LETTERS

Late Pliocene Greenland glaciation controlled by a decline in atmospheric CO_2 levels

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It is thought[1,2] that the Northern Hemisphere experienced only ephemeral glaciations from the Late Eocene to the Early Pliocene epochs (about 38 to 4 million years ago), and that the onset of extensive glaciations did not occur until about 3 million years ago[3,4]. Several hypotheses have been proposed to explain this increase in Northern Hemisphere glaciation during the Late Pliocene[5–11]. Here we use a fully coupled atmosphere–ocean general circulation model and an ice-sheet model to assess the impact of the proposed driving mechanisms for glaciation and the influence of orbital variations on the development of the Greenland ice sheet in particular. We find that Greenland glaciation is mainly controlled by a decrease in atmospheric carbon dioxide during the Late Pliocene. By contrast, our model results suggest that climatic shifts associated with the tectonically driven closure of the Panama seaway[5,6], with the termination of a permanent El Niño state[7–9] or with tectonic uplift[10] are not large enough to contribute significantly to the growth of the Greenland ice sheet; moreover, we find that none of these processes acted as a priming mechanism for glacial inception triggered by variations in the Earth's orbit.

During the Early and Middle Eocene (~56–40 Myr ago), when proxy data indicate high-latitude continental winter temperatures as high as 2 °C (ref. 12), Greenland was mostly free from ice[13]. There is some evidence of North Atlantic ice-rafted debris (IRD) in the Late Eocene and Early Oligocene (~38–30 Myr ago), indicating early ephemeral glaciations[1], and continued evidence for IRD through the Miocene[2]; however, the entry into an 'icehouse' world in the Northern Hemisphere, with extensive glaciation over much of Greenland, is thought to have occurred in the Late Pliocene around 3 Myr ago[3,4]. Several explanations have been proposed for this increase in glaciation during the Late Pliocene. Here we focus on their implications for the development of the Greenland ice sheet.

The 'Panama hypothesis'[5,6] suggests that the tectonically driven closure of the Panama seaway, between about 13 Myr and 2.5 Myr ago, led to an increase of the salinity contrast between the Pacific and Atlantic oceans, increased oceanic northward heat transport, and warmer and more evaporative surface water masses in the North Atlantic. This led to increased atmospheric moisture in the Arctic, greater snowfall over Greenland and ultimately an increase in ice volume. This hypothesis is supported by the coincidental timing of changes in salinity gradient between the Caribbean basin and the East Pacific, and pulses of increased IRD on the Icelandic Plateau[4].

The 'ENSO hypothesis' states that a 'permanent El Niño' state existed in the Early Pliocene and terminated in the Late Pliocene, evidence for which comes in the form of an increasing zonal gradient in sea surface temperature during this time period, reconstructed from the ratio Mg/Ca (ref. 7), oxygen isotope data ($\delta^{18}O$)[7] and alkenone data from sediment cores[8] in the eastern and western Equatorial Pacific. It has been suggested[9] that the transmission of El Niño-like anomalies from the tropics through large-scale planetary waves may have warmed the high latitudes of the Northern Hemisphere, and thus a permanent El Niño state may have acted to retard the onset of Northern Hemisphere glaciation. Therefore the loss of a permanent El Niño state in the Late Pliocene acted as a positive forcing mechanism for the onset of glaciation on Greenland.

The 'uplift hypothesis'[10] suggests that the Cenozoic uplift of the Rocky Mountains and Himalayas influenced atmospheric circulation, by causing larger Rossby wave amplitude and jet-stream deflection, to bring cooler air masses and increased moisture and snowfall over the incipient Greenland ice sheet.

