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Illuminating a Warmer World: Insights from the Paleogene

Key Points:

- The early Paleogene hothouse caused coral reef collapse but only few reef coral extinctions
- Reef corals can proliferate during hot climates without building reefs
- Coral reefs decline in warm climates regardless of the rate of warming

Supporting Information:

Supporting Information may be found in the online version of this article.

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Minor Coral Diversity Loss but Long-Lasting Coral Reef Crises in the Early Paleogene Hothouse

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Abstract The future of tropical coral reefs is severely threatened by rising global temperatures and relies on the persistence of two key attributes: (a) coral biodiversity, and (b) the reef-building capacity. In order to understand how these attributes responded to a climate warming, we investigated corals and coral reefs in the early Paleogene "hothouse" interval. We focused on the Mediterranean region, which was the global center of reef coral diversity and provides the most complete record for this time interval. We computed biodiversity dynamics of reef corals based on a new compilation of Paleocene to Eocene reef coral occurrences and compared these with coral reef development recorded in the PaleoReefs Database. Extinctions and diversity were within background fluctuations across the Paleocene-Eocene Thermal Maximum (PETM). Coral diversity increased rapidly in the aftermath of the PETM and remained high across the entire Eocene. But reef building collapsed at the PETM and recovered to late Paleocene levels only by the late Eocene. We document that reef corals have demonstrated an excellent resilience within the hothouse, whereas coral reefs were much more vulnerable and took much longer to recover. Our findings suggest that although coral reefs might disappear in the near future, corals will persist and could begin reconstructing reefs once environmental conditions allow.

Plain Language Summary Coral reefs are among the most vulnerable ecosystems to human-induced climate warming. Reef corals are also thought to be at elevated extinction risk. We studied the consequences of an ancient rapid warming event 56 million years ago that was followed by a period of sustained warmth. The warming event caused a collapse of coral reefs but surprisingly negligible extinctions among reef corals. Also, coral reefs could not recover during the warm period that lasted until around 40 million years before present, whereas coral diversity peaked already 5 million years after the initial warming pulse. Our findings suggest that coral reefs are more sensitive to climate warming than reef corals.

1. Introduction

Modern coral reefs are one of the most diverse and valuable ecosystems on Earth but are also among the most vulnerable to climate change (Eddy et al., 2021; Hughes, Barnes, et al., 2017; Pandolfi et al., 2003). Coral reefs around the world are suffering from warming waters, ocean acidification, and localized stressors, such as pollution or overfishing, with projections of a near total collapse before the end of this century under high levels of global warming (Hoegh-Guldberg et al., 2007; Hughes, Kerry, et al., 2017; IPCC, 2022). Reef corals, which are building this crucial ecosystem, are supposed to be under elevated extinction risk including from climate change (Carpenter et al., 2008), although some argue that this is not the case (Dietzel et al., 2021).

The future of coral reefs is thus based on the persistence of two key-aspects: (a) the maintenance of coral biodiversity; and (b) the reef-building capacity which is represented by the amount of calcium carbonate produced by corals and is reflected in the formation of volumetrically well-developed reefs. Understanding how these two coral features will respond to the unfolding climate crisis is challenging, in particular if we are interested to predict a long-term response.

The geological archive stands as the singular repository of observable data that can be used to achieve this goal, offering invaluable insights for better understanding the responses of ecosystems like coral reefs to temperatures significantly higher than those of today (Dee et al., 2019; Pandolfi & Kiessling, 2014; Tierney et al., 2020).

Comparative analyses between coral diversity and reef development in the past have already been performed, but with contradictory results. On the one hand there is evidence for a positive correlation on longer time scales (Bosellini et al., 2021; Kiessling, 2005), but there is also evidence for decoupling of diversity and reef growth

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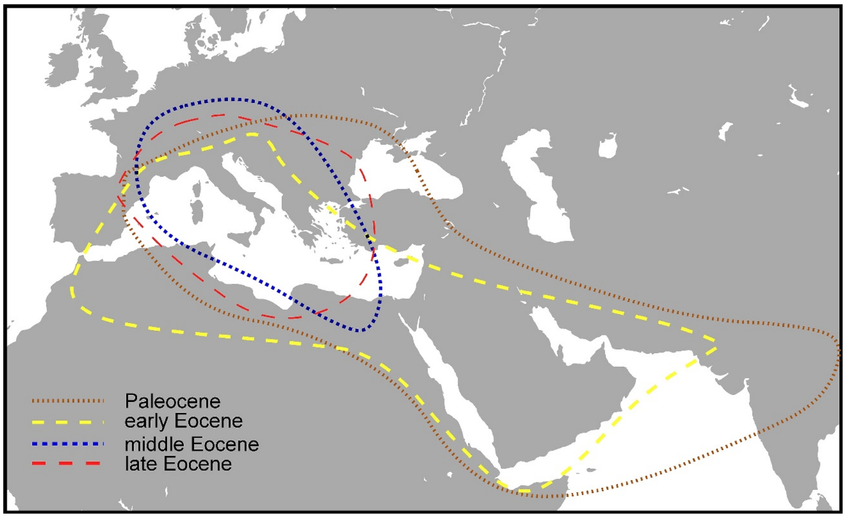

Figure 1. Geographic distribution of the reef coral occurrences in the PalEoCoral data set for the Paleocene and early, middle, and late Eocene. Details on the localities are provided in Bosellini, Benedetti, and Kiessling (2024).

(Bosellini et al., 2022; Harrison et al., 2023; Johnson et al., 2008; Perrin & Bosellini, 2013). Biodiversity hotspots may thus not necessarily imply the presence of large massive reef frameworks or vice versa.

