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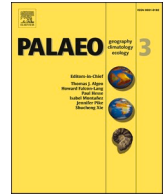
Unparallel resilience of shallow-water tropical calcifiers (foraminifera and scleractinian reef corals) during the early Paleogene global warming intervals

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ABSTRACT

Investigating the fossil record to provide evidence about the response of shallow-water tropical calcifiers to past warming events is crucial considering that they are severely threatened by current global warming. We thus focused our attention on scleractinian reef corals (SRC) and shallow-water foraminifera (SWF), both mainly symbiont-bearing organisms, analysing and comparing their diversity patterns during the Paleocene and Eocene from datasets of the Neothetyan circum-Mediterranean region. In particular, at both genus and species level, we analysed changes in diversity, together with origination and extinction rates.

Despite some biases related to biostratigraphic resolution of SRC and SWF data, our results show that they reacted differently to the major warming events of the Early Paleogene. The K/Pg mass extinction caused the disappearance of almost all SWF, whereas several corals passed this crisis and persisted up to the end of Paleocene, when the Paleocene-Eocene Thermal Maximum (PETM) caused a relatively small decrease of coral diversity together with a global collapse of coral reefs. On the other hand, a rapid radiation of nummulitids and alveolinids occurred at species level. The impact of the Early Eocene Climatic Optimum (EECO) was apparently more severe for SWF than for SRC. After the Middle Eocene Climatic Optimum (MECO), the general cooling trend led to the fading of Eocene SWF genera and species, whereas SRC began their rapid diversification from Bartonian to Priabonian and culminating in the Chattian.

Our results suggest that rapid warming events favoured speciation in SWF, whereas the slow cooling trend (e. g., after the MECO) favoured diversification of SRC. Our data also underline that SWF reacted differently to warming events as compared to deep-sea smaller benthic foraminifera and that the same events in the planktonic realm are not strictly coeval with those occurring in shallow-water environments.

On a wider perspective, we observe that shallow-water calcifiers demonstrate a good degree of resilience to global temperature increases, even if undergoing to more or less marked reduction of biodiversity. We provide evidences for the recovery of past ecosystems from both short and long stressors.

1. Introduction

Our planet has faced many global changes during geologic time, with ecosystems responding to paleoenvironmental stressors in different ways and at different speeds. Sometimes, these global events were so severe that they permanently changed the abundance and variety of marine calcifying organisms.

The last greenhouse megacycle of the Earth history peaked and started its decline during the Paleogene. In particular, the Paleocene and Eocene epochs were characterised by some major warming events such as the hyperthermal Paleocene-Eocene Thermal Maximum (PETM), the Early Eocene Climatic Optimum (EECO), and the Middle Eocene Climatic Optimum (MECO).

The PETM (e.g., Thomas and Shackleton, 1996; Schulte et al., 2013) was a ~ 170 ky-long (Zeebe and Lourens, 2019) warming event signed by a carbon cycle perturbation occurred about 56 million years ago. The average global temperature is estimated reaching 25.2 °C (Scotese et al., 2021), or even 31.6 °C according to Inglis et al. (2020); for comparison, the average global temperature during the 20th century was 13.9 °C (NOAA, 2023).

The EECO (e.g., Zachos et al., 2001; Luciani et al., 2016) was a long-lasting phase (53.3–49.1 Ma: D'Onofrio et al., 2020) occurred in the

Ypresian, with average global temperature of 25.1 °C (Scotese et al., 2021; 27.0 °C according to Inglis et al., 2020), accompanied by a marked increase of atmospheric CO_2 (Rae et al., 2021).

The MECO (e.g., Bohaty and Zachos, 2003) was a ~ 300 ky-long event of global warming occurred in the Bartonian (40.51–40.21 Ma: Rivero-Cuesta et al., 2019), with average global temperature of 23.1 °C (Scotese et al., 2021) and temporarily interrupting the general cooling trend started in the middle Eocene.

Among shallow-water calcifiers, larger foraminifera (with symbiont algae) and scleractinian reef corals (SRC; zooxanthellate) are particularly sensitive to climate changes.

Larger foraminifera are an informal group of single-celled protists, mostly with calcitic test, characterised by their inner complex morphology, consisting of different structural elements occurring in unrelated families. The larger foraminifera are usually considered as K-strategists, even if Hottinger (1999) suggested that A forms (gamonts) can be considered more opportunistic, acting more like r-strategists, whereas B forms (agamonts) are indeed more specialists (strictly K-strategists). K-strategists are favoured by stable conditions, i.e., oligotrophic environment, good illumination, constant values of salinity, pH and dissolved oxygen, and relatively high temperatures; whereas unstable conditions linked to decrease in temperature, eutrophication, high salinity, insufficient food or light, turbidity, low pH and oxygen depletion, tend to promote r-strategy.

Nummulitids, alveolinids, orthophragmines, miscellaneids, large soritids, larger conical agglutinated species, and some rotaliids (for rotaliids see also Benedetti and Papazzoni, 2022) are part of the group here considered under the name of shallow-water foraminifera (SWF), usually considered as K-strategists, having marked dimorphism and reaching remarkable size. Small-sized porcelaneous, such as most miliolids, agglutinated and hyaline taxa (several rotaliids species; see Benedetti and Papazzoni, 2022; Sinanoğlu et al., 2022; Benedetti and Sinanoğlu, 2022), are instead r-strategists lacking true or evident dimorphism and showing generally small embryonic apparatus.

Modern larger foraminifera host symbionts such as red and green algae, dinoflagellates and diatoms (e.g., Hohenegger, 2011). Dramatic environmental and temperature changes may lead to shift in symbiont organisms (Prazeres, 2018) up to loss of the symbiotic microalgae or pigments (bleaching sensu Glynn, 1996). Recent larger foraminifera species show different thermal tolerances that seem to be also dependent on their symbionts (Pinko et al., 2020).

Scleractinian reef corals are mainly colonial and thrive in shallow-water tropical settings representing the main component of modern coral reefs. The capacity of these corals to build reefs, and their survival and adaptation to climate changes, are basically controlled by photosymbiosis, a mutually relationship with zooxanthellate algae. On one hand, these endosymbiotic zooxanthellae support coral metabolism by transferring nutrients derived from photosynthesis through rapid translocation processes, allowing these corals to flourish even in nutrient-poor tropical waters. On the other hand, symbiont algae benefit from protection and moderated light conditions within coral tissues, while also receiving recycled metabolic products from the coral (Trench, 1993).

Stressors like changes in temperature, light, nutrients and also ocean acidification (Anthony et al., 2008) may lead to the breakdown of photosymbiosis, with loss of zooxanthellae (bleaching) and harmful consequences for the functioning of the entire reef ecosystem (Glynn, 1996).

The fossil record, in fact, shows that this mutualistic relationship has been crucial in the evolution of reef ecosystems since the Late Triassic period (Stanley, 1981, 1988), and that reef collapses during mass extinctions have been linked to the loss of algae, while subsequent recoveries have been associated with the renewal or recovery of the symbiotic relationship (Rosen and Turnšek, 1989; Rosen, 2000; Kiessling and Baron-Szabo, 2004; Kiessling and Kocsis, 2015). It is thus clear that the most striking effect of increasing sea water temperature is represented by the expulsion of photosymbionts (bleaching) in both SWF and SRC (e.g., Pandolfi et al., 2011; Prazeres et al., 2016), with strong influence on their diversity and survival rate.

Few papers are focused on large-scale diversity of SWF (Hottinger, 2001; Whidden and Jones, 2012; Benedetti and Papazzoni, 2022) and SRC (Kiessling and Baron-Szabo, 2004; Weiss and Martindale, 2019). In these papers the diversity of the two different groups has been analysed separately, and is usually considered as inversely correlated to climate warming (e.g., Pomar et al., 2017). In particular, Hottinger (2001) provided a detailed biodiversity analysis of both specific and generic diversity of Paleogene SWF suggesting the occurrence of phases of community maturation for K-strategists in response to the occurrence of competitors or immigrants.

Herein we aim to test the mutual resilience of this two major groups of shallow-water calcifying organisms to some climatic perturbations of the Paleocene-Eocene interval. In order to test this relationship quantitatively, we provide for the first time a comprehensive analysis of two new datasets for SRC and SWF from the Neothetyan circum-Mediterranean region, which are so far the most rich and complete for the early Paleogene.

The present research aims to contribute to understand how marine shallow-water calcifiers reacted to global stressors, such as some of the global warming intervals of the Paleogene period, and to determine how these stressors impacted on biodiversity and turnover rates.

