Eocene greenhouse climate revealed by coupled clumped isotope-
Mg/Ca thermometry

David Evans\textsuperscript{a,1,2}, Navjit Sagoo\textsuperscript{b}, Willem Renema\textsuperscript{b}, Laura J. Cotton\textsuperscript{b,c,d}, Wolfgang Müller\textsuperscript{e,f}, Jonathan A. Todd\textsuperscript{f}, Pratul Kumar Saraswati\textsuperscript{b}, Peter Stassen\textsuperscript{b}, Martin Ziegler\textsuperscript{b}, Paul N. Pearson\textsuperscript{i}, Paul J. Valdes\textsuperscript{m,n}, and Hagit P. Affek\textsuperscript{a,o}

\textsuperscript{a}Department of Geology & Geophysics, Yale University, New Haven, CT 06511; \textsuperscript{b}Naturalis Biodiversity Center, 2300 RA Leiden, The Netherlands; \textsuperscript{c}Florida Museum of Natural History, University of Florida, Gainesville, FL 32611; \textsuperscript{d}Department of Geosciences, University of Florida, Gainesville, FL 32611; \textsuperscript{e}Institute of Geosciences, Goethe University Frankfurt, 60438 Frankfurt, Germany; \textsuperscript{f}Department of Earth Sciences, Royal Holloway University of London, Egham, TW20 0EX, United Kingdom; \textsuperscript{g}Department of Earth Sciences, Natural History Museum, London, SW7 5BD, United Kingdom; \textsuperscript{h}Department of Earth Sciences, Indian Institute of Technology Bombay, Mumbai 400076, India; \textsuperscript{i}Department of Earth and Environmental Sciences, Katholieke Universiteit Leuven, B-3000 Leuven, Belgium; \textsuperscript{j}Royal Belgian Institute of Natural Sciences, B-1000 Brussels, Belgium; \textsuperscript{k}Department of Earth Sciences, Utrecht University, 3584 CS Utrecht, The Netherlands; \textsuperscript{l}School of Earth & Ocean Sciences, Cardiff University, Cardiff, CF10 3AT, United Kingdom; \textsuperscript{m}CABOT Institute, University of Bristol, Bristol, BS8 1UJ, United Kingdom; \textsuperscript{n}School of Geographical Sciences, University of Bristol, Bristol, BS8 1SS, United Kingdom; and \textsuperscript{o}Institute of Earth Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

Edited by Mark H. Thiemens, University of California, San Diego, La Jolla, CA, and approved December 15, 2017 (received for review August 21, 2017)

Past greenhouse periods with elevated atmospheric CO\textsubscript{2} were characterized by globally warmer sea-surface temperatures (SST). However, the extent to which the high latitudes warmed to a greater degree than the tropics (polar amplification) remains poorly constrained, in particular because there are only a few temperature reconstructions from the tropics. Consequently, the relationship between increased CO\textsubscript{2}, the degree of tropical warming, and the resulting latitudinal SST gradient is not well known. Here, we present coupled clumped isotope ($\Delta_{47}$)-Mg/Ca measurements of foraminifera from a set of globally distributed sites in the tropics and midlatitudes. $\Delta_{47}$ is insensitive to seawater chemistry and therefore provides a robust constraint on tropical SST. Crucially, coupling these data with Mg/Ca measurements allows the precise reconstruction of Mg/Ca$_{w}$ throughout the Eocene, enabling the reinterpretation of all planktonic foraminifera Mg/Ca data. The combined dataset constrains the range in Eocene tropical SST to 30–36 °C (from sites in all basins). We compare these accurate tropical SST to deep-ocean temperatures, serving as a minimum constraint on high-latitude SST. This results in a robust conservative reconstruction of the early Eocene latitudinal gradient, which was reduced by at least 32 ± 10% compared with present day, demonstrating greater polar amplification than captured by most climate models.

clumped isotope | Eocene | tropical sea-surface temperatures | polar amplification | seawater Mg/Ca

