**Contrasting response of the calcareous nannoplankton communities after the Eocene
hyperthermal events in the tropical Atlantic Ocean**

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1. Introduction

Superimposed on the long-term global warming from the late Paleocene through early Eocene were a series of hyperthermal events (Thomas and Zachos, 2000), among which, in descending magnitude, are the Paleocene–Eocene Thermal Maximum (PETM; 55.93 Ma), the Eocene Thermal Maximum 2 (ETM2, 54.02 Ma) and the slightly younger H2 event (54.01 Ma). These intervals appear to have been geologically brief episodes characterized by significant Earth surface warming, massive carbon input to the ocean-atmosphere system, and pronounced environmental change (see McInerney and Wing, 2011 for a review). As such, these hyperthermals share key biogeochemical characteristics with current anthropogenic global warming caused by light-carbon release from the burning of fossil fuels (Hönisch et al., 2012), and provides a possible blueprint for assessing the future impact of modern global warming on the Earth’s ecosystem.

The PETM is characterized by a >3.5‰ negative carbon isotope excursion (CIE) in global marine and continental records (e.g., McInerney and Wing, 2011). This CIE implies a massive introduction of over 3×10^{18} g ^{13}C -depleted carbon and a fundamental perturbation to the atmosphere and ocean systems (Dickens et al., 1997; Panchuk et al., 2008; Zeebe et al., 2009). The resulting abrupt global warming heated the surface ocean by ~5–9 °C and the deep sea by ~4–5 °C at all latitudes (Kennett and Stott, 1991; Zachos et al., 2003; Tripathi and Elderfield, 2004; Sluijs et al., 2006; Aze et al., 2014; Hollis et al., 2015), and triggered

significant changes in marine and terrestrial ecosystems (e.g., Kennett and Stott, 1991; Kelly et al., 1996; Wing and Harrington, 2001; Penman et al., 2014; Stassen et al., 2015). The relatively mild ETM2 and H2 events involved smaller amounts of carbon release and consequently resulted in less severe environmental changes associated with 3-5°C and 2°C of warming, respectively (Lourens et al., 2005; Sluijs et al., 2009; Stap et al., 2010). The PETM perturbation caused significant population changes in calcareous nannoplankton communities in both deep ocean and nearshore settings (e.g., Bralower, 2002; Gibbs et al., 2006; Jiang and Wise, 2006; Bown and Pearson, 2009; Raffi et al., 2009). Previous studies have discovered that there existed a scaled biotic response (e.g., extinction and calcification) of marine calcifiers to the amount of carbon released during various-magnitude hyperthermal events (Gibbs et al., 2012; Foster et al., 2013). This suggests that biotic response can be used to predict how ecosystems respond to larger perturbations and highlights the need to further explore the population change across each environmental perturbation (Norris et al., 2013). In particular, these successive environmental perturbations of varying magnitude provide a unique opportunity to gauge the resilience of the marine ecosystem regarding light carbon tolerance.

Here we quantitatively document and compare temporal population changes in calcareous nannofossil assemblages from one of the most complete and expanded, low-latitude PETM, ETM2 and H2 sections in the tropical Atlantic (Fig. 1). We attempt to 1) demonstrate in detail how marine primary producers responded to global warming in a tropical setting; and

2) explore the response of the tropical surface marine ecosystem under varying-magnitude warming events. This study provides ancient analogs for assessing the ecological consequences of modern ongoing global warming.

2. Materials and Methods

The ETM2 and H2 records were obtained from Ocean Drilling Program (ODP) Site 1258 (paleodepth ~2000 m), and the PETM records from adjacent Sites 1259 and 1260 (paleodepth ~1500 and 1700 m, respectively). These three sites, drilled during ODP Leg 207 in 2003, lie in 3192.2 m, 2354 m and 2549 m of water depth, respectively, in the western equatorial Atlantic (Fig. 1). The PETM, ETM2 and H2 intervals were identified based on the magnitude and stratigraphic position of the CIE as universally accepted.