Here, we investigate the relationship between coral diversity and reef proliferation during the early Paleogene hothouse, when global mean temperatures may have been up to 12°C higher than today (Westerhold et al., 2020; Zachos et al., 2001). In particular, we aim to characterize the impact of significant warming episodes that marked the Paleocene and Eocene epochs: the hyperthermal Paleocene-Eocene Thermal Maximum (PETM), the Early Eocene Climatic Optimum (EECO), and the Middle Eocene Climatic Optimum (MECO).

The PETM (Schulte et al., 2013; Thomas & Shackleton, 1996), occurring approximately 56 million years ago, lasted about 170 thousand years (Zeebe & Lourens, 2019) and was characterized by a profound disruption of the carbon cycle. Global temperatures surged, with estimates placing the average surface temperature at 25.2°C (Scotese et al., 2021), or even as high as 31.6°C (Inglis et al., 2020), compared with 15.0°C today.

The EECO (Luciani et al., 2016; Zachos et al., 2001), spanning from 53.3 to 49.1 million years ago during the Ypresian stage, witnessed a prolonged phase of elevated temperatures, with global averages around 25.1°C (Scotese et al., 2021) or 27.0°C (Inglis et al., 2020). This time also saw a significant rise in atmospheric CO_2 levels (Rae et al., 2021).

The MECO (Bohaty & Zachos, 2003), lasting roughly 300 thousand years, occurred in the Bartonian stage (40.51–40.21 Ma) (Rivero-Cuesta et al., 2019). The MECO represented a global warming event that temporarily interrupted the general Eocene cooling trend. Global temperatures reached around 23.1°C (Scotese et al., 2021).

We investigated the early Paleogene record of corals and reefs in the Mediterranean region. Although the region comprises more than just areas bordering the modern Mediterranean, we chose to include the western and central Neotethys for a more comprehensive regional assessment (Figure 1). The data derived from the literature are unevenly distributed across time and space, and particularly concentrated in certain regions. We outlined the investigated areas through time; however, it should be noted that the better sampled localities were always in the central-western Mediterranean (Figure 1). This Mediterranean region comprised in the Paleogene a coral province similarly distinct as the modern Caribbean and Indo-Pacific provinces. In the Paleogene, the three regions were interconnected by the westward flowing Tethyan seaway. In particular, the Mediterranean was the global center for marine diversity in the Early Paleogene (Renema et al., 2008; Yasuhara et al., 2022). This region is extremely rich in Paleogene coral reef localities and coral collections, studied since the 19th century, thus providing a continuous and more complete record with respect to the more fragmentary records of the Caribbean and Indo-Pacific. Moreover, the good and continuously updated regional biostratigraphic calibration based on larger foraminifera Shallow Benthic Zones (Serra-Kiel et al., 1998), allows in many cases to date the coral deposits at the stage level which is not always expected in shallow water settings.

2. Materials and Methods

2.1. Data

At the Mediterranean scale, a data set (i.e., REEFCORAL database) has already been created for Oligocene and Miocene scleractinian corals at the genus level (Bosellini & Perrin, 2008; Perrin & Bosellini, 2012, 2013). In order to complete the Cenozoic record of the region, we have assembled over the past couple of years the PalEoCoral data set focusing on the Paleocene and Eocene epochs (Bosellini, Benedetti, & Kiessling, 2024). This new compilation consolidates data concerning the reef corals, which in being mostly colonial and presumably zooxanthellate have the capacity to build coral reefs, in the Mediterranean region (Figure 1).

We focus on reef corals because, due to their great sensitivity to environmental and climatic changes, these shallow-water hypercalcifying organisms represent an ideal laboratory to track climate changes in the shallow seas during a period of time characterized by strong climatic fluctuations, from the hyperthermal events of the early Paleogene toward the stepwise transition to Icehouse conditions.

In the PaleEoCoral data set, we compiled occurrence data at the finest possible taxonomic level using three different data sources: published literature, studies of coral collections in museums (e.g., Bosellini et al., 2022), and also our personal collections. A cross-check with the Paleobiology Database (https://paleobiodb.org/) has been performed in order to fill potential gaps. All colonial corals were included, together with some solitary corals that we considered as zooxanthellate.

All coral occurrences have been systematically revised at the genus level (if necessary), considering recent taxonomic revisions (Budd et al., 2012; Budd & Stolarski, 2009), which were informed by molecular data of extant species (Fukami et al., 2004, 2008). Revisions also considered the World Register of Marine Species (WoRMS). Geographic and stratigraphic information was also added, together with the attribution of the coral symbiotic status following the approach of Perrin and Bosellini (2012). We dedicated particular attention in checking and revising the age of the coral localities in the data set. Shallow Benthic Zones (SBZ) are routinely identified from the Paleocene-Eocene interval of the western Neotethys (Serra-Kiel et al., 1998) and have been recently recalibrated (e.g., Benedetti et al., 2024; Papazzoni et al., 2023; Scheibner & Speijer, 2009; Serra-Kiel et al., 2020). This detailed biostratigraphic framework based on shallow water foraminiferal associations turned out to be particularly useful for updating the age of shallow-water, tropical reef localities at the stage level. The PalEoCoral data set currently provides information on 1,345 coral occurrences from more than 100 localities in the Mediterranean region (Bosellini, Benedetti, & Kiessling, 2024).

