

Global mean sea level over the past 4.5 million years

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Abstract

Changes in global mean sea level (GMSL) during the late Cenozoic remain uncertain. Here we use a new reconstruction of changes in $\delta^{18}\text{O}$ of seawater to reconstruct GMSL since 4.5 million years ago (Ma) that accounts for temperature-driven changes in the $\delta^{18}\text{O}$ of global ice sheets. Between 4.5 and 3 Ma, sea-level highstands remained up to 20 m above present while the first lowstands below present suggest onset of Northern Hemisphere (NH) glaciation at 4 Ma. Intensification of global glaciation occurred from 3 Ma to 2.5 Ma, culminating in lowstands similar to the Last Glacial Maximum lowstand at 21,000 years ago and that reoccurred throughout much of the Pleistocene. We attribute the middle Pleistocene transition in ice-sheet variability (1.2 Ma to 0.62 Ma) to modulation of 41-kyr obliquity forcing by an increase in ~ 100 -kyr CO_2 variability.

The record of $\delta^{18}\text{O}$ measured in benthic foraminifera shells ($\delta^{18}\text{O}_b$) (Fig. 1A) is widely used to represent the long-term evolution of combined changes in ocean temperature and global mean sea level (GMSL) over the Cenozoic (1-5) as well as to evaluate the response of the climate system to forcings on orbital and tectonic timescales (10^4 - 10^6 yr) (6-9). The fidelity of this record as a global signal has improved with the stacking of multiple records that increases the signal-to-noise ratio (10-12) and the use of several independent dating methods that provide a robust chronology (1, 11, 13, 14). Different strategies have then been used to decompose the $\delta^{18}\text{O}_b$ record into its temperature ($\delta^{18}\text{O}_T$) and seawater ($\delta^{18}\text{O}_{sw}$) components, with the former reflecting the temperature that the benthic foraminifera shells formed in (larger $\delta^{18}\text{O}_T$ in lower temperature) and the latter largely reflecting global ice volume (larger $\delta^{18}\text{O}_{sw}$ when more land ice). Although these strategies share the same goal, their different underlying assumptions have resulted in solutions with pronounced differences during the late Pliocene, early Pleistocene (beginning 2.6 Ma), and the middle Pleistocene transition (MPT) (defined herein as 1.2-0.62 Ma), thus confounding understanding of these critical periods of late-Cenozoic climate and GMSL change (fig. S1).

We address these issues by reconstructing GMSL for the past 4.5 million years (Myr) that circumvents several shortcomings associated with previous reconstructions (see supporting information, section 1). Using our new reconstruction of changes in global mean ocean temperature (ΔMOT), we previously decomposed a $\delta^{18}\text{O}_b$ stack (12) that includes a correction for some possible combination of diagenesis (15, 16) and the carbonate-ion effect on foraminifera (17) into its $\delta^{18}\text{O}_T$ and $\delta^{18}\text{O}_{sw}$ components (18). Here we convert our $\delta^{18}\text{O}_{sw}$ reconstruction (fig. S2C) to GMSL by applying a mass-balance approach that conserves $\delta^{18}\text{O}$ changes of the global ocean and the North American (Laurentide and Cordilleran) (NAIS), Eurasian (EUR), Greenland (GRN), and Antarctic (ANT) ice sheets, including loss of marine-based ANT ice (19, 20) (see the

supplementary materials, section 2). In doing so, our model accounts for time-varying temperature (21) and ice-volume effects on the $\delta^{18}\text{O}$ of ice sheets ($\delta^{18}\text{O}_i$) over the past 4.5 Myr that yields a variable relationship between $\delta^{18}\text{O}_{\text{sw}}$ and sea level (fig. S3), as opposed to methods that convert $\delta^{18}\text{O}_{\text{sw}}$ to sea level using a constant linear scaling between $\delta^{18}\text{O}_{\text{sw}}$ and sea level (22-26) or a variable scaling developed for just the last glacial cycle (27, 28).

Global mean sea level over the past 4.5 Myr

Our new reconstruction (Fig. 1C) shows that GMSL was largely above present from 4.5-4.0 Ma, with sea-level highstands of ~ 20 m and sea-level fluctuations of 5-20 m suggesting contributions likely from some combination of changes in GRN and ANT ice sheets although contributions from NAIS or EUR ice sheets cannot be excluded. Subsequent highstands between 4 and 3 Ma remained 15-20 m above present but lowstands now began to extend regularly below present by as much as -50 to -80 m thus marking the onset of extensive NH (NAIS, EUR) glaciation at ~ 4 Ma. The intensification of NH glaciation from 3 Ma to 2.5 Ma was marked by highstands that decreased to near-modern levels and lowstands that progressively decreased from -55 ± 29 m at 3 Ma to -151 ± 25 m at 2.52 Ma, which is comparable to or lower than the Last Glacial Maximum (LGM, 21 ka) lowstand (-132 ± 15 m) (Fig. 1C). Since 2.5 Ma, sea-level highstands have been within +10 m of present except between 2.25 Ma to 1.45 Ma when they remained as much as 50 m below present, suggesting incomplete deglaciation of NH ice sheets, while fluctuations of large LGM-size ice sheets continued throughout the Pleistocene.

Three factors used to derive our GMSL reconstruction combine to indicate that early Pleistocene ice sheets were comparable in volume to the LGM in contrast to most previous reconstructions that suggest that such large ice sheets did not appear until after the MPT (fig. S6A-D). First, with a ΔMOT that is $\sim 50\%$ of a corresponding change in global mean sea surface

temperature (Δ SST) before the MPT (18), the increasing (cooling) trend of $\delta^{18}\text{O}_\text{T}$ is smaller in our reconstruction than if $\Delta\text{MOT}:\Delta\text{SST}=1$ is assumed throughout the Pleistocene. Being a residual from the observed $\delta^{18}\text{O}_\text{b}$, our $\delta^{18}\text{O}_\text{sw}$ is thus more negative during the Pliocene and has a larger increasing trend between 3.0-2.5 Ma (compare figs. S2A and S2B). Second, because $\Delta\text{MOT}:\Delta\text{SST}$ was smaller during the early Pleistocene, so was glacial-interglacial MOT variability (15), limiting the contribution of $\delta^{18}\text{O}_\text{T}$ to glacial cycles in $\delta^{18}\text{O}_\text{b}$, in contrast to the middle and late Pleistocene when ocean temperature and ice volume exerted similar-size controls on $\delta^{18}\text{O}_\text{b}$. Third, we find that higher global mean surface temperatures (GMST) during the early Pleistocene caused the ice sheets to be isotopically heavier (fig. S3D). This reduced their influence on $\delta^{18}\text{O}_\text{sw}$ relative to the isotopically lighter ice sheets during the middle and late Pleistocene. At the same time, given our reconstructed $\delta^{18}\text{O}_\text{T}$, Ref. (18) identified the need to remove a spurious increasing trend from the $\delta^{18}\text{O}_\text{b}$ stack attributed to diagenesis (15, 16) or the carbonate-ion effect on benthic foraminifera (17) that, if unaccounted for, would have resulted in even more positive Pliocene $\delta^{18}\text{O}_\text{sw}$ values and larger early Pleistocene ice volumes than in our reconstruction (compare figs. S2B and S2C and figs. S2E and S2F).