The 'CO_2 hypothesis' states that decreased radiative forcing associated with a lowered concentration of atmospheric CO_2 led to cooler melt-season temperatures and decreased ablation, resulting in the net annual accumulation of snow necessary to grow an ice sheet. In contrast to the Quaternary, for which ice cores provide detailed and robust records[14] of past CO_2, pre-Quaternary atmospheric CO_2 concentration is a challenge to reconstruct owing to the lack of direct indicators. Estimates from the $^{13}C/^{12}C$ ratio of alkenones in marine sediments and boron isotopes in marine carbonates[15,16] suggest Eocene atmospheric CO_2 of the order of 1,000 p.p.m.v., falling to levels as low as 200 p.p.m.v. in the Middle Miocene, and then rising through the Miocene to levels similar to pre-industrial in the Early Pliocene[17]. Estimates from the $^{13}C/^{12}C$ ratio of marine organic matter[18] indicate mid-Pliocene (3.3–3.0 Myr ago) atmospheric CO_2 values of around 400 p.p.m.v., which is in broad agreement with estimates from the stomatal density of fossilized leaves[19] from the same period. The CO_2 hypothesis suggests that it is the fall from these mid-Pliocene values to lower values typical of the Quaternary that favoured the development of Northern Hemisphere glaciation and the growth of the Greenland ice sheet. It does not suggest what may have caused the variations in CO_2 through the Cenozoic; these variations may themselves have been ultimately tectonically driven[11], but this is distinct from the direct tectonic and orographic forcings of the Panama and uplift hypotheses.

It has also been suggested that none of the above hypotheses were capable of causing glacial inception on their own, but instead provided a 'priming' mechanism, with full glaciation triggered by variations in the Earth's orbit. This 'orbital-trigger hypothesis' is supported by the coincident timing of increased IRD with particularly large-amplitude oscillations on precessional timescales of boreal summer insolation[3].

To test the four main hypotheses—Panama, ENSO, uplift and CO_2—and the influence of orbital variations, we carried out a suite of simulations using a fully coupled atmosphere–ocean general circulation model (GCM), and used the modelled temperature and precipitation over Greenland to drive an off-line ice-sheet model. See Methods and Supplementary Information for details.

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Figure 1 shows the GCM-predicted temperature and precipitation changes in the Greenland region associated with the four non-orbital hypotheses. The closure of the Panama seaway has a significant effect on the simulated global ocean circulation, leading to increased overturning in the Atlantic and increased northward transport of warm surface waters[20]. This ocean-driven temperature signal is advected over continental regions, and there is a resulting increase in summer temperature over Greenland (Fig. 1a). Associated with the surface warming is increased evaporation and precipitation. This strong correlation between temperature and precipitation change is common to all the simulations presented here. In particular, in this case, precipitation in the North Atlantic (where the changes in sea surface temperature are largest) increases significantly on closure of the Panama seaway. This results in increased snowfall over Greenland itself, in particular in the southeast (Fig. 1e), where the high-altitude coastal mountain ranges amplify the precipitation increase.

The termination of the permanent El Niño state leads to an increase in northward heat transport in the Atlantic, which increases surface temperatures in the North Atlantic, just south of Greenland (Fig. 1b). However, this temperature signal does not extend over Greenland itself, where the summer temperatures are relatively unchanged. There is an increase in annual mean precipitation over Greenland associated with a northward shift of the Atlantic storm track (Fig. 1f); again this change is concentrated in the southeast.

The uplift of the Rocky Mountains leads to local cooling in western North America because of the higher surface elevation and associated increase in snow cover, especially in winter. In summer, this signal is advected downstream over much of Canada and the North Atlantic, and into Greenland itself (Fig. 1c). Additionally, uplift on the west coast of Greenland leads to localized cooling. The cooler surface temperatures in the Northern Hemisphere result in a generally drier climate over Greenland following uplift; however, a slight northward deflection of the Atlantic storm track does lead to greater precipitation on the southern margins of Greenland (Fig. 1g).

Decreasing CO_2 during the Late Pliocene leads to global cooling of 1.3 °C. Consistent with simulations carried out under present-day boundary conditions[21], the temperature response is greatest at high latitudes, primarily owing to albedo feedbacks related to changes in snow and sea-ice coverage. In contrast, the cooler planet and increased meridional temperature gradient in the low-CO_2 simulation results in increased overturning strength in the North Atlantic, leading to greater northward oceanic heat transport, and a slight increase in temperature in the Barents Sea (Fig. 1d). Over Greenland, however, the direct CO_2 response dominates, and there is a summer cooling. The globally cooler climate results in generally decreased evaporation from the Earth's surface, and a global average decrease in precipitation. This is also true over Greenland itself, where the annual mean precipitation decreases (Fig. 1h), again consistent with high-CO_2 simulations carried out under present-day boundary conditions[21].

