



NOTE

Is the Coral Triangle's future shown in a Pliocene reef gap?

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Abstract Although Pliocene temperature and pCO₂ are similar to those predicted in the IPCC RCP4.5 scenario, the distribution of coral reefs in the center of maximum coral diversity, the Coral Triangle, during this period has not been explored. We discovered a significantly lower occurrence of reefs during the Pliocene, which we refer to as the Pliocene Reef Gap, but this decrease was not associated with a drop in coral genus richness. While some of the multiple local causes that drove this decline, such as sea level rise, are analogs to drivers of Anthropocene reef decline, neither warming nor increasing pCO₂ are among them.

Keywords Pliocene · Neogene · Coral triangle · Paleontology · Anthropocene · Coral reef decline

Introduction

Forecasting the severity and effects of Anthropocene reef decline (Donovan et al. 2021; Eddy et al. 2021) is critical since coral reefs are bastions of biodiversity (Hughes et al. 2002) and provide economic benefits and ecosystem services to human society (Eddy et al. 2021). Anthropogenic climate warming is regarded as a global cause of coral mortality

(Keller et al. 2009). Increasing frequency of local hyperthermal events directly kills coral reef builders (Donovan et al. 2021) and ocean acidification from increasing pCO₂ hampers their recovery (Holcomb et al. 2014). Since the Coral Triangle is the hotspot for diversity of coral reef-associated taxa in the Anthropocene (Renema et al. 2008), understanding future trajectories of change is crucial to understand the fate of reefs and their constituent coral taxa.

The Pliocene (2.58–5.33 Ma) has been used as an analog for future conditions because Pliocene atmospheric pCO₂ was around 400 ppm (Pagani et al. 2010; de la Vega et al. 2020), comparable to present values (NOAA 2022), and temperatures (Haywood et al. 2013; Burke et al. 2018) were close to what the IPCC predicts the world will experience in the next 100 yrs under the RCP4.5 scenario (Burke et al. 2018). Previous studies have proposed a Pliocene reef decline, but this gap was mostly attributed to the loss of the Mediterranean reef province during the Messinian Salinity Crisis (Flügel and Kiessling 2002; Perrin 2002); regional analyses are needed to detect reef declines in other provinces. Thus, understanding changes in coral reef abundance in the Pliocene can serve as a proxy to project future trajectories.

Since diversity of reef building taxa is often linked with various metrics of reef health (Edinger and Risk 2000; Hoey and Bellwood 2009; Komyakova et al. 2013), preserving coral diversity is also treated as synonymous with reef conservation (Coles and Riegl 2013). However, the link between diversity of reef builders and reef building capacity has been questioned both on geological time scales (Pandolfi 1999; Kiessling 2005; Johnson et al. 2008) and in modern reefs (Hoey and Bellwood 2009). If the link between diversity of reef building taxa and reef building capacity is weak or nonexistent, it would have implications for conservation strategies. Comparing reef distribution through geological

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timescales with the diversity of reef builders in those time bins is one way to test this link.

Methods

Literature review

We found publications by querying Google Scholar and Web of Science using the following search terms for time bins and locations. The search terms used for time bins were “Pleistocene”, “Pliocene”, “Miocene”, “Piacenzian”, “Zanclean”, “Messinian”, “Tortonian”, “Serravalian”, “Langhian”, “Burdigalian”, and “Aquitainian”. The search terms for location were “Indonesia*”, “Malaysia*”, “Phillipin*”, “Australia*”, “New Guinea*”, “South China Sea”, “Dangerous Grounds”, “Guam”, and “Timor”. Finally, “Reef” or “Platform” were appended to the end of the search term. One term from each of the three categories was chosen for each search; this was run until permutations of these terms were searched. For example, “Pleistocene Indonesia* Reef” would be one full search term. References cited in publications recovered from these searches were further mined for relevant publications not found in the initial search. Additionally, the Naturalis archives (archives.naturalis.nl) were queried for PhD theses with usable data. Experts who work in the studied areas were queried for publications that were not digitally available or were missed by those search terms. Data locations were plotted on present-day maps to search for data gaps; data gaps were targeted with more specific searches to determine if the data-gap was genuine or was an artifact of the search terms combined with the ages coming from the studies published in the study region. Data from 92 papers were utilized. This compilation is available with the paper (SI Table 1).