The spectral characteristics of our GMSL reconstruction are dominated by 41-kyr variance until ~ 1.2 Ma. This is followed by the full emergence of a ~ 100 -kyr signal by 0.62 Ma (Fig. 2A) representing the ice-sheet expression of the MPT. There have been similar concentrations of ~ 100 -kyr and 41-kyr variance and a small concentration of 23-kyr variance over the past 0.8 Myr (Fig. 2A, 2B), with the latter being consistent with a long-term increase in precessional forcing from eccentricity modulation (29) rather than increasing southward expansion of NH ice-sheet margins during the MPT (30, 31). A 41-kyr filtered sea-level signal displays long-term (1 Myr) amplitude modulation of obliquity forcing until ~ 1 Ma, with lowest coherence between both occurring during

intervals of lower amplitude variations (i.e., nodes) (Fig. 2C, 2D). The increase in amplitude after the first node centered on 3.3-3.1 Ma may reflect a threshold response to the increase in obliquity forcing that led to the intensification of NH glaciation (32). The below-present highstands and reduced variability between 2.25 Ma and 1.45 Ma (Fig. 1F) are associated with the second node at ~1.8 Ma (Fig. 2C, 2D). The decrease in amplitude after the third node ~1 Ma reflects the decrease in size of 41-kyr ice sheets relative to those that characterized the Pleistocene prior to 1 Ma, with large ice sheets now occurring less frequently (every ~100 kyr) (Fig. 1C).

The evolution of changes in sea-level variability over the past 2.5 Myr as measured by sea-level terminations (defined as the maximum rate of sea-level rise during deglaciations) (Fig. 3D) shares the same relationship to obliquity as similarly defined GMST terminations (Figure 3B). This includes the occurrence of terminations between 2.5 Ma and 1.2 Ma for every (near-) maximum in obliquity, as previously found with an independent age model (13), except during the node in obliquity modulation centered on 1.8 Ma (Fig. 2C, 2D) when a small concentration of precessional variance appears (Figure 3F).

Over the past 1.2 Myr, we identify eight intervals (M8-M1) that begin and end with sea-level terminations associated with rising or peak obliquity (Fig. 3), with good agreement (within 0.5-4 kyr) between the mean ages of terminations during the past 1 Myr derived here and those derived from radiometric dating (14, 33, 34). Each of the eight intervals brackets 1-2 obliquity peaks without a corresponding termination (Fig. 3D, 3E), consistent with previous work (13, 35, 36). This low-frequency signal first appears at 1.19 Ma during the 72-kyr M8 interval. This pattern is repeated for the 78-kyr M7 interval between Terminations X (0.87 Ma) and IX (0.79 Ma) and the 89-kyr M6 interval between Terminations VIII (0.71 Ma) and VII (0.62 Ma), with each of these two intervals followed by a shorter length interval when a termination accompanies an obliquity

maximum. A similar interval of one skipped obliquity cycle between Terminations X and XII was inferred from a $\delta^{18}\text{O}_b$ record (14) but our ΔGMST and GMSL reconstructions show that the intervening Termination XI was as large as some earlier terminations (Fig. 3B, 3D). Five more intervals with 1-2 skipped obliquity cycles (M5-M1) span all of the past 0.53 Myr except for one brief 29-kyr interval between M3 and M2 (34) which reflects a temperature and sea-level oscillation during Marine Isotope Stage 7 associated with the strongest obliquity forcing since 2.5 Ma (Fig. 3C). The average duration of the M7-M1 intervals is 93.9 ± 13.4 kyr, resulting in the “100-kyr cycle” seen in the late-Pleistocene spectra of ΔGMST and GMSL (Fig. 3F) and their rates of change (Figs. 3B, 3D). One notable difference is that GMSL terminations throughout the Pleistocene only occur after sea level falls below -80 m followed by the next increase to (near-) obliquity maxima (Fig. 3E), suggesting that ice sheets become unstable when exceeding this size, whereas GMST terminations have no comparable temperature threshold.

Our reconstruction of Pliocene highstands and the onset of NH glaciation between 4 and 3 Ma is in good agreement with other studies (37-39) including one that subtracted local temperature from $\delta^{18}\text{O}_b$ to derive $\delta^{18}\text{O}_{\text{sw}}$ and sea level as done here (40) (fig. S5). A similar local temperature-based reconstruction reproduces the intensification of NH glaciation that culminated in a LGM-like sea-level lowstand at ~ 2.5 Ma (26) (fig. S5) while another reproduces large ice sheets throughout the Pleistocene (41) (fig. S6E). To first order, the similarity between temperature-based sea-level reconstructions and our GMSL reconstruction is due to the local temperature reconstructions being nearly the same as our ΔMOT reconstruction (18). Several additional lines of evidence identify early Pleistocene NH ice sheets that were at or beyond their LGM extents by ~ 2.5 Ma, including well-dated terrestrial (42, 43), marine (44, 45), and geophysical (46) records

(Fig. 1D) and ice-rafted debris records in the North Atlantic (47) and North Pacific (48) oceans (Fig. 1E), consistent with them being volumetrically as large as at the LGM.

In contrast, changes in Pleistocene GMSL inferred from the $\delta^{18}\text{O}_b$ record (49, 50) (Fig. 1A) and from several reconstructions derived from it (9, 22, 25, 27, 28) find that the culminating lowstand at 2.5 Ma was only ~40% that of the LGM lowstand. Subsequent lowstands then remained at a similar intermediate level (~ -50 m) until the MPT when they furthered lowered, reaching LGM-like levels by 0.8 Ma (fig. S6A-D). Given the robust evidence for spatially extensive early Pleistocene ice sheets (Fig. 1D, 1E), the associated intermediate-size lowstands imply low-aspect ratio ice sheets relative to those following the MPT (i.e., on average thinner, since the ice volume is less but the area the same). This was the basis for the regolith hypothesis for the MPT (51). We attribute these findings of intermediate-size early Pleistocene ice sheets to the underlying methods that, by default, preserve the variability of the $\delta^{18}\text{O}_b$ record, including the increase in the size of glaciations during the MPT, with a further underestimation of early Pleistocene glaciations due to the lack of accounting for the long-term decrease in GMST on $\delta^{18}\text{O}_i$ (Fig. S3) (see the supplementary materials, section 1). Lastly, the good agreement between our reconstruction and all those that cover the past 0.8 Myr (fig. S7) suggest a robust understanding of GMSL since the MPT.

Towards resolving the paradox of large early Pleistocene ice sheets

A well-known paradox posed by early Pleistocene GMSL reconstructions is that their spectra are dominated by 41-kyr variability despite peak summer insolation being dominated by precession (52). Coupled climate and ice-sheet models have reproduced NH ice-sheet 41-kyr variability when accounting for albedo feedbacks, the integrated summer insolation forcing, and thin ice sheets with ablation zones that remained poleward of 60°N (36, 53, 54). However, such

ice sheets are inconsistent with the geologic evidence for their southern margins in North America reaching 39°N during the early Pleistocene (Fig. 1D) (42, 55) and they would not dominate the variability seen in our reconstruction. Another hypothesis proposes that higher early Pleistocene temperatures caused the response of the ANT ice sheet to precessional forcing to be out of phase with NH ice sheets, thus cancelling the 23-kyr signal in sea-level records (56). However, hemispheric Δ SST reconstructions show a dominant in-phase 41-kyr signal with virtually no precessional power (21) and this hypothesis cannot account for the large obliquity-driven NH ice sheets in our reconstruction which had about twice the volume as modeled by Ref. (56).

