



Earth Ice Age Dynamics: A Bimodal Forcing Hypothesis

Zhongping Lai^{1,2,3}*, Yantian Xu¹ and Peisong Zheng¹

¹Institute of Marine Sciences, Guangdong Provincial Key Laboratory of Marine Biotechnology, Shantou University, Shantou, China, ²School of Geography and the Environment, University of Oxford, Oxford, United Kingdom, ³Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), Zhuhai, China

The Earth has gone through multiple ice ages in the past million years. Understanding the ice age dynamics is crucial to paleoclimatic study, and is helpful for addressing future climate challenges. Though ice ages are paced by variations in Earth's orbit geometry, how various climatic system components on the Earth respond to insolation forcing and interact with each other remains unclear. A prevailing view argues that the initial responses occur in the northern high latitudes (i.e. the northern high-latitude hypothesis, NHH). This opinion is challenged by recent reports, such as the lead of climate change in the Southern Hemisphere (SH) relative to that in the Northern Hemisphere (NH), the southern control on Atlantic meridional overturning circulations (AMOC), and the potential significance of Southern Hemisphere (SH). Alternatively, the tropical hypothesis (TH) argues for a leading role of the tropics. Both the NHH and the TH belong to a single-forcing mechanism, and have difficulty in interpreting phenomena, such as the saw-tooth pattern of the ice ages. Here we present a new proposal concerning the Earth's ice age dynamics: the bimodal forcing hypothesis (BFH). The essential assumption of this hypothesis is that for glacialinterglacial cycles, the cooling (glaciation) starts from the northern high latitudes, whereas the warming (deglaciations) starts from the SH. Particularly, the BFH emphasizes the significance of SH oceans in accumulating and transferring heat for deglaciations. Thus, it is capable to reasonably explain the saw-tooth pattern. We compiled 100 paleotemperature records globally for validation. The BFH is consistent with most of these records, and provides a straightforward and comprehensible way to interpret ice age on Earth.

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*Correspondence:

Zhongping Lai zhongping.lai@yahoo.com

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INTRODUCTION

How the Earth's climate would respond to increasing anthropogenic atmospheric carbon dioxide concentration concerns the human society (IPCC and Stocker, 2013; Steffen et al., 2018). Resolving this problem requires insights from both the current and paleoclimatic studies (e.g. Zheng et al., 2021). Climate of the past ~2.6 million years (Myr) is characterized by repeated growth and decay of large continental ice sheets, with astronomical cycles at ~23 thousand years (kyr), ~41 kyr, and ~100 kyr (Milankovitch, 1941; Hays et al., 1976). Although variations in Earth orbital geometry have been widely accepted as the ultimate cause of glacial-interglacial cycles, the process that translates the insolation oscillations into periodic climate change is still in debate (Imbrie et al., 1992, 1993; Denton et al., 2010). A long-lasting enigma is the saw-tooth pattern of ice ages, i.e., relatively long periods of ice-sheet growth followed by relatively short periods of ice-sheet decay (Broecker and Donk, 1970; Lisiecki and Raymo, 2005). How do symmetric insolation fluctuations result in asymmetric ice age cycles? Internal feedbacks in Earth's climate system are



FIGURE 1 | Climatic records during the last deglaciation. (A) 65°N June 21 insolation (black) (Laskar et al., 2004). 65°S averaged mean longitude spring insolation (August 21 to November 20, blue) (Laskar et al., 2004; Stott et al., 2007). 77°S summer duration (red), which is measured as the number of days whose diurnal average insolation exceeds 250 W/m2 (Huybers and Denton, 2008). (B) North Atlantic core OCE326-GGC5 ²³¹Pa/²³⁰Th ratios for the overall strength of AMOC. Red and green are ²³⁸U-based value and ²³²U-based results, respectively. Increasing values (plotted downward) indicate reduced overturning strength (McManus et al., 2004). (C) Atmospheric CO2 from EPICA Dome C (EDC) ice core (Monnin et al., 2001). (D) δ^{18} O from North Greenland Ice Core Project (NGRIP) ice core (grey. Black for 20 points smoothed data). (Rasmussen et al., 2006). (E) δ^{18} O from West Antarctic Ice Sheet Divide (WDC) ice core, (grey. Black for 30 points smoothed data) (WAIS Divide Project Members, 2015). (F) Northern Hemisphere (NH; blue), Southern Hemisphere (SH; orange), and global (pink) surface temperature stacks with 1σ error range (Shakun et al., 2012). (G) Ice-volume equivalent sea level plotted with 2o (Continued)