In order to assess reef development and compare it quantitatively with coral diversity, we used the Paleoreefs Database (https://www.paleo-reefs.pal.uni-erlangen.de/). This database compiles geometrical and compositional data of Phanerozoic reef sites (Kiessling & Flügel, 2002). Here the database was filtered to outcropping Cenozoic coral reefs of the same Mediterranean region as used for corals (Figure 1) (Bosellini, Benedetti, & Kiessling, 2024). Coral reefs were defined as reef structures in which corals were at least the second most prevailing reef builders. We limited the data set to exposed reefs because the dimensions of subsurface reefs tend to be overestimated (Kiessling & Flügel, 2002) introducing a bias when reefs have economic value (e.g., as hydrocarbon reservoirs). Following Kiessling et al. (2000), we estimated reef volume by multiplying thickness and lateral dimensions assuming a simple cuboid geometry. Missing values were replaced with estimates that were inferred from reefs with known dimensions. Reef volume estimates are provided with and without estimates of reef tract dimensions (e.g., when reefs were reported to be aligned in a reef tract but not individually recorded in the database). Coral reef volume was estimated to be 70% of the total reef volume when corals were the dominant reef builders and 30% if they were secondary reef builders. We report cumulative sums of reef volume per stage and standardized by the duration of the stage (km^3 my^{-1}).

2.2. Age Resolution

Our stratigraphic scheme was guided by available data and is thus not strictly by established geological stage (Table S1 in Supporting Information S1). Although the subdivision of the Paleocene into three stages has been formalized since 1989, historically the Selandian was often included within the lower Thanetian (e.g., Speijer et al., 2020). This implies that the stratigraphic resolution of most literature data from middle to late Paleocene suffers from heterogeneous stratigraphic concepts. In this work, for the numerical analysis, we merged the Selandian and Thanetian into a single interval. As concerns the lower Eocene, that is Ypresian, in order to highlight the response of reef corals to the PETM and EECO events, we divided this stage into two bins, corresponding to the regional stages Ilerdian (i.e., lower Ypresian) and Cuisian (i.e., upper Ypresian), that are still routinely adopted for the central-western Neotethys shallow-water biozonation (Benedetti et al., 2024; Serra-Kiel et al., 2020).

All diversity, turnover and reef volume data were computed at this stratigraphic resolution. Although proxy-based temperature estimates are available at much finer stratigraphic resolution (Gaskell et al., 2022; Westerhold et al., 2020), we binned these data to the same stratigraphic resolution as the reef data for statistical comparison. We did this by computing the mean of all values reported within respective bins.

2.3. Statistical Analysis

Diversity and turnover estimates of reef corals were computed with the divDyn *R* package (Kocsis et al., 2019). We report range-through and sampled-in-bin diversity estimates per stratigraphic bin using the same temporal resolution as for reefs. Range-through diversity assumes a continuous occurrence of a taxon within a range by inferring its presence in intermediate bins, when it is not documented. This method may contribute to overestimating diversity. Sampled-in-bin diversity is based only on direct fossil evidence, but may underestimate diversity when the fossil record is incomplete.

Extinction and origination rates for both genera and species were calculated following the equations of Foote (2000) but, following Foote (2005), without standardizing for the duration of stages. The method implies that turnover rates cannot be computed for the first interval with occurrences and because our data set does not comprise Cretaceous coral occurrences, the Selandian-Thanetian is the first interval for which turnover rates could be computed.

To assess turnover rates of coral genera, we merged the PaleEoCoral and the REEFCORAL data set (Bosellini & Perrin, 2008; Perrin & Bosellini, 2012, 2013), which allowed us to avoid edge effects at the end of the Eocene. Since no species occurrences are included within REEFCORAL, we avoided to provide species turnover rates for the investigated intervals. Sampling-standardized turnover rates were computed using shareholder-quorum subsampling (Alroy, 2010). Finally, we performed a statistical comparison of estimated reef volume and coral diversity. We applied both parametric (Pearson) and non-parametric (Spearman rank) correlation tests of first differences. All statistical analyses were conducted in *R* 4.4.1 (R Core Team, 2024).

3. Results

3.1. Coral Diversity and Turnover

The raw data, for both species and genus coral diversity (Figure 2) show an overall trend of increase through time from the Paleocene to the late Eocene.

In detail, the number of species and genera is rather constant during the Paleocene from Danian to Thanetian. Across the PETM our data document a slight decline for the species in the lower Ypresian, whereas diversity remained stable for genera, especially if we consider range-through diversity. Both genus and species diversity increased rapidly in the late Ypresian, that is into the advent of the EECO. Diversity at the genus and species level remained essentially constant from the late Ypresian up to the Lutetian. After the MECO, both genus and species diversity increased slightly until the end of the Priabonian stage.

Turnover dynamics at the genus level during the Paleocene-Eocene interval suggests a major origination pulse in the late Ypresian, whereas extinction rates are greatest at the end of the Eocene (Figure 2). The late Ypresian origination pulse occurred during the EECO, roughly corresponding to the maximum in atmospheric $p\mathrm{CO}_2$, and it is followed by a sharp decline in the Lutetian. A less marked increase is registered in the Bartonian, possibly linked to the MECO.

Extinctions mostly involved genera that passed the K/Pg mass extinction event but were rare and geographically restricted, with one or two occurrences in our data set. Instead, originations include some more widespread genera that will later become important reef builders such as the extant *Porites*, *Colpophyllia*, *Agaricia*, and the extinct *Antiguastrea* that was very common in many Oligocene reefs worldwide (Figure 3). Minimum extinction values are reached during the EECO and during the Bartonian, close to the MECO. The end-Eocene rise of extinction