We propose that obliquity forced variations in the Southern Ocean carbon cycle during the early Pleistocene caused dominant $[\text{CO}_2]_{\text{atm}}$ variability at this frequency (57). At the same time, the dominant 41-kyr signal of Southern Ocean SSTs and the temperature effects of related changes in the position of the sea-ice edge would have been advected through the shallow meridional circulation and upwelled in the equatorial Pacific (58, 59), where they combined with the SST variability from CO_2 forcing to induce the observed dominant 41-kyr SST signal at these low latitudes (21, 60). Observations (61) and modeling (62) show that changes in equatorial Pacific SSTs can strongly influence NH ice-sheet surface mass balance (SMB), with the ice-sheet changes then potentially acting as a positive feedback on equatorial Pacific SSTs (63).

Our results pose another dimension to this paradox in showing that large ice sheets existed throughout the Pleistocene while glacial GMSTs underwent a $\sim 6^\circ\text{C}$ long-term cooling (Figs. 1B, 1C), with polar amplification causing an even greater amount of cooling experienced by the high-latitude ice sheets (21). This relationship is further complicated by the strong effect that ice sheets have on their own local climate (64). We propose that the effects of higher early Pleistocene temperatures on ice-sheet SMB were mitigated by an associated increase in high-latitude

precipitation directly from warming (Clausius-Clapeyron relationship) as well as from latitudinal shifts in the westerlies as SST gradients changed (65). We can then infer that while cooling decreased accumulation over glaciated regions, the same cooling reduced surface ablation and thus caused SMB to remain positive. Similar transient relationships between other factors affecting SMB such as the influence of clouds on ice-sheet surface energy balance (66, 67) or terrestrial ecosystem emissions and atmospheric chemistry (68) can also be considered. If involved, changes in these transient feedbacks with global cooling continued to combine in such a way as to induce ice-sheet SMB that supported the growth of large ice sheets and then maintained their presence in response to obliquity forcing, suggesting an extraordinary balancing act that allowed the inception and growth of ice sheets to their maximum size under a range of GMST and $[\text{CO}_2]_{\text{atm}}$.

To explore this issue further, we conducted several experiments with the GENESIS V3.0 climate model (69, 70) to examine the sensitivity of early Pleistocene NH ice-sheet SMB to orbits, atmospheric CO_2 , and ice-sheet height (see supporting information, section 4, Table S1). We first assessed our modeling strategy by running an experiment with LGM boundary conditions and found that the simulated NH ice sheets are in or have positive SMB. Our sensitivity experiments for early Pleistocene ice sheets included various combinations of orbits corresponding to low (at 2.165 Ma) and high (at 2.145 Ma) obliquity (71), $[\text{CO}_2]_{\text{atm}}$ of 200 and 300 ppmv that covers much of the range suggested by proxies (72), and three ice-sheet configurations that assess sensitivity to ice-sheet height for a given LGM area (Table S1). Our results suggest that early Pleistocene ice sheets that were larger than LGM ice sheets could have been in SMB with low obliquity and $[\text{CO}_2]_{\text{atm}}$ of 300 ppmv. SMB becomes more negative as ice-sheet height is lowered to LGM values unless there is a compensatory decrease in $[\text{CO}_2]_{\text{atm}}$. No decrease in $[\text{CO}_2]_{\text{atm}}$ within the range of

our current understanding of its Pleistocene variability could support the low-aspect-ratio ice sheets in SMB inferred by the regolith hypothesis (51).

We thus conclude that the extra height of the early Pleistocene ice sheets relative to the LGM was critical to them being in SMB during glaciations. Given our finding that the large ice sheets shared a common size threshold throughout the Pleistocene equivalent to sea level below -80 m that, when exceeded, triggered ice-sheet instabilities that culminated in a termination (Fig. 3E), we have narrowed this aspect of the paradox to understanding how different boundary conditions and feedbacks may have contributed to the inception and growth of the early Pleistocene ice sheets.

Towards resolving the paradox of the middle Pleistocene transition and the origin of the ~100-kyr cycle

The longstanding MPT paradox relates to the increase in amplitude and decrease in frequency of GMSL variability during the MPT in the absence of any corresponding change in orbital forcing (4). Our finding that large ice sheets existed throughout the Pleistocene, however, challenges several key aspects of their behavior that are usually invoked to explain this paradox: (i) that large ice sheets developed during the MPT in response to long-term changes internal to the climate system (4, 51, 73-78), (ii) that the time constant for growth of large ice sheets is significantly longer than for ice-sheet decay, giving rise to ~100-kyr cycles (79-81), and (iii) that through their large inertia and influence on climate, the large ice sheets drove the ~100-kyr cycle in the rest of the climate system (8, 82, 83).

We first note that because pre-MPT ice sheets were as large as those after the MPT, their albedo forcing should have remained largely the same throughout the Pleistocene and thus cannot explain the large increase in orbital-scale GMST variability during the MPT (Fig. 1B). Instead, we

attribute that increase to an increase in CO₂ variability associated with changes in the Southern Ocean carbon cycle. Ref. (21) proposed that the gradual cooling of the Southern Ocean through the early Pleistocene initiated the MPT in GMST at ~1.5 Ma when average extratropical Southern Hemisphere SSTs first decreased below pre-industrial, increasing the sensitivity of sea ice to the dominant obliquity forcing at these high latitudes. Increased cooling of the Southern Hemisphere also led to an equatorward shift of the westerly winds (84), an increase in dust flux to the Southern Ocean (85), and greater stratification of surface waters (86). Through their impacts on the Southern Ocean carbon cycle (84, 85, 87-90), these changes increased carbon storage during glaciations, thus increasing obliquity-scale variability of [CO₂]_{atm} and GMST. However, a further decrease and then stabilization of Southern Ocean ΔSSTs at the end of the MPT in GMST ~0.8 Ma then muted the response of the Southern Ocean carbon cycle to obliquity forcing that may have dominated [CO₂]_{atm} variability during the early Pleistocene, with an attendant large decrease in the concentration of 41-kyr variance in [CO₂]_{atm} and GMST (21).

We similarly attribute the decrease in large-ice-sheet 41-kyr variance across the MPT (Fig. 2A, 2B) to modulation of obliquity forcing by the newly established decrease in [CO₂]_{atm} and GMST variance. Specifically, prior to reaching their maximum size at the end of each of the M intervals, ice-sheet response to low obliquity was modulated by periods of higher [CO₂]_{atm} and GMST, and vice versa, with times of maximum ice-sheet growth only occurring when the next obliquity low combined with low [CO₂]_{atm} and GMST (Figs. 4A, 4B, 4C). The initial retreat of large ice sheets in response to the next increase in obliquity then triggered a sequence of events and feedbacks leading to a termination every ~100 kyr (34). Among these feedbacks are large-ice-sheet instabilities that sustained ice-sheet retreat (8, 80, 91-94) which, through its influence on the Atlantic meridional overturning circulation, induced warming of the Southern Ocean with an

associated retreat of sea ice, deterioration of the Southern Ocean halocline, and poleward shift in the westerlies. These changes then led to the release of CO₂ from the deep ocean (90) which combined with obliquity (Fig. 4D) to fully deglaciate NH ice sheets and usher in the next interglaciation.

