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Despite recent advances, the link between the evolution of atmospheric CO₂ and climate during the Eocene greenhouse remains uncertain. In particular, modelling studies suggest that in order to achieve the global warmth that characterised the early Eocene, warmer climates must be more sensitive to CO₂ forcing than colder climates. Here, we test this assertion in the geological record by combining a new high-resolution boron isotope-based CO₂ record with novel estimates of Global Mean Temperature. We find that Equilibrium Climate Sensitivity (ECS) was indeed higher during the warmest intervals of the Eocene, agreeing well with recent model simulations, and declined through the Eocene as global climate cooled. These observations indicate that the canonical IPCC range of ECS (1.5 to 4.5 °C per doubling) is unlikely to be appropriate for high-CO₂ warm climates of the past, and the state dependency of ECS may play an increasingly important role in determining the state of future climate as the Earth continues to warm.
he Eocene Epoch is the most recent greenhouse period in Earth’s history. Atmospheric carbon dioxide (CO₂) and temperature peaked in the early Eocene, and both declined towards the late Eocene, ultimately leading to an icehouse state at the Eocene-Oligocene Transition (e.g. refs. 1–3). However, to better constrain the potential mechanisms driving the early Eocene warmth and the subsequent cooling, high-resolution records of CO₂ and temperature are required. While obtaining continuous marine records of temperature through this interval has been an ongoing effort (e.g. refs. 1,2), similar records for CO₂, need for improved constraints on the nature and evolution of spheric CO₂ is higher in warm climates than in cooler periods, the state-dependency of climate sensitivity. That is, the magnitude of modelling studies that have highlighted the possible existence of a state-dependency of climate sensitivity. That is, the magnitude of global mean temperature change following a doubling of atmospheric CO₂ is higher in warm climates than in cooler periods, including the modern climate system (e.g. refs. 16–8). In the Eocene, this is thought to result from non-linearities in the albedo response related to cloud feedbacks rather than snow and ice feedbacks6–8. These feedbacks are further modulated by changing palaeogeography, potentially linked to ocean area and deep water formation8. Given the major implications such a state dependency may have on the amount of warming by 2100 and beyond under high-emission scenarios (e.g. RCP8.5), there is a pressing need for improved constraints on the nature and evolution of climate sensitivity in different climate states.

In order to achieve this, we generate a new CO₂ record, spanning the Eocene Epoch with an average sampling resolution of 1 sample per 0.25 million years (Myr), using boron isotopes (δ¹¹B) in planktonic foraminifera from five pelagic sites located in the Atlantic and Pacific: International Ocean Discovery Program (IODP) Sites 1407 and 1409, Newfoundland margin; Ocean Drilling Program (ODP) Sites 1258 and 1260, Demerara Rise, and ODP Site 865, Allison Guyot, (Fig. 1). This record, coupled to existing δ¹¹B-CO₂ reconstructions5,9–11 and novel Global Mean Temperature (GMT) estimates, is used to provide proxy evidence of the state dependency in climate sensitivity, with higher sensitivity during the warm period of the early Eocene, and lower towards the transition to the colder, late Eocene.

Results and discussion

Reconstructions of seawater pH. We followed established methods to calculate seawater pH and CO₂ from foraminiferal δ¹¹B measurements4,12–14 (“Methods”). We employ the δ¹¹B proxy on mixed-layer species of planktonic foraminifera in all core sites to first reconstruct surface ocean pH. The majority of Paleogene foraminiferal species selected for this study were previously identified to reflect surface mixed layer conditions4,10, and are likely characterized by a reduction in the degree of pH modification in the micro-environment surrounding the foraminifera by physiological processes compared to observations in modern foraminifera4,14. When thermocline dwelling species were used, or additional species not previously analysed, we ensured that our new analyses of δ¹¹B overlapped with previously studied mixed-layer planktonic foraminiferal species (“Methods” and Supplementary Data 1) in order to constrain site-specific intra-species offsets and thus provide consistency and confidence in the derived mixed-layer pH (as in ref. 4). Seawater temperatures for the calculation of carbonate system parameters from δ¹¹B were estimated using foraminiferal Magnesium/Calcium (Mg/Ca) ratios determined on an aliquot of the same solution used for δ¹¹B analyses, assuming Eocene seawater Mg/Ca of 2.2 ± 0.1 mol/mol4,14 and the seawater adjusted Mg/Ca thermometer15.