Greenhouse periods in the geological past have received much attention as indicators of the response of the Earth to elevated CO\textsubscript{2}. Of these, the Eocene is the most recent epoch characterized by pCO\textsubscript{2} at least twice preindustrial, i.e., >560 ppm (1). Furthermore, as the quantity of paleoclimate reconstructions has increased the Eocene has become a target for comparison with climate models (2), as proxy data of past warm periods are required to assess model competence at elevated CO\textsubscript{2} (3). Existing geochemical proxy data suggest that the Eocene latitudinal sea-surface temperature (SST) gradient was greatly reduced: the mid to high latitude (>40°) surface oceans were 10–25 °C warmer than today throughout the Eocene (4, 5), yet there is no evidence for tropical SST warming of a similar magnitude, even during peak warm intervals such as the Paleocene–Eocene Thermal Maximum (PETM) (6, 7). In fact, several studies have reported moderate tropical warmth (30–34 °C) throughout the Eocene (8, 9). This is in contrast to most Eocene climate model simulations (10, 11), which indicate the latitudinal gradient was within 20% of modern [with notable exceptions (12), discussed below]. However, using proxies to validate model output is problematic because many paleothermometers are associated with relatively large (often systematic) errors and are sensitive to diagenetic alteration after burial in the sediment. For example, initial reconstructions of the Eocene tropics were biased by the analysis of poorly preserved material, resulting in the cool-tropics hypothesis (13). Subsequently, it was shown that well-preserved samples yield Eocene tropical SST at least as warm as present (14–16). Furthermore, carbonate-bound proxies such as foraminiferal δ\textsubscript{18}O and Mg/Ca are highly sensitive to poorly constrained secular variations in salinity and seawater chemistry (17), TEX\textsubscript{86} is associated with calibration complications (18, 19), and all proxies may be seasonally biased to summer temperatures at mid to high latitudes (20). As a result, absolute tropical SST are not constrained to better than ±5 °C at any given site (21), in part due to uncertainties over whether modern calibrations are applicable to Eocene material (20). Similarly, atmospheric processes, in particular clouds and aerosol–cloud interactions, are a large source of uncertainty within climate models (22), while variable intermodel sensitivities to CO\textsubscript{2} (10) complicate the use of these to directly constrain absolute Eocene temperatures. Given these uncertainties in both the data and models, there is no consensus regarding the degree of polar amplification or the precise response of the tropical oceans to increasing CO\textsubscript{2}. Specifically, much debate has focused on whether the tropics underwent substantial warming and the latitudinal gradient was only moderately reduced (23, 24), or if tropical warmth was limited and the gradient

Significance

Reconstructing the degree of warming during geological periods of elevated CO\textsubscript{2} provides a way of testing our understanding of the Earth system and the accuracy of climate models. We present accurate estimates of tropical sea-surface temperatures (SST) and seawater chemistry during the Eocene (56–34 Ma before present, CO\textsubscript{2} >560 ppm). This latter dataset enables us to reinterpret a large amount of existing proxy data. We find that tropical SST are characterized by a modest warming in response to CO\textsubscript{2}. Coupling these data to a conservative estimate of high-latitude warming demonstrates that most climate simulations do not capture the degree of Eocene polar amplification.

Author contributions: D.E., N.S., and H.P.A. designed research; D.E. performed research; D.E. analyzed data; D.E., W.R., L.J.C., J.A.T., P.K.S., and P.N.P. collected samples; H.P.A. directed clumped isotope analysis; W.M. directed laser ablation analysis; and D.E., N.S., W.R., L.J.C., W.M., J.A.T., P.K.S., P.S., M.Z., P.N.P., and H.P.A. wrote the paper. The authors declare no conflict of interest. This article is a PNAS Direct Submission. Published under the PNAS license.

\textsuperscript{1}Present address: School of Earth and Environmental Sciences, University of St Andrews, St Andrews, KY16 9AL, United Kingdom.

\textsuperscript{2}To whom correspondence should be addressed. Email: de32@st-andrews.ac.uk.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1714744115/-/DCSupplemental.
Eocene Surface Ocean Temperature from Foraminifera Clumped Isotopes

The carbonate clumped isotope thermometer (26, 27), hereafter denoted Δ847, is based on the increasingly preferential binding of heavy isotopes to each other (e.g., 13C-18O in carbonate) at lower temperatures. The principal advantage over existing geochmical temperature proxies is that there is no resolvable dependence on seawater elemental or isotopic composition (28), and uncertainty is dominated by analytical noise so that, unlike other carbonate-bound proxies, paleotemperature errors are random rather than systematic.