2. Material and methods

2.1. Construction of datasets

Our work is primarily based on three main datasets produced in the last years by the research group of the Modena and Reggio Emilia University. As regards SRC of the Neotethys, the REEFCORAL dataset (Bosellini and Perrin, 2008; Perrin and Bosellini, 2012, 2013) was focused on Oligocene to Miocene epochs of the Neothetyan circum-Mediterranean region. During the last two years we produced the PalEoCoral dataset, focused on the Paleocene-Eocene interval. This new dataset groups information about scleractinian corals (mainly colonial and subordinately solitary corals) occurring in the western Neothetyan circum-Mediterranean region. The PalEoCoral dataset includes data collected from three different sources: recently published literature, data derived from study of coral collections in museums (e.g., Bosellini et al., 2022), and also from our own collections. For each occurrence, we provided a systematic attribution at least at genus rank, and possibly, when available, at species rank; all the occurrences have been systematically revised (if needed) and also geographic and stratigraphic information have been added. Finally, a symbiotic status was attributed to each genus following the approach of Perrin and Bosellini (2012). The PalEoCoral dataset currently provides information on coral occurrences from >100 localities in the Neothetyan circum-Mediterranean region. A total of 480 different colonial scleractinian species belonging to 89 genera have been identified in addition to an incomplete inventory of solitary taxa (71 species belonging to 12 genera). The obtained dataset has been also compared to that available for free in the Paleobiology database (https://paleobiodb.org/).

We focused on the Neothetyan circum-Mediterranean area because of the significant number of studies in respect to other areas, and especially because of the good biostratigraphic control given by larger foraminifera. The fossil record is inherently incomplete and the first and last occurrences of a species may depend on the lack of good (lucky) preservation of the first appearances of species in sedimentary successions. Signor-Lipps (Signor III and Lipps, 1982) and Jaanusson (1976) effects can produce delayed recoveries of first and last appearances of taxa, but we here refer simply on the first occurrence and last occurrence in the investigated basin, taking into account that some taxa can be documented before (in the Cretaceous) the investigated interval in other sedimentary basins. Moreover, the occurrence of both investigated

groups is strongly controlled by the preservation of sedimentary successions recording shallow-water environments. This could depend on both tectonic and erosional processes or even on the sampling methods and on the quality of paleontological analysis. The accumulation and preservation of shallow-water carbonate factories may depend also by pH and temperatures (e.g., Coletti et al., 2022) that influence directly the relative abundance of shallow-water calcifiers, taking also into account possible preservation biases of aragonitic vs calcitic tests. The following results and discussions derive from a huge amount of literature data that represent the consequence of more than one hundred years of paleontological investigations and we retain that the overall dataset obtained is sufficiently reliable to characterize the diversity trends of both groups. As concerns SWF, we provide a list of over 1200 species collected from selected groups of larger foraminifera (e.g., Hottinger, 1960, 1974, 2014; Drobne, 1977; Schaub, 1981; Less, 1987; Sirel and Acar, 2008; Benedetti and Papazzoni, 2022; Özcan et al., 2022) and on tens of recent scientific articles listing and illustrating benthic foraminifera (not exclusively larger foraminifera) from shallow-water environments. We started extracting data from the stratigraphic charts in Serra-Kiel et al. (1998) and from the above monographs. The taxonomy and systematics of each species has been updated by a comparison and review of recent occurrences documented by specialists from the western to easternmost Neotethys, up to Tibet and eastern India. We updated the stratigraphic distribution of each genera and species and added all the new taxa described in the last 25 years. As concerns orthophragmines, whose taxonomy is based on biometrical ranges of selected characters (e.g., Less, 1987), we took into account both chronospecies and chronosubspecies, when available (Özcan et al., 2022). The complete lists of both SWF and SRC are provided respectively in Supplementary Table 1 and Supplementary Table 2.

2.2. Ghost taxa

As recently assessed by Benedetti and Papazzoni (2022), we completed the list of our datasets with ghost taxa, i.e., those species that are still missing from the fossil record. Ghost taxa refer to hypothetical taxa (in our analysis genera or species) that are inferred to have existed based on gaps in the fossil record, but have left so far no direct fossil evidence. There are several reasons why ancient benthic organisms might not have left any fossil evidence. For example, the individuals may have been very small or fragile, or they may have lived in environments that were not favourable to fossilization, or simply they have not yet been described, or left in open nomenclature. Additionally, the fossil record is intrinsically incomplete, and many potential fossil sites have been destroyed by erosion or other geological processes. Moreover, the sampling process is patchy and discontinuous: there are some historically well-known sedimentary successions (especially in the circum-Mediterranean area) but also several sites that have never been investigated at all. A ghost species allows us to fill the gaps in the stratigraphic range of a genus due to the incompleteness of the current knowledge.

First of all, we filled the gaps in the earliest Paleocene by investigating the known stratigraphic range of both foraminiferal and coral genera, by means of literature data (mainly Baron-Szabo, 2004, 2006, 2008) and PBDB for colonial scleractinians, and atlases and monographs (e.g., Loeblich and Tappan, 1987; Hottinger, 2014) for shallow-water foraminifera, in addition to some tens of more recent articles. Then, to obtain a reliable distribution for the latest Eocene, we compared our datasets with lower Oligocene REEFCORAL (Perrin and Bosellini, 2012, 2013) for scleractinian corals, and with our own data, the scheme by Cahuzac and Poignant (1997) and other published atlases and articles for larger foraminifera. After compiling the list of species occurrences, we filled the gaps in the stratigraphic record for each species and added the ghost species, if needed, for each genus. We chose to add only one ghost taxon for each vacant time interval. This choice is supported for those foraminiferal or coral taxa that are characterised by few genera or species — or are often monospecific — as for many rotaliids (Hottinger,

2001, 2014), considering each poorly-represented group as monophyletic.

2.3. Time scale accuracy

The stratigraphic distribution of shallow-water foraminifera follows the biozonal scheme by Serra-Kiel et al. (1998) for the Paleocene-Eocene of the Neotethys. A total of 20 Shallow Benthic Zones (SBZ) is routinely recognizable for the investigated time interval, 4 for the Paleocene and 16 for the Eocene. The SBZ have been further recently recalibrated thanks to integrated works for the Paleocene (Scheibner and Speijer, 2009; Serra-Kiel et al., 2020; Papazzoni et al., 2023), early-middle Eocene (Costa et al., 2013; Silva-Casal et al., 2021; Rodriguez-Pintó et al., 2022; Benedetti et al., 2024) and middle-late Eocene (Luciani et al., 2020; Agnini et al., 2021). The Paleocene-Eocene SBZ are Oppelzones based on the concomitant occurrence of different phylogenetically unrelated taxa (e.g., Pignatti and Papazzoni, 2017), not only larger foraminifera, but their boundaries cannot be clearly constrained to the geochronological scale at the current state of knowledge. Recently Papazzoni et al. (2023) proposed a revision of Paleocene biozonation based on larger foraminiferal biohorizons instead of marker species to allow to provide chronological constraints for biozonal boundaries, calibrated by means of nannofossils biostratigraphy. Unfortunately, the biohorizons are not yet available out of the Paleocene, therefore we build our graphs putting the datum in the centre of each biozone.

As concerns the scleractinian corals, the occurrence time was binned at the stage level, although for some selected localities we have associated foraminifera that would allow us to have a biozonal resolution, in absence of more reliable and continuous constraints furnished by, often indirect, literature data. We are aware that the different time resolution of the two groups under study does not allow a perfect correlation between them but the data analysis has been made trying to maintain the maximum homogeneity when making comparisons.

2.4. Data elaboration

For each time interval (biozone or stage) we counted the total number of species and genera of both corals and foraminifera. In addition, we provided an estimation of origination and extinction rates by means of number of first (FO) and last (LO) occurrences. We excluded from the latter counts the singletons, i.e., the taxa whose stratigraphic distribution is limited to a single bin.

In addition, to obtain a more reliable estimate of diversity per each stage and biozone, we normalised the data of occurrence (FO and LO) per million years.

To provide an estimate of both origination and extinction rates, other than FO and LO, we used the equations proposed by Alroy (2008) that focus on occurrence data instead of simple range, thus removing the edge effects. These measures are called three-timer rates since they take into account the occurrences crossing the base of a bin and continuing over the top. The three-timer extinction rate is calculated as follows:

$$\mu = log\left(^2t_i/^3t\right) + log(P_s)$$

where ^2t_i are the two-timer taxa sampled immediately before and within the ith bin; ^3t are the three timer taxa occurring in three consecutive bins; P_s is calculated as $^3t/(^3t + ^Pt)$ where the part-timers ^Pt are those taxa sampled before and after, but not within a bin.

The three-timer origination rate is calculated as follows:

$$\lambda = log\left(^2t_{i+1}/^3t\right) + log(P_s)$$

where $^2t_{i+1}$ are the taxa sampled immediately after and within the ith bin.