Database assembly

Publications with cores, seismic data, well logs, outcrop studies, or other stratigraphic data dated to the stage level were selected for entry in the database, generating 175 sites with data extending from the Early Miocene to Pleistocene (23.04–0.011 Ma). Only localities between 90 and 160° E longitude and 25° N to 25° S latitude were entered. For each stage, we recorded whether there was a reef, non-reefal sediments, or no data. All Pleistocene (2.58–0.011 Ma) stages were combined in this study due to the extremely short duration of both stages and the paucity of studies which distinguish between them. Cores with lower stratigraphic resolution were excluded. Only sites which included a coral reef somewhere in their stratigraphy were included.

The category “Reef” was recorded if a stage was sampled at a site and a coral reef was found at some point during that stage. The definitions of coral reefs varied between

publications, including patch reefs, pinnacle reefs, reef atoll, and barrier reef systems; all of the above were simply categorized as “Reef”. “Other” was recorded if a stage was sampled but at no point in that stage was a coral reef found. If both coral reefs and non-reefal sediments were found in a stage, “Reef” was recorded. “Absent” was recorded in cases where the stage in question was represented by an unconformity, the study did not analyze that part of the section, or the section did not extend to that stage. Additionally, the site name and the publication from which the data were extracted were recorded.

The 2020 Geologic Time Scale (Gradstein et al. 2020) was used for stage boundaries. Stratigraphic information was extracted in multiple ways depending on what data was reported in a figure. If data were presented in text or in figures with stage boundaries explicitly stated, this was usually preferred. The exception was for the Pliocene; many publications were written before the Gelasian was moved to the Pliocene. In studies where the Pleistocene was present, we used other data such as radiometric dates to determine if the Gelesian was counted as Pliocene or Pleistocene in that publication. Sometimes the stage was not directly stated but samples had radiometric dates associated with them. In this case, those dates were used to determine the exact stage by referencing stage boundaries in the 2020 Geologic Time Scale. If neither stages nor dates were available, planktonic foraminifera zones were used. Publications often reported the foraminifera biozones found in Blow (1969), so we were forced to use these while correlating them with the more calibrated zones reported by Wade et al. (2011). Agnini et al. (2014) were used for calcareous nanofossils when foraminifera were not available. Disagreement between Agnini, Wade, and Blow was not observed at the level of precision of this study.

Statistical analysis

Sites were first binned by stage and spatially binned to 1° Latitude by 1° Longitude grid cells based on their modern location to reduce bias from heavily sampled areas (Beck et al. 2014). The gridding was sufficient since this study was conducted relatively close to the equator and number of reefs in a cell was not considered beyond presence or absence. The spatial binning was accomplished by scanning each grid cell within the study area and recording if the data contained either a record of a reef in that time bin and grid cell or, if there was no record of a reef in the specified time bin and grid cell, did that grid cell contain records of non-reefal sediment in the specified time bin. If neither a reef nor non-reefal sediments were recorded from that time bin and grid cell, the grid cell was excluded from further analyses for that time bin. If both a reef and non-reefal sediments were recorded in the same grid cell at a specific time bin, the

record of a reef overrode the non-reefal sediments. Sampling effort, defined as the number of grid cells in a time bin that contained records of a reef or non-reefal sediments (hereafter called “sampled grid cells”), was extremely uneven with the Pleistocene having 67 grid cells with data and the Aquitanian (23.04–20.45 Ma) only having 35. To lessen this bias toward recent stages, and in order to test how sensitive the observed trends are to missing datapoints, 15,000 bootstrap resampling runs were performed. For bootstrapping, spatially binned data from each stage was resampled with replacement separately down to 70% of the sampled grid cells in the time bin with the fewest sampled grid cells. Coral reef abundance, defined as the percent of sampled grid cells which contained coral reefs, was calculated for each resampling run in each time bin. The 5th and 95th percentiles of coral reef abundance across resampling runs were calculated to generate error bars for charts. Resampling runs were then divided into 1000 groups of 15 runs each, which allowed Wilcoxon tests to be run on the variety of data to determine the significance of observed differences in reef abundance between individual stages as well as between the overall Miocene, Pliocene, and Pleistocene. Bonferroni corrections were used to account for the large number of statistical tests performed. The mean *W*-statistics and *p*-values were used along with the percent of groups of 10 resampling runs that produced non-significant *p* values to determine significance. Since the Zanclean (5.33–3.60 Ma) and Piacenzian (3.60–2.58 Ma) are shorter than the Miocene stages, analyses were rerun with them combined to test the effect of stage length on reef abundance. Mean reef abundance for each stage was plotted in a time series plot using the ‘divDyn’ package in R (Kocsis et al. 2019) along with the aforementioned 5th and 95th percentiles. Furthermore, the log ratio of changes in mean reef abundance between stages was plotted to visualize the drop from the Messinian to the Zanclean and the rise from the Piacenzian to the Pleistocene. Mean reef abundance and sampling effort were plotted against each other and tested for correlation with a Spearman Rank Correlation test; autocorrelation was corrected by using generalized first differences.

