PNAS COMMENTARY

Unraveling ecological signals from a global warming event of the past

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As we face the increasing threat of global warming and its associated effects, paleontologists and paleoclimatologists alike look to the geological record to investigate how rapid, natural global warming events of the past have impacted the Earth system. One of the most important archives for investigating climate change in the geological past is the marine sediment record (1). In the open oceans, sediment particles, organic matter, and the shells of marine microorganisms, are constantly raining down on the seafloor and accumulating as marine sediments (1). In the relative quiescence of the deep sea, these sediments can build up relatively undisturbed for millions of years (1). Analysis of the chemical signals in these sediments that are influenced by temperature has allowed for the reconstruction of changing global climates throughout the last 70 million years (2).

The first half of the Cenozoic (66 million years to 34 million years ago) was characterized by "hothouse" and "warmhouse" climates, when global temperatures were between 5 °C and 10 °C warmer than the present day (2), and atmospheric CO_2 was estimated to be between 500 and 3,000 parts per million (3). Against this backdrop of an already warm world, between 56 million and 46 million years ago, there were a series of rapid global warming events called "hyperthermals" (2). These hyperthermal events are geologically brief, typically <200,000 y in duration, and associated with sharp negative carbon isotope excursions (2). The Paleocene–Eocene thermal maximum (PETM), which occurred ∼56 million years ago, was the largest of these events (2). It was first discovered in the early 1990s as a pronounced shift in the climate records of a deep-sea sediment core from the Southern Ocean (4). Since that time, the PETM has become the most studied Cenozoic hyperthermal, and, due to its potential analogy to anthropogenic climate change, it remains a key interval of Earth history for climatological research.

The PETM was driven by the release of a massive quantity of isotopically light carbon into the ocean–atmosphere system, as indicated by a distinct negative carbon isotope excursion (5). Since the discovery of the PETM, there has been considerable uncertainty about the amount of carbon that was released, its source, and the rate of release (5). The carbon isotope excursion recorded in different geological archives mostly varies in magnitude between −2.5‰ and −5.5‰ due to fractionation effects and postdepositional processes, and likely resulted in a significant dampening of the carbon isotope signal from marine microfossil archives (Fig. 1*A* and ref. 5). Recent work suggests the triggering carbon source was volcanic in origin (6–8) and released in less than 5,000 y (9). The volume and geologically rapid nature of this carbon release is what makes the PETM a useful analog for modern-day CO_2 emissions, although it should be noted that the rate of carbon release is over significantly different timescales: hundreds of years in the present day, in comparison to thousands of years during the PETM (7).

The carbon injection into the ocean–atmosphere system during the PETM drove profound changes in the Earth system, such as global sea surface temperatures increasing by ∼4 °C to 5 °C (Fig. 1*B* and ref. 9), major changes to hydrological and biogeochemical cycles (10), and rapid ocean acidification (11, 12). Despite these substantial environmental impacts, the PETM is not classified as a mass extinction event, as significant levels of extinction are limited to just a handful of taxonomic groups, and overall extinction rates do not increase beyond background levels (13). Despite this muted extinction signal, biotic impacts were severe, and studies have found the PETM to be dominated by taxonomic turnover and originations in various marine groups (Fig. 1*C* and refs. 14 and 15) and land mammals (16), and by latitudinal migrations and range shifts of many groups, including marine plankton (13) and land plants (17).

Despite this wealth of evidence, our ability to fully unravel the stories locked up in marine sediments has been hampered by the quality of that archive of the PETM. Widespread dissolution of marine carbonate due to ocean acidification has resulted in many PETM records being truncated (11). Additionally, mixing of deep-sea sediments that occurs due to the burrowing activities of sediment-dwelling organisms and the action of ocean currents can result in mixing of sediments that span thousands to tens of thousands of years (18). This is a particular challenge for events as short lived as the PETM, with an estimated duration of ∼170,000 y (6, 11, 12). Disentangling the ecological signals of open-ocean marine calcifying plankton during the PETM is crucial, as they play a key role in sequestering carbon in the deep sea (1). Being able to quantify how the abundances and distributions of these plankton groups might change in response to rapid global warming is critical to accurately predicting oceanic carbon drawdown in the future.

In their contribution in PNAS, Hupp et al. (19) aim to address these sedimentary complexities by revisiting