The temporal resolution of our analysis is limited by the biozonal interval for foraminifera and by stage duration for scleractinian corals. Regarding the Ypresian, to highlight the response of reef corals to the

EECO event, we divided this interval in two bins, corresponding to the regional stages Ilerdian and Cuisian. We solve and provide a correction of the equations by dividing all the values for the time interval Δt.

Finally, the obtained curves were compared with isotopic and temperature data to see possible correlations.

3. Results

3.1. Generic and specific diversity (raw data)

The raw data of both foraminifera and corals are reported in Fig. 1.

As concerns SWF, with special emphasis on larger foraminifera, the generic radiation precedes the species-level differentiation. In particular, most of the Paleocene genera are monospecific or characterised by 2–4 species (for details about rotaliids see also Benedetti and Papazzoni, 2022). The generic radiation was very quick and started already in the late Danian, then diversity stands rather constant throughout the Paleocene. Right after the PETM, there was a rapid radiation at the species level, especially within the genera *Alveolina, Nummulites, Discocyclina, Orbitoclypeus,* and *Assilina.* These are all K-strategist taxa widely occurring in the Eocene shallow-water environments of the Neotethys. The EECO falls within two long biozonal intervals, SBZ10 and 11, characterised by the occurrence of several larger foraminifera, but possibly overestimated because of relative sampling density. In fact, lower to middle Cuisian platforms are very well-documented and investigated in the central-western Neotethys, whereas much less is known for example for the lower Ypresian interval, also known as Ilerdian in the non-standard regional stratigraphy.

As concerns the coral diversity, we record an apparent increase in diversity from the Danian to the Thanetian, taking into account that data from Selandian, i.e., middle Paleocene, are possibly incomplete and not completely reliable due to the relatively recent use of threefold subdivision of Paleocene (Speijer et al., 2020), that prevents to assign unambiguously to this stage the taxa described at least before 1989. A

slight but evident decrease is recorded at the beginning of Ypresian, after the PETM event. An increase in both genera and species is then recorded during the Ypresian, from the Ilerdian to the Cuisian, followed by a slow decline up to Bartonian, with a relatively high diversity in the Priabonian.

3.2. Generic and specific diversity (normalised data)

To obtain more comparable data, we re-calculated our data in terms of number of genera and species per million year within each biozone, to avoid biases due to the different length of the biozones. In this way, we obtained a quite different picture (Fig. 2). The first main peak in diversity of SWF is indeed documented right after the PETM, during the SBZ5 and especially in SBZ6. With normalised data, also the EECO shows a minimum in diversity, with a second peak occurring in SBZ12, right after the warming event. The last peak occurs just before the MECO, after which we assist to the final decline of most Eocene SWF.

As concerns the reproductive strategies, r-strategists were dominant only during the Danian, after the K/Pg mass extinction that caused the disappearance of almost all the major groups of Cretaceous larger foraminifera except rotaliids that, in fact, dominated the Danian shallow-water sedimentary record (e.g., Benedetti and Papazzoni, 2022; Sinanoğlu et al., 2022). After the PETM, an increase in K-strategist species is noteworthy as also documented by the rapid differentiation at species level of the genera *Alveolina* and *Nummulites* (Fig. 3). While the drop in SBZ9 could be an artefact due to the poorly-preserved sedimentary successions in the late Ilerdian, the SBZ10–11 interval, roughly coinciding with EECO, seems to record an increase of both r- and K-strategists with special regards to nummulitids, alveolinids and orthophragmines (Fig. 3). Again, normalised data suggest a quite different scenario, with a decrease at genus rank followed by a resilient response right after the Ypresian warming event. The decline of very shallow water groups, such as rotaliids and alveolinids is concluded in the late Eocene. Nummulitids and orthophragmines, that thrived in deeper
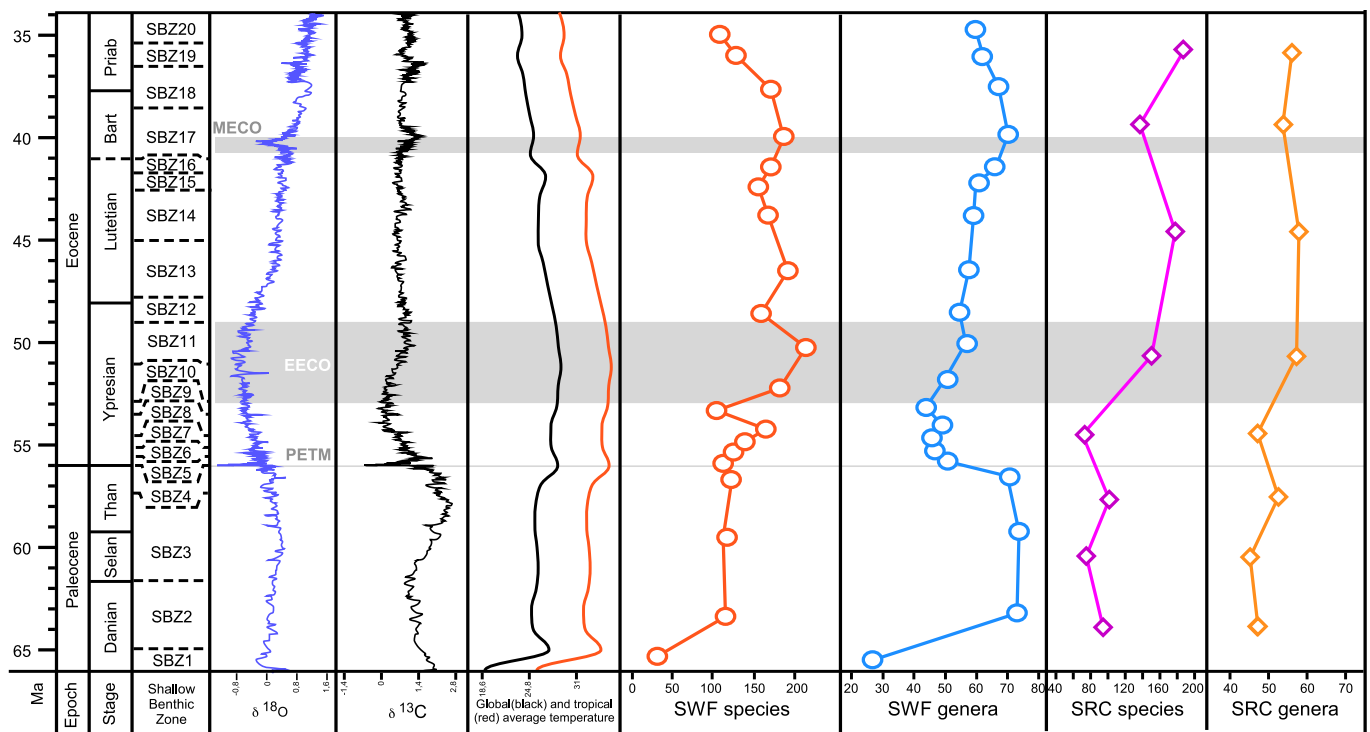