The epifaunal foraminifera utilized here live at approximately the same depth as planktonic species considered to be surface dwelling (29) (<50 m, within 1 °C of SST in the tropics; SI Appendix, Fig. S6), and calcify at a constant rate in locations characterized by a seasonal cycle (30). Therefore, our paleotemperatures reflect mean annual SST. The abundance of the nummulitids in the Eocene tropics and midlatitudes, where they are rock-forming in some locations, demonstrates that they were well-adapted to the climate at the time. Three LBF species live-collected from seven locations are characterized by a Δ847-temperature slope within error of the Yale abiogenic calcite calibration (27) (SI Appendix, Fig. S1 and Table S1), and there is no evidence for a significant vital effect influence on shell δ18O. These observations provide the basis for the use of this calibration to reconstruct paleotemperatures from extinct LBF of the family Nummulitidae and Mg/Ca (29) (this study). Three LBF species live-collected from seven locations are characterized by a Δ847-temperature slope within error of the Yale abiogenic calcite calibration (27) (SI Appendix, Fig. S1 and Table S1), and there is no evidence for a significant vital effect influence on shell δ18O. These observations provide the basis for the use of this calibration to reconstruct paleotemperatures from extinct LBF of the family Nummulitidae.

All fossil samples were analyzed by laser-ablation inductively coupled plasma mass spectrometry (ICPMS) for a suite of trace elements to assess their geochemical preservation, together with SEM images (SI Appendix, Fig. S4 and Table S3). Trace element ratios indicative of contamination and overgrowths (Al/Ca and Mn/Ca) show no correlation with Mg/Ca, indicating the absence of any Mg-bearing secondary phase. SEM images of broken specimens show that Eocene and modern foraminifera are characterized by equivalent chamber wall microtextures, demonstrating the absence of micrometer-scale recrystallization.

Furthermore, high-Mg calcite, such as that of LBF shells, recrystallizes fully to low-Mg, low-Sr calcite during diaGenesis (SI Appendix, Fig. S5), enabling the unambiguous identification of chemically well-preserved material. On the basis of these screening techniques, only samples that were exceptionally well-preserved were utilized for Δ847 analysis, i.e., those with no discernible diagenetic modification. Finally, because these foraminifera live at shallow depths, there is no potential for a large difference between calcification and diagenetic temperature, unlike typical planktonic species (15).

The mean tropical SST derived from samples that passed this rigorous screening is 32.5 ± 2.5 °C (Fig. 3A). The maximum reconstructed Eocene Δ847 temperature is 36.3 ± 1.9 °C from Java at ~39 Ma (all uncertainties are 1 SE), with a paleolatitude of 6°S (30), possibly located within an expanded Indo-Pacific warm pool. Samples spanning the early Eocene (55.3–49.9 Ma) from Kutch, India, which was within 5° of the equator at that time, are characterized by temperatures of 30.4 ± 2.5 to 35.1 ± 2.6 °C. The difficulty in precise temporal correlation between shallow sites means that we cannot definitively assign these samples to specific intervals, although the youngest and warmest Kutch sample probably falls within the Early Eocene Climatic Optimum (EECO; ~52–50 Ma). Although the peak temperature from equatorial India in the early Eocene is marginally cooler than that from middle Eocene Java, the two are within error, and this small difference may be explained by regionally cooler SST on the west coast of India compared with the West Pacific. A latest Eocene sample from Tanzania (33.9 Ma; 21°S) records 29.7 ± 3.1 °C.

In addition, samples spanning the early-middle Eocene from northwest Europe were analyzed for Δ847 and Mg/Ca. The principal aim of doing so was to fill temporal gaps in our seawater chemistry reconstructions (see below), but these also provide Eocene SST for this region. We observe a 9 °C warming between the earliest Eocene (18–20 °C) and the EECO (28–31 °C), followed by a long-term cooling trend through the Mid-Eocene to 23.1 ± 2.5 °C at 42.5 Ma. This pattern of global change is in good agreement with mid-to-high-latitude TEX86 (31) (SI Appendix, Fig. S8).