Map generation

The grid cells generated for statistical analysis were further binned to the sub-epoch (Early Miocene, Middle Miocene, Late Miocene, Pliocene, Pleistocene) level to generate paleo-maps. The ‘Chronosphere’ package in R (Kocsis and Raja 2019) was used to rotate these points to their paleo-coordinates. Chronosphere is designed to allow modern GPS points to be rotated using the GPlates software (Müller et al. 2018). The Müller et al. (2016) tectonics model was used for most reconstructions with van Hinsbergen et al. (2015) being used to reconstruct points in areas not covered by Müller

et al. (2016). Miocene landmass reconstructions found on GPlates (Müller et al. 2018) for the studied area were not sufficiently accurate for the purposes of these maps, with many reef areas being placed in the middle of dry continents. Maps for the Miocene sub-epochs were modified using local reconstructions (Hall 2013; Morley et al. 2017) and to account for these errors in the global-scale maps.

Coral genera data

Previously generated genus-level data on corals (Johnson et al. 2015; Santodomingo et al. 2016; Saw et al. 2019) were compiled from the Miocene through the Anthropocene into a single datasheet containing only the first and last occurrences of each genus. Since there have been no genus-level extinctions of corals in the studied area since the Pleistocene, the Pleistocene is used as a baseline for Coral Triangle reefs in the absence of human interference (Merlín-Hernández et al. 2021). Data cleaning was conducted to update nomenclature and to remove azooxanthellate coral genera. Diversity dynamics were calculated using divDyn (Kocsis et al. 2019). Extinction rates, origination rates, and range-through diversity were all examined against reef abundance for correlations via Spearman Rank Correlation tests; autocorrelations were corrected by using generalized first differences. Range-through diversity was added to the previously generated time series plot.

Results and discussion

We found that coral reef abundance remained relatively constant throughout the Miocene but showed a significant drop in the Pliocene (Fig. 1, Fig. 2, SI Fig. 1, SI Fig. 2, $W = 2691$, $p = 3.77 * 10^{-16}$, Zanclean and Piacenzian separated; $W = 2679$, $p = 9.45 * 10^{-16}$, Zanclean and Piacenzian combined). During the Pleistocene an increase in reef abundance was observed (Fig. 1, $t = 223$, $p = 2.40 * 10^{-4}$, Zanclean and Piacenzian separated; $W = 218$, $p = 0.00105$, Zanclean and Piacenzian combined). The Pliocene stages were not significantly different from each other but were significantly different from all other stages, which is reflected in the 5th and 95th percentiles for the Pliocene stages not overlapping with the means of any of the Miocene stages or the Pleistocene (Fig. 1a, SI Tables 2–4). However, the 5th and 95th percentiles of all the Miocene stages and the Pleistocene overlapped with the means of each stage, suggesting that there were no relevant changes in reef abundance within the Miocene and that Miocene reef abundance was equivalent to that of the Pleistocene (Fig. 1a, SI Tables 2–4). Combining the Pliocene stages to account for unequal stage length did not modify any of the outcomes (SI Tables 2–4). Finally, a time series plot shows that the drop in reef abundances