Reconstructions of atmospheric CO₂. The derived surface seawater pH estimates from foraminiferal δ¹¹B were combined with the latitude-specific estimates of calcite saturation in surface waters (from cGENIE3), which we assume remains within a range of ±1, thereby accounting for uncertainty in both absolute value and any short-term variability16. Full error propagation was carried out using a Monte Carlo approach as described in ref. 4. The CO₂ record was then smoothed using varying span LOESS curve with the degree of smoothing optimised using generalised cross validation (Michael Friendly: https://tolstoy.newcastle.edu.au/R/help/05/11/15899.html). The 95% confidence intervals were then estimated from smoothing the residuals between the LOESS curve and the CO₂ data.

Eocene time-series of δ¹¹B-derived pH and CO₂. Our new continuous and high-resolution record of δ¹¹B-derived pH and CO₂ (Fig. 2, Supplementary Fig. 1) overlaps with existing low-resolution δ¹¹B-based records from Tanzania4,5, and records from the Middle Eocene Climatic Optimum (MECO; ~40.1–40.5 Ma)3, Eocene Thermal Maximum 2 (ETM2; 54.1 Ma)9, and the Paleocene-Eocene Thermal Maximum (PETM; ~56 Ma)10,11 (all re-calculated for consistency, see “Methods” and Supplementary Data 3), and demonstrates the validity of our multi-species treatment of δ¹¹B in deriving mixed-layer pH and CO₂ concentrations. This continuous view of the evolution of CO₂ confirms that the highest CO₂ levels, outside of the short-lived increase in CO₂ at the PETM9,10,17, occurred during the Early Eocene Climatic Optimum (EECO; 49–53 Ma9). Pre-PETM CO₂
Drivers of the ca. 51 Ma decoupling between δ13C and CO2. Although the timing of major weathering regime changes and volcanic events coincide with large variations in our CO2 curve, there is structure within our record that require the action of additional processes. Previous work indicates that δ13C and δ18O values are tightly coupled on short-term orbital scales and across hyperthermals such as the PETM (e.g. ref. 38); however, they decouple on longer timescales, including in the marked transition from ca. 51 to 51.5 Ma, characterized by a 1–2‰ increase in benthic foraminiferal δ13C records during the sustained warmth of the EEO (Fig. 3)39,40. Our CO2 record demonstrates for the first time that this increase in δ13C is not associated with a systematic change in CO2.

Large scale circulation changes could cause this δ13C-CO2 decoupling, but they preceded the EEO by ca. 6 Ma41, except the short-lived changes in deep water formation during hyperthermal events, such as the PETM42. Additionally, cessation of North Pacific deep-water formation43, a more inter-basin thermohaline circulation δ13C pattern44 (Fig. 3f), and establishment of a proto-Antarctic Circumpolar circulation (proto-ACC) associated with the gradual Drake Passage opening (ref. 45) and the Tasman Seaway widening (refs. 46,47) followed the EEO CO2 and temperature decline (post 47 Ma). Therefore circulation changes are unlikely to have been the main drivers of the δ13C and CO2 decoupling within the EEO.

Alternatively, this decoupling could arise from multiple changes in carbon sources and sinks. Volcanic carbon emissions could have been associated with a nearly neutral atmospheric δ13C signal while still elevating CO2 concentrations, such as the case of metamorphic degassing of carbonates, whereas the positive δ13C excursion can be explained by enhanced burial of δ13C depleted organic carbon48. Although the amount of organic
carbon burial across the early Eocene remains debated\(^{49,50}\), the most striking evidence for organic carbon burial increase is the S isotope record obtained from foraminifera calcite\(^{51}\) (Fig. 3e) and sedimentary barite\(^{52,53}\), which reveals a sharp increase in $\delta^{34}S_{\text{sof}}$ seawater sulfate starting at ca. 52 Ma and is potentially linked to a change in the locus of organic carbon burial and an increase in the burial of organo-sulfides\(^{51,52,54}\).