Finally, calculated δ18Osw derived from δ18O measured simultaneously with Δ847, yield values that are in agreement with an ice-free world. Specifically, all δ18Osw reconstructions from our tropical samples are within error of −1‰e, with the exception of
Paleotemperatures, together with the LBF Mg/Ca curve (Fig. 2) is based on our LBF and data (Fig. 2) demonstrate that those models of the same specimens allows us to significantly change seawater Mg/Ca (Mg/Ca$_{sw}$), our LBF Mg/Ca data discussed below must also represent normal seawater conditions (59). See SI Appendix for references.

These data further demonstrate that our samples are well-preserved, and that the sample site salinity was not substantially lower than open ocean (all δ$^{18}$O$_{sw}$ within 3% of mean Eocene seawater). Because a >10-psu salinity reduction is necessary to significantly change seawater Mg/Ca (Mg/Ca$_{sw}$), our LBF Mg/Ca data discussed below must also represent normal seawater conditions (59).

Our samples do not include the PETM, and only one falls within the EECO. Therefore, our results do not preclude warmer tropical temperatures during those time intervals (6). Nonetheless, we find no evidence for tropical SST >38 °C based on our Δ$_{47}$ data. Indeed, all of our tropical data are within uncertainty of each other, and could be interpreted as indicating stable warm conditions in the tropics throughout the Eocene (32.5 ± 2.5 °C), in line with several previous studies (8, 14, 32), although possible temporal trends will be discussed below. To assess whether a similar picture is evident in other proxy SST data, and therefore to address the broader question of the Eocene evolution of tropical SST and early Eocene polar amplification, we use these Δ$_{47}$ paleotemperatures, together with Mg/Ca analyses of the same samples, to accurately and precisely reconstruct Mg/Ca$_{sw}$. This allows us to reevaluate all Eocene planktonic foraminifera Mg/Ca data, providing an additional constraint on tropical SST at higher temporal and spatial resolution than the Δ$_{47}$ data alone. Furthermore, by combining information from these proxies we create a large dataset consisting mostly of open ocean data, suitable for comparison with climate simulations. Doing so minimizes potential bias associated with the regional paleoceanography of any individual site.

Tanzania (−0.2‰), δ$^{18}$O$_{sw}$ at our midlatitude sites is temporally variable and characterized by overall more negative values, consistent with midlatitude freshwater contribution to these proximal sites (−4 to −1.5‰). These data further demonstrate that our samples are well-preserved, and that the sample site salinity was not substantially lower than open ocean (all δ$^{18}$O$_{sw}$ within 3% of mean Eocene seawater). Because a >10-psu salinity reduction is necessary to significantly change seawater Mg/Ca (Mg/Ca$_{sw}$), our LBF Mg/Ca data discussed below must also represent normal seawater conditions (59).

Our samples do not include the PETM, and only one falls within the EECO. Therefore, our results do not preclude warmer tropical temperatures during those time intervals (6). Nonetheless, we find no evidence for tropical SST >38 °C based on our Δ$_{47}$ data. Indeed, all of our tropical data are within uncertainty of each other, and could be interpreted as indicating stable warm conditions in the tropics throughout the Eocene (32.5 ± 2.5 °C), in line with several previous studies (8, 14, 32), although possible temporal trends will be discussed below. To assess whether a similar picture is evident in other proxy SST data, and therefore to address the broader question of the Eocene evolution of tropical SST and early Eocene polar amplification, we use these Δ$_{47}$ paleotemperatures, together with Mg/Ca analyses of the same samples, to accurately and precisely reconstruct Mg/Ca$_{sw}$. This allows us to reevaluate all Eocene planktonic foraminifera Mg/Ca data, providing an additional constraint on tropical SST at higher temporal and spatial resolution than the Δ$_{47}$ data alone. Furthermore, by combining information from these proxies we create a large dataset consisting mostly of open ocean data, suitable for comparison with climate simulations. Doing so minimizes potential bias associated with the regional paleoceanography of any individual site.

