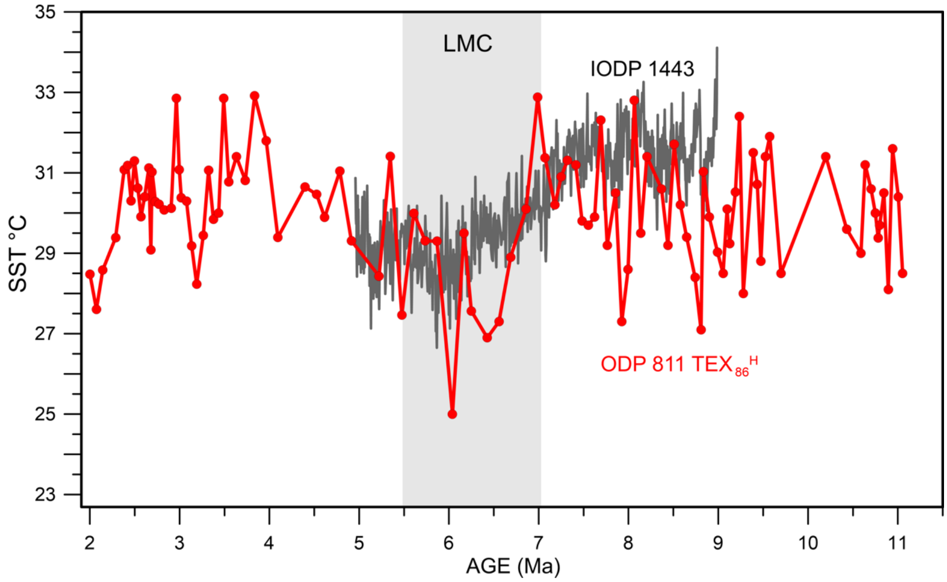

Figure 4: ODP site 811 TEX_{86}^{H}-derived SSTs compared to the Mg/Ca-derived SST record from IODP site U1443 in the Bay of Bengal (Fig 1) (Martinot et al., 2022). The gray bar marks the LMC as defined in Herbert et al. 2016

However, as mentioned, this degree of cooling has been seen elsewhere in the tropics, with an Mg/Ca SST record from IODP Site U1443 in the northern Indian Ocean showing a very similar degree of cooling (Martinot et al., 2022) (Fig. 4). In the study at IODP Site U1443, the authors used existing models to show that the amount of cooling in the tropical Indian Ocean was not an anomaly. They showed that the amount of cooling they saw in the tropical Indian Ocean would be explainable by a decrease in CO_2 (Burls et al. 2021). The cooling at ODP site 811 roughly fits the model data presented in this article, which suggests SSTs of around 28 °C and a cooling of about 2 °C at ODP site 811 (Martinot et al., 2021). Therefore, the cooling at ODP Site 811 fits the model for the LMC.

Explaining the apparent difference between the different tropical records is important to understanding the dynamics of the LMC. The original study of the LMC was based on U^{K}_{37}' SSTs (Herbert et al., 2016). These have a saturation limit of 28 to 29 °C (Müller et al., 1998) when the proportion of the $C_{37:3}$ isomer used for calculation approaches zero. Especially in a lithology such as carbonates without high organic preservation, U^{K}_{37}' SSTs are considered unreliable above 26-27 °C (Pelejero and Calvo, 2003; Grimalt et al., 2001). Therefore, models show that many parts of the tropical and sub-tropical Miocene ocean were too warm to reconstruct SST with U^{K}_{37}' (Burls et al., 2021). In fact, except for ODP Site 722, all the sites used for the U^{K}_{37}' reconstruction were located in the East Pacific Equatorial Upwelling Zone (Herbert et al., 2016). ODP Site 722 is in the Arabian Sea upwelling cell and thus actually defined by localized monsoonal wind patterns forcing upwelling in the western Arabian Sea (Bialik et al., 2020). Therefore, it is possible that the U^{K}_{37}' data reflects more

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reduced cooling in upwelling cells than global tropical cooling. Furthermore, the individual records that make up the TEX_{86} stack show that there was cooling at the individual sites during the LMC (Liu et al., 2022). All the sites show a cooling of 2-3 degrees between 7-5 Ma (Liu et al., 2022; Zhang et al., 2014). The major difference seems to be that the cooling is not as rapid, and not all sites show the post-cooling recovery seen at ODP site 811 and IODP site U1443 (Fig. 4). This seems to suggest that while the timing and rapidity of the cooling differed across the Central Indo-Pacific, there was about a 2 degree cooling at all the sites during the LMC.