FIGURE 1 | uncertainty (Lambeck et al., 2014). All data are on their published timescale. Periods of Last Glacial Maximum (LGM), Henrich stadial 1 (HS1), Bølling-Allerød (B/A), Younger Dryas (YD) and Holocene are separate by grey dashed lines.

believed to be the answer. Different understandings of internal feedbacks with emphasis on different climate components lead to multiple climate hypotheses, such as the northern high-latitude hypothesis (NHH; e.g. Denton et al., 2010) and the tropical hypothesis (TH; e.g. Cane, 1998; Clement et al., 2001; Chiang, 2009; Beck et al., 2018; Wang, 2021). The NHH and the TH, both belong to a single-forcing mechanism (Ding, 2006), argue for a leading role of the northern high latitudes and the tropics, respectively. However, a single-forcing mechanism has difficulty in interpreting phenomena like the saw-tooth pattern.

The bimodal forcing hypothesis (BFH) we proposed here assumes cooling/glaciation starts from the northern highlatitudes while warming/deglaciation from the SH. We tested this hypothesis with a compilation of 100 global paleotemperature records. The BFH is compatible with most of them, and can better explain puzzles like the saw-tooth problem. In the following, we first outline the NHH and its drawbacks, then illustrate the logic of the BFH, and finally discuss future directions of this new hypothesis.

THE NORTHERN HIGH-LATITUDE HYPOTHESIS AND ITS DRAWBACKS The Key Points of Northern High-Latitude Hypothesis

So far, the NHH has been the most prevailing ice age hypothesis. Essentially, it argues for a uniquely triggering role of the summer insolation at 65°N in both hemispheres (e.g. Kawamura et al., 2007). A concomitant assumption is that initial responses to insolation forcing happen in northern high latitudes, no matter in ice age onsets (e.g. Imbrie et al., 1992; 1993) or terminations (e.g. Denton et al., 2010). Besides, the 'switch' of Atlantic meridional overturning circulation important (AMOC), which exerts an effect on interhemispheric heat redistribution, is assumed to lie in the northern North Atlantic (e.g. Broecker and Denton, 1989; Clark et al., 2002). After the pioneering interpretation of glacial-interglacial cycles from a northern perspective (Imbrie et al., 1992; 1993), a comprehensive NHH-based picture of working processes during the last deglaciation was presented (Denton et al., 2010).

In summary, the rising NH summer insolation at the end of Last Glacial Maximum (LGM) (**Figure 1A**, black curve) initiated ice-sheet melting and delivered freshwater into the North Atlantic. This freshwater forcing shut down the AMOC during the Heinrich stadial 1 (HS1) interval (**Figure 1B**; Ganopolski and Rahmstorf, 2001; McManus et al., 2004; Liu et al., 2009), resulting in the deglacial warming in the SH through the bipolar seesaw mechanism (Crowley, 1992; Broecker, 1998; Stocker and Johnsen,



15 kyr) initial warming. The early deglacial warming observed in some tropical and NH mid-latitude records (e.g. West Pacific) may partly arise from the influence of lowlatitude insolation (Xu et al., 2013; Wang, 2021). Details about the database for this map can be found in supplementary materials.

2003). Meanwhile, reduced AMOC and expanded sea ice in North Atlantic caused the southward shift of SH westerlies and the release of CO_2 from the deep ocean to the atmosphere (**Figure 1C**; Toggweiler et al., 2006; Anderson et al., 2009). The last deglaciation was accomplished when atmospheric CO_2 was raised above threshold.

The seemingly self-consistent NHH actually has unsolvable problems, and there is an increasing number of studies challenging the NHH. We summarize three aspects of these challenges, i.e., the lead of climate change in the SH with respect to that in the NH, the southern control on AMOC variations, and the potential significance of SH insolation.

The Lead of Climate Change in the Southern Hemisphere with Respect to That in the Northern Hemisphere

Orbital-scale climate changes in the NH do not always lead those in the SH or the tropics (Shackleton and Pisias, 1985; Sowers et al., 1991, 1993; Pichon et al., 1992; Broecker and Henderson, 1998; Paillard and Parrenin, 2004; Bouttes et al., 2011, 2012; Paillard, 2015; Mariotti et al., 2016). Changes in sea surface temperature (SST) from the SH Indian Ocean (Hays et al., 1976) and the tropical Pacific (Lea et al., 2000; Visser et al., 2003) led variations in NH ice sheets by up to a few thousand years. Particularly, an early deglacial warming prior to the LGM has been observed from the SH mid/low-latitude SST records (Pahnke and Sachs, 2006; Santos et al., 2017).