Fig. 1. Generic and specific diversity in shallow-water foraminifera (SWF) and scleractinian reef corals (SRC) through the Paleocene and Eocene epochs, according to our datasets. Shallow benthic zones after Serra-Kiel et al. (1998) with modification (see text); oxygen and carbon curves after Cramer et al. (2009), global temperatures after Scotese et al. (2021).
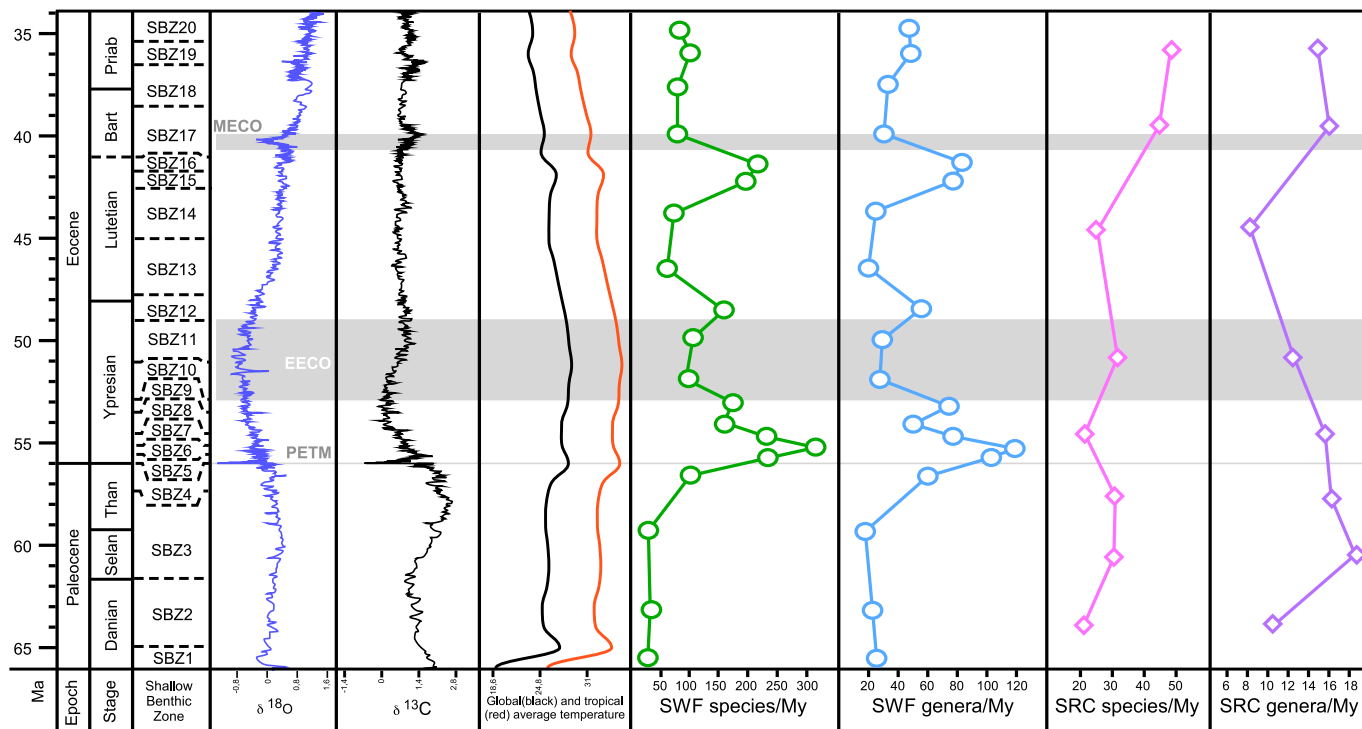
Fig. 2. Generic and specific diversity in SWF and SRC, normalised per million years.
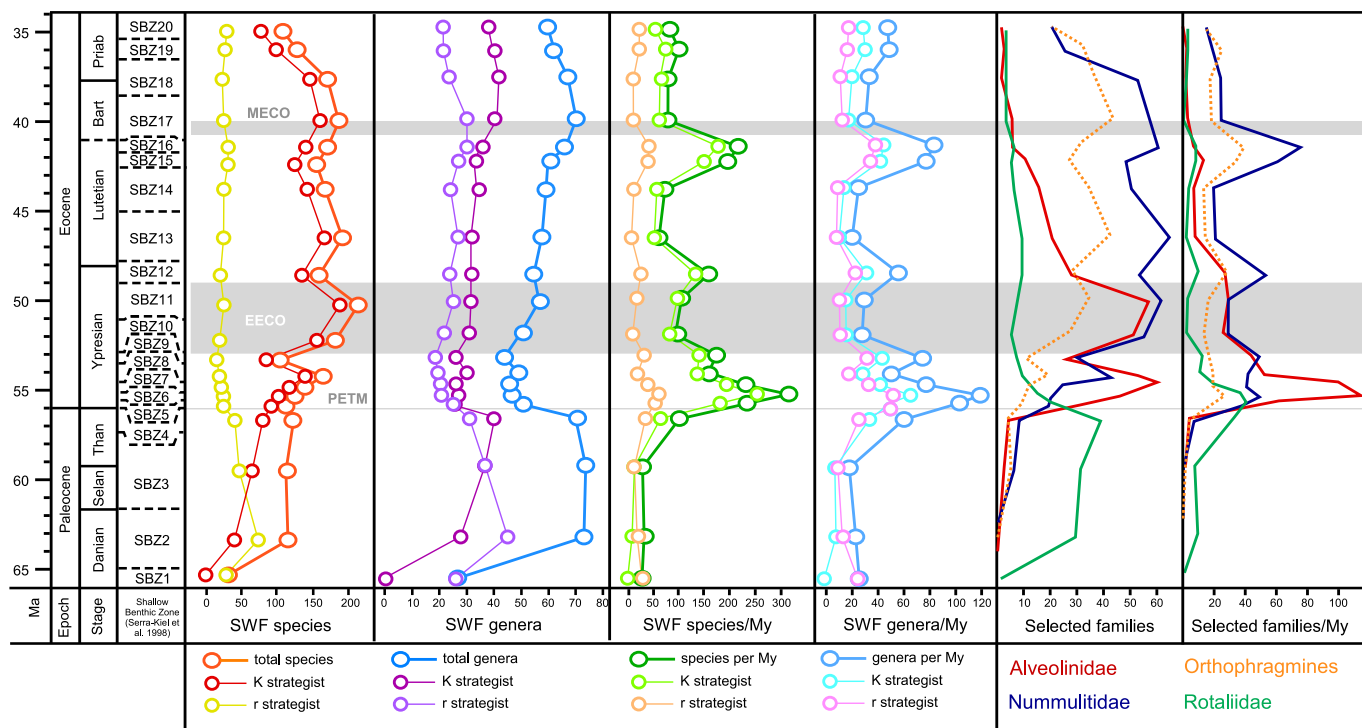

Fig. 3. Generic and specific diversity of K-strategist and r-strategist SWF through the Paleocene and Eocene; data raw and normalised per million years. The distributions of the families Alveolinidae, Nummulitidae, orthophragmines (Discocyclinidae + Orbitoclypeidae), and Rotaliidae are also given.

environments, show a very similar trend. This suggests that SWF biodiversity is not controlled by water depth or local changes, rather it depends on global events.

As regards corals, looking at the normalised data (Fig. 2) the increase in both genera and species from Danian to Thanetian is more marked, as it appears also for the decline of generic diversity in the Ypresian and

Lutetian. The species number apparently shows a peak during the EECO, then it underwent a decrease during the Lutetian followed by a new increase up to the Priabonian. Faunal turnovers are evident at the Paleocene/Eocene transition and at the end of Eocene. A genus-level radiation is apparent in the Bartonian.

3.3. Origination and extinction rates

First and last occurrences in SWF show, as expected, inverse patterns, especially from the late Paleocene upwards. Raw data (Fig. 4) suggest a first radiation of shallow-water foraminifera in the late Danian SBZ2, but normalised data per million years evidence an extremely rapid radiation after the PETM, mainly due to the sudden bloom of species belonging to genera *Alveolina* and *Nummulites* and subordinately to orthophragmines. A second peak in new occurrences is then documented in SBZ10, followed by an important increase in last occurrences in SBZ11, during the EECO. The three timers origination and extinction rates (Fig. 5) are mostly consistent with FO and LO. Major originations are recorded in the late Danian, after the PETM, in the lower Cuisian SBZ10 (initial EECO interval), after the EECO, and possibly after the MECO (from raw data, not visible from normalised data, Fig. 4) and at the end of the Eocene. Extinctions are usually diachronous in respect to originations, and they occur mainly at the end of Paleocene, in the lower Ilerdian SBZ6, when some taxa that passing the PETM got extinct also in the eastern Neotethys (e.g., Zhang et al., 2013; Kamran et al., 2021b; Benedetti and Papazzoni, 2022). Two new extinction events are then recorded just before and after the EECO interval, before the MECO, and before the final dramatic extinction of several Eocene species at the Eocene-Oligocene transition.

The origination rate for SRC shows a decrease from the Danian up to the Thanetian where a peak in number of extinct taxa is evident (Fig. 5C-D). Our data cannot permit us to evaluate the importance of the PETM on the coral communities, but an inverse relationship between origination and extinction trends is noteworthy in the Ypresian and Lutetian intervals. The Bartonian is characterised by a relatively low rate of both originations and extinctions, whereas at the end of Priabonian most Eocene species become extinct and new species did their first appearance (Fig. 5C-D).

The temporal diversity distributions of foraminifera and corals here investigated prevent a direct correlation between the two taxonomic groups, so we decided to lump diversity data at the stage level also for the foraminifera (Fig. 6). The obtained curves (Fig. 6C) show a similar

trend up to Bartonian when, possibly due to a different response to the MECO, aragonitic corals and calcitic foraminifera diversities diverge. Origination rates are quite comparable up to the Lutetian (Fig. 6A-B), then they diverge considerably (Kendall's tau = 0.24, $p = 0.45$), while extinction rate curves clearly diverge only in the Selandian and Ypresian (Kendall's tau = 0.62, $p = 0.05$).