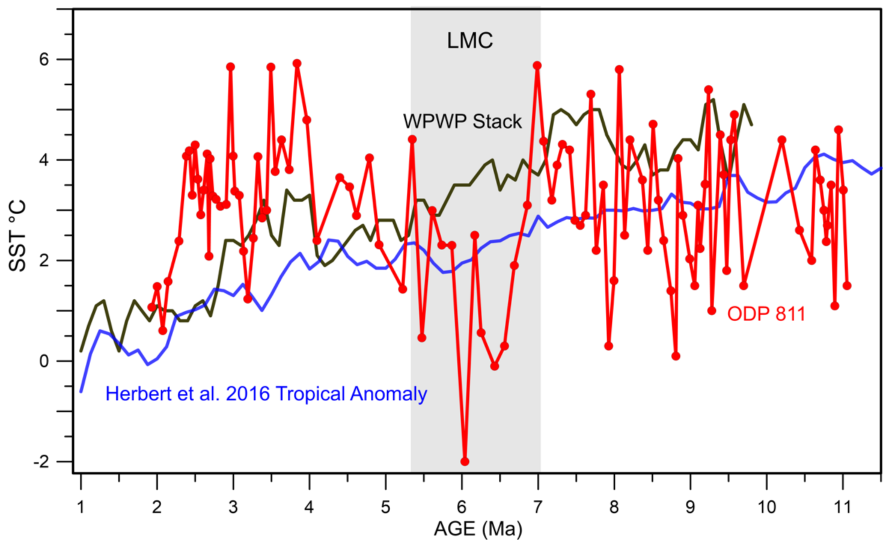

Figure 5: SST data for this plot has been normalized to modern temperatures to better compare with the anomaly data presented by Herbert et al. (2016). This was done for ODP site 811 and the WPWP stack by subtracting modern SSTs from the data. ODP Site 811 (red) change compared to the Tropical Anomaly data (blue) (Herbert et al., 2016) and the WPWP stack (black) (Liu et al., 2022). The gray bar delineates the LMC as defined by Herbert et al. (2016)

4.2 Loss of Carbonate Platforms in the Central Indo-Pacific

There was an extensive coral reef system on the Queensland Plateau during the Early-Mid Miocene (Feary et al., 1991; Betzler and Chaproniere, 1993). This is confirmed by microfacies analysis, which showed the presence of reef corals and other tropical species (Betzler et al., 1995). However, after 11 Ma, the coral reefs appear to retreat (Isern et al., 1993, 1996). Some authors put the collapse of this system to 13 Ma and relate it to changes in the bottom water current strength (Betzler and Eberli, 2019).

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Large benthic foraminifera-based reconstructions of sea level show a gradual increase in relative water depth between 13-8 Ma (Katz and Miller, 1993). This matches both an increase in sea level (Miller et al., 2023) and a subsidence event that has been seen in the coral sea (DiCarpio et al., 2010). A major transition between 14-11 Ma reduced the coral coverage in the coral sea (Betzler et al., 2024). However, it is unclear whether this led to the collapse of reef systems on the Queensland Plateau or whether there were active atolls after the initial collapse, as there is still shallow water bank material in ODP Site 811 until around 8 Ma (Betzler, 1997). However, it is clear that the loss of corals in the northern coral sea predates the cooling of LMC and is probably a result of the rise in sea level, changing currents, and high SSTs, as we suggested previously (Petrick et al., 2023).

However, while local processes might have caused the early collapse of the Queensland Plateau, other reefs in the Coral Sea and surrounding areas have evidence of a much later collapse. Interestingly, a similar timing of coral reef loss is seen in the Southern Coral Sea on the Marion Plateau. Areas in the northern part of the platform with no evidence of reefs drowned around 13 Ma, while the southern part, where coral reefs have been found, survived until around 7 Ma (Isern et al., 2004; John and Mutti, 2005; Bashah et al., 2024). On the other side of Australia, the NW shelf great barrier reef did not fully drown until around 7 Ma (Rosleff-Soerensen et al., 2012; McCaffrey et al., 2020). Finally, the studies on the Early Pliocene sediments, even on the Queensland Plateau, show pelagic sedimentation even on the shallow carbonate platforms (Droxler et al., 1993). Therefore, there is abundant evidence of coral reef collapse in Australia during the LMC.