Contrasting temperature and ice-sheet responses to CO₂ forcing over the past 0.8 Myr are clearly expressed in their variance spectra, with a dominant ~100-kyr cycle in GMST (21) that is shared by CO₂ (fig. S9A) whereas the concentration of GMSL variance is nearly equally distributed between 41 kyr and ~100 kyr (Fig. 2B, fig. S9B). Insofar as the variance characteristics of GMST are shared by GMSST, MOT, and thus $\delta^{18}\text{O}_\text{T}$ (18) and those of GMSL are shared by $\delta^{18}\text{O}_\text{sw}$, we can similarly evaluate the relative contributions of $\delta^{18}\text{O}_\text{T}$ and $\delta^{18}\text{O}_\text{sw}$ to the variance of the $\delta^{18}\text{O}_\text{b}$ record since the MPT. The $\delta^{18}\text{O}_\text{b}$ record has long been used to argue that the dominant post-MPT ~100-kyr signal in that record (Fig. 5A) is from ice-sheet dynamics (8, 14, 95-97), but our results show that its origin is largely in the $\delta^{18}\text{O}_\text{T}$ component due to changes in the carbon cycle (Fig. 5B), as first recognized by Ref. (78). Overall, however, terminations present in both $\delta^{18}\text{O}_\text{T}$ and $\delta^{18}\text{O}_\text{sw}$ were set by the threshold of when ice sheets exceeded a limiting size beyond which they responded nonlinearly to obliquity forcing and helped drive a termination. This threshold was reached for nearly every obliquity cycle of the Pleistocene prior to the MPT (Fig. 3D, 3E). Afterward, the development of the ~100-kyr cycle arising from the long-term cooling enhanced the ability of the Southern Ocean carbon cycle to sequester CO₂ and modulate the response of $\delta^{18}\text{O}_\text{T}$ and $\delta^{18}\text{O}_\text{sw}$ to obliquity forcing until the growth of the next large ice sheet.

Conclusions

We find that between 4.5 and 3 Ma, sea-level highstands remained ~20 m above present suggesting large decreases in AIS and GrIS volume relative to today. Beginning at 4 Ma, sea-level

lowstands began to episodically extend below present by as much as -50 to -80 m suggesting the onset of Northern Hemisphere (NH) glaciation. Sustained intensification of NH glaciation occurred from 3 Ma to 2.5 Ma, with highstands decreasing to near-modern levels while lowstands decreased to levels comparable to or lower than the Last Glacial Maximum (LGM) lowstand ~21 ka that continued throughout much of the Pleistocene.

Our finding that large ice sheets existed throughout the Pleistocene modifies as well as adds several fundamental challenges to our understanding of ice sheet-climate interactions and their joint responses to external forcing. Underlying each of these challenges is the fact that the dominant orbital-scale GMSL variability and its changes over the past 3 Myr is not the one that would be predicted solely by the associated orbital forcing, suggesting internal feedbacks of the climate system that we propose are largely driven by changes in the Southern Ocean carbon cycle and their effect on $[\text{CO}_2]_{\text{atm}}$ and GMST. High-resolution ice-core CO_2 records that extend beyond 0.8 Ma are needed to test our hypotheses. Finally, the presence of large ice sheets throughout the MPT indicates that the hypothesis of regolith removal to explain the change in ice-sheet sensitivity to orbital forcing (5, 51) can be rejected.

Materials and Methods

Assessment of GMSL reconstructions

Two different approaches have been used to decompose the $\delta^{18}\text{O}$ record measured in benthic foraminifera ($\delta^{18}\text{O}_b$) into its two primary components: the temperature ($\delta^{18}\text{O}_T$) and the $\delta^{18}\text{O}$ of seawater ($\delta^{18}\text{O}_{\text{sw}}$) that the benthic foraminifera shells formed in, with the latter largely reflecting sea level. Ref. (24) developed an approach that regresses independently known sea-level data (e.g., from corals) on $\delta^{18}\text{O}_b$ for the last glacial cycle and then uses this regression to reconstruct sea level from $\delta^{18}\text{O}_b$ records for the last four glacial cycles. Sea level is then converted to $\delta^{18}\text{O}_{\text{sw}}$

using a constant relation of $\Delta\delta^{18}\text{O}_{\text{sw}}:\Delta\text{GMSL}$. Refs. (98) and (25) extended the regression over the last two glacial cycles to reconstruct sea level from $\delta^{18}\text{O}_b$ records over the last 5 Myr (figs. S1B, S6C). Refs. (27, 28) further extended the regression over the last 800 kyr using the LR04 $\delta^{18}\text{O}_b$ stack and a stack of sea-level records from Ref. (99) (fig. S7C) to reconstruct sea level over the last 40 Myr (figs. S1B and S6A show last 4.5 Myr). Refs. (27, 28) also accounted for $\delta^{18}\text{O}$ variations in land ice ($\delta^{18}\text{O}_i$) over the last glacial cycle which they then applied to their sea-level record to derive $\delta^{18}\text{O}_{\text{sw}}$ from $\delta^{18}\text{O}_b$, but this did not include the effect of increasing temperatures on $\delta^{18}\text{O}_i$ prior to 0.8 Ma. In any event, applying this regression approach to a $\delta^{18}\text{O}_b$ record will, by default, reproduce the variability of the $\delta^{18}\text{O}_b$ record, including the increase in the size of glaciations during the mid-Pleistocene transition (MPT), with the early Pleistocene low-amplitude variability further reinforced by not accounting for higher temperatures on $\delta^{18}\text{O}_i$.

Refs. (9) and (100) reconstructed sea level using a simple scaling relationship that determines the fraction of the LGM sea-level lowstand (-120 m in their case) from the fraction of the $\delta^{18}\text{O}_b$ value at any given time relative to the LGM $\delta^{18}\text{O}_b$ value. As with the regression method, this relationship reproduces the $\delta^{18}\text{O}_b$ variability throughout the Pleistocene as well as does not account for the effect of increasing temperatures on $\delta^{18}\text{O}_i$ prior to 0.8 Ma, resulting in smaller early Pleistocene ice sheets than in our reconstruction (figs. S1B, S6D). Finally, these approaches imply a stationary partitioning of $\delta^{18}\text{O}_b$ between temperature and ice volume, and thus do not capture the larger ice volume component relative to temperature that we identify before the MPT (18).

Another approach that is similar to ours subtracts independently reconstructed seawater temperature as $\delta^{18}\text{O}_T$ from $\delta^{18}\text{O}_b$ to derive $\delta^{18}\text{O}_{\text{sw}}$ (22, 23, 41, 101-103) which can then be converted to GMSL using a relation of $\Delta\delta^{18}\text{O}_{\text{sw}}:\Delta\text{GMSL}$ (22, 23). Ref. (22) used a reconstruction of bottom water temperature (BWT) that is similar to ours in showing lower ΔBWT than ΔSST

during the early Pleistocene (18). However, this is a 2-Myr smoothed record and thus does not capture the increase in orbital variability across the MPT (18) (figs. S1B, S6B) which contributes to larger early Pleistocene ice sheets in our reconstruction. Ref. (22) also applied a constant 0.013‰ m⁻¹ relationship to derive sea level from their $\delta^{18}\text{O}_{\text{sw}}$ which does not account for the effect of warmer early Pleistocene temperatures on $\delta^{18}\text{O}_i$, and thus $\delta^{18}\text{O}_{\text{sw}}$. Moreover, this relationship is more appropriate for warmer climates with just the Greenland and Antarctic ice sheets (19) as opposed to the 0.008‰ m⁻¹ relationship that is more suitable for deriving sea level after 0.8 Ma. Accordingly, their sea-level lowstands are generally higher than in our reconstruction throughout the Pleistocene (figs. S6B, S7B).