4. Discussion

4.1. Aftermaths of the K-Pg crisis

Shallow-water foraminifera suffered a dramatic turnover with the extinction of the K-strategists at the end of the Maastrichtian (e.g., Hottinger, 2001). Very few larger foraminifera passed the K/Pg boundary and, among them, *Laffitteina* disappeared without leaving descendants during the Paleocene, in the lower Thanetian (e.g., Benedetti and Papazzoni, 2022), resulting a "dead clade walking" sensu Jablonski (2002). Hottinger (2001) suggested that, after the K/Pg boundary event, practically no K-strategists occurred for a long interval estimated to be at least 4 million years (the number of 8–10 million years mentioned in the text is clearly wrong, because the SBZ1, depicted in his fig. 17, is clearly shorter than the whole Paleocene). However, the recent recalibration of Paleocene SBZ (Serra-Kiel et al., 2020) and the new proposal by Papazzoni et al. (2023), together with the increasing description of new assemblages (e.g., Sinanoğlu et al., 2022) allow us to underline a more rapid recovery, started around 2 million years (or even less, ~1.2–1.5 My according to Serra-Kiel et al., 2020 and Papazzoni et al., 2023, respectively) of shallow-water foraminiferal communities after K/Pg in respect to what has been previously retained (e.g., Hottinger, 2001). This rise culminated right after the PETM, about 10 million years after K/Pg (Fig. 3). We also notice that the K/Pg mass extinction apparently did not affect the deep water benthic foraminifera, especially agglutinated taxa, that are mostly cosmopolitan and persist in the Paleogene (e.g., Kaminski and Gradstein, 2005) with time of recovery varying from 200 kyr to 400 kyr (Alegret and Thomas, 2004; Alegret et al., 2004).
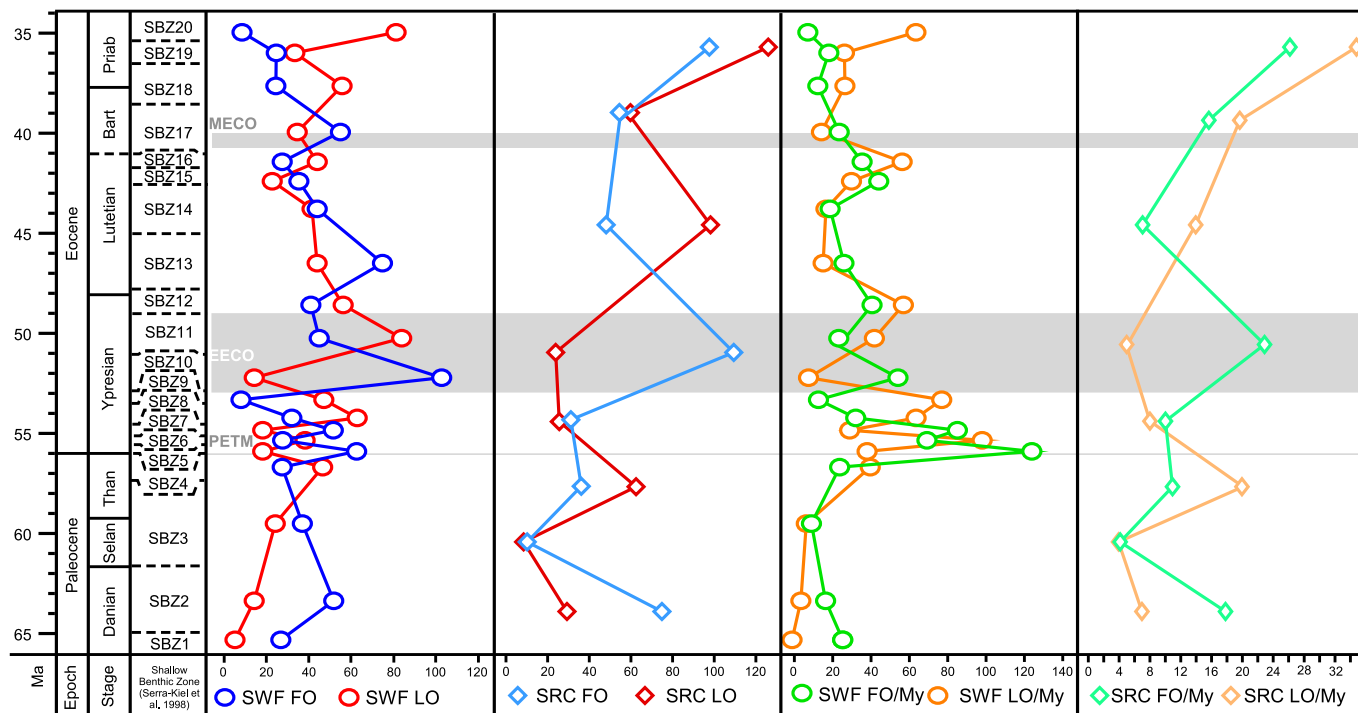

Fig. 4. Estimation of origination and extinction rates (species level) for SWF and SRC by means of number of FO and LO per each biozone (SWF) and stage (SRC); raw data and normalised per million years.
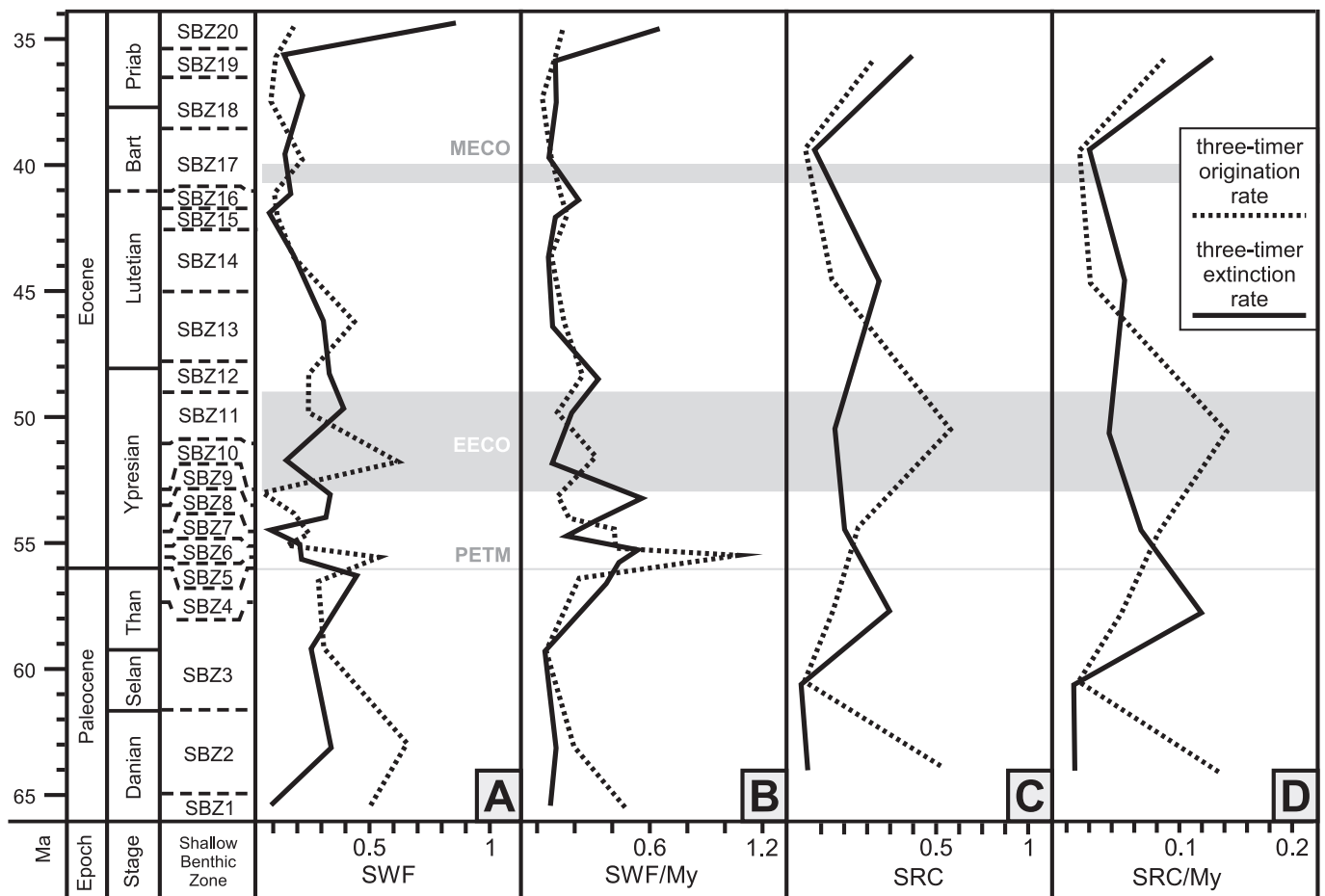
Fig. 5. Three-timer estimates of origination (dashed line) and extinction (continuous line) rates according to the equation by Alroy (2008) of A. SWF, B. SWF per million years; C. SRC, D. SRC per million years.

Among SRC, only a few species belonging to typical Mesozoic genera survived the mass extinction of the end-Cretaceous, but later on they got extinct either during the late Paleocene or at the PETM (e.g., Kiessling and Baron-Szabo, 2004; Baron-Szabo, 2008).