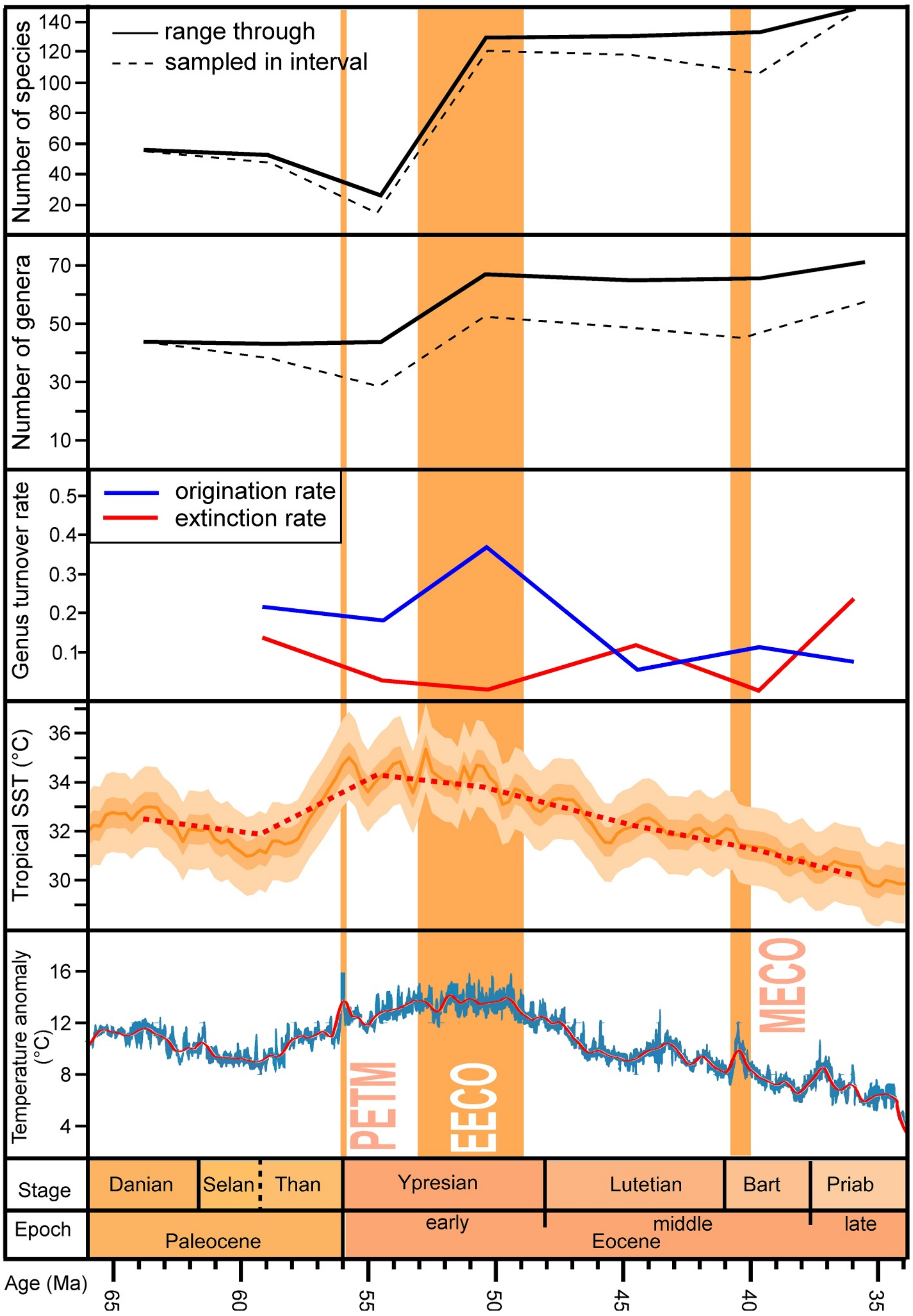

Figure 2. Raw data of coral diversity at both genus and species level and turnover rate (origination and extinction) of reef coral genera during the Paleocene-Eocene interval. Results are compared with tropical sea-surface temperatures from Gaskell et al. (2022), averaged to the same temporal bins as diversity metrics (dotted red line). Temperature anomalies from Westerhold et al. (2020) are shown at original temporal resolution (red line marks the running mean) to demarcate short-term events, such as the PETM, and other warming events such as the EECO and MECO.

rate is mostly in the rare genera, some solitary zooxanthellate (i.e., *Cycloseris*, *Trochoseris*, *Circophyllia*) but also some that were very common during all the Paleocene-Eocene interval such as *Pachygyra*.

3.2. Coral Reef Volume

The trajectory of estimated coral reef volume (Figure 4) shows that coral reefs were on the rise after the Cretaceous-Paleogene boundary, but declined after the PETM. Coral reef volume gradually dropped further