Seawater Mg/Ca Reconstruction

Coupling Mg/Ca−Δ$_{47}$ data of the same specimens allows us to simultaneously reconstruct temperature and Mg/Ca$_{sw}$ because shell Mg/Ca is a function of both, and we independently constrain the temperature component of Mg incorporation using Δ$_{47}$. Although much work has focused on reconstructing past variation in Mg/Ca$_{sw}$ (33, 34), a different approach is required. While these studies show that Mg/Ca$_{sw}$ has approximately doubled since the Oligocene (35), precise reconstructions for most of the Paleogene are lacking, and models covering the Phanerozoic (35, 36) do not agree on epoch-scale variation in seawater chemistry. This has precluded reliable Mg/Ca-derived paleotemperatures with sufficient accuracy for assessing model SST competency (17). To overcome this, we use Δ$_{47}$ data of LBF spanning the Eocene–early Oligocene to solve the Mg/Ca$_{sw}$−Mg/Ca$_{ash}$-temperature calibration for the foraminifera (37). The uncertainty in these reconstructions is ~2–5 times lower than previous estimates, reducing the Mg/Ca$_{ash}$-derived error on existing planktonic foraminifera temperatures to <2.5 °C. This is possible because nummulitid Mg/Ca is more sensitive to Mg/Ca$_{ash}$ than to temperature, and unlike planktonic species there are no resolvable salinity or carbonate chemistry effects (30, 37). The composite Paleogene Mg/Ca$_{ash}$ curve (Fig. 2) is based on our LBF and data from inorganic calcium carbonate veins (CCV) (33), as the uncertainty on these latter data is also relatively small and the two records are in excellent agreement where they overlap. This reconstruction delineates the Eocene–early Oligocene as a period of stable Mg/Ca$_{ash}$ between 2.1 and 2.5 mol/mol, ~45% of modern. Previously, the lack of data before 40 Ma required box-model estimates (35, 36) to be used to assess the impact of secular change in seawater chemistry on fossil Mg/Ca measurements. The precise LBF-derived Mg/Ca$_{ash}$ data (Fig. 2) demonstrate that those models are inaccurate in the early Eocene, with a large effect on Mg/Ca$_{ash}$-derived temperatures. For example, early Eocene tropical SST
Evolution of tropical (www.pnas.org/cgi/doi/10.1073/pnas.1714744115) and pH on Mg/Ca, and 2 SE for TEXΔ123) and coherence of tropical early Eocene data from the Arctic Coring Expedition (ACEX) (42) (~80°N), ODP Site 1172 (5) (~54°S), and Wilkes Land (43) (~60°S) greatly exceed deep-ocean temperatures derived from deep-benthic foraminifera Mg/Ca and δ18O (44), suggesting either a seasonal bias, the influence of local warm surface currents, a more stratified ocean, and/or uncertain calibrations (20). To avoid these complications, we use the deep-benthic foraminifera-Mg/Ca temperature stack (44) as a lower limit on high-latitude SST. Present-day mean SST at high latitudes is within 2 °C of the deep ocean (SI Appendix), and the coolest Eocene high-latitude Δ47 data based on long-lived shallow benthic mollusks from Seymour Island (45) are within error of coeval deep-ocean temperatures where both are available (Fig. 3 B and C). Although the coherence of these reconstructions supports the use of deep-ocean Mg/Ca as a minimum constraint on high-latitude SST through time, model evidence suggests that Eocene deep-water formation in the Southern Ocean may have been limited to winter (20), resulting in colder deep water compared with mean annual high-latitude SST. Therefore, we emphasize that using the benthic foraminifera Mg/Ca dataset as a proxy for high-latitude SST produces an estimate of the maximum steepness of the latitudinal SST gradient and does not necessarily represent the mean annual gradient. Similarly, it does not in itself provide a means of assessing high-latitude SST proxy data given that these may be biased toward a different season, and there is evidence for a zonal SST heterogeneity in the Eocene Southern Ocean (45). The merit in this approach is that it provides a conservative constraint on the degree to which the gradient was reduced in the Eocene, and therefore represents the minimum value model simulations must achieve to be considered representative of Eocene climate. We calculate the early Eocene latitudinal gradient as the difference between the mean tropical and deep-ocean data between 48 and 56 Ma (±2 SE variability in both datasets); it is therefore representative of background early Eocene conditions [i.e., not the PETM, for which there is evidence for a further reduction in the latitudinal SST gradient (21)].

