Causes of ice age intensification across the Mid-Pleistocene Transition

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During the Mid-Pleistocene Transition (MPT; 1,200–800 ky), Earth’s orbitally paced ice ages cycles intensified, lengthened from ~40,000 (~40 ky) to ~100 ky, and became distinctly asymmetrical. Testing hypotheses that implicate changing atmospheric CO$_2$ levels as a driver of the MPT has proven difficult with available observations. Here, we use orbitally resolved, boron isotope CO$_2$ data to show that the glacial to interglacial CO$_2$ difference increased from ~43 to ~75 μatm across the MPT, mainly because of lower glacial CO$_2$ levels. Through carbon cycle modeling, we attribute this decline primarily to the initiation of substantive dust-borne iron fertilization of the Southern Ocean during peak glacial stages. We also observe a twofold steepening of the relationship between sea level and CO$_2$-related climate forcing that is suggestive of a change in the dynamics that govern ice sheet stability, such as that expected from the removal of subglacial regolith or interhemispheric ice sheet phase-locking. We argue that neither ice sheet dynamics nor CO$_2$ change in isolation can explain the MPT. Instead, we infer that the MPT was initiated by a change in ice sheet dynamics and that longer and deeper post-MPT ice ages were sustained by carbon cycle feedbacks related to dust fertilization of the Southern Ocean as a consequence of larger ice sheets.

Significance

Conflicting sets of hypotheses highlight either the role of ice sheets or atmospheric carbon dioxide (CO$_2$) in causing the increase in duration and severity of ice age cycles ~1 Mya during the Mid-Pleistocene Transition (MPT). We document early MPT CO$_2$ cycles that were smaller than during recent ice age cycles. Using model simulations, we attribute this to post-MPT increase in glacial-stage dustiness and its effect on Southern Ocean productivity. Detailed analysis reveals the importance of CO$_2$ climate forcing as a powerful positive feedback that magnified MPT climate change originally triggered by a change in ice sheet dynamics. These findings offer insights into the close coupling of climate, oceans, and ice sheets within the Earth System.

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evidence that CO₂ decline was most pronounced during glacial stages. Here, we build on that work with the aim to resolve the coupling of CO₂ and climate on orbital timescales to address major unanswered questions regarding the role of CO₂ change in the MPT.

To better quantify the role of CO₂ during the MPT, we present two orbitally resolved, boron isotope-based CO₂ records generated using the calcite tests of surface-dwelling planktonic foraminifera from Ocean Drilling Program (ODP) Site 999 in the Caribbean (Fig. 3 and Figs. S1 and S2). Boron isotopes (δ²⁹B) in foraminifera have proven to be a reliable indicator of past ocean pH (18, 19) and with appropriate assumptions regarding a second carbonate system parameter (Materials and Methods and Fig. S3), allow reconstruction of atmospheric CO₂ levels. Site 999 likely remained near air–sea CO₂ equilibrium through time (20), and this is further supported by agreement of our data (blue and red in Figs. L4 and 3) with published low-resolution δ¹³C-based CO₂ data from ODP Site 668 in the equatorial Atlantic (11) (purple squares in Figs. L4 and 3B) and with the ice core CO₂ compilation (14).

Fig. 2. Changing relationship between CO₂ climate forcing and ice sheet size. Three scenarios (A–C) for the MPT intensification of glacial cycles compared with observations (D). Reconstructed SL is taken here to reflect continental ice sheet size in relationship to CO₂ climate forcing (ΔRCO₂) calculated (33) from our orbitally resolved CO₂ data. In all panels, red and blue represent conditions during our two sampling intervals before and after the MPT (i.e., eMPT and LP260), respectively. The end member scenarios posit (A) a change in ice sheet dynamics, causing ice volume to become more sensitive to unchanged G-I-G climate forcing, and (B) an unchanged sensitivity of ice sheet size to forcing, with glacial intensification driven by additional CO₂ drawdown. Neither one of these two scenarios adequately describes both observed changes of increased ice sheet sensitivity (greater slope) and additional glacial CO₂ drawdown (more negative climate forcing). Here, we argue for a hybrid scenario with a change in ice sheet dynamics (possibly caused by regolith removal of ref. 8 or ice sheet phase-locking of ref. 10), allowing ice sheets to grow larger and to trigger a positive ice–dust–CO₂ feedback that promotes additional glacial intensification. In D, the regression confidence intervals account for uncertainty in both SL and ΔRCO₂ (SI Forcing to SL Relationship), but to avoid clutter, we only display the regression based on the Mediterranean SL reconstruction (4) and the uncertainty on the slope rather than the individual data points. We refer the reader to SI Forcing to SL Relationship and Fig. S7 for other SL records and full treatment of data uncertainties.
Ocean and Atlantic mechanisms thought to have contributed to the most recent Late Pleistocene G-IG CO₂ cycles (22). For this, we force the CYCLOPS carbon cycle model (23) with ODP 1090 sedimentary iron mass accumulation rates (24), ODP 1094 Ba/Fe ratios (25), and ODP 982/U1313 (Fig. S1) benthic Δδ³¹C variations (26, 27) to represent, respectively, (i) sub-Antarctic dust-borne iron fertilization; (ii) combined changes in polar Antarctic stratification, nutrient drawdown, and export production; and (iii) transitions in the geometry and depth structure of the Atlantic Meridional Overturning Circulation (AMOC) (Fig. S5). These mechanisms and their model sensitivities have been documented elsewhere (23). Here, we invert the model and the forcing to minimize the mismatch between simulated atmospheric CO₂ levels and the ice core CO₂ record of the last 800 ky (residual rms error of 12.3 μatm) (SI Carbon Cycle Modeling) and then, to predict atmospheric CO₂ levels back to 1,500 ky (Fig. S5) for comparison with our data.