On first inspection the results shown in Fig. 1 could provide support for each of the hypotheses; for instance, both the Panama and ENSO anomalies are characterized by increases in precipitation over Greenland, and both the uplift and CO_2 anomalies are characterized by decreases in temperature. However, these climate anomalies are not sufficient on their own to draw conclusions about possible impacts on Greenland glaciation. The mass balance of an ice sheet is a complex function of the geographical and temporal distribution of accumulation, ablation and underlying bedrock, and is influenced by ice dynamics. Therefore we made use of a high-resolution ice-sheet model, which includes a representation of these processes, given the temperature and precipitation predictions from the GCM. The role of albedo feedbacks in these simulations is discussed in the Supplementary Information.

The resulting equilibrium configurations for the Greenland ice sheet are shown in Fig. 2. The closure of the Panama seaway actually reduces the volume of the ice sheet (compare the control configuration, Fig. 2c, with Fig. 2a). The warmer Greenland summer surface temperatures in the closed-seaway Pliocene control case result in increased ablation around the margins of the ice sheet, enough to remove the ice cap in the south of the island that is present in the open-seaway configuration. The increased precipitation results in a small increase in the maximum height of the ice cap in the east. The net change is a decrease of 0.8 m sea level equivalent (SLE) of the total ice volume on closure of the Panama seaway.

The termination of the permanent El Niño state also leads to a small decrease in volume of the ice sheet (0.3 m SLE; compare Fig. 2c with Fig. 2b). In this case, the limited response of the ice sheet is due to the relatively small changes in temperature and precipitation over Greenland (Fig. 1b, f).

Tectonic uplift does lead to a slight increase in Greenland ice volume (0.5 m SLE; compare Fig. 2d with Fig. 2c), with localized

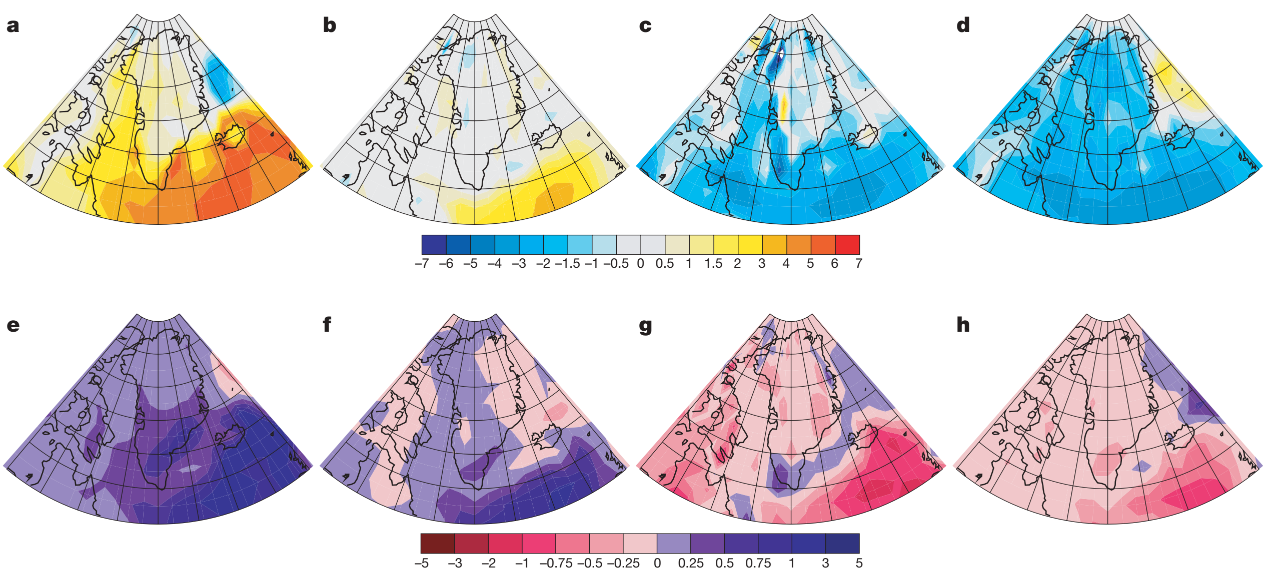

Figure 1 | Surface climate anomalies associated with the four hypotheses considered. a–d, Simulated surface temperature change (°C) during Northern Hemisphere summer due to closure of the Panama seaway (**a**), termination of a permanent El Niño state (**b**), tectonic uplift (**c**), decreasing CO_2 (**d**). **e–h**, Simulated annual precipitation change (mm day^{-1}) due to closure of the Panama seaway (**e**), termination of a permanent El Niño state (**f**), tectonic uplift (**g**), decreasing CO_2 (**h**).