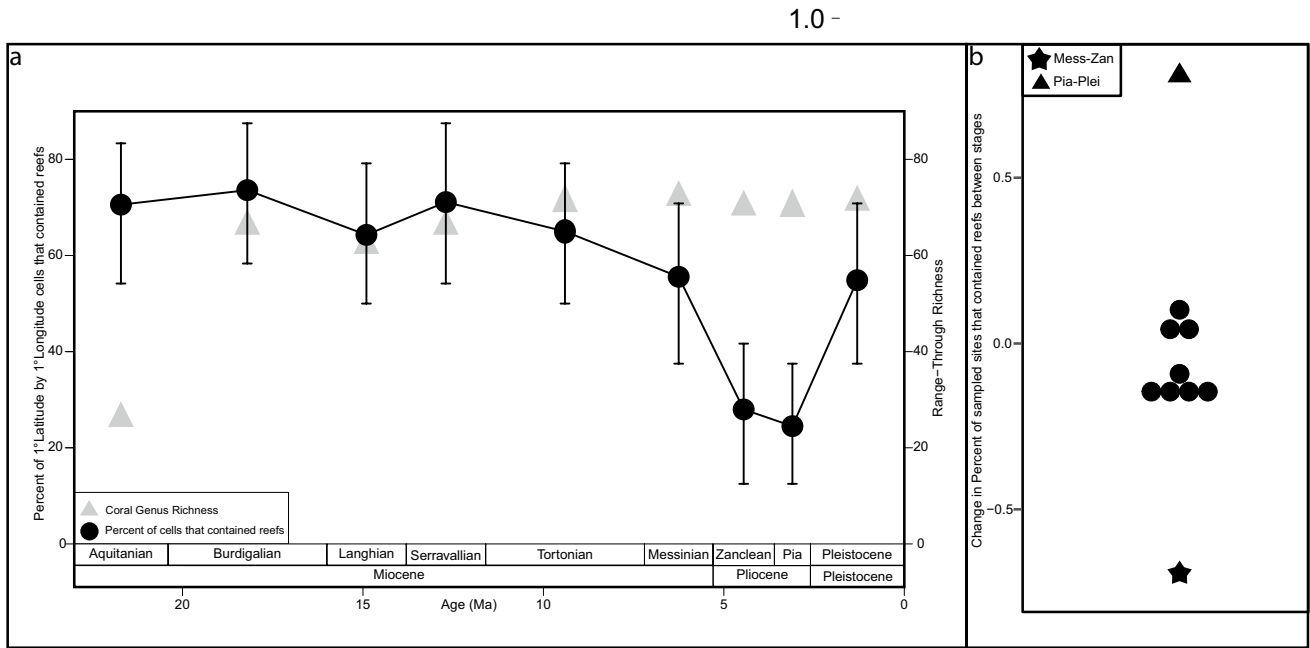


Fig. 1 a The black circles and line represent the mean reef abundance and the error bars indicate the 5th and 95th percentiles in each time bin. Gray triangles represent range-through richness of coral genera. b A time series plot showing changes in abundance of reefs

between periods. The star represents the change in reef abundance between the Messinian and the Zanclean and the triangle represents the change in reef abundance between the Piacenzian and the Pleistocene