Other studies that used independent orbital-scale temperature records to derive $\delta^{18}\text{O}_{\text{sw}}$ from $\delta^{18}\text{O}_b$ suggest small GMSL variability in the late Pliocene that increases into the early Pleistocene and continues across the MPT (26, 40, 41). We used our method to convert $\delta^{18}\text{O}_{\text{sw}}$ data from Refs. (41) and (26) to sea level (see section 2 of this Supplementary Materials) and find generally good agreement with our GMSL reconstruction (figs. S5, S6E). However, the temperature records in Refs. (41) and (26) are local and so may not be representative of mean ocean temperature (MOT). Finally, other than Refs. (27) and (28), none of the reconstructions using either approach account for changing $\delta^{18}\text{O}_i$ on $\delta^{18}\text{O}_{\text{sw}}$ (28, 104).

Finally, Refs. (105, 106) reconstructed changes in water depth using grain size variations in uplifted marine sedimentary sequences preserved in New Zealand (fig. S1, S8), with inferred water depths being supplemented by estimates from benthic foraminifera. Unconformities in the sedimentary sequence are assigned a maximum water depth of -32.5 m, and the authors assume the missing part of the sea-level record to be <5 m. Water depth is converted to relative sea level using back stripping methods that account for sediment compaction and tectonic subsidence. Their

reconstruction cannot be referenced to Holocene sea level, but it does identify long-term trends as well as the frequency and amplitude of sea-level change on orbital timescales. Comparison of their reconstruction to other sea-level reconstructions (fig. S1) and to our reconstruction (fig. S8) shows a similar concentration of 41-kyr variance but disagrees with these other reconstructions in showing no trend of increasing lowstands (i.e., greater amplitude) during the intensification of Northern Hemisphere glaciation.

Conversion of $\delta^{18}O_{sw}$ to sea level

We develop a simple model to translate $\delta^{18}O_{sw}$ to sea level that conserves global water and ^{18}O mass as they are redistributed between the ocean and the North American (NAIS) (Laurentide and Cordilleran ice sheets), Eurasian (EUR), Greenland (GRN), and Antarctic (ANT) ice sheets. The model also accounts for the changing isotopic composition of each ice sheet through time as a function of changes in its volume and global temperature, which allows us to separate their isotopic effects. This is important because our reconstructions suggest that there is not a constant scaling between global temperature and ice volume over the past 4.5 Myr.

The method is based on conservation of global water and isotopic ^{18}O mass, extending similar treatments in Ref. (19) and Ref. (20). A simple expression is used for the mean $\delta^{18}O$ of each ice sheet as a linearized function of its size and global mean surface temperature (GMST), and a parameterization is assumed for the relative size of each ice sheet to the others at all times. After some tedious but straightforward algebra, this yields a quadratic equation yielding total ice volume over flotation (and hence global sea-level rise) as a function of $\delta^{18}O_{sw}$ and GMST.

While $\delta^{18}O_{sw}$ is often converted to sea level using a constant scaling of ~ -0.008 ‰/m based on Last Glacial Maximum values (i.e., a ~ 1 ‰ $\delta^{18}O_{sw}$ enrichment (107) and ~ 130 m sea level lowering (108)), our model accounts for time-varying temperature and ice-volume effects on ice-

sheet $\delta^{18}\text{O}_i$ (fig. S3D), yielding a variable relationship between $\delta^{18}\text{O}_{\text{sw}}$ and sea level (fig. S3A, S3B). As a result, relative to linear scaling, applying our model to our $\delta^{18}\text{O}_{\text{sw}}$ reconstruction produces lower sea levels during early Pleistocene glaciations because less-negative $\delta^{18}\text{O}_{\text{ice}}$ then (due to higher temperatures) requires greater ice growth to explain $\delta^{18}\text{O}_{\text{sw}}$ enrichments, and thus lower sea levels during Pliocene interglaciations because more-negative $\delta^{18}\text{O}_{\text{ice}}$ then (due to NAIS and EIS absence) requires less ice loss to explain $\delta^{18}\text{O}_{\text{sw}}$ depletions (fig. S3A).

In the Supplementary Materials, we explain the details of our model. Section 1 derives separate equations for differing climates relative to today. Section 2 outlines how we estimate the coefficients in the expression for mean ice-sheet $\delta^{18}\text{O}$ based on observed quantities and published general circulation model (GCM) experiments. Section 3 explains the scheme we use to account for the residence time of ice in each ice sheet, and a list of prescribed quantities is given in section 4. Finally, section 5 assesses the sensitivity of our sea-level reconstruction to the various parameters in our model. Finally, section 6 provides the MATLAB code for converting $\delta^{18}\text{O}_{\text{sw}}$ to sea level.

Time series analyses

We characterized the temporal variability and covariability of the different time series in four ways, using: 1) evolutionary spectra (Fig. 2A); 2) “global” multitaper spectral analysis (Fig. 2B); 3) bandpass-filtered time series of ΔGMST and SL at the 41 kyr obliquity period (Fig. 2C); and 4) the rolling coherence between the filtered series and obliquity (Fig. 2D). Evolutionary spectra (109) were calculated using the R astrochron package (110, 111). The function eha() in the astrochron package implements a moving-window application of the multi-taper method (MTM) spectral-analysis procedure (112). We used a window width of 500 kyr, a time step of 10 kyr between adjacent window positions, and a “standard” MTM time-bandwidth product of 4. Prior to

analysis, the time series were detrended using a smoothing spline with 10 degrees of freedom using the `spline.smooth()` function in the R base stats package (111). This detrending step removes the very long-period variability from the time series but does not obscure or overly emphasize the eccentricity band variations in the data. The spectral density was rescaled to “normalized amplitude” values—in each window, the amplitudes (the square root of the spectral density) at each frequency were divided by the maximum amplitude across all frequencies. This facilitates judging the relative importance of variations across periods. We did not do any significance testing of the results because the presence of variability in the time series at orbital frequencies is really not in question, and white-noise or low-order autoregressive null-hypothesis spectra are rather naïve. On Fig. 2A, the dominant periods in insolation variations at orbital periods are indicated by horizontal lines (eccentricity: $E_1 = 400$ kyr, $E_2 = 96$ kyr; obliquity: $T = 41$ kyr and precession: $P_1 = 23$ kyr, $P_2 = 19$ kyr).

Global (as opposed to evolutionary) spectral analysis was performed for blocks of data, as indicated by the black horizontal bars on Fig. 2A. We used the multitaper method here as well. We bandpass-filtered the time series at the 41 kyr obliquity period using the `butter()` (Butterworth filter) function from the R signal package (113). The band limits were 39.0 and 43.1 kyr, 0.95 and 1.05 times the obliquity frequency of $1/41.0 = 0.0244$ cycles kyr⁻¹. The coherence between obliquity and Δ GMST and SL was calculated using a moving window approach. Cross-spectral analyses were done following the Blackman-Tukey method using the `SPECTX2` function from the ARAND software package (114). The number of lags used correspond to $\sim 1/3$ the length of the interval analyzed.