Fifty-four samples bracketing the ETM2 and H2 events were taken from Core 1258B-14R. Each sample was assigned an orbital age via interpolation based on the high-resolution Fe cyclostratigraphy by Westerhold and Röhl (2009). Sample spacing varied depending on sample availability and proximity to the magnetic susceptibility spike that approximates the CIE; it was generally ~10 cm close to the events and 20-30 cm farther away, temporally equivalent to about 4-10 ka. Calcareous nannofossils were prepared following the modified “glass beads” method (Okada, 1992; Jiang and Wise, 2009) that allows random counts to be converted into absolute coccolith numbers per g of sediments, and their identification

followed the commonly used taxonomy in Perch-Nielsen (1985) and Bown (1998). No mechanical settling or concentration was applied and two slides were made for each sample to ensure better representation of the original fossil assemblages. Specimens representing more than half of a complete fossil were identified and counted under a Zeiss Axiophot II microscope (Florida State University, Tallahassee, USA) at 1000x magnification from fields of view with materials evenly distributed. Counting continued until the following three thresholds were reached: 1) >400 specimens were tallied; 2) >150 glass beads were counted; and 3) specimens were counted from within ≥ 20 fields of view randomly selected from the two slides. The preservation state of a fossil assemblage was quantified using the ratio of indeterminate to identifiable *Toweius* specimens following Gibbs et al. (2006), with smaller values indicating better preservation. The PETM nannofossil records from Sites 1259 and 1260 were previously studied following the same or similar methodology (Jiang and Wise, 2006; Mutterlose et al., 2007).

Another subset of samples from the same depths was pretreated with 10% hydrogen peroxide for 24 h to remove organic matter prior to bulk-isotopic analysis. The freeze-dried samples were then homogenized, and a suitable aliquot weighed for isotopic analysis. The stable C- and O-isotopic ratios were measured on a Gas Bench II Auto-Carbonate device interfaced to a Finnigan Mat Delta plus XP mass-spectrometer housed at the National High Magnetic Field Laboratory of Florida State University in Tallahassee, USA. All results were calibrated against international and internal laboratory standards, and reported in delta

notation relative to the Peedee Belemnite (PDB) standard. Analytical precision is better than $\pm 0.03\text{‰}$ for C isotopes and $\pm 0.04\text{‰}$ for O isotopes.

Nonmetric multidimensional scaling (NMS) was used to analyze and compare temporal changes in the nannofossil assemblage (Jiang and Wise, 2006; Mutterlose et al., 2007) across the PETM, ETM2 and H2 events. NMS is an ordination technique that makes no assumptions about the distribution of the underlying data and is one of the most robust unconstrained ordination methods in community ecology (Minchin, 1987). During the analyses the Bray-Curtis distance measure was used and 100 random initial starting configurations chosen to avoid a local stress minimum. The 2-dimension solutions can explain >90% of the information from the original datasets using the after-the-fact method (McCune and Grace, 2002). The analyses and calculation of community indices were implemented with the Vegan package on an R platform (www.r-project.org).

3. Results

3.1 Nannoplankton population changes across the ETM2 and H2

The ETM2 occurred at 54.02 Ma (Westerhold et al., 2015) and lies approximately at the lower boundary of calcareous nannofossil Zone NP11 (~54 Ma), a gap zone from the last occurrence of *Tribrachiatus contortus* to first occurrence of *Discoaster lodoensis* (Martini,

1971). Therefore, the absence of these two marker species, together with the co-occurrence of *Tribrachiatus orthostylus* and *Sphenolithus villae* (Agnini et al., 2007a), constrains the entire study interval at Site 1258 to the lowermost part of nannofossil Zone NP11. This age assignment is consistent with the Fe cyclostratigraphy age model at the same site by Westerhold and Röhl (Westerhold et al., 2007). Therefore, the CIE (-1.5‰) centered at 133.1 meters below sea floor (mbsf) corresponds to the ETM2 and the CIE (-1.1‰) at 131.5 mbsf to the H2 (Fig. 2; Table S1).

The nannofossil assemblages are moderately preserved throughout except within the CIE peaks where the preservation deteriorated from moderate to moderate-poor levels (Fig. 2; Table S2). Species richness steadily increases upward, and Shannon-Wiener (S-W) index and evenness show prominent spikes across the ETM2 and H2 where there is a corresponding trough in kurtosis (Fig. 2).

Total coccolith number and most major taxa share the same temporal variation pattern, showing abundance minima within the ETM2 and H2 core intervals (Fig. 3). *Toweius* and *Coccolithus* (mainly *C. pelagicus*) dominate the nannofossil assemblages throughout the study interval, making up 1/3 and 1/4 of the population, respectively. Across the ETM2, *Coccolithus*, *Toweius*, and *Chiasmolithus* decrease to less than half their pre-event abundances, and *Z. bijugatus* essentially disappears. However, *Discoaster* steadily increases, and *Tribrachiatus* shows a prominent peak.