Based on this analysis, we find a reduction of at least 32 ±10% in the mean difference between tropical and high-latitude SST during the early Eocene (48–56 Ma), relative to present day (Fig. 5 A). The quantity (n = 123) and coherence of tropical early Eocene data from Δ47 and two other proxies means that we can confidently use this as a conservative estimate to assess model competency. Splitting the early Eocene into intervals approximating the EECO (50–52.5 Ma) versus post-EECO (55–52.5 Ma) does not significantly alter our finding as the latitudinal gradient for both intervals is within the uncertainty of the early Eocene data overall. Therefore, for the purposes of model-data comparison we do not split the early Eocene in this way because the overall sparsity of data may result in a regionally biased comparison.

Eocene Model-Data Comparison

Polar amplification in climate models of past warm periods has received much attention as it has long been suggested that simulations may not capture the extent to which the latitudinal SST gradient is reduced. In the Eocene, this debate has focused in part on the magnitude of tropical warming (23). For example, if tropical SST were far higher than at present and if high-latitude proxy data were summer-biased, then some models would be in overall agreement with the data (20). Our Δ47 reconstructions and SST compilation (Figs. 3 and 4) demonstrate that early Eocene tropical warming was of a substantially lower magnitude than in most models, and therefore indicate that the proxy data are irreconcilable with these simulations even when accounting for complicating factors in the high latitudes. Other simulations indicate SST exceeding the proxy estimates in both the tropics and high latitudes. For
example, the FAMOUS model simulation (46) shown in the context of the early Eocene proxy data in Fig. 3D is notable because it produces a substantially reduced latitudinal SST gradient. However, the parameter changes used to achieve this gradient reduction result in tropical SST that are ∼7 °C warmer than the proxy data.

Extending this comparison (Fig. 5A) by comparing the Eocene data latitudinal gradient to a number of climate simulations shows that HadCM3L (47) and GISS (48) are characterized by SST gradients within 10% of their preindustrial simulation. In contrast, CCSM (as configured by refs. 49 and 50) approaches the proxy gradient at four CO₂ doublings (4,480 ppm), while the CCSM models of ref. 12 (hereafter CCSMKS) and the warmest FAMOUS simulation (46) fall within the range of the proxy data, achieving latitudinal gradients below 80% of modern at 560 ppm CO₂. The common feature of these latter models is that both have substantially modified parameters related to cloud formation resulting in a reduction in low-level stratiform cloud, increased precipitation rates, and an increase in incoming shortwave radiation. Such clouds are more prevalent at high latitudes, resulting in preferential surface warming of these regions.

Although models with modified cloud properties are within error of a conservative latitudinal gradient, this does not imply agreement in terms of absolute temperatures (e.g., compare FAMOUS to the data in Fig. 3D). Therefore, to assess the ability of models to reconstruct both absolute SST and the latitudinal gradient, and to avoid the potential bias introduced by condensing model-data comparison into a latitudinal transect, the offsets between the proxy data and the nearest model grid cells were calculated to produce a location-specific proxy-model comparison. Figs. 5B and SI Appendix, Figs. S11–S14 display the result of this exercise in terms of the average tropical and high-latitude proxy-model offset, i.e., the mean of location-specific offsets between the model and data for the two regions (as above, the high-latitude proxy-model offset was conservatively estimated based on deep-ocean temperatures; SI Appendix). Models with Eocene latitudinal gradients similar to present day such as HadCM3L and ECHAM (Fig. 5A) consistently underestimate high-latitude SST. Moreover, we find that no simulation captures our conservative estimate of the latitudinal gradient and the absolute proxy temperatures. Specifically, most models that lie close to the 1:1 line in Fig. 5B, representing agreement in terms of the latitudinal gradient, overestimate both tropical and high-latitude SST and require pCO₂ greater than that indicated by the proxy data. Nonetheless, three CCSM simulations fall within 2–3 °C of the origin in Fig. 5B, indicating that these are close to reproducing our conservative analysis of the early Eocene latitudinal gradient, as well as the absolute proxy temperatures. CCSMKS, with modified cloud properties, achieves this with pCO₂ within the range of proxy data (1). However, we stress that our derivation of the early Eocene latitudinal gradient is conservative.