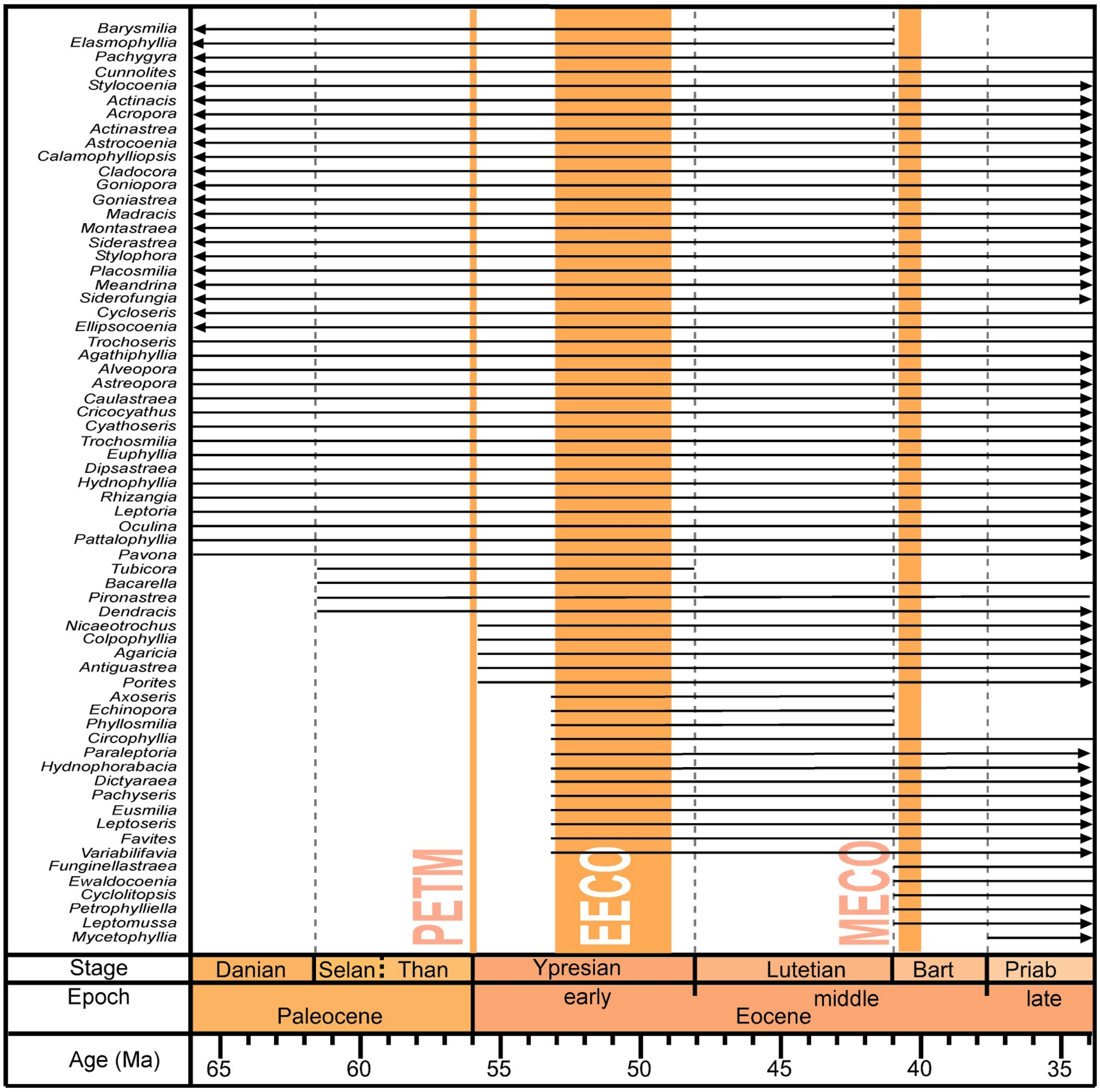

Figure 3. Stratigraphic ranges of colonial and solitary zooxanthellate genera with more than two occurrences in the PalEoCoral data set. The range refers only to the distribution in the Mediterranean region considered in this study. Arrows indicate the occurrence of the genera before and/or after the Paleocene-Eocene interval as derived from the Paleobiology Database and by Bosellini and Perrin (2008) for the Oligocene-Miocene time interval. The major warming events and their duration are also shown.

reaching a minimum in the Lutetian. The recovery started in the Bartonian, with considerable reef volumes similar to those of the late Paleocene reached again in the Priabonian.

3.3. Statistical Comparisons Between Reefs and Corals

The decoupling of reef building and coral diversity is statistically confirmed. There is no correlation between genus diversity and coral reef numbers or coral reef volume across the Paleocene-Miocene time series or just the Paleocene-Eocene. There are no significant cross-correlations regardless of the combination of range-through, sampled-in-bin, reef volume with and without reef tract estimates and regardless whether raw data or first-differences (to account for autocorrelations) are being applied. For example, the Pearson correlation between the first differences of Paleogene reef volume (without reef tract) estimates and range-through genus diversity estimates was $R = 0.06$, $p = 0.91$. The species-diversity trajectories of the Paleocene and Eocene also yielded no significant cross-correlation with reef proliferation estimates (rho $= 0.15$, $p = 0.77$ for the same setup as for genera).

