Non-trivial role of internal climate feedback on interglacial temperature evolution

https://doi.org/10.1038/s41586-021-03930-4

Received: 2 March 2021

Accepted: 18 August 2021

Published online: 1 December 2021

Check for updates

Xu Zhang[1,2]✉ & Fahu Chen[1,2]

ARISING FROM S. Bova et al. *Nature* https://doi.org/10.1038/s41586-020-03155-x (2021)

Quantifying seasonal bias in proxy reconstructions (for example, sea surface temperature (SST)) has been a long-standing challenge, hampering our understanding of past climate evolution (for example, the Holocene temperature conundrum)[1,2]. Recently, Bova et al.[3] proposed a seasonal to mean annual transformation (SAT) method that seems to effectively remove SST signal caused by seasonal insolation change. To extract mean annual SST (MASST) change for the Holocene epoch (12–0 thousand years before present (kyr BP)), Bova et al.[3] selected SST records that additionally cover the last interglacial (LIG; 128–115 kyr BP) period, for which SST is assumed to be solely attributed to variations in local solar insolation, hence allowing for reliable quantification of seasonal bias in SST records. However, this assumption is fundamentally incorrect because it overlooks the roles of internal Earth system feedback (for example, sea ice) on LIG temperature change, indicating that their findings are effectively biased by overcorrecting insolation-induced seasonal bias in SST proxies.

We agree that global ice volume and greenhouse gas concentrations were relatively stable during the LIG (Fig. 1a, b) and their direct contributions to seasonally unadjusted SST (SST_{sn}) changes might be trivial, in comparison to the seasonal insolation change. However, this does not mean that contemporary internal feedbacks of the system also have a trivial role. Among various internal feedbacks (for example, sea ice, cloud, vegetation and so on), sea ice is one representative example for the LIG because it experienced significant contemporary advances as suggested by reconstructions[4,5] and climate models[5–7].

Sea ice–albedo feedback is a well-acknowledged effectively positive feedback on temperature changes. Recently, England et al.[8] conducted a sensitivity experiment applying a Representative Concentration Pathway 8.5 sea-ice scenario—including an approximately 35% winter sea-ice loss in the Southern Ocean and an approximately 70% summer sea-ice loss in the Arctic (perennial sea-ice remnants persist)—under an otherwise present-day climate background. They found that the polar sea-ice loss can directly cause an increase of tropical MASST by more than 0.6 °C (Fig. 2). In particular, all of the core locations used in Bova et al.[3] are characterized by mean annual warming with magnitudes in a range between 0.4 and 1 °C.

During the peak warm period of the LIG (128–125 kyr BP), both polar regions experienced significant sea-ice losses[4,5] (for example, Antarctic winter sea ice may have retreated by up to 65% (ref. [6]) and a summer sea-ice-free condition probably happened in the Arctic[7]) that were more than those imposed in ref. [8]. Following that, sea-ice volume increased markedly (note that their driving mechanisms might be different—the former is mainly driven by obliquity-induced mean annual insolation while the latter is driven by precession-induced summer insolation[9,10]), probably reaching present-day levels by the end of the LIG[4,5] (that is, 115 kyr BP; for example, Fig. 1c). Therefore, it is reasonable to infer that the sea-ice expansions could have caused MASST to decrease by at least about 0.6 °C during the LIG without any additional changes in the climate background (for example, insolation, greenhouse gas concentrations and ice volume) (Figs. 1a–c and 2). This indicates that part of the MASST component in SST_{sn} change is directly attributed to the sea-ice expansion and should be eliminated before applying the SAT method. Of particular importance is that if this part is equivalent to, or perhaps larger than, the seasonal insolation-induced component, the phase between a corrected SST_{sn} and insolation would be different from that in Bova et al.[3]. These lines of evidence therefore raise questions about the representativeness and reliability of the MASST stack of Bova et al.[3] in representing mean annual temperature change (Fig. 1f).