We find that changes in the periodicity of simulated CO₂ levels closely match those in the ice core CO₂ record, in the benthic foraminiferal oxygen isotope record, and in our δ¹³B-based CO₂ reconstruction (Fig. S6). Within the relative age uncertainty between the model forcing and our δ¹³B record, we find that the model explains more than 60% of the variance observed in our eMPT CO₂ reconstruction, in line with model and reconstruction uncertainties. The model inversion does not include any secular change in the silicate weathering cycle (11) (SI Carbon Cycle Modeling), so that simulated CO₂ change is exclusively related to carbon redistribution within the ocean–atmosphere system and associated CaCO₃ compensation dynamics (22, 23).

**Results**

Our two datasets span an early portion of the Mid-Pleistocene Transition (eMPT) from 1,080 to 1,250 kya (n = 51) and for validation against the ice core CO₂ record, the Pleistocene interval from 0 to 260 kya (LP260; n = 59, including 32 recalculated data points from ref. 18), yielding a similar median sampling interval of ~3.5–4.5 ky for both records. Our LP260 CO₂ dataset has a confidence interval of ±20 μatm (2σ) and is offset by a mean of +7 μatm from the ice core CO₂ data when accounting for both CO₂ and age uncertainties (21) (Fig. S8B and SI Methodology). Comparison between our two CO₂ records reveals that eMPT glacial on average were associated with higher CO₂ levels than LP260 glacial (eMPT: 241 ± 21 μatm vs. LP260: 203 ± 14 μatm; 2σ), whereas interglacial levels were indistinguishable between the two time slices (eMPT: 284 ± 17 μatm vs. LP260: 277 ± 18 μatm; 2σ).

We evaluate the reconstructed G-IG CO₂ change across our study interval with a carbon cycle model inversion of Southern

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**Fig. 3.** Reconstructed ice age CO₂ cycles before and after MPT. (A) Boron isotope data from ODP 999 (Fig. S1) shown in blue (LP260) and red (eMPT) along with the LR04 deep sea benthic foraminiferal oxygen isotope stack (black) (26). (B) CO₂ levels calculated from boron isotopes (same colors as above) compared with ice core (black) (14) and previous low-resolution boron-derived CO₂ data (purple) (11). Probabilistic assessments are shown as the colored bands, with the probability maximum shown within a dark band that represents its 95% probability envelope (±6 ppm) and a lighter band that represents the full 95% envelope of the sampled distribution. As illustrated by B, Inset, comparison between our (red) eMPT and (blue) LP260 records reveals that glaciads on average experienced higher CO₂ levels during eMPT than LP260 (eMPT: 241 ± 21 μatm vs. LP260: 203 ± 14 μatm; 2σ), whereas interglacial levels were indistinguishable between the two time slices (eMPT: 284 ± 17 μatm vs. LP260: 277 ± 18 μatm; 2σ).