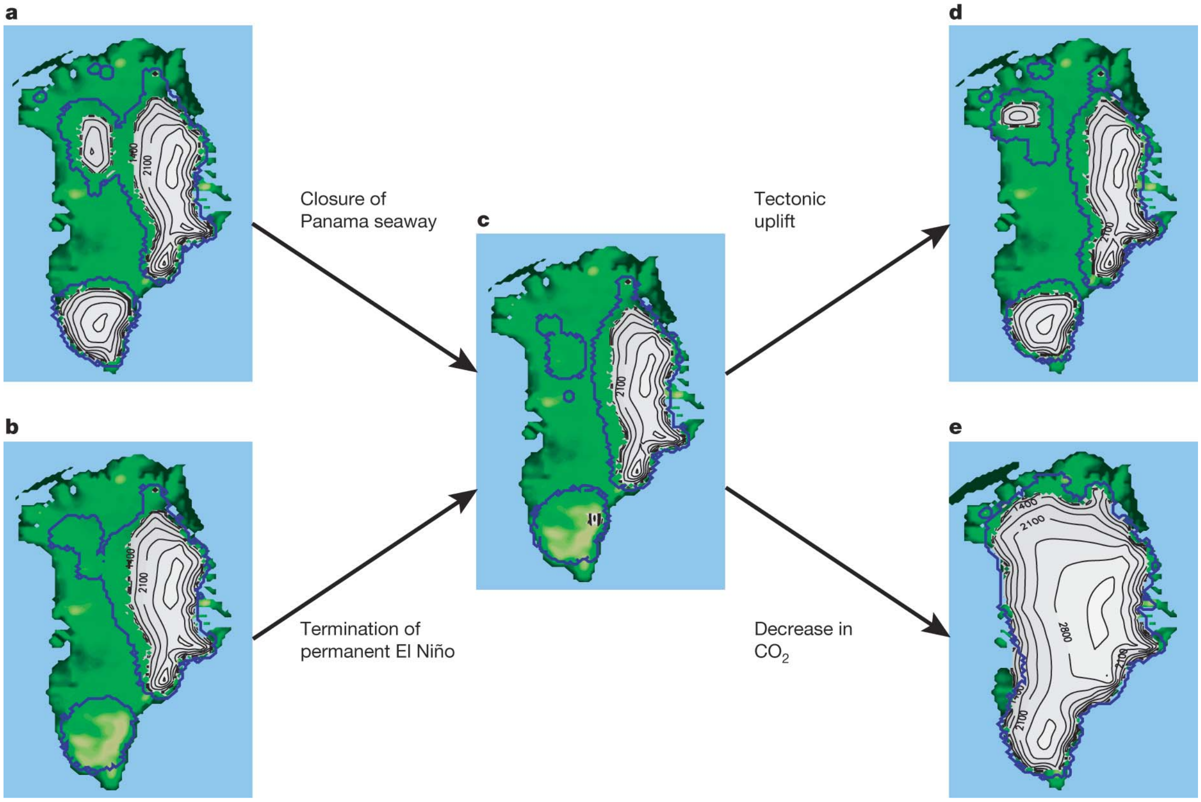

Figure 2 | Ice-sheet configurations. a–e, Pliocene ice-sheet configuration with open seaway (**a**), permanent El Niño (**b**), closed seaway, dynamic ENSO, low orography and high CO_2 (the Pliocene control) (**c**), high orography (**d**) and low CO_2 (**e**). The blue line represents the extent of the ice sheet under orbital conditions favourable for inception. The arrows represent the direction of geological time.

inception occurring in the south and northwest of the island, where temperature anomalies are the greatest (Fig. 1c). However, this is not extensive enough to be considered entry into full glaciation. Decreasing CO_2 has a considerable effect on the evolution of the ice sheet (compare Fig. 2e with Fig. 2c). The cooler summer temperatures under low-CO_2 conditions result in decreased ablation of the ice sheet, an effect that dominates over the decrease in accumulation. The net change is a large increase in volume of 6.3 m SLE. Notably, as well as being larger in volume, the low-CO_2 ice sheet also has the most extensive marine margin, capable of producing greater IRD.