Global mean temperature and climate sensitivity. Regardless of the causes of the evolution of CO$_2$ through the early Cenozoic, our new CO$_2$ record clearly resembles long-term deep-sea and surface seawater temperature (SST) records as compiled in refs. \(^{1,2,38–40,55}\), (see “Methods”, Fig. 4). To further explore the relationship between CO$_2$ and the global mean temperature evolution during the Eocene, we first computed GMT (Methods). However here, rather than using multi-site, non-continuous foraminiferal $\delta^{18}O$ records\(^{8}\), which have also been shown to be impacted by diagenesis\(^{56,57}\), we use the continuous TEX$_{86}$-SST record from the equatorial Atlantic (ODP 959)\(^1\) and the model simulations with the NCAR Community Earth System Model version 1 (CESM 1) in ref. \(^1\), which provide a transfer function from SST at ODP 959 to a global mean in four specific time windows (54–49, 48–46, 42–42, 38–35 Ma; Supplementary Fig. 2).

The relative change in climate forcing (W m$^{-2}$) within the Eocene attributable to CO$_2$ change relative to preindustrial (PI) CO$_2$ (278 ppm) ($\Delta$CO$_2$) is calculated using the formulation of ref. \(^{58}\). Earth System Sensitivity (ESS), defined as the mean temperature response to all radiative perturbations\(^{59}\), can then be computed from the change in global mean temperature relative to preindustrial ($\Delta$GMT), using the equation:

$$\text{ESS} = \frac{\Delta\text{GMT}}{\Delta\text{FCO}_2} \times 3.87$$

where the 3.87 W m$^{-2}$ expresses the ESS as the temperature change due to a CO$_2$ doubling. However, to isolate the climate change due purely to changes in CO$_2$, we must first account for the influence of paleogeography and solar constant on GMT. To
do this we subtract a time variant correction following ref. 8 estimated to ~0.5 °C in the late Eocene and 1.5 °C in the early Eocene (Supplementary Data 2). Finally, we provide an estimate of Equilibrium Climate Sensitivity (ECS) by accounting for the contribution to Eocene GMT of the changes in the land-ice sheets (equivalent to 1.5 ± 0.5 °C, refs. 60, 61), a slow-climate feedback not considered in climate models (PALAEOSENS59). To calculate ECS in this way we use Eq. (1), but we first subtract from GMT the estimated temperature changes due to solar constant, paleogeography, and ice sheets (Fig. 5a and Supplementary Data 2). Note that we do not provide any corrections for other greenhouse gasses. Finally, to examine the robustness of our findings to our chosen record of GMT we use an independent alternative approach for calculating GMT from ref. 8 using foraminiferal δ18O (related to deep water temperature) as in Fig. 2c.

Recently, a number of studies have focused on non-linearities of the climate system during the Eocene, such as those related to changes in paleobathymetry affecting ocean area and deep water formation6, and short-wave cloud feedbacks linked to cloud microphysics, amplifying surface warming through changes in clouds6. Here we compare our GMT vs. ΔFCO2 relationship for the Eocene to climate model derived relationships for different boundary condition and processes (Fig. 5b). Largely independent of the approach used for calculating GMT, the majority of our reconstructions fall within the range of Paleogene simulations in refs. 6, 7. Our time-evolving record of ECS (and ESS) through the Eocene, even when considering the large uncertainty it inherits from the individual GMT and CO2 values used for its calculation, shows that the highest ECS estimates occur consistently during the warm intervals of the Eocene, such as the PETM, ETM2, EECO and MECO, and progressively decline towards the EOT (Fig. 5a).