3.2 NMS ordination

NMS ordination reveals distinct clusters consisting almost solely of pre-, mid- or post-ETM2/H2 assemblages separated along NMS Axis 1 (Fig. 4A&B). Assemblages from within the ETM2 and H2 CIE peaks spread out on the right, while those from the pre-CIE and recovery intervals cluster together on the left, and assemblages immediately adjacent to the CIE peaks lie in between but overlap with the left clusters (Fig. 4A; see Fig. 4B for definition of different intervals). The strong correlation ($R^2=0.75$, $n=54$, $p=0$) between sample scores and $\delta^{13}\text{C}$ values (Fig. 4B), and the horizontally contrasting ordination of excursion taxa (equivalent to the *Rhomboaster* spp.-*Discoaster araneus* association temporally restricted to the CIE; Kahn and Aubry, 2004) with normal dominant taxa of Paleogene oceans (e.g., *Coccolithus*, *Toweius*; Fig. 4A) indicate that Axis 1 corresponds to an environmental gradient associated with ^{13}C -depleted carbon addition.

In contrast, a distinct separation of pre- and post-PETM assemblages occurs along NMS Axis 1 (Fig. 5A). At both Sites 1259 and 1260, the pre-PETM assemblages stand alone as a separate cluster without any overlap with assemblages from the CIE and recovery intervals. The contrasting NMS ordination of nannofossil taxa with different ecologies (Fig. 5A) and the close resemblance between sample score-depth plot and $\delta^{13}\text{C}$ -depth plot (Fig. 5B)

suggest that Axis 1 also reflects environmental conditions related to the addition of ^{13}C -depleted carbon.

4. Discussion

4.1 Quality assessment of the ETM2 and H2 fossil records

Four lines of evidence suggest that the Site 1258 ETM2 and H2 nannofossil records are stratigraphically complete, despite relative poor preservation in the CIE peak intervals (Fig. 2, Table S2). Firstly, the prominent negative excursions in bulk carbonate $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are 1.5‰ and 1.8‰, respectively, and are as large as those recorded at the South Atlantic Site 1263 (paleodepth 1500 m) which is considered to be a complete ETM2 section (Lourens et al., 2005). Note that other sites in the South Atlantic and elsewhere have much smaller CIEs (Fig. 1), and therefore are considered to be incomplete. Secondly, Site 1258 ETM2 has a calculated duration of ~100 ka (Fig. 2), essentially the same length as at Site 1263 (Stap et al., 2009). Thirdly, within the ETM2 and H2 CIE peak intervals there also exists *D. araneus*, a PETM excursion species that has been previously observed within the Site 1263 ETM2 interval (Raffi and De Bernardi, 2008). Lastly, the nannofossil assemblages at Site 1258 are generally moderately preserved, which is comparable to, if not better than, those in the South Atlantic (Dedert et al., 2012). The preservation of such a complete, nannofossil-rich ETM2 and H2 section allows for further community analyses.

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185 Variation in preservational state may override the assemblage change signals because
186 dissolution, as a result from ocean acidification associated with PETM and ETM2 carbon
187 release, can selectively remove susceptible taxa from the fossil record, and therefore severely
188 alter the primary community structure. At first glance, the peak in *Discoaster* and *Tribrachiatus*
189 abundance across these intervals could appear to suggest that dissolution was the controlling
190 factor at Site 1258. However, the increase in rarefied species richness during the ETM2 CIE
191 interval where the observed preservation was comparatively poor (Fig. 2) suggests otherwise.
192 Preferential removal of susceptible taxa was negligible and the primary biogeochemical
193 signal was preserved, otherwise decreased species numbers would be expected. Therefore,
194 the absolute abundances are primarily a function of export productivity by nanoplankton in
195 the photic zone. In addition, the nannofossil assemblages from the ETM2 and H2 CIE peaks
196 should have similar environmental indicators, but would plot separately in the NMS
197 ordination space if differing preservation states had altered their original environmental
198 signal (Fig. 2). Instead, these two sets of assemblages plot together on the right side of NMS
199 Axis 1 (Fig. 4A) and thus have a similar environmental implication. This suggests that
200 postmortem depositional diagenesis did not significantly alter the primary signal of
201 population change, and therefore variation in preservation did not statistically compromise
202 the community analyses. This may be because our NMS analyses were primarily based on
203 genus-level data that were readily classified under varied preservational states. Typically,
204 nannofossil genera represent robust groupings of morphospecies with very similar ecologies,

and it is a routine to group species counts at the genus level before further multivariate analyses are performed because rare taxa often form outliers (Gibbs et al., 2012; Schneider et al., 2013). These analyses and the comparable preservation state for the assemblages from pre- and post-event intervals (Fig. 2) provide a basis for comparing nannofossil assemblage changes across the PETM, ETM2 and H2 events.