If high-latitude mean annual SST were in fact warmer than the deep ocean, then the model-data comparison would be considerably less favorable. Similarly, evidence for further polar amplification during the PETM (21) predicts a less-favorable comparison. Therefore, our analysis indicates that a further mechanism of polar amplification is likely to be required to fully reconcile models with peak Eocene warmth, given that CCSMKS (the best-performing simulations in our analysis) is characterized by a similar latitudinal SST gradient when run under pre-PETM and PETM conditions (Fig. 5A).

Our coupled Δα₂₃-Mg/Ca data and subsequent reanalysis of planktonic Mg/Ca temperatures via the precise reconstruction of Mg/Ca₀ demonstrate that the early Eocene mean latitudinal SST gradient was at least 32 ± 10% shallower than modern. Based on a location-specific comparison that avoids latitudinal averaging, we find that few modeling efforts (12) are close to reproducing both this gradient and the absolute proxy SST. Further work is required to capture the possible additional reduction in this gradient during peak warm intervals, or if Eocene mean annual high-latitude SST were warmer than the deep ocean. The most accurate Eocene simulations with respect to SST independently achieved this by modifying aerosol and cloud properties, highlighting the importance of this research direction as a potential mechanism for polar amplification (51).

Materials and Methods
All fossil samples come from clay or sand horizons (e.g., ref. 30) and none contained noticeable carbonate infillings that may bias the data. Additionally, broken chamber wall sections of key samples were imaged by SEM to confirm that micrometer-scale recrystallization had not taken place.

Samples were analyzed by laser-ablation ICPMS using the RESolution M-50 system at Royal Holloway University of London (RHUL) (52). The procedure for nondestructive analysis of LBF has been described in detail elsewhere (37), and was modified only in that the Agilent 7500 triple-quadrupole ICPMS used in that study was replaced with an Agilent 8800 triple-quadrupole ICPMS partway through the analytical period. Before clumped isotope measurement every specimen was analyzed by laser-ablation ICPMS to assess preservation on an individual specimen basis. The only exception to this was sample W10-3c and EF11/2, which contained abundant foraminifera, and all specimens analyzed were found to be geochemically well-preserved. Therefore, screening of every foraminifera was unnecessary. Aside from widely used preservation indicators such as Al/Ca for clay contamination and Mn/Ca for overgrowths, Mg/Ca and Sr/Ca are also useful preservation indicators as the Mg and Sr concentration of high-Mg calcite decreases upon recrystallization to values substantially lower than well-preserved Eocene LBF specimens (pervasively recrystallized samples are shown for comparison in SI Appendix, Fig. S5).

The clumped isotope analytical procedure at Yale University is described in detail elsewhere (45, 53). Larger specimens were crushed before cleaning; smaller specimens were analyzed as multiple whole shells. Modern samples were ultrasonicated for 30 min in ∼7% H₂O₂ rinsed three times in distilled


ACKNOWLEDGMENTS. We thank the editor, and reviewers for their constructive comments, which greatly improved this paper. D.E. and H.P.A. acknowledge support from Yale University and the Yale Analytical and Stable Isotope Center and from Grant 171/16 of the Israel Science Foundation. W.R. and L.J.C. were supported by NWO Grant ALW 822 01 009. The Tanzania Commission for Science and Technology (COSTECH) and the Tanzania Petroleum Development Corpora- tion supported the Tanzania Drilling Project (TDP) that recovered the Tanzanian specimens. Laser-ablation ICPSM project was funded by naturally a National Environmental Research Council (NERC) Capital Equipment Grant (Ref. CC073). The Research Foundation Flanders is acknowledged for financial support (To P.S.). M.Z. acknowledges support from the Netherlands Earth System Science Center and Horizon 2020 Grant MSCA-IF-2014-655073.

Evans et al.