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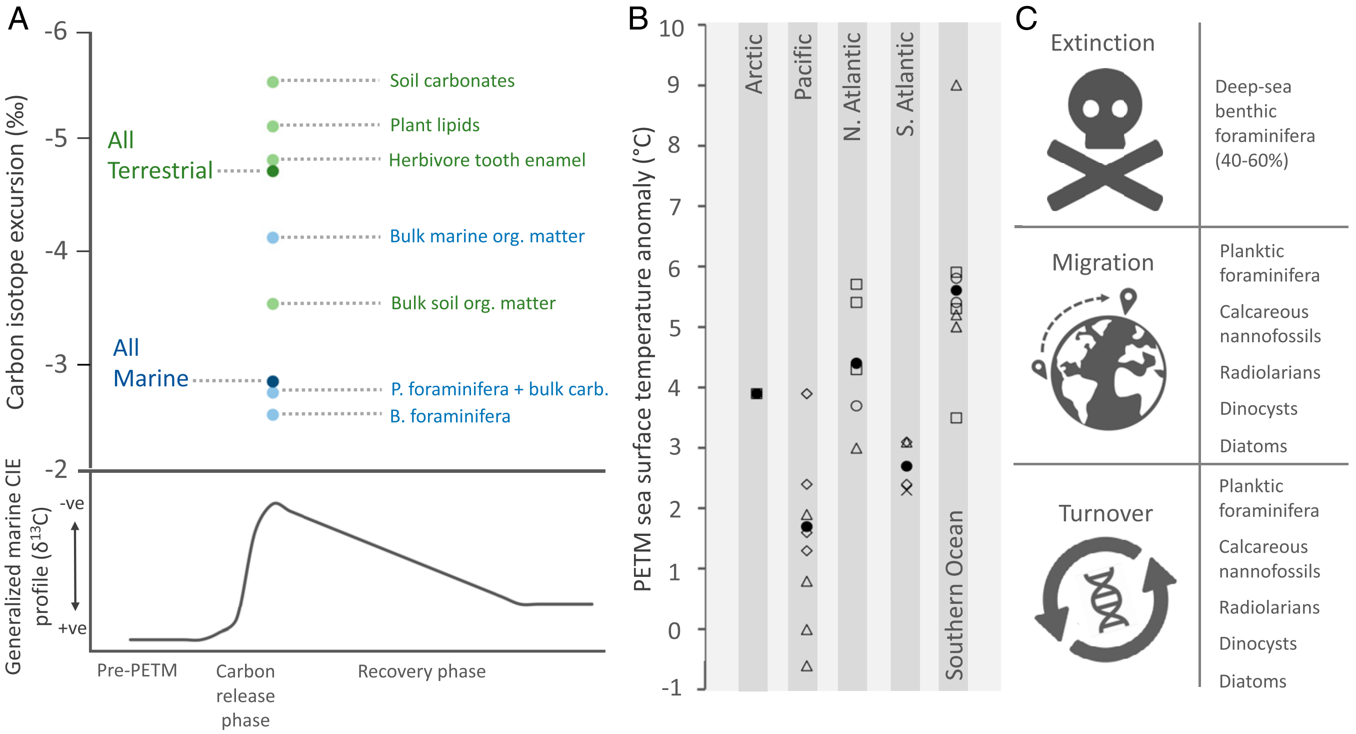

Fig. 1. (*A*) The mean magnitudes of the PETM negative carbon isotope excursion as recorded by different carbon isotope archives [data from McInerney and Wing (5)]. P. foraminifera, planktic foraminifera; B. foraminifera, benthic foraminifera; bulk carb., bulk carbonate. The curve indicates the typical expression of the PETM negative carbon isotope excursion in marine sedimentary archives, such as IODP Site 865. CIE, carbon isotope excursion; $\delta^{13}C$, carbon isotopes ratios; -ve, more negative values; +ve, more positive values. (*B*) PETM sea surface temperature (degrees Celsius) anomalies for the Arctic, Pacific, North (N.) Atlantic, South (S.) Atlantic and Southern Oceans [data from Dunkley Jones et al. (9)]. Open triangles, surface-dwelling planktonic foraminifera oxygen isotope derived temperatures; open circles, thermocline-dwelling planktonic foraminifera oxygen isotope derived temperatures; open diamonds, surface-dwelling planktonic foraminifera Mg/Ca ratio derived temperatures; crosses, thermocline-dwelling planktonic foraminifera Mg/Ca ratio derived temperatures; open squares, glycerol dialkyl glycerol tetraether derived temperatures. (*C*) Summary of the main biotic impacts on key marine microfossil groups [data from Speijer et al. (13)].

open-ocean sediment archives from Ocean Drilling Program Site 865, which was located at a paleolatitude just a few degrees north of the equator in the Atlantic Ocean during the PETM. In their study, the authors analyze the carbon isotope signals recorded in the calcite shells of a group of single-celled marine plankton called planktonic foraminifera (PF). A total of 548 single-specimen PF carbon isotope measurements were combined with bulk sediment carbon isotope measurements and assemblages counts to determine the extent to which sedimentary mixing had impacted the PETM record at this site. The authors find a distinctly bimodal distribution in the PF carbon isotope data between more positive pre–carbon isotope excursion (CIE) values and distinctly negative CIE values and, by applying an "isotopic filtering" approach, are able to identify that 49.5% of all individual PF shells found in PETM sediments were contaminants from earlier in the record. One of the interesting aspects of this pattern, however, is that it is only seen in the taxa which live in the surface mixed layer of the ocean and was not seen in the species that are known to live deeper in the water column. The deeper-dwelling taxa were found in significantly lower abundances during the PETM, and all had pre-CIE carbon isotope values, indicating that they were reworked in the sediment, and none were present at this site during the PETM. This pattern was also true of a handful of surface-dwelling taxa, which then appear later in the record after the main body of the PETM, with carbon isotope values and abundances typical of those from before the event. Thermal stress and acidification are implicated in the expatriation of the surface dwellers that were absent from this record, and deoxygenation of intermediate waters is implicated as a driver for the deeper-dwelling taxa.

The implications of these findings are that assemblage counts from PETM sediments that have not been subject to "isotopic filtering" will be significantly overestimating standing diversity, and in a nonsystematic way, as not all taxa responded equally to the environmental pressures of the event. These findings lend credence to the suggestion that many organisms managed to survive the PETM by migrating to environments that were more favorable, for the duration of the event (14). Indeed, there is evidence of typically tropical marine plankton being found in high-latitude sites throughout the event, which are then found at lower latitudes again afterward (14). This work highlights the sensitivity of tropical plankton communities to extreme global warming, with organisms evacuating tropical regions, due to overwhelming environmental stress. By more widely employing isotopic filtering to existing tropical deep-sea records, we can start to build a clearer picture of open-ocean diversity changes. Initial indications of what this means for the future of marine calcifying plankton, however, are bleak. The rate of carbon release during the PETM was an order of magnitude slower than modern-day emission rates; organisms had more time to respond, and the oceans had a longer time to equilibrate the carbon inputs. As such, the rapid rate of modern-day climate change may well be the greatest challenge these communities have faced for the last 66 million years.

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