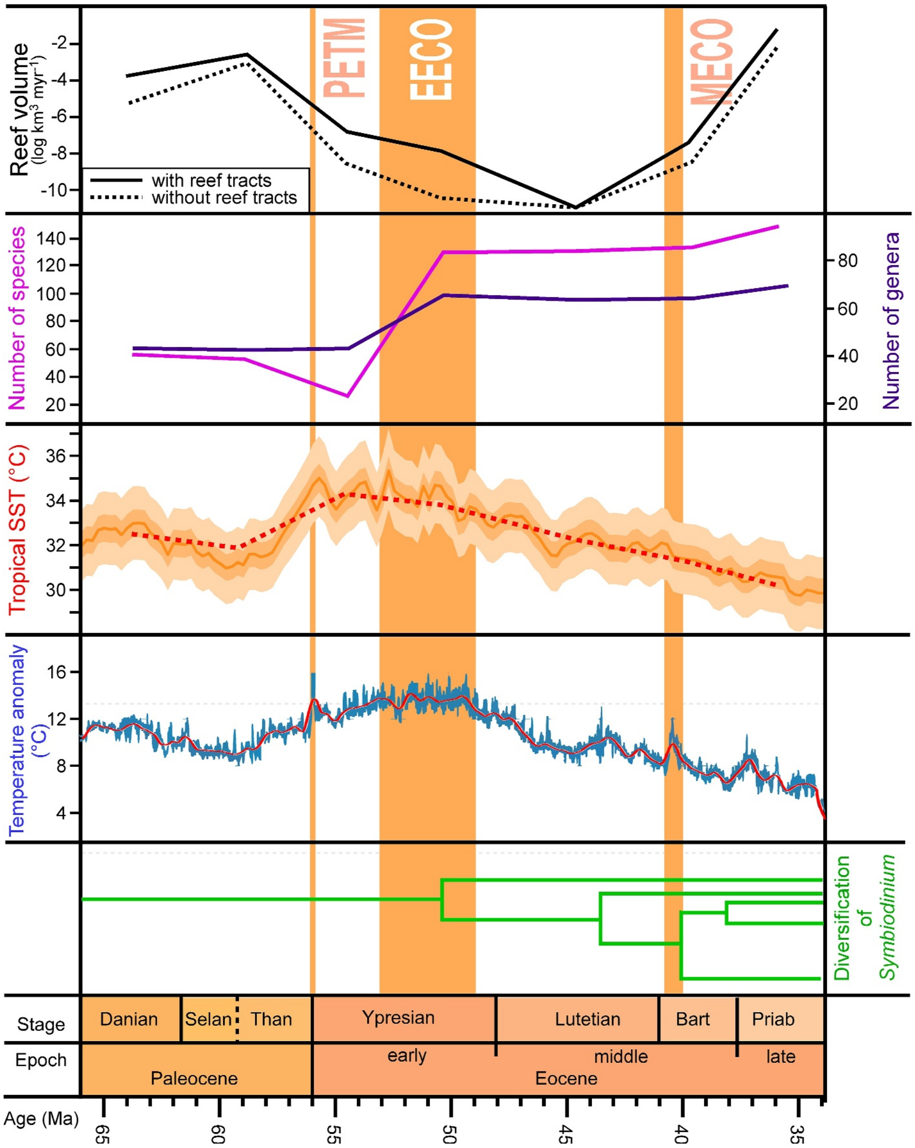

Figure 4. Values of estimated coral reef volume (log km^3 myr^{-1}) during the Paleocene-Eocene interval. Results are compared to coral diversity (species and genera), the diversification of *Symbiodinium* dinoflagellates (Pochon et al., 2006), and tropical sea surface temperature (Gaskell et al., 2022). The dotted red line represents the values of SST averaged to the same temporal bins as diversity metrics as in Figure 2. Temperature anomalies from Westerhold et al. (2020) are shown at original temporal resolution (red line marks the running mean) to demarcate short-term events, such as the PETM, and other warming events such as the EECO and MECO.

There are, however, strong correlations among our diversity estimates at genus and species level, respectively. The Pearson correlation between genus and species level range-through diversity is $R = 0.98$ and that between sampled-in-bin diversity is $R = 0.95$ ($R = 0.92$ and 0.99, respectively for first differences, all p-values $<< 0.01$).

4. Discussion

4.1. Coral Diversity Versus Coral Reef Development in the Cenozoic

Undoubtedly, the optimal conditions for coral reef ecosystems correspond to their ability to maintain a high coral diversity and a good reef-building capacity. However, these two crucial requirements, now threatened by global warming and associated environmental stressors, were not always characterized in the past by a positive cross-correlation.

The reef record of the Cenozoic shows several examples of decoupling and mismatches (Johnson et al., 2008; Kiessling & Baron-Szabo, 2004; Perrin & Bosellini, 2013; Zamagni et al., 2012), suggesting that reef development and coral diversity may be controlled by different drivers. There were cases in which coral diversity was high but reefs were rare and poorly developed, and others in which the opposite occurred. In the Caribbean, reef development was unrelated to coral diversity, with the largest reef tracts (Late Oligocene, Late Pliocene-Pleistocene) forming when diversity was low and after important extinction events (Oligocene/Miocene transition and in the late Pliocene) (Johnson et al., 2008). In the Mediterranean, the most striking example is reported from the Messinian, when reef complexes were very frequent and well developed but built by a very poorly diversified coral fauna, strongly dominated by *Porites* (Bosellini & Perrin, 2008; Perrin & Bosellini, 2013). According to Pomar and Hallock (2008), Mediterranean reef development during the late Miocene was promoted by the global cooling associated to low $p\mathrm{CO}_2$ values, and by the coeval diversification of zooxanthellae associated to widespread aragonite precipitation. In contrast, the low coral diversity has been mainly related to the gradual regional climatic cooling resulting from the northwards slow migration of the Mediterranean realm outside of the tropical-subtropical belt, superimposed on the global cooling, and to the closure of the Indian Gateway that ended the potential faunal exchange with the Indo-Pacific coral fauna and limited the genetic pool of z-corals within the Mediterranean (Perrin & Bosellini, 2013).

Paleocene coral reefs were on a rise after the end-Cretaceous mass extinction (Baceta et al., 2005; Zamagni et al., 2012). However, this rise rapidly ended at the PETM, causing a collapse of reef building (Flügel & Kiessling, 2002; Kiessling & Simpson, 2011; Scheibner & Speijer, 2008). This coral reef collapse has been attributed to a combination of warming seawater temperature and ocean acidification associated with the PETM hyperthermal event, that significantly impacted coral reef development and likely favored the expansion of marginal settings where corals had a limited frame-building capacity (Scheibner & Speijer, 2008; Zamagni et al., 2012). Despite the loss of coral reefs, previous global database analyses reported that coral generic diversity increased during this interval (Kiessling & Baron-Szabo, 2004; Zamagni et al., 2012) due to low extinction and high origination rates. Simpson et al. (2011), by combining the molecular and fossil record, underlined just small changes in coral diversity, origination and extinction rates during the late Paleocene-early Eocene. More recently, Weiss and Martindale (2019), analyzing the Paleobiology Database (PBDB), documented almost no changes in generic and species richness of colonial corals throughout the late Paleocene and early Eocene.