The declining ECS for the Eocene, and the overlap between our early Eocene climate sensitivity estimates and the model output of ref. 8 (Fig. 5b), provide a strong confirmation of state dependency of ECS likely driven by changes in cloud-microphysics6. This finding is robust to the uncertainties in final estimates of ECS as it is present in all processing scenarios we consider which largely influence our estimates of absolute ECS, not the pattern of its evolution through time. The decrease in GMT that we observe post 39 Ma (Fig. 5b), however, is not sufficiently described by this early Eocene model, implying that non-CO2 boundary conditions may be playing a role in changing climate at this time, such as changes in paleogeography and/or associated changes in ocean circulation, and the presence of ice sheets8, 47, 62–65.

Our new compilation of δ11B-CO2 from planktonic foraminifera from multiple open ocean sites provides a comprehensive

Fig. 4 Comparison of the δ11B-derived CO2 to temperature records. a CO2 compilation as in Fig. 2a, b Sea surface temperature (SST) records, as compiled in ref. 1 (see “Methods” for the list of references used in the compilation). Purple dotted line connects the TEX86 record from ODP 9591. c Benthic foraminifera δ18O (related to deep water temperature) as in Fig. 2c.
picture of the evolution of CO₂ through the Eocene, greatly improving on recent CO₂ compilations (ref. 3 and Supplementary Fig. 3) and allowing for the first direct comparison with high-resolution records of climate variability. Our reconstructions, while still underlining the importance of CO₂ in driving the evolution of Eocene climate, provide evidence of strong non-linearities between climate and CO₂ forcing, likely related to both cloud feedbacks for the early-mid Eocene, and changing paleogeography and ice sheets for the late Eocene. This reveals climate-state dependent feedbacks and elevated ECS operated during the warmest climates of the last 65 million years.

Methods

Site information and age models. Boron isotopes ($\delta^{11}B$) from mono-specific samples of planktonic foraminifera were obtained from a number of deep-sea, open-ocean Paleogene-age core locations (Fig. 1). Sites ODP 865 and ODP 1258 and 1126 were positioned in subtropical/tropical paleolatitude and Sites IODP 1407/1409 was likely within temperate latitudes (Fig. 1), and all sites were located within deep-bathyal water depths throughout the Eocene above the calcite compensation depth (CCD). Age models for IODP 1407/1409 and ODP 1258/60 were updated to ref. 39 timescale.

The age-depth model used for site 865B (Supplementary Table 1 and Supplementary Fig. 4) in this study was based on that from ref. 69, with refinements in this study including re-adjustment to the GTS201268 timescale. The model uses a linear fit, but it is solely based on planktonic foraminiferal events (excluding nannofossils), because of suspected winnowing bottom water currents that may have mobilized the fine fraction containing nannofossils, making them suspect.

We only used datums for which GTS2012 ages were available and in which we had significant confidence (Supplementary Table 1), such as those without obvious signs of reworking. At Sites IODP 1407 and 1409 the planktonic foraminifera exhibit glassy test textures and appear minimally influenced by post-depositional recrystallization68, while at ODP 1258/1260 and ODP 865 the foraminifera specimens are frosty in appearance67, indicative of partial or complete recrystallization, with the most altered site being ODP 865, without hampering identification of individual species. Nevertheless, it has been shown that at least at ca. 40.3 Ma, ODP 865 $\delta^{11}B$ values are indistinguishable from that of glassy, well-preserved foraminifera from the Tanzania Drilling Project (TDP)73.

Records of $\delta^{13}C$ and $\delta^{18}O$ displayed in Fig. 2 to Fig. 4 were generated from ODP Sites 1258, 1262, 1263, 1265 and 1267 and 1209 in refs. 40, 55, 74–81, and the ref. 39 age model, and from Deep Sea Drilling Project and ODP sites in ref. 38.

Sample preparation. Approximately 3 mg of 73 mono-specific planktonic foraminiferal carbonate samples of a narrow size fraction (Supplementary Data 1) were separated from 2 to 10 cm of core material for tandem analyses of boron isotopes and trace element composition. Identification of planktonic foraminifera followed ref. 37, and samples were cleaned following established methods82–84.