Polar ice cores offer another opportunity to compare temporal relationship between hemispheres. A pioneering attempt to synchronize ice core records from the Antarctica and the Greenland showed that the onset of warming in Antarctica occurred ~3 kyr prior to that in Greenland during the last deglaciation (14.7 kyr ago; **Figure 1D**; Sowers and Bender, 1995). A surface air temperature record from the West Antarctic Ice Sheet Divide ice core (WDC; **Figure 1E**) revealed that significant warming in West Antarctica began by 20 kyr ago during the last deglaciation, confirming an earlier deglacial warming in Antarctica (WAIS Divide Project Members, 2013). Additionally, Antarctic Vostok temperature rising occurred ~4–9 kyr prior to the ice-sheet melting during the last four ice age terminations (Petit et al., 1999).

Compilations of surface temperature reconstructions during the last termination further confirm early warming in the SH and the tropics. Assessment of deglacial SST development in the Pacific Ocean revealed that the timing of initial deglacial warming was generally early (before 18 kyr ago) in the south, late (later than 15.5 kyr ago) in the north, and mixed with both early and intermediate (between 18 and 15.5 kyr ago) signals in the tropics (Kiefer and Kienast, 2005; Tachikawa et al., 2009). A lead of deglacial warming in the SH relative to that in the NH was confirmed at a global scale as well (**Figure 1F**; Shakun et al., 2012).

We also compile 100 paleotemperature records during the last deglaciation (see Material and Methods), including land/ sea surface and deep ocean temperatures, and compare their initial timings of the last deglacial warming (**Figure 2**). Two points stand out from this temporal-spatial warming pattern of the last deglaciation. First, initial warming in the SH (mostly centered between 20 and 18 kyr ago) is earlier than in the NH (mostly centered after 18 kyr ago). Second, warming started prior to 20 kyr ago in some SH surface records, and prior to 18 kyr ago in two deep ocean records. This early and strong warming is inconsistent with the NHH view that bipolar seesaw initiates deglacial warming in the SH.

The Southern Control on Atlantic Meridional Overturning Circulations Variations

An ²¹³Pa/²³⁰Th record recovered from the subtropical North Atlantic has demonstrated that a nearly total shutdown of AMOC occurred between 17.5 and 15 kyr ago, followed by an abrupt resumption at ~14.7 kyr ago (McManus et al., 2004; Böhm et al., 2015). The near-collapse of AMOC during the HS1 interval was regarded as the cause of SH warming in NHH, and was usually attributed to catastrophic iceberg discharge into the North Atlantic (e.g. Ganopolski and Rahmstorf, 2001; Liu et al., 2009). However, recent studies favor that episodic Heinrich events with huge iceberg discharge were the results rather than the causes of AMOC reduction. According to a sedimentary record from the northeast Atlantic, for the majority of abrupt climate changes over the past four glacial cycles, iceberg arrived too late to trigger cooling (Barker et al., 2015). And episodic icedischarge events were probably a consequence of increased basal melting rate due to increased subsurface temperature caused by an inactive AMOC (Shaffer et al., 2004; Liu et al., 2009). A northwest Atlantic record showed that, for four Heinrich events (H1, H3, H5a and H6), the subsurface water started to warm approximately 1-2 kyr before each Heinrich event (Marcott et al., 2011). New evidence also suggested that the small amount of meltwater from ice-sheet margins during early deglaciation was unable to induce near-complete collapse of AMOC (e.g. Colin de Verdière et al., 2006; Sévellec et al., 2010).