The mean annual cooling is also supported by other lines of evidence. For instance, a global stack of benthic foraminifera $\delta^{18}O$ ($\delta^{18}O_c$; where $\delta^{18}O$ represents the $^{18}O/^{16}O$ composition), which reflects mean ocean characteristics given the weak seasonal cycle in deep ocean, has a significant enriching trend from 123 to 115 kyr BP[11] (Fig. 1d). The $\delta^{18}O_c$ stack reflects changes in ambient temperature and the oxygen isotopic composition of seawater, which itself is a function of global ice volume[11]. The stable global ice volume during the last part of the LIG[12] (Fig. 1b) therefore indicates that the isotopic trend should be attributed solely to mean cooling, very probably associated with the sea-ice expansion[4,5] (for example, Fig. 1c). This, as Bova et al.[3] assumed that there were no effects from sea-ice change on SST changes, contradicts a neutral LIG temperature evolution as indicated by the SAT-calculated MASST stack (Fig. 1f).

A further problem in Bova et al.[3] is the model experiment used to support their LIG SST results. The model setup has two fundamental flaws that prevent it from being a reasonable and reliable reference. First is the 100×-accelerated orbital change. This appears to effectively induce biases in surface climate (for example, sea ice) in high latitudes where deep ocean water masses reach the surface[13] and, in turn, in the global climate—a consequence of overlooking the role of slow feedback on the fast feedback. Second is the ignoring of changes in ice volume and greenhouse gas concentrations. Interglacial climate evolution appears to depend on the climate change of the preceding deglaciation period[14]. This setup overlooks the associated slow and fast internal feedbacks during the penultimate deglaciation period[12], giving rise to evident underestimation of polar warming/ice loss particularly in the Antarctic realm during the peak warm periods[15]. Therefore, without

[1]Alpine Paleoecology and Human Adaption Group (ALPHA), State Key Laboratory of Tibetan Plateau Earth System, Resources and Environment (TPESRE), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China. [2]Key Laboratory of Western China's Environmental Systems (Ministry of Education), College of Earth and Environmental Science, Lanzhou University, Lanzhou, China. ✉e-mail: xu.zhang@itpcas.ac.cn