Trace element to calcium ratios were determined as in ref. 84 and Al/Ca ratios were typically <150 μmol/mol signifying efficient surficial clay removal during the foraminiferal cleaning procedure84. For all core sites used in this study, there was no relationship between Al/Ca μmol/mol and foraminiferal $\delta^{11}B$ measurements, suggesting that any clay remnants did not bias the measured $\delta^{11}B$ values18.

Mg/Ca analyses, temperature reconstructions. Trace element to calcium analyses were carried out using a Thermo Scientific Element XR sector-field inductively-coupled-plasma mass spectrometer (SF-ICPMS) at the University of Southampton. The long-term precision (2 s.d.) of an in-house carbonate standard was 2% for Mg/Ca (mmol/mol) and Al/Ca (μmol/mol). Seawater temperature was estimated from each sample using foraminiferal Mg/Ca ratio on a aliquot of the same solution used for $\delta^{11}B$ analyses, assuming Eocene seawater Mg/Ca of 2.2 ± 0.1 mmol/mol24 and Mg/Ca-temperature calibration sensitivity was adjusted based on the seawater Mg/Ca value15. The temperature uncertainty is set to a range of ±2 °C and it is fully propagated into our carbonate system estimates (see below).

Relative $\delta^{11}B$ offsets. Identification of planktonic foraminiferal depth habitats in this study are based on relationships between stable isotope foraminiferal geochemistry and ecology in relationship to $\delta^{11}B$ offsets (e.g., refs. 68, 69, and references therein). Additional foraminifera species used here (M. aragonensis, A. incerta, T. frontosa, Truncorotalia decussata, T. ampliapertura) were cross-calibrated against previously known species (A. pseudopatellina, A. praetopilensis, A. solidoaenesis, G. mutabilis) using the same time interval and core site and site-specific species $\delta^{11}B$ were not identified. In site ODP 865, the $\delta^{11}B$ composition of Turborotalia decussata, T. frontosa, and T. ampliapertura are offset from the mixed layer species A. rohri, A. praetopilensis and A. topilensis by on
average 1.02 ± 0.04 (2 s.e., n = 3) ‰, confirming previous estimates for T. ampliapertura4, but showing less of an offset for the species T. cerroazonus compared to TDP4. We used the site-specific offset here for this species, propagating the uncertainty of this offset correction through the calculations. Sites 1407 and 1409 are dominated by A. bulloides in the late Eocene which recorded variably lower δ18O values than known shallow mixed layer species and so were excluded from the time series compilation. For consistency, we have included previously published δ18O records generated from planktonic foraminiferal species we have tested for relative vital effects and interspecies offsets in our timeseries. Therefore, we excluded the M. velascoensis record of the PETM17, since this species is randomly offset from our tested species A. soldaikienensis when comparing five samples from site 1209 and at similar ages (δ18O 38.2‰ ± 0.6‰ 2σ.d.3,7). Also, A. neptunei and G. klugeri records from the MECO1 are excluded, because the former showed variable habitat depth and δ18O offsets in TDP4, and the latter is not sufficiently tested for within site interspecies offsets.

Boron isotope proxy and analyses. Boron isotopes in planktonic foraminifera have been used extensively to reconstruct past ocean pH and thus CO2 concentrations e.g. refs. 4,18,42,62. Here we use the Thermo Scientific Neptune multi-collector ICP-MS at the University of Southampton. External reproducibility of δ11B analyses is calculated from the long-term precision of consistency standards, and two relationships depending on the amplifiers used for the Faraday cups:

For 1012 amplifiers : 129690 ± e−214‰(δ11Bsw) + 0.339 ± e−1.54‰(δ11Bsw) (2)

For 1014 amplifiers : 2.251 ± e−2.61‰(δ11Bsw) + 0.278 ± e−6.59‰(δ11Bsw) (3)