In addition, the coupling of AMOC variations and sea level changes during the last deglaciation was at odds with a northern freshwater-forcing scenario, which predicts association of more freshwater input (i.e. larger sea level rise) with a less active AMOC. Within the duration when the AMOC was significantly reduced (17.5–15 kyr ago), a rise of ~25 m at a rate of ~12 m kyr⁻¹ only occurred during the latter half of the interval (~16.5–15 kyr ago) after a period of near-constant sea level between ~18 and 16.5 kyr ago (**Figure 1G**; Lambeck et al., 2014). In contrast, the most prominent meltwater pulse (MWP-1A; ~20 m in less than



FIGURE 3 | Schematic of the bimodal forcing hypothesis. (A) During glacial inception, high northern latitudes first respond to decreasing insolation, and the coeval vigorous AMOC helps to deliver cooling signal to the rest of the Earth. (B) AMOC switches from a warm to cold mode when ice age is near its maximum, and this mode change results in heat accumulation in the SH. (C) The accumulated heat together with SH insolation cause the deglacial warming in the Southern Ocean and Antarctica. This warming and associated sea-ice retreat and CO₂ release terminate glacial conditions. Particularly, warming in the SH leads to AMOC resumption during deglaciations, this resumption is accompanied by AMOC overshoot (Skinner et al., 2013) and transported a huge amount of heat from the SH to the NH.



FIGURE 4 | Climatic records since the last interglacial period. **(A)** 65°N June 21 insolation (Laskar et al., 2004). **(B)** EDC temperature reconstruction based on ice δD (Jouzel et al., 2007). **(C)**. Composite sea level in one σ error (Spratt and Lisiecki, 2016). North Atlantic core ODP 1063 ²³¹Pa/²³⁰Th **(D)** and ¹⁴³Nd/¹⁴⁴Nd (ϵ Nd) **(E**; Böhm et al., 2015) records. ϵ Nd is a proxy for changes in sources and mixing of water masses. Increasced values (plotted downward) indicate shoaling of the AMOC. **(F)** Western South Atlantic core GL-1090 SST data (Santos et al., 2017). All data are on their published timescale. The mode shifts of AMOC derived from the combined ²³¹Pa/²³⁰Th and ϵ Nd records is showed in the bottom (Böhm et al., 2015). Grey and orange shadings mark cold periods (MIS 2, 4) and the last interglacial (MIS 5e), respectively.

500 years) coincided with a sharp resumption of AMOC at \sim 14.6 kyr ago (Deschamps et al., 2012).

To overcome deficiencies in modulating AMOC with a northern origin, some researchers argue for a southern control on the AMOC variability. A numerical simulation revealed that a gradual warming and sea-ice retreat in the Southern Ocean during deglaciations would induce an abrupt resumption of AMOC (Knorr and Lohmann, 2003). Another simulation also showed that freshwater perturbations to the regions of Antarctic Intermediate Water (AAIW) formation would induce a shift of North Atlantic Deep Water (NADW) formation from the "off" to the "on" mode (Weaver et al., 2003). This driving mechanism well explains the synchronicity of MWP-1A with AMOC resumption during the last deglaciation.

The Potential Significance of Southern Hemisphere Insolation

The NHH view that NH summer insolation drives terminations is questioned by recent proposals that local insolation is at least equally important in driving terminations in the SH. For example, due to the non-linear relationship between radiation and temperature, the seasonal distribution of the solar energy could control the annual temperature of the Antarctic (Huybers and Denton, 2008). This radiation-driven temperature (proportional to the local summer duration) was rising from about 25 kyr ago (Huybers and Denton, 2008). Alternatively, increased springtime insolation over the Southern Ocean (Stott et al., 2007) along with retreating sea ice due to the positive feedback between temperature and sea ice area (Levermann et al., 2007), could account for early onset of deglacial warming in the SH. Particularly, the retreat of sea ice would lead to decreased stratification in the Southern Ocean by inducing enhanced Ekman transport, both contributing to the subsequent rise in atmospheric CO₂ (Stephens and Keeling, 2000; Stott et al., 2007; Basak et al., 2018). Moreover, there are doubts that Antarctic temperature records derived from ice cores were biased, and the orbital component of the bias-corrected temperature record can be explained by local insolation without involving the NH (Laepple et al., 2011).

In summary, the astronomical-forcing theory nicely explains the dominant periods within glacial-interglacial cycles, but fails to illustrate explicitly the response of different climate system components to insolation forcing.

THE BIMODAL FORCING HYPOTHESIS

A single-forcing mechanism such as the NHH seems unsatisfactory in explaining ice age dynamics, thus we put forth the BFH. In this conceptual model, glaciations (cooling) start from the NH while deglaciations (warming) begin from the SH (**Figure 3**). Here we present an interpretation of the onset and termination of the last glacial period (~120–10 kyr ago) under the framework of BFH, which fits better with available paleoclimatic records and model simulations.