To test the alternative hypothesis that one of these mechanisms acted in conjunction with favourable orbital conditions to produce an increase in glaciation, we repeated the five ice-sheet model simulations but included an additional time-varying forcing component, peaking at values appropriate for a cold orbit favourable for inception in the Northern Hemisphere. For more details see Methods and Supplementary Information.

The maximum ice-sheet extent from these transient orbital simulations, representing the Pliocene glacial configuration of the Greenland ice sheet, is represented in Fig. 2 as a blue line. As expected, the ice sheet expands for all five of these glacial simulations. However, with the exception of the larger low-CO_2 ice sheet, all of the ice sheets are similar in size. Therefore, there is no evidence that any of the tectonic and oceanographic changes modelled here have a 'priming' effect that promotes glaciation under favourable orbital conditions.

This study indicates that the decrease in atmospheric CO_2, from the high values of the mid-Pliocene to the lower values of the Quaternary, drove a significant increase in Greenland glaciation. It shows that the climatic shifts associated with the tectonically driven closure of the Panama seaway, with the termination of a permanent El Niño state, or with tectonic uplift, were not large enough to contribute significantly to this increase. In addition, it suggests that none of these processes acted as a priming mechanism for inception, triggered by orbital variations. It does, however, support the assertion that some ice did exist on Greenland before the onset of extensive glaciation, and that this waxed and waned on orbital timescales, a conclusion that is consistent with orbital timescale variations in benthic $^{18}O/^{16}O$ ratios before 3 Myr ago[22]. Further confidence in our results can be gained by noting that the dominant role of CO_2 compared with the other hypotheses is robust to variations in key parameters in the ice-sheet model, and also holds under warm-orbit conditions (see Supplementary Information). The work highlights the need for detailed multi-proxy CO_2 reconstructions through the Cenozoic, and expansion of the IRD record from the North Atlantic.

METHODS SUMMARY

We used the UK Met Office model HadCM3 (ref. 23) to carry out the suite of GCM simulations. As well as a Pliocene control, these were simulations with an open Panama seaway (to test the Panama hypothesis), a permanent El Niño (to test the ENSO hypothesis), modern orography (to test the uplift hypothesis), low-CO_2 (to test the CO_2 hypothesis) and a cold-orbit (to test the orbital-trigger hypothesis). We used the UK ice-sheet model GLIMMER[24] to carry out the ice-sheet model simulations. In the non-orbital ice-sheet simulations, the temperature and precipitation from the GCM were used to force the ice-sheet model to equilibrium. In the orbital ice-sheet simulations, the cold-orbit GCM was used to create a 10,000-year synthetic orbital cycle, covering half a precession cycle. For more details, and descriptions of the models used, see online Methods and Supplementary Information.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions D.J.L. carried out the GCM and ice-sheet model simulations, except for the permanent El Niño GCM simulation, which was provided by P. Valdes at the University of Bristol, UK. A.M.H. contributed to setting up the Pliocene control and permanent El Niño GCM simulations. D.J.L., G.L.F. and A.M.H. were involved in the study design. E.J.S. devised parts of the ice-sheet model driver and experimental set-up. All authors discussed the results and commented on the manuscript.

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METHODS

Here we describe the GCM and ice-sheet simulations analysed in this paper. Further details can be found in the Supplementary Information.

The Pliocene control GCM simulation is a 580-year extension of the equivalent Pliocene control simulation described by Haywood and Valdes[25]. The open-seaway simulation is a 200-year extension of the equivalent simulation of Lunt *et al.*[20]. This allows a closer degree of equilibrium to be obtained than in those studies. The permanent El Niño simulation is the same as the 'PlioPacific*Dateline*' simulation discussed by Haywood *et al.*[26]. The uplift and CO_2 simulations are both 200 years long, and are initialized from the end of the Pliocene control simulation of Lunt *et al.*[20].

The Pliocene control GCM simulation conforms to the PRISM2 (Pliocene Research, Interpretation and Synoptic Mapping-2) standard[25]. It has been found to be in reasonable agreement with global proxy data and, in particular, in excellent agreement with Arctic palaeobotanical data and palaeotemperature estimates[27].

To test the Panama hypothesis we carried out an open-seaway perturbation simulation, representing a time period prior to the control, in which a connection of 350 m depth was made between the Pacific and Atlantic in the region that forms the Panama Isthmus in the Pliocene control simulation, in agreement with proxy data appropriate for this time interval[28].