Ice-sheet surface mass balance

We assessed the sensitivity of the surface mass balance (SMB) of early Pleistocene Northern Hemisphere ice sheets to orbits, atmospheric CO₂, and ice-sheet height by conducting experiments with the GENESIS V3.0 climate model (69, 70) (Table S1). The GENESIS climate model comprises a T31 atmospheric model (horizontal resolution of approximately $3.75^\circ \times 3.75^\circ$ latitude by longitude) coupled with the land-surface model LSX ($2^\circ \times 2^\circ$ resolution). SSTs were computed by the 50-meter mixed layer ocean model in GENESIS. SMB is computed from annual precipitation, runoff, and evaporation over the ice sheets on the $2^\circ \times 2^\circ$ grid of the LSX land surface model. The fraction of runoff retained through refreezing is computed as a function of temperature and precipitation using the method of Ref. (115). We ran the simulations for 100 years and analyzed the last 70 years to exclude spin-up artifacts.

Our sensitivity experiments used orbits corresponding to low (glacial) and high (interglacial) obliquity at 2.165 Ma and 2.145 Ma (71), respectively, and atmospheric CO₂ values of 200 and 300 ppmv which cover much of the early Pleistocene range suggested by proxies (57, 116, 117). We used three ice-sheet configurations to assess sensitivity to ice-sheet height for a given LGM area (Table S1). The GLAC-1D LGM ice sheets are from Ref. (118). The HIGH ice sheets are intended to represent the largest of the early Pleistocene ice sheets, with ~30 m of additional lowering of sea-level relative to the LGM sea-level lowstand (Figs. 1C, 3E). We derived the HIGH ice-sheet heights by calculating the volume of 30 m of global sea level and distributing the height equivalent of the volume uniformly over the GLAC 1-D LGM North American (NA) (20 m) and Eurasian (EU) (10 m) ice-sheet complexes, accounting for the density ratio of water to ice ($1028 \text{ kg m}^{-3}/910 \text{ kg m}^{-3}$). The LOW ice sheet was derived by reducing the GLAC 1-D LGM ice-sheet height to an equivalent of 60% of the full LGM sea-level volume and is intended to represent the low-aspect ratio ice-sheet geometry inferred from the regolith hypothesis (51).

Experiment EXP1 shows the model's ability to simulate NH (GLAC-1D) ice sheets that are in SMB or have positive SMB under LGM boundary conditions (Table S1). Experiments EXP2 and EXP3 assess the effect of orbital changes on NH ice-sheet SMB (Table S1). In both experiments, NH MATs north of 40°N are 8 K to 9 K colder than the PI due to the presence of the ice sheets while North Atlantic SSTs are 3 K to >5 K colder due to advection of cold air off the NA ice-sheet complex and southward expansion of sea ice (fig. S10A). Warming of the oceans elsewhere partially offsets the NH cooling such that global SSTs are the same as PI and global MATs are 2 K colder than PI (Table S1). The net effect of the boundary conditions yields a glacial NA ice-sheet-complex SMB of 5 m yr⁻¹ (fig. S10B) and an interglacial SMB of -11 m yr⁻¹. Comparison of the NA and EU ice-sheet-complex SMB in EXP2 to that of EXP3 indicates that glacial-interglacial obliquity accounts for 16 m yr⁻¹ over NA and 2 m yr⁻¹ over EU (Table S1, fig. S10C).

Experiments EXP2 and EXP4 assess the effect of CO₂ changes on NH ice-sheet SMB. Over the 200 to 300 ppm range evaluated here, CO₂ accounts for 15 m yr⁻¹ in the NA ice-sheet complex SMB and 8 m yr⁻¹ in the EU ice-sheet complex SMB, which are comparable to the effect of obliquity (Table S1). Experiments EXP2 and EXP5 and experiments EXP4 and EXP6 assess the effect of ice-sheet height on NH ice-sheet SMB (Table S1). Lowering the ice-sheet height from HIGH (EXP2) to GLAC-1D (EXP5) results in SMB becoming more negative by 35 m yr⁻¹ for the NA ice-sheet complex and 11 m yr⁻¹ for the EU ice-sheet complex (Table S1). The effect of height on mass balance is most evident along the margin of the NA ice-sheet complex (fig. S10D) where the higher margin blocks penetration of precipitation into the interior (orographic shadowing) and positions more ice area at or above the zero-degree isotherm. The marginally more positive SMB

over the interior of the NA ice-sheet complex for the lower ice sheet where precipitation is slightly greater than that of the high ice sheet reflects the effect of desertification.

Lowering the ice sheet from HIGH (EXP4) to LOW (EXP6) results in SMB becoming more negative by 84 m yr^{-1} for the NA ice-sheet complex and by 4 m yr^{-1} for the EU ice-sheet complex (Table S1). We note that the strongly negative SMB of the LOW ice sheet in EXP6 (Table S1) indicates that such an ice sheet could not have existed even under glacial orbitals and LGM CO_2 levels.

In summary, our sensitivity tests suggest that early Pleistocene ice sheets that were larger than LGM ice sheets could have been in SMB with low obliquity and CO_2 levels of 300 ppm. SMB becomes more negative as ice-sheet height decreases towards LGM values unless there is a compensatory decrease in CO_2 , but no decrease in CO_2 within the range of our current understanding of its Pleistocene variability could support the low-aspect-ratio ice sheets in SMB inferred by the regolith hypothesis (51). We note that while our experiments using LSX and a mixed layer ocean model are a first-order assessment of the sensitivity of ice-sheet SMB to changes in boundary conditions, the model does not account for feedbacks such as changes in global ocean circulation and ice-sheet dynamics that, when investigated with a full Earth System model, would further refine our results. The challenge remains for modeling the inception and growth of the ice sheets.