4.2 Surface water oligotrophy during hyperthermal events in the tropical Atlantic

Because calcareous nannoplankton as a whole prefer warm temperatures and low nutrient conditions (Brand, 1994), most of these microorganisms seem to benefit from these hyperthermal events as indicated by the reduced kurtosis but increase in diversity and evenness of the communities during the CIE peaks (Figs. 2 and S2, Supplementary Material). Across ETM2 and H2, there occurred a sudden shift in population dominance as indicated by the abrupt decrease in *Toweius* and *Coccolithus pelagicus*, accompanied by a decrease in *Chiasmolithus* and an increase in *Discoaster* and *Tribrachiatus* (Fig. 3). Similar changes have been previously reported across the PETM at these sites (Jiang and Wise, 2006; Mutterlose et al., 2007). *Discoaster* is thought to have preferred warm, oligotrophic waters (Haq and Lohmann, 1976; Wei and Wise, 1990) based on their high abundance in tropical and subtropical open-ocean sites, and therefore has been established as a K-selected specialist (Aubry, 1998b; Bralower, 2002). The *Rhomboaster-Tribrachiatus* lineage is considered to be highly specialized towards oligotrophic conditions (Aubry, 1998a;

Mutterlose et al., 2007), and the evolution of the short-lived “excursion” *Rhomboaster-*
-Discoaster assemblage may have resulted from warming-induced oligotrophy in the open
ocean (Bralower, 2002). *Chiasmolithus* was an r-selected opportunist that preferred cool,
eutrophic conditions, and *Toweius* was considered to have preferred eurythermal and
mesotrophic conditions (Bralower, 2002; Gibbs et al., 2006) but has recently shown to be
ubiquitous (Schneider et al., 2013). *Coccolithus pelagicus* is cosmopolitan and prefers a
wide nutrient range (Haq and Lohmann, 1976; Gibbs et al., 2006; Mutterlose et al., 2007;
Schneider et al., 2013). Therefore, the overall population change across the PETM, ETM2
and H2 warming episodes appears to suggest reduced nutrient supply to warmed surface
waters.

Prevailing tropical oceanic oligotrophy due to warmed surface sea temperatures may explain
the >75% drop in nannofossil absolute abundances across each hyperthermal event at these
sites. During hyperthermal events, sea surface temperature increases were amplified toward
the poles (Kennett and Stott, 1991; Shellito et al., 2003; Zachos et al., 2003). The greater
warming at high latitudes flattened the equator-to-pole thermal gradient, and thereby would
have weakened the trade winds and consequently reduced wind mixing and equatorial
upwelling (Vecchi et al., 2006). Reduced nutrient supply to the photic zone from diminished
upwelling of cold, nutrient-rich deep water created warmer surface-water conditions that
favored oligotrophic/thermophilic *Discoaster* and *Tribrachiatus* but discriminated against
cold-loving, eutrophic *Chiasmolithus*. The resulting decrease in productivity during ETM2 is

consistent with the tropical Pacific Site 1209, but is in contrast to the South Atlantic Site 1265 (Dedert et al., 2012). Similarly, during the PETM, nannofossils with oligotrophic preferences increased in abundance in open ocean environments (Bralower, 2002; Tremolada and Bralower, 2004; Gibbs et al., 2006), while those preferring eutrophic conditions thrived in shelf and marginal-sea settings (Gibbs et al., 2006; Agnini et al., 2007b), highlighting the geographic heterogeneity of the trophic regime in response to global warming (Schneider et al., 2013).