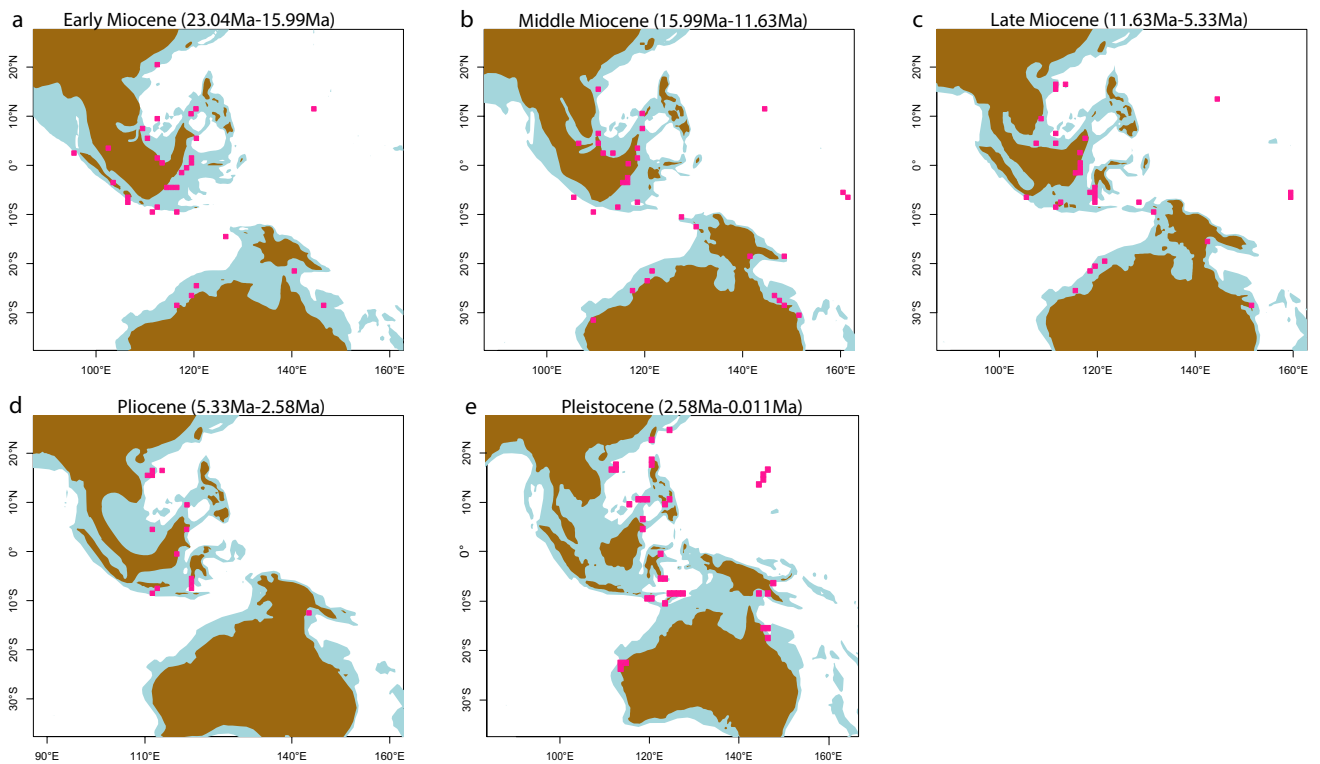


Fig. 2 Map of reef occurrences in the a Early Miocene, b Middle Miocene, c Late Miocene, d Pliocene, and e Pleistocene. The brown area represents land, and the light blue is shallow seaways. The pink

boxes represent 1° Latitude by 1° Longitude grid cells that contained at least one reef during the studied time interval

from the Messinian to the Zanclean and the rise from the Piacenzian to the Pleistocene are outliers compared to the fluctuations between the other stages (Fig. 1b). Reef abundance and sampling effort did not correlate ($\rho = 0.323$, $S = 56.838$, $p = 0.435$, SI Fig. 1). In contrast to the decline in regional reef abundance, the richness of reef coral genera was not significantly different between the Miocene and the Pleistocene (Fig. 1a). Despite the low number of reefs in the Pliocene (Figs. 1, 2), reef-building coral taxa (Fig. 1), similar to other reef-associated taxa like bryozoans (Di Martino et al. 2015) and foraminifera (Prazeres and Renema 2019), did not experience a loss of diversity on the genus level. No correlations were found between reef abundance and coral genus extinction rate, origination rates, or range-through diversity (Fig. 1, SI Table 5).

Even though we observed a decline in reef occurrences from the Middle Miocene to Pliocene in all regions, trajectories of Miocene to Pliocene reef development were regionally different. In the Coral Triangle most Miocene reefs developed on top of detached carbonate platforms (Wilson 2002). Uplift drove carbonate platform decline within the Coral Triangle by subaerially exposing platforms during the Middle-Late Miocene; reefs then occurred in patches on turbid, land-attached shelves (Santodomingo et al. 2016). In contrast, high subsidence rates in tandem with sea-level rise drowned carbonate platforms and platform-top reefs across Northern Australia (Clift and Sun 2006), drove platform top reefs out of the photic zone faster than they could accrete. During the Late Miocene only a few atolls and pinnacle reefs persisted there (Fig. 2). Simultaneously, reefs in the South China Sea declined sharply in the Late Miocene when wind-driven currents caused by the intensification of the Asian summer monsoons removed too much sediment for platform accretion to keep pace with subsidence and sea-level rise (Mathew et al. 2020). Patch reefs are the only reef type that appeared in all regions throughout the studied time intervals but they are less common in and after the Pliocene than in the Miocene.