The seawater boron isotopic composition (δ11Bsw) for the Eocene has been estimated in ref. 4 based on two scenarios, one involving no vital-effect corrections (38.2–38.7‰) and one using the modern surface dwelling Tribolitus sacculifer11 δ11B composition (38.5±6‰). For the targeted Eocene planktonic foraminiferal species, δ11B vital effects as observed in modern (extant) species are likely not applicable4. If vital effects are present in Eocene foraminiferal δ11B, these only played a minor role4,17, supported by the demonstration that during periods of reduced δ11Bsw, vital effect corrections on δ11B are also reduced14, especially for when targeting small size fraction foraminifera as in this study (Supplementary Data 1). Nonetheless, we also apply the modern T. sacculifer calibration19 (for the 300 to 355 μm size fraction), adjusting the intercept of the calibration to Eocene-specific δ11Bsw as described in ref. 14. (T. sacculifer δ11B-PH proxy intercept = 1.748 for average δ11Bsw = 38.75‰.)

This provides an upper limit on potential δ11B vital effects in the Eocene planktonic foraminifera selected here. Notably, our calculated pH and CO2 estimates for both approaches are largely within uncertainty (Supplementary Data 1).

Second carbonate parameter. After computing seawater pH using Eocene δ11Bsw and foraminiferal δ11B, an additional carbonate parameter is required to calculate CO2 concentrations at any given seawater salinity and temperature. Here, the second parameter we use is the surface oceanic saturation of calcite (surface Ωcalc = [Ca2+]s/[CO32−]pKsp), estimated at different paleolatitudes4. For IODP 1407/1409, Ωcalc is estimated at 4.5 ± 1, for ODP 865 and ODP 1258/1260 Ωcalc is estimated at 6.5 ± 1, for the re-processing of the δ18O data of δ34S from DSDP 401 we used Ωcalc 4.5 ± 1, and the data from ODP1209/1210 and ODP 1265 in ref. 19 we used Ωcalc = 6 and 4.5 ± 1, respectively. In support of the narrow range of potential Ωcalc, a variety of carbon cycle modelling studies of the early Cenozoic oceans show that surface water Ωcalc remains, within ±1, essentially constant and independent of model boundary conditions16,83,86.

Monte Carlo pH–CO2 estimates from planktonic foraminiferal δ11B. We followed established methods to calculate seawater pH and CO2 from foraminiferal δ11B12–14. Atmospheric CO2 was calculated using a Monte Carlo approach to solve the relevant carbonate system equations with 1000 iterations, deriving mean, upper and lower bounds of 95% of the simulations. We use the seawater Ca and Mg concentrations and salinity constraints in ref. 4 and the equation in ref. 12,13 to calculate the carbonate ion product of 100 realization of TEX86-temperature reconstruction and analytical uncertainty1, randomly sampled within its 95% CI uncertainty envelope, including the standard errors of the regression (Supplementary Fig. 2).

GMT calculations. We convert the ODP 959 TEX8E SST record of ref. 1 to GMT, employing previously published model simulations with the NCAR CESM version 1 with CAM 4, which essentially provides a transfer function from SST at ODP 959 to a global mean in four specific time windows (54–49, 48–42, 42–36, 36–35 Ma, Supplementary Fig. 2). The regression is then:

\[
\text{GMT} = 0.91 \pm (0.04) \times \text{SST (ODP 959, TEX8E)} - 6.66 \pm (1.3) \times (1\text{s.d.})
\]


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Author contributions
E.A. conducted the boron isotope and trace element analyses, calculated and drafted the manuscript. E.H., P.F.S. prepared foraminifer samples and provided taxonomic and age model expertise. P.N.P. led the taxonomy and foraminifera and age model selection. A.R. provided constrains on carbon cycling. T.L.B. with T.B.C. completed a subset of IODP 1409 boron isotope and elemental analyses. D.J.L. advised on climate sensitivity calculations, and D.J.L., R.D.P. and G.L.F. assisted on refining the discussion section. All co-authors contributed to the final text.

Competing interests
The authors declare no competing interests.

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