The reappearance of *Discoaster araneus*, a characteristic "excursion taxa" species (Kahn and Aubry, 2004) that was previously considered exclusive to the PETM, ~50 m above the PETM in Core 1258B-14R corroborates the presence of ETM2 and H2 at Site 1258. Raffi and De Bernardi (2008) reported *D. araneus* from the ETM2 interval in South Atlantic, suggesting that this excursion nannofossil is a good indicator of hyperthermals in the Atlantic, if not globally. This species is one of a peculiar group of discoasterids with variable ray number, free ray length and inter-ray angles, with short-lived occurrences in transient CIE peak intervals. They are interpreted as rapidly evolving opportunists that were able to take advantage of the unusual conditions that developed during hyperthermal events (Bown and Pearson, 2009). Its reappearance during the ETM2, however, suggests that it is more likely to be a morphological variant of existing *Discoaster* species that responded to changing surface-water chemistry (Jiang and Wise, 2006; Agnini et al., 2007b; Raffi et al., 2009; Self-Trail et al., 2012; Bralower et al., 2015). Thus, community changes in calcareous

nannoplankton may reflect the multiple aspects of environmental consequences resulting from the massive introduction of light carbon into the Earth's ecosystem during late Paleocene-early Eocene hyperthermal events, among which are the most notable shift in temperature-driven nutrient regime and CO₂-driven aquatic chemistry (McInerney and Wing, 2011).

4.3 Contrasting response of nannoplankton community and implications

Resilience to C disturbance measures the amount of light carbon input that an ecosystem can tolerate without collapsing into a qualitatively different state that is controlled by a different set of processes (Carpenter et al., 2001). A regime shift, an abrupt change in the structure and function of ecosystems, occurs when the threshold resilience is reached or crossed (Fig. 5), and then the ecosystem enters another state of operation that is difficult to anticipate and costly to reverse (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Despite numerous ecological studies in the marine realm, regime shifts are only occasionally detected (e.g., Hare and Mantua, 2000) because they mostly result from changes at decadal or longer scales (Steele, 1998). Since various amounts of light carbon were involved in the PETM, ETM2 and H2 (Zeebe et al., 2009; Supplementary Material), a comparison of their ecological consequences would allow for empirically gauging the resilience of the Paleogene marine ecosystem to light carbon input. This would in turn provide a reference for understanding the impacts of anthropogenic global warming on the modern marine biome.

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290 Two findings emerged from the NMS ordination of temporal changes in nannofossil
291 assemblages across the PETM, ETM2 and H2 perturbations in the tropical Atlantic. First,
292 sample scores of nannoplankton assemblages on NMS Axis 1 closely resemble the $\delta^{13}\text{C}$
293 trend (Figs. 4B & S2), suggesting that the nannoplankton community was sensitive to
294 changes in the C cycle. In particular, the wide separation of the CIE peak assemblages from
295 those pre- and post-CIE assemblages (Fig. 4A) indicates that, even during the relatively mild
296 ETM2 and H2, a relatively small amount of light carbon (700 and 160 Pg C of methane,
297 respectively; Supplementary Material) triggered significant change in the nannoplankton
298 community.

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300 Second and more interestingly, the distinct separation of pre- and post-event assemblages in
301 the NMS ordination space across the PETM stands in stark contrast to the largely
302 overlapping pattern across ETM2/H2 (Figs. 4A & 5A), suggesting that the surface marine
303 ecosystem in the tropical Atlantic experienced changes of different magnitudes that resulted
304 in distinct responses. The comparable pre-event nannofossil absolute abundances between
305 ETM2 and PETM (2.78×10^9 vs. 3×10^9 specimens/g sediment) (Mutterlose et al., 2007)
306 indicates similar paleoceanographic background settings prior to these two perturbations.
307 The pre-ETM2/H2 assemblages closely cluster together and overlap with those from the
308 post-event interval (Fig. 4A). This pattern suggests that, despite significant change in
309 nannoplankton communities during the ETM2/H2 peak, the surface marine ecosystem

rapidly returned to a pre-event state in ~20 ka period. In other words, the pre-ETM2/H2 ecosystem in the tropical Atlantic was capable of tolerating a ~700 Pg C change in the methane scenario without causing a regime shift (Fig. S1, Supplementary Material).

In contrast, the pre-PETM assemblages from Sites 1259 and 1260 are clearly separated along NMS Axis 1 from those within CIE peak and post-event intervals (Fig. 5A). The slight deviation of Site 1259 assemblages from Site 1260 along Axis 2 may be attributed to local environmental heterogeneity, water depth-related differences in preservational processes, and/or even different species concepts between the two groups of authors (Jiang and Wise, 2006; Mutterlose et al., 2007). The stand-alone cluster of the pre-PETM samples at both sites, however, more likely suggests that the pre-PETM nanoplankton assemblages were substantially different from the post-PETM (recovery) interval, indicating that the surface marine ecosystem underwent a regime shift and entered a substantially different state (Fig. 6). This is consistent with a previous study that showed disruption in nanoplankton community structure was scaled with the amount of carbon released during a series of hyperthermal events in early Eocene, and above-background variance was observed for both the PETM and ETM2 (Gibbs et al., 2012). Furthermore, it did not recover to the pre-PETM state during the study interval (~170 ka) but persistently remained disturbed long after the carbon-cycle perturbation had stopped (Bornemann et al., 2014). Such a regime shift signifies that the PETM environmental perturbation exceeded the resilience threshold of the pre-PETM ecosystem (Fig. 6), thus bracketing the threshold tolerance of methane for the Eocene