4.2. The Early Paleogene Decoupling of Reef Growth and Coral Diversity in the Mediterranean

Our results, summarized in Figure 4, confirm the global reef crisis in the aftermath of the PETM already recognized by previous studies (Kiessling & Baron-Szabo, 2004; Kiessling & Simpson, 2011; Scheibner & Speijer, 2008; Zamagni et al., 2012), and characterize in detail the decoupling with coral diversity for the Paleocene-Eocene time span and the diachroneity of responses to short-term (PETM, MECO) and long-term warming events (EECO).

Mediterranean coral reef development experienced a profound crisis after the PETM, and started to flourish and recover again only after the MECO. Its trajectory is testified by a broad suite of reef localities and reef types summarized below.

The Danian was characterized by carbonate platforms with quite well-developed coralgal reefs, ranging from small isolated patch reefs and mounds to large reef complexes such as the upper Danian Lizzaraga reef complex in the Pyrenees (northern Spain) (Baceta et al., 2005). Other examples of Danian patch reefs and mounds with abundant algae and corals are reported from Egypt (Schuster, 1998), Libya (Pawelek, 2009), the northern Adriatic platform (Turnšek & Drobne, 1998) and other localities reported by Zamagni et al. (2012).

Selandian-Thanetian coralgal buildups were also quite common and well-developed in many areas of the entire region, for example, Somalia (Carbone et al., 1993), Egypt (Scheibner et al., 2003; Schuster, 1998), Sirt Basin, Lybia (Spring & Hansen, 2004; Vršič et al., 2021), Pyrenees, Spain (Baceta et al., 2005; Eichenseer, 2003), Apennines, central Italy (Vecsei & Moussavian, 1997), northern Adriatic platform (Zamagni et al., 2009), and other localities reported by Zamagni et al. (2012).

At the end of the Paleocene, paleoclimatic and paleoceanographic changes that triggered the PETM hyperthermal event caused profound changes in shallow-water settings and in carbonate production (Pomar et al., 2017). The decrease in coral reef volume that followed this event has been to some extent balanced by the increase of carbonate production by larger foraminifera (especially nummulitids and alveolinids) that flourished after the PETM (Scheibner & Speijer, 2009).

During most of the Eocene coral buildups declined, in both size and relative abundance. The early Ypresian carbonate platforms were mostly characterized by few and small coralgal mounds (Eichenseer, 2003; Eichenseer & Luterbacher, 1992) and *Solenomeris* (an encrusting foraminifer) reefs (Plaziat & Perrin, 1992). The late Ypresian, despite generally considered as barren in coral reefs (Pomar et al., 2017), shows patch reefs from Slovenia and northeastern Italy (Bosellini et al., 2022; Vescogni et al., 2016; Zamagni et al., 2012), the latter developed during the EECO. These coral patch reefs were overwhelmed by foraminiferal shoals dominated by alveolinids and nummulitids, which were abundant during the whole Ypresian up to the middle Bartonian (Pomar et al., 2017).

During the Lutetian, coral reef volume reached the minimum values in the Mediterranean region and carbonate platforms were dominated by large benthic foraminifera (Pomar et al., 2017). In the Bartonian, after the MECO, and up to the Priabonian, coral buildups crop out extensively increasing their volume both in deltaic, mixed carbonate-siliciclastic setting, like in northern Spain (Alvarez et al., 1995; Morsilli et al., 2012; Taberner & Bosence, 1995) than in pure carbonate settings, such as the Nago Limestone in northern Italy (Bosellini, 1998) and the Eisenrichterstein limestone complex in southern Germany (Darga, 1990).

At a global scale, it has been documented that from the late Paleocene to the early Eocene, the proportions of corals in pure carbonate depositional settings decreased markedly, whereas those living in mixed carbonate-siliciclastic settings increased (Weiss & Martindale, 2019; Zamagni et al., 2012). This pattern is confirmed also for the Mediterranean region, where coral assemblages during the early Eocene mostly occupied, with few exceptions such as the small coral buildups at Monte Postale, northern Italy (Vescogni et al., 2016), marginal mixed carbonate-siliciclastic settings, possibly turbid-mesophotic. Although it is beyond the scope of this paper to discuss the role of mesophotic reefs, it should be underlined that these types of ecosystems are considered quite resilient with respect to global warming both currently (Morgan et al., 2017; Sully & van Woesik, 2020) and in the geological record (Bosellini, Vescogni, et al., 2024; Dimitrijević & Kiessling, 2023).

Looking at coral diversity, the most recent paper that investigates coral diversity and coral traits during the early Paleogene at the global scale shows that no extinction occurred at the generic level and just a little extinction at the species level, thus leading to an increase in generic and species richness of colonial corals throughout the late Paleocene and early Eocene (Weiss & Martindale, 2019). Our data instead shows a different pattern, underlining a clear decrease in species richness from the Thanetian to early Ypresian, followed by a marked increase in both generic and species richness in the late Ypresian, during the EECO. This pattern is also confirmed by the peak of genus origination rates. This peak of diversity is most probably related to the coral hotspot recently described from northeastern Italy, where a total of 37 genera and 103 species have been reported, and the EECO and post-EECO phases characterized by an accurate specimen-based systematic revision of museum collections associated to a detailed biostratigraphic calibration (Bosellini et al., 2022). This coral hotspot was the most diverse at global scale during the Ypresian and was hosted within a deltaic and mesophotic depositional setting, where rapid sediment accumulation, enhanced nutrient delivery and stressful climatic conditions reduced coral size and frame-building capacity but served as a suitable refuge for maintaining a well-diversified pool of shallow-water coral species escaping warming seawater. After this peak, indeed, coral richness remained stable with a very slight increase in the Priabonian.