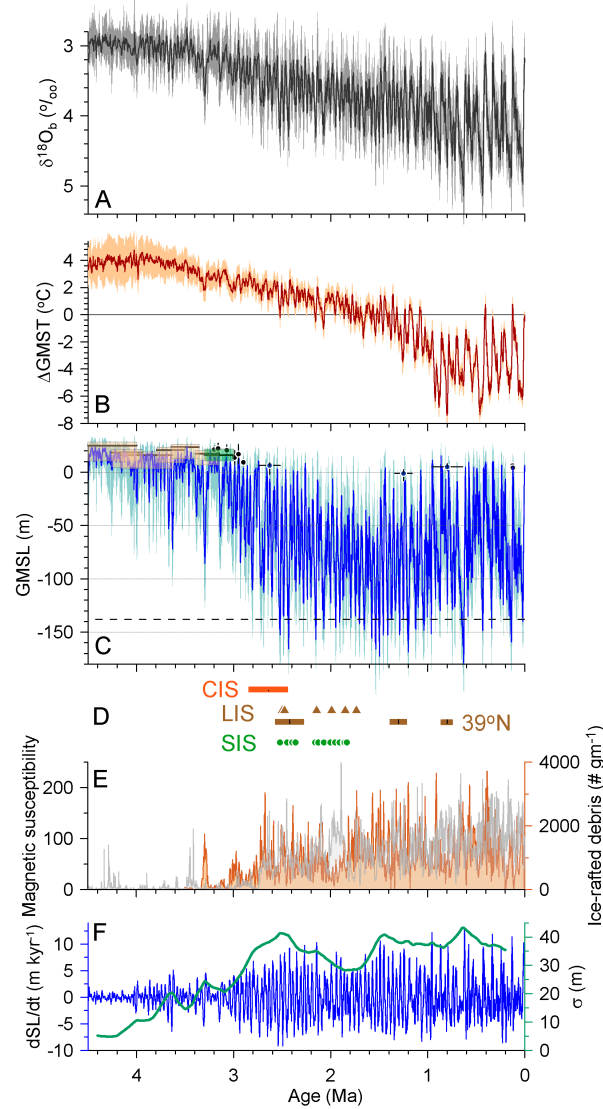


Fig. 1. Global mean temperature and sea-level changes over the past 4.5 Myr. (A) Prob-stack $\delta^{18}\text{O}_b$ record (12). (B) Global mean surface temperature difference (ΔGMST) (brick red with 1σ uncertainty) referenced to PI. (C) Global mean sea level (GMSL) (blue line with 1σ uncertainty). The uncertainty on $\delta^{18}\text{O}_{\text{sw}}$ (converted to sea level) is calculated as the square root of the sum of squares of the uncertainty in the Prob-stack $\delta^{18}\text{O}_b$ record (12) and in the ΔMOT reconstruction (as $\delta^{18}\text{O}$) (18). Also shown are published Pliocene (37-39) and Pleistocene (119, 120) sea-level highstands. Dashed horizontal line is referenced to the LGM lowstand (-130 m). (D) Geologic evidence of extensive margins of early-to-middle Pleistocene Cordilleran Ice Sheet (CIS, orange symbols) (43), Laurentide Ice Sheet records at 39°N (LIS, brown symbols) (42, 44), and Scandinavian Ice Sheet (SIS, green symbols) (46). Newer evidence suggests a more-limited extent of the SIS in the North Sea prior to 1.1 Ma (121) than inferred by Ref. (46), but the difference in extent, and its contribution to GMSL, is negligible. (E) Records of ice-rafted debris from the North Pacific (gray) (48) and Nordic Seas (orange) (47). (F) Rate of change (12-kyr running average) (dark blue line) and standard deviation (σ , 200-kyr centered) (green line) of GMSL.

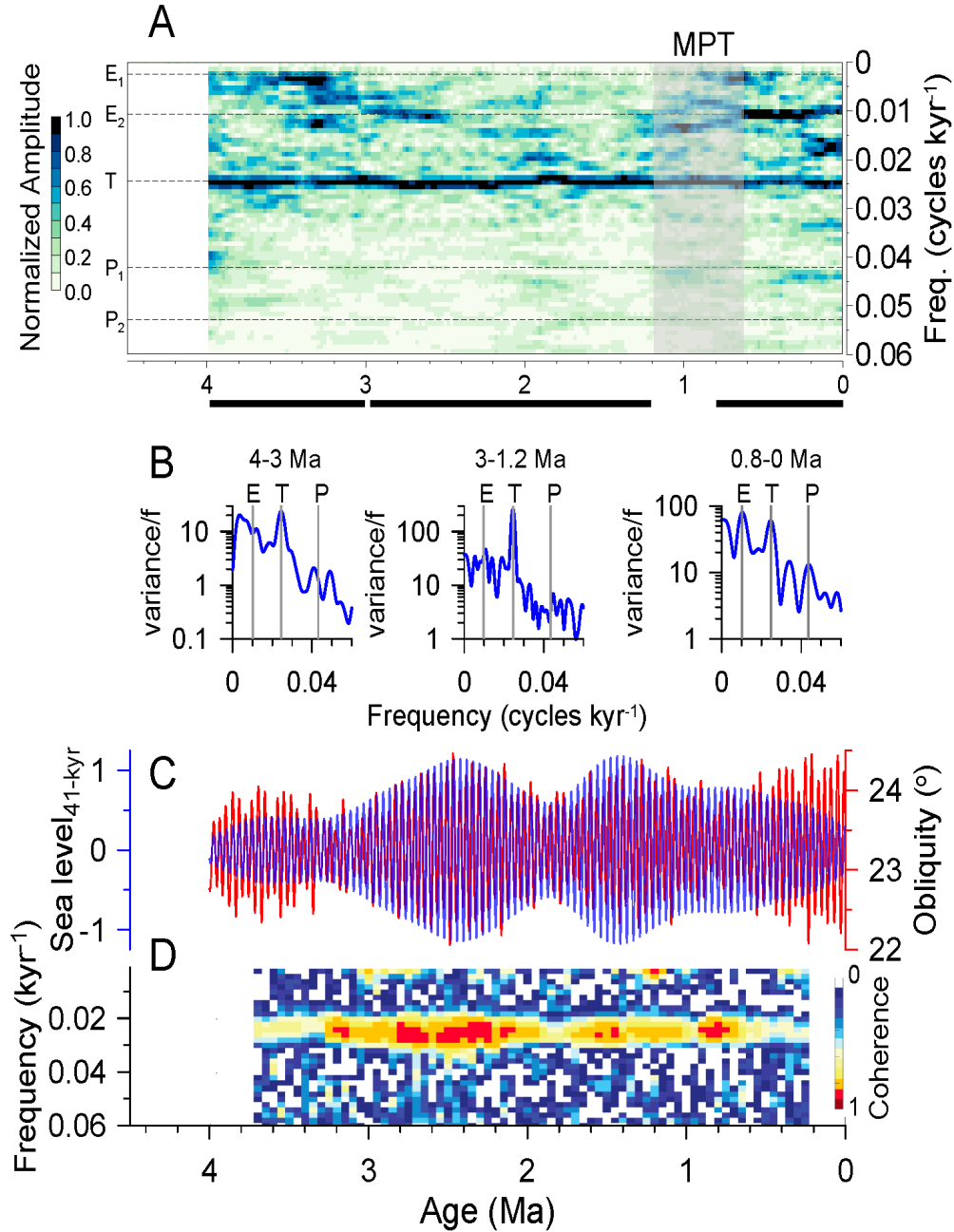


Fig. 2. Spectral characteristics of global mean sea level. (A) Evolutionary spectra of global mean sea level (GMSL). The dominant periods in insolation variations at orbital periods are indicated by horizontal lines (eccentricity: E₁ = 400 kyr, E₂ = 96 kyr; obliquity: T = 41 kyr and precession: P₁ = 23 kyr, P₂ = 19 kyr). Vertical gray rectangle represents the middle Pleistocene transition (MPT). (B) Spectral density of GMSL (variance per frequency) for three periods corresponding to horizontal black bars shown in (A) (3-4 Ma, 1.2-3 Ma, 0-0.8 Ma). Orbital periods are indicated by vertical lines (E = eccentricity (96 kyr), T = obliquity (41 kyr), and P = precession (23 kyr)). Note scale change for y-axes (variance/f). (C) Filtered GMSL using a 41-kyr filter (blue line) and obliquity (red line). (D) Coherence between 41-kyr filtered GMSL and obliquity.