Major Anthropocene drivers of reef decline, such as heat stress and increased sediment stress appear to have played smaller roles in the formation of the Pliocene reef gap. Even though the Pliocene is often referred to as a warm period in climate history (Haywood et al. 2013; Burke et al. 2018), it is in the middle of a cooling trend of Neogene climate. For example, the Late Miocene was the same temperature as the Pliocene while the Middle Miocene, when coral reefs were most abundant in the Coral Triangle, was even warmer (Zachos et al. 2008; Haywood et al. 2013; Burke et al. 2018). Pliocene $p\text{CO}_2$ (Burke et al. 2018) was not higher than Miocene $p\text{CO}_2$, so that cannot have been a driver either (Burke et al. 2018). Furthermore, Miocene reefs developed abundantly in turbid conditions (Santodomingo et al. 2016), so turbidity from sediment

shedding may not have driven this decline. Since modern modes of carbonate production developed in the Miocene (Betzler and Eberli 2019; McCaffrey et al. 2020) under these turbid, warm conditions, neither heat nor turbidity are plausible drivers of the Pliocene reef gap. Regional tectonics and sea-level rise remain as the last potential drivers Pliocene Reef Gap in the Coral Triangle that cannot be dismissed with present data, which suggests that researchers need to be cautious when drawing analogies between the Pliocene and Anthropocene in the Coral Triangle related to the future of reef growth.

Reefs reestablished in the Pleistocene. The onset of glacial sea-level fall returned drowned pinnacle reefs back into the accretion window (Shao et al. 2017). In addition, the uplift of islands in the Coral Triangle resulted in the development of fringing reefs around these islands (Fig. 1). Following the mid-Pleistocene transition, modern barrier systems, such as the Great Barrier Reefs, were initiated (Davies 2011; Renema et al. 2016) (Fig. 2).

The regional coral genus pool in the Miocene reefs is almost identical to that of Anthropocene reefs, but the contributions of taxa to the reef framework are radically different. *Acropora* dominated Pleistocene to Anthropocene reefs, while *Porites* dominated the framework of Miocene reefs with major contributions by other genera (Renema et al. 2016; Santodomingo et al. 2016). While the range-through values used in this study cannot be used to determine that local extirpation did not occur, there is evidence in favor of a high regional genus richness interpretation. For example, the Era Beds (PNG) alone contain 47 genera of reef-building coral (Veron and Kelley 1988), compared to the 70 genera estimated by our range-through analysis (Fig. 1). Our findings suggest survival of coral genera in non-reefal environments and the few remaining reefs, although extirpation and recolonization cannot be excluded.

The genera-rich but reef-poor state in the Pliocene Coral Triangle, exemplified in the Era Beds (Veron and Kelley 1988), contrasts with the Pleistocene Caribbean, which is genera-poor and has many coral reefs (Johnson et al. 2008). The decoupling of reef abundance from coral richness in the Pliocene and Pleistocene reinforces the notion that carbonate production was independent from reef builder diversity at those times. Kiessling (2005) found a general Phanerozoic correlation between carbonate production and reef builder diversity, but Pandolfi (1999) noted that carbonate production can vary greatly, even on reefs with a stable taxon-pool, which suggests the survival of coral taxa does not guarantee the maintenance of the fundamental function of coral reefs as carbonate factories. Therefore, conservation initiatives may benefit from treating preserving coral diversity and coral reef frameworks as related but separate conservation goals.

Conclusions

In conclusion, this study presents the first evidence for the existence of a Pliocene Reef Gap in the Coral Triangle and North Australian reef provinces. The sharp drop in coral reef occurrences in the Pliocene is likely a response to a combination of regional and local drivers, mostly subaerial exposure from uplift or drowning from subsidence combined with sea-level rise. High temperatures are not a plausible driver due to earlier, warmer time bins having higher reef abundances. Anthropocene reefs are also affected by diverse local and regional stressors, some of which lack Pliocene analogs, such as pollution, coastal development, and fisheries (Jones and Steven 1997; Slade and Kalangahe 2015; Santodomingo et al. 2021; Andreello et al. 2022), which demonstrate the need to mitigate local anthropogenic stressors on coral communities. Finally, this study highlights the disconnect between the survival of individual coral genera and the ability of those corals to build reefs. This means that the survival of coral genera through past greenhouse climates does not guarantee they built or will build reefs. Coral reef conservation should consider maintaining coral diversity and coral reef frameworks as related but separate goals which may require different management strategies.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Employment All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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