Throughout the Central Indo-Pacific, a similar trend is seen (Fig. 2). The highest reef density exists during the mid-Miocene, followed by a slight decrease towards the Late Miocene (Harrison et al., 2023). However, there seems to have been a major loss in coral reefs by the Early Pliocene. This suggests that the major loss of corals occurred between the Messinian and the beginning of the Early Pliocene (7 – 4 Ma). Harrison et al. (2023) ascribes the loss to multiple individual changes for individual reefs. These include changes in tectonics, sea level, and increases in terrestrial input. Furthermore, they suggested different drivers for coral reef loss in different parts of the Central Indo-Pacific. However, given the amount of coral reef loss within such a narrow window of time, there is likely some regional change that might have combined with changes in local conditions to drive the loss of coral reefs. The authors reject climate change because they argue that SSTs during the late Miocene are similar to modern ones, and there is no evidence of major warming across this time (Harrison et al., 2023). However, as mentioned above, there is some evidence that the warm water belt both cooled and contracted during the LMC (Martinot et al., 2022; Liu et al., 2022). Furthermore, in the WPWP, this cooling is part of a long-term cooling trend (Liu et al., 2022). Finally, as pointed out above, there is evidence that the corals here had adapted to the warmer but stable Late Miocene SSTs, with lower growth and calcification rates than modern corals (Brachert et al., 2020). The ODP 811 record shows a major SST shift prior to the Pliocene reef gap. Therefore, it is necessary to understand if cooling during the LMC could be a key factor in the loss of coral reefs in the Central Indo-Pacific.

4.3 Potential stressors in the Central Indo-Pacific

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In the last paper on ODP Site 811, we proposed that high temperatures together with additional stressors might have contributed to the loss of the reef systems in the Coral Sea between 8-11 Ma (Petrick et al., 2023). These additional stressors include changes in the aragonite saturation of seawater (Brachert et al., 2020), an increase in the sea level (Katz and Miller, 1993; DiCaprio et al., 2009), and changes in the location and strength of ocean currents (Betzler and Eberli, 2019). So, the question is how the LMC might have impacted these already stressed reefs in the Coral Sea and the wider central Indo-Pacific reef province.

As shown above, ODP site 811 experienced a rapid and strong cooling associated with the LMC. Furthermore, SSTs did not recover until at least 5 Ma, well into the "Pliocene Reef Gap." Therefore, it seems likely that the cooling could have had an impact and led to the loss of the carbonate platform ecosystems. However, the absolute temperatures at the site during the LMC raise some issues with this interpretation. SSTs are around 27 °C during the late Miocene. These are similar to modern-day SSTs in the Coral Sea (World Ocean Atlas 2018). Research shows that 27 °C is ideal for coral reef development in the modern ocean (Lough and Cantin, 2014). Therefore, colder SSTs during the LMC alone should not have caused a collapse of these coral reefs, despite their adaptation to warm temperatures, as pointed out before (Petrick et al., 2023).

As shown above, many stressors impacted the carbonate ecosystems even before the LMC (Petrick et al., 2023). While the high SSTs between 11-8 Ma, changes in sea level, changes in nutrients, tectonic changes, changes in turbidity, and changes in circulation might not cause the loss of shallow carbonate ecosystems individually, together, they might have led to a system under stress and on the verge of collapse (Petrick et al., 2023). In a system like this, a major change, such as an SST drop, might be the final trigger that causes a collapse. (Note that both warm and cold temperatures may contribute to coral reef loss (Higuchi et al., 2015; Nakabayashi et al., 2019; Hoegh-Guldberg and Fine, 2004).

Also, there might be additional stressors besides SST associated with the LMC. Oceanic current changes might also be linked with the LMC, as with other major coolings (Petrick et al., 2018, 2019). This might have led to some of the erosional characteristics that mark the top of these platforms, making it harder for reefs to re-establish themselves after the cooling (Betzler and Eberli, 2019). This has been shown recently on the Marion Plateau around 7 Ma (Bashah et al., 2024). Changes in terrestrial input could also result from changes in temperature gradients, as there is evidence that cooling during the Late Miocene leads to shifts in the rain belts northward (Santodomingo et al., 2016; Groeneveld et al., 2017). This could result in changes in the amount of terrestrial input due to more rainfall. As a result, the LMC can be associated with numerous stressors beyond the SST drop.

Therefore, the LMC was associated with a number of major environmental changes that could act as stressors, which would have led to major impacts on the coral reefs, causing widespread drowning. This is similar to modern coral systems, where current climatic changes are accompanied by multiple other environmental stressors, such as sea-level rise, impacting coral reef systems (Cornwall et al., 2021). While coral reefs might be able to adapt to single stressors, such as higher sea levels, multiple stressors may add up synergistically and cause the coral reef to collapse much quicker than normal (Darling and Côté, 2013).