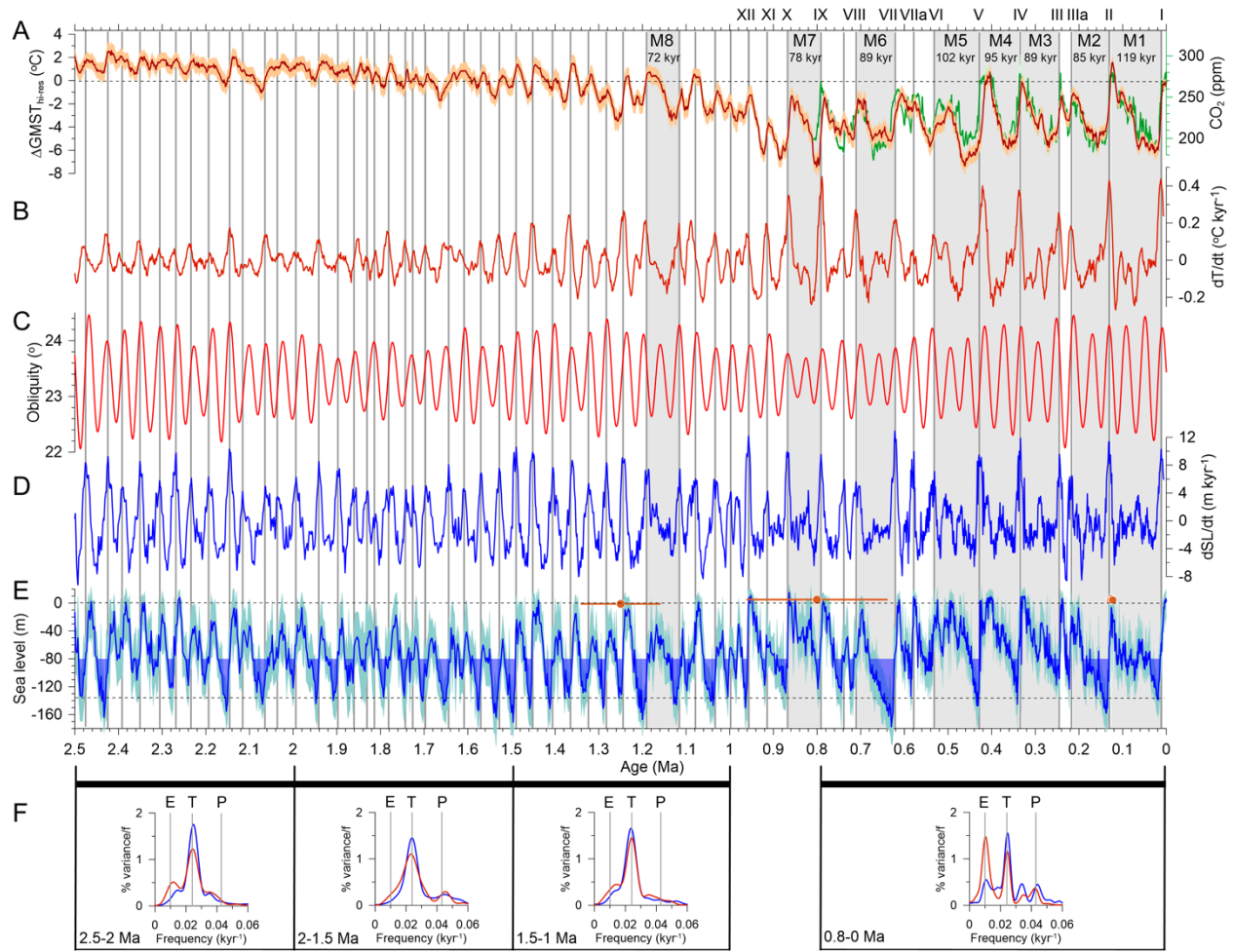


Fig. 3. Global temperature and sea-level changes over the past 2.5 Myr. (A) Global mean surface temperature change (ΔGMST) (brick red with 1σ uncertainty,) referenced to PI, and atmospheric CO_2 (green) (122) placed on the AICC2023 chronology (123). (B) Rate of change of ΔGMST . (C) Obliquity (71). (D) Rate of change of global mean sea level (GMSL) (12-kyr running average), whose maxima are highlighted by vertical lines across (A-E). (E) Global mean sea level. Sea-level threshold of -80 m that, when exceeded, is followed by a termination upon next increase in obliquity (see text) is shown by filled blue sea-level intervals. Dashed horizontal lines correspond to present (0 m) and LGM (-130 m) sea levels. Brick-red symbols with 1σ age uncertainty are published Pleistocene sea-level highstands (119, 120). (F) Spectral density of rate of change of ΔGMST (brick red) and GMSL (blue) for four periods corresponding to horizontal black bars shown in (E). Eccentricity (E, 100-kyr), tilt (T, 41-kyr) and precession (P, 23-kyr) frequency bands noted by vertical lines.

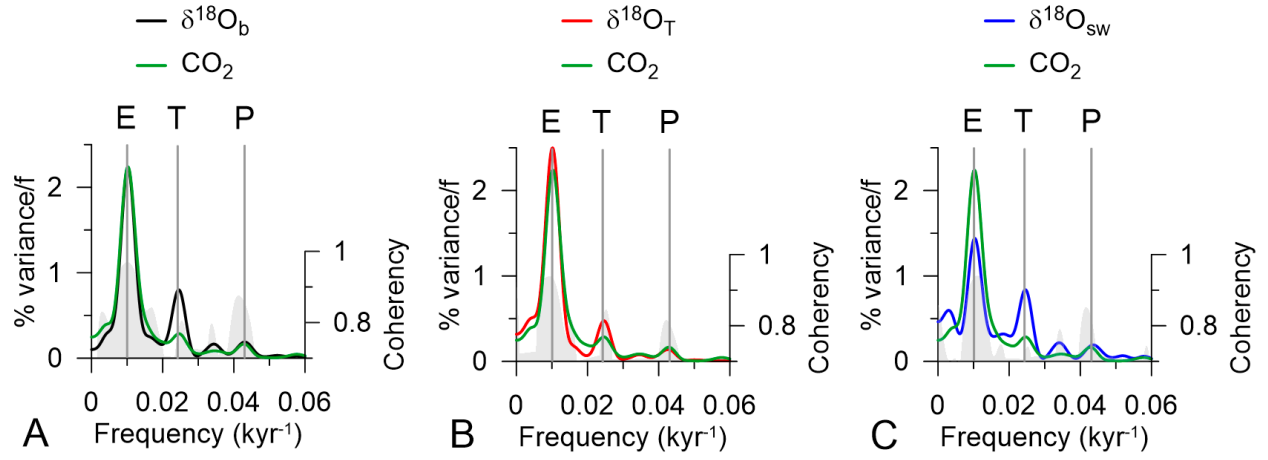


Fig. 5. Spectral density of the $\delta^{18}\text{O}_b$ record, its components, and atmospheric CO_2 for past 0.8 Myr. (A) Spectral density (normalized variance) of the Prob-stack $\delta^{18}\text{O}_b$ record (12) and atmospheric CO_2 (green) (122). (B) Spectral density (normalized variance) of the temperature component ($\delta^{18}\text{O}_T$) of the $\delta^{18}\text{O}_b$ record (18) and atmospheric CO_2 (green) (122). (C) Spectral density (normalized variance) of the seawater component ($\delta^{18}\text{O}_{sw}$) of the $\delta^{18}\text{O}_b$ record (18) and atmospheric CO_2 (green) (122)

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Supplementary Materials

Equations and parameters to convert $\delta^{18}\text{O}_{\text{sw}}$ to sea level

Figs. S1 to S10

Table S1

References (125-131)