4.2. Paleocene and PETM

The bioconstruction power of SRC was not relevant throughout the Paleogene: the Paleocene-Eocene epochs are characterised by the scarcity or absence of extensive coral buildups (Pomar et al., 2017), even if some limited examples have been recorded, among which the lower Eocene Monte Postale buildups (Vescogni et al., 2016); shallow-water settings were then mostly dominated by calcareous algae and larger foraminifera, often linked to seagrass meadows (Tomassetti et al., 2016; Benedetti, 2018; Sinanoğlu et al., 2022). Due to its complexity, the topic of coral reef crises is not covered here: a separate, in-depth exploration is forthcoming. Here, we only remark that Kiessling and Simpson (2011) pointed out that reef crises and biodiversity crises were not always contemporaries.

At the very end of the Paleocene, the abrupt increase in temperature marked by a drop in δ^{18}O and δ^{13}C caused dramatic changes in shallow-water settings. Most of the well-known shallow-water sedimentary successions recording the onset of PETM are located in the eastern Neotethys, such as Tibet (e.g., Zhang et al., 2013, 2019; Jiang et al., 2021), India (Sarkar et al., 2022), Pakistan (Kamran et al., 2021b; Ali et al., 2024), while less is know from the central-western part with sections investigated in Egypt (Scheibner et al., 2005; Scheibner and Speijer, 2009) and Pyrenean basin, Spain (Scheibner et al., 2007; Pujalte

et al., 2009). Despite the few works dedicated to the PETM, the Paleocene-Eocene SWF are well-documented also from Turkey (e.g., Sirel and Acar, 2008) and Italy (e.g., Papazzoni et al., 2023).

Weiss and Martindale (2019) documented few changes in both specific and generic diversity of scleractinian corals passing from the Paleocene to the Eocene, with differences linked only to substantial ecological changes. On the contrary, our data clearly evidence a change in diversity both at genus and species ranks. The decreases in corals at the P/E boundary has been generally linked to the change in global conditions such as the rise in temperature and the ocean acidification which affect mainly aragonitic corals (Pomar et al., 2017).

In Fig. 7 we provide a synthetic diagram of our data showing the diversity, origination, and extinction rates of both analysed groups in response to the major global warming occurring close to the Paleocene-Eocene boundary. An unparallel variation in normalised diversity is clearly recorded for the investigated taxonomic groups across the PETM (Figs. 2, 7).

It is here evident that the extinction of the K-strategist larger foraminiferal typical of Paleocene such as miscellaneids and most rotaliids (Hottinger, 2001; Scheibner and Speijer, 2008; Benedetti and Papazzoni, 2022) was also affected by the PETM event. Our data (Fig. 2 and Fig. 5B) evidence a very high origination rate in foraminiferal species occurring in the lower Ilerdian (lowermost Ypresian) SBZ5, roughly coincident with the PETM.

As concerns SRF, it seems that the origination rate is more or less constant, whereas the extinction rate, which is maximum at the end of Paleocene, attains lower values in the lower Ypresian (Fig. 4).
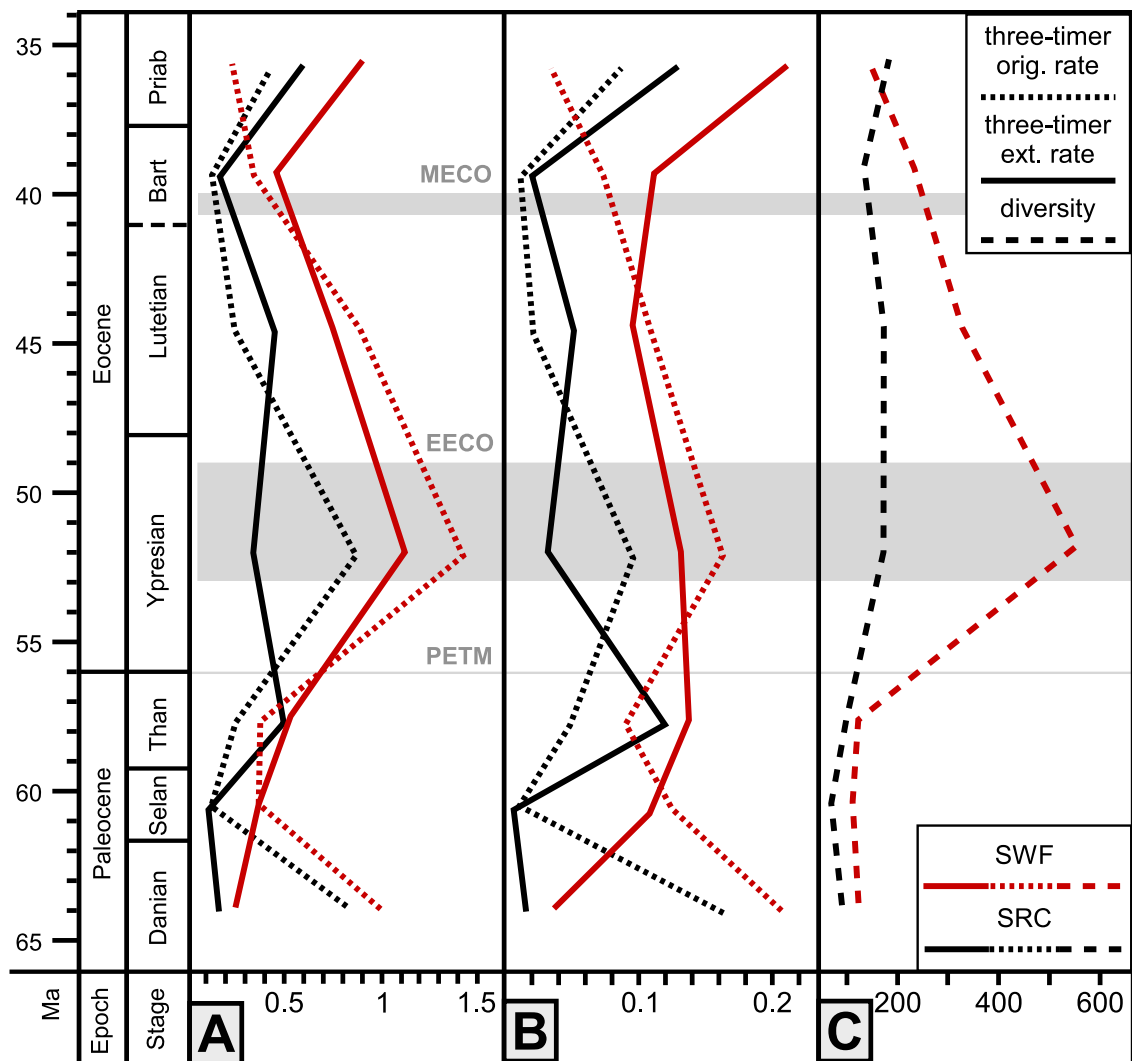
Fig. 6. Comparison at the same scale resolution of SRC (black lines) and SWF (red lines). A. Three-timer estimates of origination (dashed line) and extinction (continuous line) rates according to the equation by Alroy (2008); B. corrected origination (dashed line) and extinction (continuous line) rates per stage duration; C. number of species per stage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. Early Eocene (EECO)

The early Eocene interval is indeed characterised by the absence of relevant coral buildups (Pomar et al., 2017; Bosellini et al., 2022); the Ilerdian (i.e., early Ypresian) carbonate platforms were mostly dominated by nummulitids and alveolinids (Fig. 3) that flourished after the PETM (Turnšek and Košir, 2004). Anyway, the few coral patch reefs from Ilerdian (i.e., lower Ypresian: Eichenseer and Luterbacher, 1992; Plaziat and Perrin, 1992; Košir, 1997) and Cuisian (i.e., upper Ypresian: Zamagni et al., 2012; Vescogni et al., 2016; Bosellini et al., 2020, 2022), were overwhelmed by foraminiferal shoals dominated by alveolinids and nummulitids, which are relatively abundant in the whole Ypresian up to the middle Bartonian (Fig. 3). In fact, during the EECO, in the lower-middle Cuisian, the Neothetyan basins were mainly characterised by larger foraminiferal-dominated ramps (e.g., Ćosović et al., 2004; Di Carlo et al., 2010; Benedetti, 2018). Despite the absence of extensive coral buildups during the whole Ypresian, we here report a very high diversity at both genus and species levels with a total of 170 species documented in literature belonging to 61 genera, most of which derived from recent revision of museum collections of Friuli (Italy, Bosellini et al., 2022) and our own unpublished data from northern Italy. Similarly, the apex of larger foraminifera has been generally reported as coincident with the EECO SBZ10–11 (Hallock and Pomar, 2008;

Hottinger, 2001), i.e., with the highest temperatures and pCO$_2$ values. Our data suggest that this is an artefact, partly due to the abundance of shallow-water deposits, providing the chance to identify and recognize several species, and partly due to the length of the SBZ10 and 11, which are the longest biozones in the Ypresian: in fact, normalising the data per million years the results are quite different (Fig. 3; see also Whidden and Jones, 2012), with the maximum diversity at the beginning of the Eocene and a second peak in the upper Lutetian.