To test the ENSO hypothesis, we carried out a simulation in which Pacific sea surface temperatures between 40° north and south of the Equator were forced towards a constant value, typical of the western Pacific. This represents the permanent El Niño state which may have existed earlier than the control, and is in contrast to the fully dynamic ENSO of the Pliocene control simulation.

To test the importance of orographic changes, we carried out a high-orography perturbation simulation, representing a time period after the control, in which the orography was prescribed to be that of the present day, in contrast to the PRISM2 orography used in the Pliocene control simulation. The exception is in the glaciated regions of Greenland and Antarctica, where the Pliocene orography was used. The most important changes are in North America, where the Rocky Mountains in the PRISM2 data set are up to a kilometre lower than the present day. There are also regions of low orography in the PRISM2 data set on the west and east coasts of Greenland itself, which is consistent with data indicating late Cenozoic uplift around the North Atlantic[29].

To test the CO_2 hypothesis, we carried out a low-CO_2 simulation, again representing a time period after the control. In this simulation, atmospheric CO_2 was prescribed to be 280 p.p.m.v., a value appropriate for the pre-industrial period, in contrast to 400 p.p.m.v. in the Pliocene control, which is at the upper end of mid-Pliocene atmospheric CO_2 estimates[18] from carbon isotope ($\delta^{13}C$) data. To test the importance of orbital effects, we carried out a Pliocene cold-orbit simulation, in which the orbital configuration was set to be identical to that of 115,000 years before present (115 kyr BP, the most recent glacial inception, following the last interglacial). The orbit at 115 kyr BP is characterized by cold boreal summers, and at 65° north in July results in less insolation than any orbital configuration between 5 and 2 Myr ago[30] (see Supplementary Information).

More details of the experimental set-up, spin-up and boundary conditions of all the GCM simulations are given in the Supplementary Information.

For the non-orbital ice-sheet simulations, we used the temperature and precipitation fields from the GCM to force the ice-sheet model for a total of 50,000 years, long enough for equilibrium with the driving climate to be reached. The GCM simulations were carried out using the modern orbital configuration, which results in an insolation at 65° north in July close to, but slightly colder than, the long-term average of the past 5 million years. The non-orbital ice-sheet simulations are therefore intended to represent a long-term average configuration of the Greenland ice sheet, in equilibrium with near-average orbital conditions. More details of the experimental set-up of the ice-sheet simulations are given in the Supplementary Information.

The transient orbital ice-sheet experiments represent the forcing experienced during a transition from near-average orbital conditions to glacial orbital conditions, and back again. The orbital-trigger hypothesis states that under favourable orbital conditions, one of the Panama, uplift, ENSO or CO_2 mechanisms could have produced a significant change in volume of the Greenland ice sheet. However, given that the orbital forcing is transient, it is not appropriate just to repeat the five GCM simulations including a constant favourable orbit. This would overestimate the orbital effect, as in reality the insolation at high latitudes varies in response to the ~20-kyr precessional cycle, the 'favourable' orbit being the maximum of this cycle.

Therefore, we create a synthetic orbital cycle, by applying a time-varying anomaly on top of the five original GCM simulations, and use this to force the ice-sheet model. We simulate the 'cold' half of the cycle (10 kyr) only, as it is this that is appropriate for testing the orbital-trigger hypothesis. The maximum of this anomaly (calculated relative to the Pliocene control with modern orbit) is obtained from the GCM simulation carried out under orbital conditions for 115 kyr BP, but otherwise Pliocene boundary conditions. For each orbital ice-sheet simulation, the initial condition is the equilibrium state from the corresponding non-orbital simulation. This corresponds to the fact that the non-orbital experiments are simulating an average ice-sheet configuration over many orbital cycles, whereas the orbital experiments represent a deviation from this long-term average state. Given that the 115-kyr orbit is fairly extreme in the context of the past 5 million years, this provides a strong test of the orbital-trigger hypothesis—for example, if the control cold-orbit ice sheet were significantly larger than the open-seaway cold-orbit ice sheet, this would imply that the closure of the Panama seaway acted as a 'priming' mechanism for glaciation, triggered by the favourable orbital conditions. More details of the orbital ice-sheet simulations are given in the Supplementary Information.

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