surface marine ecosystem between 700 and 3000 Pg C, since the ETM2 and H2 perturbations did not cause regime shift (Fig. 6). It is true that this resilience threshold was deduced from the Paleogene greenhouse climate, and therefore may not be directly applicable to the modern ocean in the context of icehouse climate, considering the modernday faster rates of carbon cycle change and different oceanographic background. However, this estimate represents a first-order attempt to constrain the surface marine ecosystem threshold regarding light carbon tolerance, which cautions the urgent possibility of regime shift under present faster carbon emissions (Cui et al., 2011), and meanwhile affords reference to future marine biotic response to modern ongoing global warming.

5. Conclusions

We quantitatively document and compare the community changes in calcareous nannoplankton across the PETM, ETM2 and H2 environmental perturbations from Sites 1258, 1259 and 1260 in the tropical Atlantic. The decrease in total abundance of eutrophic and mesotrophic taxa, and corresponding increase in oligotrophic and thermophilic taxa suggest that oligotrophy prevailed in the warmed tropical Atlantic surface waters during these three hyperthermal events. An NMS ordination analysis further reveals that the surface marine ecosystem rapidly recovered to the pre-event state immediately after the ETM2 and H2 perturbations. In contrast, the ecosystem experienced a regime shift across the PETM and entered a substantially different state, indicating that the PETM environmental perturbation exceeded the resilience threshold of the pre-PETM ecosystem and thus a certain threshold

was crossed. This constrains the threshold methane tolerance of the Eocene tropical Atlantic ecosystem to between 700 and 3000 Pg C.

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Figure Captions

Figure 1. Location of ETM2 records at studied (filled star) and reference sites (solid circle) on a 53-Ma paleogeography map (www.odsn.de). Reference sites include the land section at Bighorn Basin (Koch et al., 2003), and oceanic sections at Mead and Dee Streams (Nicolo et al., 2007), Passago (Agnini et al., 2007), Dababiya (Stassen et al., 2012), DSDP Sites 550 & 577, ODP Sites 690, 1051 (Cramer et al., 2003), 1209 (Gibbs et al., 2012) and 1215 (Leon-Rodriguez and Dickens, 2010), and IODP Site M0004 (Sluijs et al., 2009). CIE based on bulk carbonate unless otherwise stated. BF=benthic foraminifer, n.d. = not determined.

Figure 2. Overall variations in nannoplankton population across ETM2 and H2 at ODP Site 1258.

Figure 3. Variations in composition of nannoplankton population across ETM2 and H2 at ODP Site 1258. All abundance numbers in 10^8 . Note the sharp reduction across each event except for *Discoaster* and *Tribrachiatus*.

Figure 4. NMS ordination for the ETM2/H2 events at Site 1258. (A) Sample and species distribution in a 2-D ordination space. Note the clear separation of CIE peak samples on the right and clustering of other samples on the left; see B for definition of different intervals. (B) Close correlation between sample scores on NMS Axis 1 and carbon isotopic values at Site 1258. (C) Close correlation between sample scores on NMS Axis 1 and carbon isotopic values.

Figure 5. NMS ordination for the PETM event at Sites 1259 and 1260 (the position of a taxon in the ordination space is located at the center of its name). (A) Sample and species distribution in a 2-D ordination space. Note the separation of pre-CIE samples from those in CIE peak and recovery intervals. See B for definition of different intervals. (B) Close correlation between sample scores on NMS Axis 1 and carbon isotopic values.

Figure 6. Conceptual fluctuations around two ecosystem regimes (thick dotted lines) under different carbon emission amounts during PETM, ETM2, and H2. The PETM perturbation crossed the threshold of the pre-PETM regime and caused a regime shift. The ETM2 and H2 perturbations fell within the resilience range of the pre-ETM2 regime and consequently did not cause regime shift. Inspired by Carpenter (2003).

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