Cooling Down: Mechanism of the Onset of the Last Ice Age

The BFH assumes that northern high latitudes firstly responded to the decline of NH summer insolation beginning at \sim 128 kyr ago (**Figure 4A**), same as the NHH. Diminishing insolation triggered the Earth moving forward into the last ice age, assisted by a series of positive feedbacks such as vegetation and sea ice (Khodri et al., 2005). An early oceanic response to insolation to the south of Greenland indicated that SST started to decrease at ~119 kyr ago and a strong ice-rafted-deposit (IRD) input occurred at ~117 kyr ago, signaling the first regrowth of the Greenland Ice Sheet during the end of last interglacial period (Irvalı et al., 2016).

This initial cooling in the northern high latitudes was propagated through oceanic and atmospheric circulations towards the rest of the world. According to studies on oceanic circulations (e.g. Broecker, 1991; Marshall and Speer, 2012; Talley, 2013; Ferrari et al., 2014), once a cooling signal was imprinted on the northern North Atlantic, the formation regions of NADW, during the onset of last ice age, temperature of the whole ocean would begin to decrease within centuries. Reconstructions of deep ocean temperatures at various sites and with different methods all reveal a significant cooling during the MIS 5e-5 days transition (~115 kyr ago; e.g. Labeyrie et al., 1987; Shackleton, 2000; Cutler et al., 2003; Adkins, 2013). For instance, a deep ocean cooling of $\sim 2^{\circ}$ C was estimated between the MIS 5e and MIS 5c for two drilling cores in the Atlantic and Pacific (Cutler et al., 2003). Also, considerable temperature reductions around the MIS 5e-5 days transition were observed worldwide at sea (e.g. Labeyrie et al., 1996; Lea et al., 2000; Tachikawa et al., 2009; Koutavas, 2018), and land surface (e.g. Jouzel et al., 2007; Figure 4B). Compared to oceanic processes, atmospheric circulations played a relatively subordinate role during the onset of last ice age, because the contribution of atmosphere to rapid deep ocean cooling is limited, and the tropics is a barrier for trans-hemispheric atmospheric processes (Manabe and Broccoli, 1985; Chiang and Bitz, 2005). The aforementioned cooling trends are apparently synchronous at a global scale, which seems in contradiction with the BFH. However, this synchronicity could be misled by dating uncertainties and low sampling resolution.

Warming up: Mechanism of the Termination of the Last Ice Age

From its beginning at ~120 kyr ago, the last ice age lasted until the deglaciation at ~18 kyr ago (Figure 4C). Within the glacial period, the Earth experienced three NH summer insolation peaks but none triggered deglaciations (Figure 4A; Cheng et al., 2016), implying that apart from insolation, internal feedbacks are also needed to determine terminations. Simultaneous measurements of ²³¹Pa/²³⁰Th and ¹⁴³Nd/¹⁴⁴Nd from North Atlantic evidenced a warm-to-cold mode shift of AMOC during the MIS three to two transition at ~27 kyr ago (Figures 4D,E; Böhm et al., 2015). As reduction in AMOC would lead to heat accumulation in SH through the bipolar seesaw, the mode shift of AMOC during the later part of last ice age was probably responsible for the early deglaciation warming registered in SH low/mid-latitudes (e.g. Pahnke and Sachs, 2006; Santos et al., 2017; Figure 4F). The rapid ice-sheet melting indicated by asymmetric saw-tooth pattern required huge amount of heat, which might partly source from the accumulated heat in the SH linked to reduced AMOC.