The "time of decoupling" is characterized by an increase in origination rates, with the appearance of several important genera (*Colpophyllia*, *Antiguastrea, Porites*, *Paraleptoria*, *Favites*, *Variabilifavia*) which, although still not frequent, will be among those that will characterize the Mediterranean Oligocene and Miocene luxuriant reefs. Moreover, the dominant corals in the rare and small coral patches and buildups of the early Eocene (*Actinacis*, *Goniopora*, *Astrocoenia*, *Stylocoenia*, *Pachygyra*, *Caulastraea*, *Siderastrea*, *Siderofungia*) were all already present since the Paleocene or even the Cretaceous, suggesting that the reduced potential to produce a consistent reef framework was not an effect of a particular community composition.

4.3. The Mutual Response to Global Drivers

Although this analysis was performed at a regional scale, it refers to a region that during the early Paleogene was the global center of coral diversity, was connected with both the still extant coral reef provinces of the Caribbean and the Indo-Pacific by the westward flowing Tethyan seaway and, with respect with these two regions, was much more explored and investigated. We can thus assume that the Mediterranean may represent a suitable “laboratory” for better understanding how coral reefs and reef corals reacted to the warming events of the early Paleogene, when catastrophic release of carbon to the atmosphere triggered abrupt increase in global temperatures.

The decoupling of reef growth and coral diversity clearly shows a different response to the global multiple stressors of this hothouse interval. The reef crisis, or reef gap, is coincident with rise of tropical sea surface temperatures (SST) (Figure 4), and with extremely high $p\mathrm{CO_2}$ values. These conditions also led to increased acidification, weathering rates and nutrient levels, and to low aragonite saturation state. The combination of these detrimental factors impacted negatively on the capacity of reef corals to produce carbonate in an efficient way to create extensive reefs, as already suggested by previous studies (Zamagni et al., 2012 for a review).

In contrast to reef development, our results show a positive feedback of reef corals that appeared extremely resilient and able to develop adaptive strategies to live and diversify during stressed and harsh conditions, as also proposed by Zamagni et al. (2012). These adaptations may have induced reduced growth rates and less effective calcification, but were not associated to a significant loss in diversity.

Previous studies that aimed to investigate the response of shallow-water calcifiers to the warming events of the early Paleogene, were all concentrated on the late Paleocene-early Eocene interval and on the PETM in particular, neglecting the immediate post-warming phase when global temperatures started to cool down, driving the Earth climate from hothouse to icehouse conditions in the Oligocene. Our data at the regional scale cover also this first Cenozoic cooling interval, interrupted during the Bartonian by the hyperthermal event known as MECO, and show that the reef crisis was gradual and has lasted longer than documented so far. The most negative effect of the climate warming, represented in our data by the minimum values of reef volume, was actually reached in the Lutetian, thus with a substantial lag with respect to the peak of the hothouse. Among all stressors, $p\mathrm{CO_2}$ experienced abrupt changes in the late Paleocene-early Eocene interval, maintaining high values in the middle and upper Ypresian, thus during the EECO. Sea-water temperature instead was constantly high. We can thus postulate that the longer EECO interval was the “killing blow” for the collapse of coral reefs, and not the PETM alone.

The recovery after the MECO was quite fast, concomitant to the decrease of tropical SST and $p\mathrm{CO_2}$ values and the increase of pH levels. The rise of coral reefs during the late Eocene is also positively correlated with the first radiation event within evolution of the *Symbiodinium* zooxanthellae, with the divergence of several clades, that occurred during the Eocene cooling, after the PETM and EECO, according to Pochon et al. (2006) (Figure 4). At the same time also diversity, at both genus and species level, slightly increased. The close relationship between evolution of *Symbiodinium* and reef development was already pointed out by Pomar and Hallock (2008), who postulated that a shallowing of coral habitats, as well as an increase in coral-building capacity that occurred during the Late Miocene in the Mediterranean region, was a consequence of a strengthening of the bathymetric thermal gradient induced by global cooling and coeval diversification of zooxanthellae. Similarly, diversification of *Symbiodinium* zooxanthellae during Bartonian and Priabonian epochs may have played a role in coral's recovery of the ability to form reefs.

5. Conclusions

Global climate change is expected to cause the collapse of living coral reefs and since ancient reefs have experienced multiple episodes of crises being repeatedly slowed or stopped during periods of climate change, the fossil record is a valuable resource for understanding how coral reefs responded to similar stressors in the geological past.

In this study we have investigated the most severe coral reef crisis of the Cenozoic, that occurred in association to the hothouse phase of the early Paleogene and was triggered by the strong and fast PETM hyperthermal event, often used as a benchmark for the modern situation. We compared reef coral diversity with coral reef development at the Mediterranean scale and the main outputs are the following:

- We document a long-term decoupling between reef coral diversity and coral reef proliferation in the Paleocene and Eocene of the Mediterranean region.
- During the warmest time in the Cenozoic, zooxanthellate reef corals were constantly present and the detrimental factors associated to the warming events inhibited the growth of well-developed and extensive reefs but not the

proliferation of diversified coral communities, suggesting that reef development and corals diversity are controlled by different drivers.

- We show that reef growth is more sensitive to climate warming than reef coral diversity. The coral reef crisis started at the PETM, but the gradual decline reached it maximum in the Lutetian, indicating that the most negative effect of the climate warming was recorded much later than the PETM and that the longer warming event of the EECO was more detrimental than the PETM alone. This suggests that warm climates per se are detrimental to coral reef growth, regardless of rates of warming.

Data Availability Statement

The data used for assessing reef coral diversity and calculating coral reef volume in the study are available at the repository ZENODO (Bosellini, Benedetti, & Kiessling, 2024). The record and files are publicly available.

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