**Fig. 4.** CO₂ change since the MPT. Quantified from different datasets: boron isotope data from ODP 999 (this study) and ODP 668 (11), CO₂ directly measured on stratigraphically disturbed ~1-My-old blue ice from the Allan Hills (17), and CYCLOPS model inversion (this study). For each dataset, we quantify the change in (Top) interglacial and (Middle) glacial CO₂ levels as well as (Bottom) the change in the magnitude of interglacial–glacial CO₂ cycles. For this analysis, we define glacial and interglacial subsets of the datasets based on a 25% cutoff criterion, subsampling the data with the 25% lowest/highest δ¹³O (marine records) or CO₂ (ice core; model). As further discussed in SI Quantification of δ¹³C CO₂, δ¹³C CO₂, and δ¹⁵N CO₂, the results are robust for a wide range of cutoff values (Fig. S4). Thick black bars denote the uncertainty on the estimated CO₂ change, while thin black bars denote the one-sided test of the sign of CO₂ change at 95% significance level. We note that the ODP 668 uncertainties do not encompass the underlying alkalinity and seawater boron isotope composition assumptions, which are included in the uncertainty propagation for our ODP 999 data. The Allan Hills ice may not capture the full range of CO₂ levels (17).
In good agreement with the δ11B-based CO2 reconstructions and the ice core CO2 measurements, the model inversion yields (i) insignificant (−1 ± 3 μatm; 2σ) eMPT to LP260 interglacial CO2 change and (ii) a ~22 ± 5 μatm (2σ) eMPT to LP260 decline in glacial-stage CO2 levels (Fig. 4 and Fig. S4). In the model, we can attribute most of the additional glacial CO2 drawdown to MPT intensification of glacial dust-borne iron fertilization of biological productivity and nutrient utilization in the Sub-Antarctic Zone of the Southern Ocean (24, 28–30) (Fig. S5). AMOC shoaling also seems to have become more prevalent after ~1,200 ky but contributes less to simulated CO2 change (23). The model reproduces relatively well reconstructed interglacial CO2 from 400 to 800 ky, because use of ODP 1094 Ba/Fe in the model inversion results in persistent polar Southern Ocean stratification as suggested previously (25). Through our eMPT sample interval, the model reproduces the ~80-ky CO2 periodicity that is evident in our eMPT δ11B data (Fig. S6), mainly because of an ~80-ky periodicity in eMPT polar Antarctic stratification and nutrient cycling recorded in ODP 1094 Ba/Fe (25). While all three forcings (iron fertilization, Atlantic circulation, coupled polar Antarctic changes) contribute to the simulated changes in CO2 periodicities that are highly coherent with the MPT change in rhythm of the climate system, the iron fertilization influence dominates the MPT intensification of ice age CO2 drawdown (Fig. S5).

Discussion

MPT intensification of glacial-stage CO2 drawdown is consistent with stabilization of continental ice sheets during increasing orbital obliquity by reduced greenhouse gas forcing, thereby helping ice sheets to grow larger and for periods longer than one obliquity cycle (scenario 2 in Fig. 2). However, when we directly compare changes in SL as a measure for ice volume against CO2 change (23). The model reproduces relatively low reconstructed interglacial CO2 from 400 to 800 ky, because use of ODP 1094 Ba/Fe in the model inversion results in persistent polar Southern Ocean stratification as suggested previously (25). Through our eMPT sample interval, the model reproduces the ~80-ky CO2 periodicity that is evident in our eMPT δ11B data (Fig. S6), mainly because of an ~80-ky periodicity in eMPT polar Antarctic stratification and nutrient cycling recorded in ODP 1094 Ba/Fe (25). While all three forcings (iron fertilization, Atlantic circulation, coupled polar Antarctic changes) contribute to the simulated changes in CO2 periodicities that are highly coherent with the MPT change in rhythm of the climate system, the iron fertilization influence dominates the MPT intensification of ice age CO2 drawdown (Fig. S5).

Materials and Methods

Globigerinoides ruber white sensu stricto (300–355 μm) were picked from sediments from ODP 999A (Fig. S1), and the age model was constructed by benthic oxygen isotopes from the same samples and X-ray fluorescence scanning data. Samples were measured for boron isotope composition using a Thermo Scientific Neptune multicollector inductively coupled plasma mass spectrometer at the University of Southampton according to methods described elsewhere (18). Analytical uncertainty is given by the external reproducibility of repeat analyses of Japanese Geological Survey Porites coral standard at the University of Southampton and is typically <0.2% (at 95% confidence). Metal element–calcium ratios (Mg, B, Al) were analyzed using Thermo Scientific XSeries II inductively coupled plasma mass spectrometer at the University of Southampton. Here, these data are used to assess adequacy of clay removal (Al/Ca < 100 μmol/mol) and to generate down core temperature estimates. CO2 was calculated using a Monte Carlo approach (10,000 replicates) with estimates of salinity and alkalinity using a flat probability spanning a generous range (34–37 psu and 2,100–2,500 μmol/kg, respectively). A normal distribution around proxy data was used for all other interpretation variables (temperature, δ11B, δ18O, δ13C, Ba/Fe). The CO2 record was then probabilistically assessed using a Monte Carlo approach that considers uncertainties in both age and CO2 values and that preserves the stratigraphic record of the last 800 ky. Significant linear correlation with and matching spectral content to our boron isotope-based CO2 data confirm the skill of the model inversion (Fig. S6). Detailed statistical analysis is carried out to identify and quantify changes in absolute glacial and interglacial CO2 as well as the G-IG CO2 range from the model inversion results, our high-resolution CO2 data, and some previous datasets (11, 17) that are not well dated or lack the required temporal resolution for comparison in the time and/or frequency domains. This analysis is based on estimation of the population means of cumulative probability density of glacial and interglacial subsamples, which were selected based on either available benthic foraminiferal δ18O or CO2 rank (Fig. 4). Factorial analysis of the validated model allows for the mechanistic attribution to sub-Antarctic iron fertilization of glacial stage-specific CO2 reduction associated with the MPT interval (Fig. S5, Bottom), which is the pattern that we identified as common between model and all three empirical datasets. More detailed descriptions of inverse modeling and model/data cross-validation and statistical quantification of CO2 change can be found in SI Carbon Cycle Modeling and SI Quantification of δ13C CO2, δ18O CO2, and δ11B CO2, respectively.

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