The deglacial warming in the Southern Ocean and Antarctica at ~20 kyr ago lagged that in the SH mid/low latitudes occurring at ~27 kyr ago, indicating a southward transmission of heat in the SH. The summer sea-ice edge around the Antarctica started to retreat at ~23 kyr ago (Collins et al., 2012), the surface air in the West Antarctica had felt the warming by ~20 kyr ago (WAIS Divide Project Members, 2013), and the Southern Ocean began to warm at ~19 kyr ago (Stott et al., 2007). This lag of deglacial warming possibly result from the existence of a thermal threshold between the Southern Ocean and the SH low/midlatitudes, which was finally reached when the SH summer duration (Huybers and Denton, 2008; Figure 1A, red curve), and/or spring insolation (Stott et al., 2007; Figure 1A, blue curve), began to increase at ~23 kyr ago. The accumulated heat associated with reduced AMOC (Santos et al., 2017), or the heat accumulation in deep Southern Ocean during the long Greenland stadial starting from 27.6 kyr ago (Skinner et al., 2020) could contribute to this initial warming. Once Antarctic sea ice had retreated and the Southern Ocean had warmed, positive feedbacks worked to release CO₂ from the deep ocean to the atmosphere (e.g. Stephens and Keeling, 2000; Toggweiler et al., 2006; Watson et al., 2015), and CO₂ helped to drive the warming in the NH (Shakun et al., 2012). Moreover, heat carried by a Southern Ocean-origin water mass led to a 3°C warming in the deep North Atlantic during the HS1, possibly resulting in the reinvigoration of AMOC at ~14.7 kyr ago (Thiagarajan et al., 2014). Simulations also support a controlling role of the Southern Ocean warming in AMOC resumption (Knorr and Lohmann, 2003; Weaver et al., 2003; Buizert and Schmittner, 2015). The resumpted AMOC transported a considerable amount of heat from the SH to the NH at an unprecedented rate in the next few hundred years and caused a rapid melting of ice sheets, the MWP-1A (Deschamps et al., 2012). By this time, the transition from the LGM to Holocene on both hemispheres seemed irreversible.

In summary, the BFH is distinct from previous single-forcing hypotheses, in that it assumes the initial response of glacial onsets is different from that of glacial terminations. When the NH summer insolation starts to decline, it is the northern high latitudes that first react. The NH ice sheets begin to grow, and the high-latitude surface temperature begin to decrease. Subsequently, through a series of atmospheric and oceanic processes, especially the global oceanic overturning circulation, the cooling signal is transmitted towards the rest of the world. As the ice age proceeds near its maximum, the AMOC switches from a warm to a cold mode due to a few possible reasons, such as a threshold value has been reached by the volume of NH ice sheets, the temperature of NADW (Adkins, 2013), or the area of Antarctic sea ice (Ferrari et al., 2014). Then heat begins to accumulate in the SH as a result of reduced AMOC. Once the accumulated heat plus the SH local insolation attains a certain value, the Antarctic surface temperature starts to increase, the sea ice around the Antarctica starts to retreat, and the CO₂ preserved in deep ocean is added back to the atmosphere. Finally, the heat stored in the SH becomes so large that the AMOC switches back to the warm mode and both hemispheres move toward another interglacial period.

FUTURE DIRECTIONS

In general, the BFH differs from previous ice-age hypotheses in two aspects. First, it assumes that different climatic components drive glaciation and deglaciation, contrasting with single-forcing hypotheses which argue for a dominant role of a single climatic component during both ice-age onset and termination. This might benefit the understanding for the saw-tooth pattern, which indicates different processes of cooling and warming. Second, the BFH recognizes the significance of SH oceans in accumulating and transferring heat for terminations.

The BFH awaits further improvement, as many issues need to be resolved. For example, a crucial idea within the BFH, that reduced AMOC at the MIS three to two transition contributed to heat accumulation in the SH, is not yet consistent with traditional bipolar seesaw which is used to explain millennial-scale oscillations. Specific mechanisms transmitting heat from the SH low/mid latitudes to the Southern Ocean and Antarctica during \sim 27- \sim 20 kyr ago remains unclear. And to which extent SH local insolation contributes to deglaciation is unsettled.

MATERIALS AND METHODS

In order to investigate the temporal-spatial distribution of the last glacial-interglacial transition (the time when temperature or proxy records have obviously shifted), we compiled 100 proxy records around the world (**Supplementary Table S1**, **Supplementary Figure S1**). Only proxy records with firm chronological control and high resolution have been collected. For records with the ¹⁴C-based age model, we recalibrated all available ¹⁴C dates using Intcal 13 and SHcal 13. Then the age model was built up by linear interpolation between ¹⁴C-dated control points. We determine the start of deglaciation by visually identifying the first obvious shift in temperature or proxy curves since 34 kyr ago. Then this age is compared to the timing given by the original author(s) if available. In case that the result has

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apparent discrepancies (the difference between two ages is over 1,000 yr), we adopt the opinion of original author(s).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

ZL proposed the hypothesis. ZL, YX, and PZ wrote the paper. PZ made figures. ZL, YX, and PZ have equal contributions.

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SUPPLEMENTARY MATERIAL

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