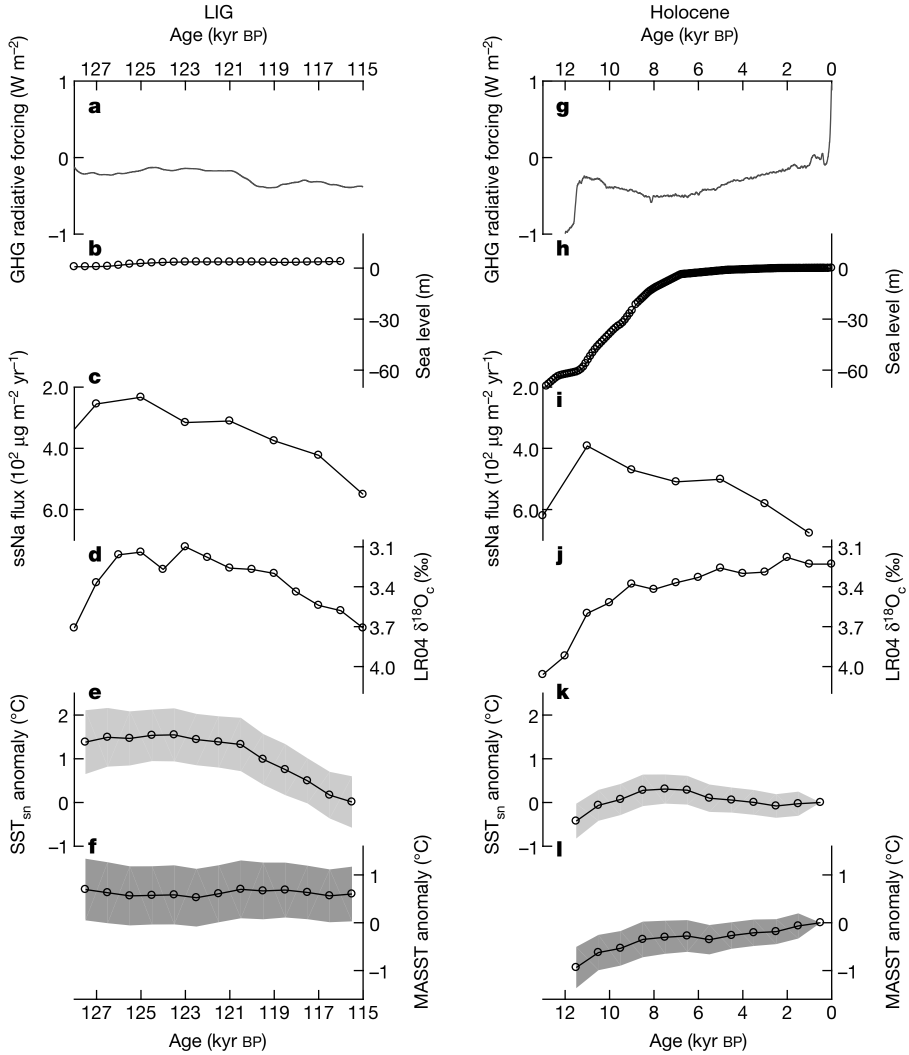

Fig. 1 | Evolution and drivers of Holocene and LIG SST. a–l, Greenhouse gas (GHG)-induced radiative forcing[3] (**a**, **g**) sea-level reconstructions[12] (**b**, **h**), Antarctic ice-core sea-ice proxy (sea-salt sodium, ssNa)[4] (**c**, **i**), global $\delta^{18}O_c$ stack[11] (**d**, **j**), seasonally unadjusted SST stack[3] (**e**, **k**) and SAT-calculated MASST stack[3] (**f**, **l**) for the LIG (**a**–**f**) and the Holocene (**g**–**l**). The age models for each record are taken from the corresponding studies.

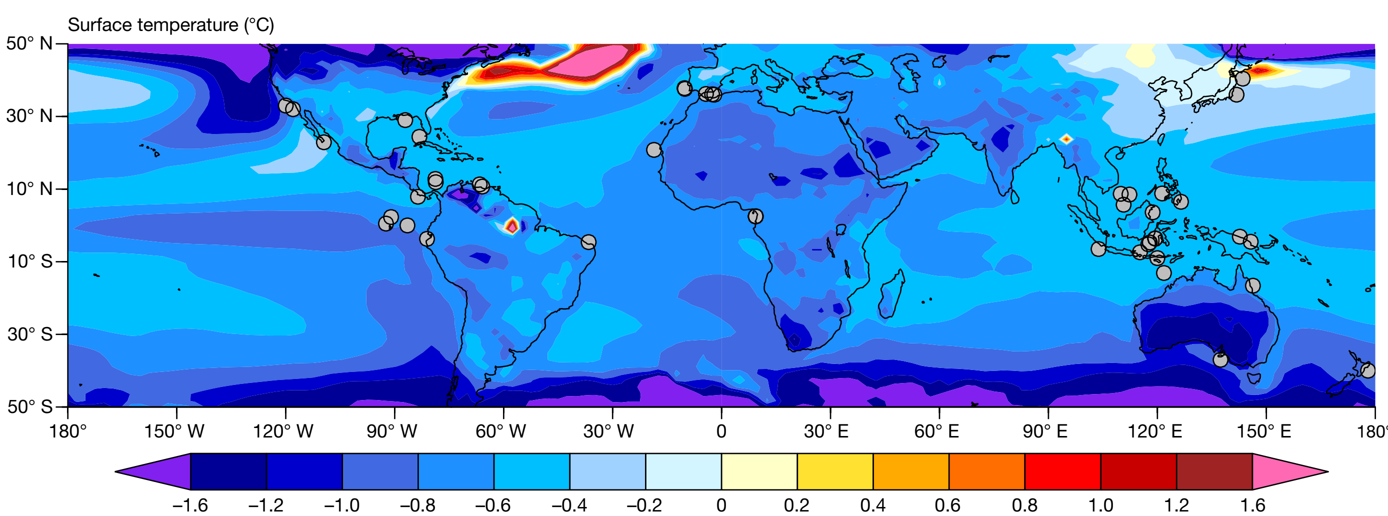

Fig. 2 | Tropical mean cooling induced by sea-ice expansion. The results are derived from the Community Earth System Model Whole Atmosphere Community Climate Model, in England et al.[8]. The plot represents the mean surface temperature anomaly between the present-day control run and the sea-ice sensitivity run (that is, temperature responses to polar sea-ice growth). The dots represent core locations used in Bova et al.[3]. This figure was generated by NCL[16].

these critical feedbacks, the experiment might artificially reproduce a climate in which orbital forcing solely dominates SST change that is linearly following variations in local insolation. In addition, model inconsistency on reproducing a coherent relationship between insolation and SST[9] may also reduce the credibility of the results derived from a single model. These issues therefore effectively limit the applicability of these modelling results to supporting their SAT-calculated results.