The next question is, could a major cooling of 2 °C cause that much damage to coral reefs in the late Miocene? Today, corals have been shown to grow in very warm SSTs >30 °C in the Red Sea (Dibattista et al., 2016; Aeby et al., 2021). While our understanding of SSTs in tropical environments during the Mid-Miocene is poor, given the SSTs found for the late Miocene means that SSTs were likely persistently warmer than modern SSTs in the Coral Sea for the Early-Mid Miocene when the coral reefs were developing (Petrick et al., 2023). Therefore, it is likely that these corals were warm water-adapted corals. As shown above, there is evidence that Miocene corals were predominantly hypo-calcifying, while modern corals are hyper-calcifiers (Brachert et al., 2020). Interestingly, this change is seen despite no major changes in species diversity (Brachert et al., 2020; Harrison et al., 2023). This might mean the Miocene corals had a growth window different from modern coral reefs, which first developed during the cooling associated with the onset of northern hemisphere glaciations (Brachert et al., 2020). The sudden change to much cooler SSTs could be a final stressor for these warm, water-adapted, stressed corals. This has been seen in the modern Great Barrier Reef, where it has been shown that anomalously cold SSTs can cause the bleaching of coral reefs (Hoegh-Guldberg and Fine, 2004). Studies also show this temperature threshold can be lower when combined with other stressors (Donovan et al., 2020). Therefore, in summary, there is good evidence that coral reefs are susceptible to rapid SST changes, particularly when combined with other stressors. Given the global nature of the LMC, this could have led to a collapse of reef systems for at least some of the reefs in the central Indo-Pacific reef province, leading to the coral "Reef Gap" during the early Pliocene.

Finally, the temperature decrease of the LMC was not related to a sea level change. However, the global sea level increased after 5 Ma (Miller et al., 2020) (Fig 2.), while temperatures at ODP Site 811 remained relatively low. This means that when SSTs returned to the Mid-Miocene SST levels during the Mid-Pliocene, the carbonate platform tops were no longer in the photic zone, allowing corals to regrow. It was noted that the establishment of coral reefs in the Coral Sea was linked to a global sea level lowering around 2.9 Ma, which would have brought the platforms back into the photic zone and allowed coral reefs to develop again (Droxler et al., 1993) (Fig 2). Therefore, it is likely that after the drowning during the LMC, the reestablishment of the reefs was more related to changes in sea level than SST.

5 Conclusions

The new TEX_{86}^{H}-derived SST data at ODP site 811 shows that the LMC in the southern part of the central Indo-Pacific reef province led to a relatively rapid drop in SSTs by about 2°C. This contradicts the idea that the tropics were not strongly affected by the LMC. It shows for the first time that a contraction of the equatorial belt happened not only in the Indian Ocean but also in the Pacific. The sudden and relatively extreme SST drop in the tropics that preceded the "Pliocene Reef Gap" could have proved to be an additional stressor leading to coral reef loss in the central Indo-Pacific reef province. The cooling could have impacted corals that had adapted to the warmer conditions of the Miocene more strongly than they would modern corals. Additionally, there is evidence that the changes in global and local SSTs triggered by the LMC have led to shifts in the ocean currents, as well as rain belts. Together with the SST changes, these multiple stressors explain some of the changes seen previously in individual reefs of the late Miocene and provide an overall driver for explaining the region-wide coral loss over such a relatively constrained period of time. Our study indicates that major climate changes may combine with and/or give rise to multiple stressors impacting coral reefs. This likely explains the massive reduction in the extent of coral reefs in the 'Pliocene Reef Gap.' Therefore, it emphasizes how detrimental climate changes are to the reefs and the importance of limiting additional stressors, such as pollution on reef ecosystems in a time of global temperature change.

Data availability

The data for this paper is available both in supplementary data one and at Zenodo with a doi of 10.5281/zenodo.10902264.

Author Contribution

All authors approved the manuscript and agreed to its submission. The corresponding author is B.P. All authors discussed the results and provided significant input to the final version of the manuscript. B.P. and L.R. designed the study. B.P. Ran the project and processed the samples. L.S. performed the biomarker analysis in his lab and interpreted data with B.P. G.A., who provided a new-age model for the site. B.P., L.S., L.R., M.P., and G.A. provided vital feedback on the article.

Competing Interests

The authors declare they have no competing interests in this paper.

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