If the PETM represented an abrupt interruption of oligotrophic conditions, leading to a dramatic larger foraminiferal turnover, the long-standing oligotrophic interval of EECO seems twofold (Figs. 4, 5B): at first, the number of FO overwhelm the LO, as in the PETM, then the opposite occurred, with a negative effect on diversity. Possibly, the persistence of stable conditions did not favour the originations while the background extinction rate was more or less constant. The time resolution of our data cannot give us further elements for a more detailed explanation.

We know that, generally speaking, oligotrophic conditions favour diversity of shallow-water symbiont-bearing biota such as larger foraminifera (Hallock and Schlager, 1986; Beavington-Penney and Racey, 2004), and possibly also their radiation, but their specialisation implies disadvantages in terms of response to rapid environmental changes or extreme conditions (e.g., Hallock and Schlager, 1986).

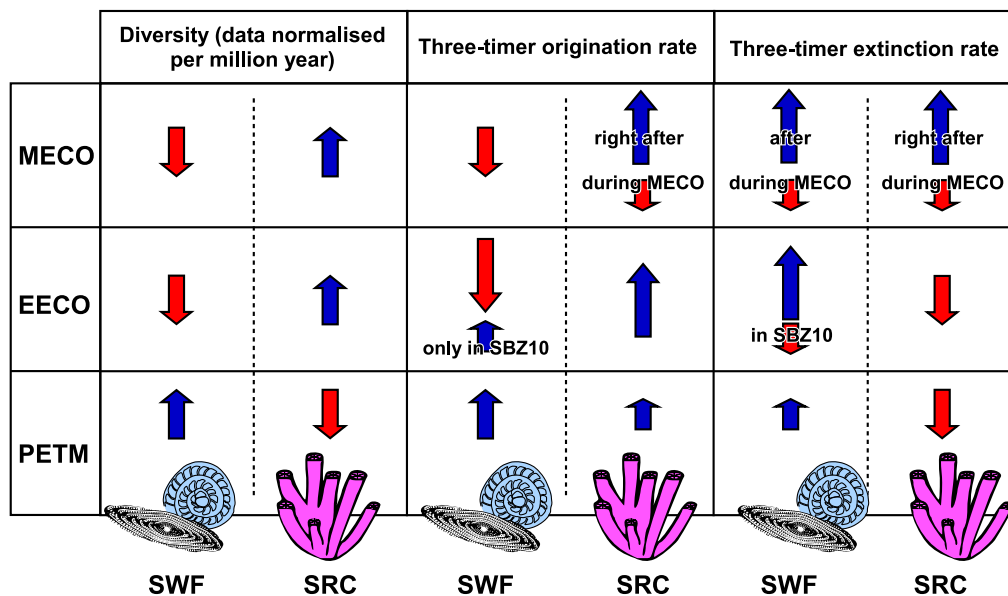|	Diversity (data normalised per million year)		Three-timer origination rate		Three-timer extinction rate	
MECO	↓	↑	↓	right after ↑ / during MECO ↓	after ↑ / during MECO ↓	right after ↑ / during MECO ↓
EECO	↓	↑	↓	↑ only in SBZ10	↑ in SBZ10 ↓	↓
PETM	↑	↓	↑	↑	↑	↓
	SWF	SRC	SWF	SRC	SWF	SRC

Fig. 7. Summary of the response of SWF and SRC to the major global warming events occurring in the Paleocene-Eocene interval. Blue arrow indicates increase, while the red one points to decrease. The length of arrows is roughly proportional to the strength of trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Both investigated groups show resilience to the warming phases, expressed by changing their strategies after a rapid recovery in diversification after EECO, as documented by dedicated works and not detectable from the herein discussed data (Bosellini et al., 2022; Benedetti et al., 2024).

Oligotrophic conditions seem to enhance asexual reproduction, which is advantageous to maintain the symbionts borne by the mother cell in the offspring. However, studies on recent *Marginopora* suggest that asexual reproduction could be drastically reduced under increase in temperature and water acidification (Reymond et al., 2022). The data here presented cannot solve this issue, even if some examples of nummulite banks from different parts of the Eocene show drastically reduced A/B ratios (Papazzoni and Seddighi, 2018; Kövecsi et al., 2022) suggesting some possible effects of high temperatures on the reproduction in the genus *Nummulites*. Nobody tried to connect the temporal distribution of nummulite banks with climate and temperature changes; however, we can notice that they are apparently confined to the Eocene and several examples are from the lower Eocene (possibly EECO) and upper middle Eocene (Bartonian: possibly MECO).

According to Weiss and Martindale (2019) zooxanthellate corals (z-corals) suffered more than taxa without symbionts in the high-temperature early Eocene interval. However, our raw and normalised data (Figs. 1–2) show a significant decrease of both species and genus diversity in the lower Ypresian and later in the Lutetian, even taking into account that our PalEoCoral dataset comprises several as yet unpublished data on both Ypresian and Lutetian corals from Friuli and Veneto (Italy).

Hottinger (2001) showed a maximum specific diversity in larger foraminifera occurring in SBZ12, during the cooling phase just following the EECO. Our raw data (Fig. 1) appear in contrast with those of Hottinger (2001), since species diversity is apparently higher in SBZ11. However, our normalised data suggest the occurrence of a (minor) peak in diversity in SBZ12, although the maximum is recorded in SBZ6 (right after the PETM), with a slightly lower peak in SBZ16. The highest value of diversity is clearly linked to the rapid differentiation at specific level of *Nummulites* and *Alveolina* radiating from ancestors rooted in SBZ5, right after the PETM.

Pinko et al. (2020) found that, among larger foraminifera, holobionts decrease their life functions and calcification power under warming conditions, but that the calcification drops more drastically in hyaline

taxa such as recent *Amphistegina* rather than in porcelaneous taxa such as *Sorites*. Similarly, during the EECO we recorded an increase in the total number of *Alveolina* species (see also Drobne et al., 2011) and a reduction of rotaliids when compared to the Ilerdian (see also Benedetti and Papazzoni, 2022).

Pomar et al. (2017) postulated an inverse correlation between corals and larger foraminifera, with a warm climate favouring calcitic larger foraminifera in calm, extremely clear and oligotrophic conditions. Accordingly, the cooling should promote increased turbulence and higher levels of dissolved nutrients also in the former relatively oligotrophic surface waters, thus favouring sessile, colonial, aragonite-producing corals (Pomar et al., 2017).

Indeed, our data do not support these statements, because during EECO (Figs. 2, 7) SWF suffered a decrease in diversity, probably related to the long-standing high temperatures and possibly also to the acidification of water given by the increasing pCO_2. In fact, the elevated pCO_2 levels reached during EECO (>1100 ppm according to Westerhold et al., 2020, up to 2000 ppm in Rae et al., 2021), associated with decreasing pH values, possibly affected the calcification of both porcelaneous and hyaline larger foraminifera (Kawahata et al., 2019; Dämmer et al., 2023), with sea-surface temperature 12 °C warmer than at present (Westerhold et al., 2020; Rae et al., 2021). This reaction to global warming may have led to variation in life cycles up to a significant loss in biodiversity. At the same time, SRC underwent a differentiation at species rank and a decrease at genus rank (Fig. 2). We underline that several species and genera persisted during the long-lasting warming interval and rapidly diversified right after the return to less extreme conditions.

The origination rates for the two groups diverge significantly (Fig. 7). In SWF, the rate slowly rises in SBZ10, dips through the end of EECO, and then increases after the end of the warming event (Fig. 5). In contrast, SRC show a steady rise from the Ilerdian to the late Ypresian, followed by a sharp decline in the Lutetian. Furthermore, extinction rates exhibit contrasting trends. Specifically, SCR show low extinction rates during the EECO, while SWF extinctions increase steadily from the beginning to the end of the warming event (Figs. 5, 7).

4.4. Middle-late Eocene (MECO)

During Lutetian (Bosellini et al., 2022; Benedetti et al., 2024; Pomar

et al., 2017) and Bartonian (Pavlovec, 1959; Álvarez-Pérez et al., 2001; Serra-Kiel et al., 2003; Astibia et al., 2016), corals are usually found together with abundant SWF. Sedimentary shallow-water successions spanning through the MECO are widespread in the whole peri-Mediterranean area (Less and Özcan, 2012), with recent descriptions of sections from northwestern Italy (Brandano and Tomassetti, 2022; Gandolfi et al., 2023) and Pakistan (Kamran et al., 2021a).

During the middle Eocene, coral reefs started to become more common up to the Bartonian (e.g., Kiessling, 2002) when, roughly corresponding with the MECO, the larger foraminifera reached a maximum in size of their B forms (e.g., Hottinger, 2001), possibly testifying the increase in frequency of asexual reproduction, because the gamont delayed their reproduction (see above). The SWF biodiversity underwent a significant decrease (with the exception of the upper Lutetian), whereas SRC showed a relatively steady increase (Fig. 2). During the MECO (Fig. 7), both groups exhibit similar patterns in extinction rates, characterised by a general decline followed by an increase (Figs. 5, 7). The main difference is in the origination rate of SWF, which is in this interval constantly low. After the Bartonian, a marked decline in K-strategists larger foraminifera preluded to the final turnover at the end of the Eocene. The calcification of foraminiferal calcitic tests suffered also during MECO, with level of pCO_2 higher than 700 ppm (Westerhold et al., 2020; Rae et al., 2021) and mean seawater temperature 10 °C warmer than present. These values affected more intensely the porcelaneous tests, as documented by the disappearance of *Alveolina*, in comparison with hyaline taxa, such as nummulitids, that survived up to the Oligocene. We know that porcelaneous foraminifera are more sensitive to dissolution with elevated pCO_2 as compared to hyaline tests, which appear to be more resilient (Kawahata et al., 2019; Bassi et al., 2024).

The post-MECO cooling led to a deep crisis in the larger foraminiferal diversity, with the extinction of large *Nummulites* and of the whole genus *Alveolina* and the rising of small nummulitids and newcomers as *Pellatispira*. McGowran (2012) suggested this crisis is due to the general spreading of eutrophic conditions in shallow-water environments.

After the MECO we record a divergent trend, with some widespread groups of larger foraminifera becoming extinct well before (*Alveolina*, large *Nummulites* and *Assilina*) or close to the end of the Eocene (orthophragmines, i.e., Discocyclinidae and Orbitoclypeidae), and scleractinian corals started an important diversification up to the Oligocene.

During Priabonian, true, modern-like coral reefs were still missing (e. g., Lombardini, 1921; Russo, 1979; Taberner and Bosence, 1993; Bosellini, 1998; Bosellini and Papazzoni, 2003; Álvarez-Pérez and Busquets, 2012; Morsilli et al., 2012), but the raw number of SRC is the highest of the whole Paleocene-Eocene interval.

To summarize, the paleoenvironments up to the end of the middle Eocene were apparently optimal for K-strategists (Hallock et al., 1991); the middle to late Eocene is characterised by the proliferation of temperate and opportunistic taxa indicating a gradual loss of oligotrophic habitats within the euphotic zone.

4.5. Global warming events and their impact on larger foraminifera and corals

The larger foraminiferal evolution seems to be mostly driven by warming events (Whidden and Jones, 2012), and also their size and growth may be possibly linked to the rise in temperature. Hottinger (2001) suggested that the disappearance of largest-sized taxa at the end of middle Eocene is not related to major environmental changes but exclusively consequence of biotic processes, such as competition, symbiotic relationships, or some kind of genetic trouble derived by repeated asexual reproduction.

Large microspheric forms of *Nummulites,* showing multispiral growth, have been firstly documented during EECO (Ferràndez-Cañadell, 2012), whereas their maximum test size and abundances have been recorded in SBZ17, possibly related to the MECO. Ferràndez-Cañadell (2012) speculated about a possible relationship between warm events and gigantism in larger foraminifera. We can notice also the occurrence of the gigantic (diameter 8–10 cm) *Eulepidina elephantina* (Lemoine and Douvillé, 1904) during Chattian, possibly related to the Late Oligocene Warming Event, LOWE and the 5 cm-long *Alveolina levantina* Hottinger, 1960 during the EECO. According to Hottinger (2001) large-sized individuals, by being exposed for a long period of time (i.e., years) to the environmental conditions, underwent high levels of adaptive pressure. Therefore, sexual reproduction is favoured when high genetic variability provides advantages.

As regards size increase, Ferràndez-Cañadell (2012) assumed a quite fast growth rate enhanced by multispiral growth, anyway indicating a lifespan of "less than 6 years" which is indeed an indication of delayed asexual reproduction possibly related to somewhat stressed conditions. The larger tests could host more symbionts even under harsh environmental conditions, and according to recent experimental results some larger foraminifera could be even favoured in calcification by quite high levels of pCO_2 (Dämmer et al., 2023), contrary to what measured on other benthic foraminifera under heat stress (Titelboim et al., 2021).

Symbiont-bearing shallow-water biota can survive to the loss of symbionts during bleaching events, but afterwards they require some time to undergo to sexual reproduction, waiting for collecting new symbionts. Thus, we argue that the possible increase in number of bleaching events linked to global warming tends to favour asexual vs. sexual reproduction and contemporary a decrease in frequency of asexual reproduction occurs. This could lead to an evolutionary stasis of symbiont-bearing taxa during global warming phases, thus explaining the occurrence of long-ranging species recorded especially during the EECO. In fact, as concerns larger foraminifera, life-cycle flexibility may offer a selective advantage under unstable conditions (Hallock and Reymond, 2022), but global warming and ocean acidification scenarios, linked to the increase of pCO_2 contribute to decrease the fecundity, and also asexual reproduction (Reymond et al., 2022).

Under stressed conditions, asexual reproduction, whether agamogeny or schizogeny, has the important advantages to sustain the population by quickly producing large-sized embryos developed directly from the parent cytoplasm and to allow the immediate transfer of algal symbionts from the parent cell to the offspring (Hallock and Reymond, 2022). The increase of asexual reproduction during global warming could be also responsible for the slight increase in r-strategists roughly coinciding with EECO and MECO (Fig. 3).

Our data confirm that, generally speaking, the SRC were negatively affected by periods of high temperatures and high pCO_2, as already pointed out by Pomar et al. (2017). In particular, the EECO shows high rates of extinction among SRC, whereas the general cooling towards the end of the Eocene is marking the recovery of coral diversity by increasing the origination rates. Unfortunately, the time resolution for corals is not high as it is for foraminifera, hampering a really detailed reconstruction of what happened during the warming episodes.

5. Conclusions

Symbiont-bearing shallow-water taxa appear sensitive to change in water temperature, as underlined by the modern observations of the bleaching phenomenon. With our work on a quite large database, we here document a different, long-lasting response to major climate changes occurred in geological time.

We can summarize their response to the major global warming events of the Paleocene-Eocene as follows:

(1) the hyperthermal PETM lead to the decrease of corals diversity, that drops in the lower Ypresian, while, as concerns SWF, caused a spectacular evolutionary radiation of nummulitids and alveolinids at species level. Unfortunately, the time resolution for SRC

(Figs. 5 and 6) does not allow us to resolve clearly the effects of the PETM on this group.

(2) The EECO, characterised by high temperature and especially high pCO$_2$ values, initially affected both corals and larger foraminifera in terms of decreasing diversity and quite high extinction rate, even if followed by a quick recovery as the new cooling phase started. In particular, our unpublished data from the revision of museum collections reveal that the SCR diversity has been usually underestimated since their number increases in the upper part of global warming and in the following interval.

(3) The MECO event had opposite effects on SWF and SRC, leading to a significant reduction in SWF diversity due to their low origination rates and increasing extinction rates.

The final crisis of the Eocene larger foraminiferal genera, with only a few species reaching the late Eocene is again due to a decrease in origination rates (Figs. 6, 7). In the meantime, especially during Bartonian and Priabonian, scleractinian corals increased their origination rate (Figs. 6, 7) and started their rapid diversification, culminating in the Chattian in the Mediterranean area.

Apparently, the larger foraminifera are a resilient group of calcifiers in the modern ocean with a good flexibility in the host-symbionts relationship and persistence under varying conditions with quite high tolerance to episodic thermal stresses. Our study confirms their resilience in surviving to warming events (even with slightly reduced and standing diversity) and differentiating rapidly right after the event.

Thus, we may conclude that shallow water organism such as foraminifera and colonial reef corals show a parallel reaction under long-lasting stress conditions and ocean acidification, whereas under relatively rapid changes they show unparallel response: in particular, rapid and intense warming events (e.g., the PETM) seem to favour larger foraminifera, whereas the long-lasting cooling trends seem to favour scleractinian corals. Moreover, our data suggest that shallow-water foraminifera show a different response to warming events with respect to deep-sea benthic foraminifera, displaying a decrease in diversity during warming events, under stressed conditions (Arreguín-Rodríguez et al., 2022).

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CRediT authorship contribution statement

Andrea Benedetti: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Cesare A. Papazzoni:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Francesca R. Bosellini:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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