Overall, the issues discussed indicate that internal feedbacks of the system can shape interglacial temperature evolution, perhaps with only a secondary role for insolation changes. During the Holocene, internal feedbacks are much more complicated than those during the LIG (Fig. 1). For instance, global ice volume reached its present-day level from the early to middle Holocene and stayed stable until now (Fig. 1h). At the same time, sea-ice volume probably increased in both the Arctic (for example, ref. [5]) and Antarctic (for example, ref. [4] and Fig. 1i). In fact, this complexity creates challenges for current model performance on internal climate feedbacks; for example, the TraCE (Transient Climate Evolution) experiment TraCE-all applying alleged realistic climate forcing falls short of capturing Holocene sea-ice evolution especially in the Southern Ocean. We applaud the strategy of Bova et al.[3] of extracting seasonal bias by using LIG SST change. Nevertheless, the assumption of simplifying the Earth system to be solely driven by Earth's orbit effectively undermines the reliability and robustness of their results. Therefore, we would suggest that the current conclusions by Bova et al.[3] not be considered as final unless combined with more supportive evidence (that is, more pertinent SST records and an improved SAT method that accounts for internal feedbacks (for example, sea ice)).

Data availability

The datasets used for this study are available in the original papers.

1. Marcott, S. A., Shakun, J. D., Clark, P. U. & Mix, A. C. A reconstruction of regional and global temperature for the past 11,300 years. *Science* **339**, 1198–1201 (2013).
2. Liu, Z. et al. The Holocene temperature conundrum. *Proc. Natl Acad. Sci. USA* **111**, E3501–E3505 (2014).
3. Bova, S., Rosenthal, Y., Liu, Z., Godad, S. P. & Yan, M. Seasonal origin of the thermal maxima at the Holocene and the last interglacial. *Nature* **589**, 548–553 (2021).
4. Wolff, E. W. et al. Southern Ocean sea-ice extent, productivity and iron flux over the past eight glacial cycles. *Nature* **440**, 491–496 (2006).
5. Stein, R., Fahl, K., Gierz, P., Niessen, F. & Lohmann, G. Arctic Ocean sea ice cover during the penultimate glacial and the last interglacial. *Nat. Commun.* **8**, 373 (2017).
6. Holloway, M. D. et al. Antarctic last interglacial isotope peak in response to sea ice retreat not ice-sheet collapse. *Nat. Commun.* **7**, 12293 (2016).
7. Guarino, M. V. et al. Sea-ice-free Arctic during the Last Interglacial supports fast future loss. *Nat. Clim. Change* **10**, 928–932 (2020).
8. England, M. R., Polvani, L. M., Sun, L. & Deser, C. Tropical climate responses to projected Arctic and Antarctic sea-ice loss. *Nat. Geosci.* **13**, 275–281 (2020).
9. Bakker, P. et al. Temperature trends during the present and last interglacial periods - a multi-model-data comparison. *Quat. Sci. Rev.* **99**, 224–243 (2014).
10. Wu, Z., Yin, Q., Guo, Z. & Berger, A. Hemisphere differences in response of sea surface temperature and sea ice to precession and obliquity. *Glob. Planet. Change* **192**, 103223 (2020).
11. Lisiecki, L. E. & Raymo, M. E. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography* **20**, PA1003 (2005).
12. Clark, P. U. et al. Oceanic forcing of penultimate deglacial and last interglacial sea-level rise. *Nature* **577**, 660–664 (2020).
13. Varma, V., Prange, M. & Schulz, M. Transient simulations of the present and the last interglacial climate using the Community Climate System Model version 3: effects of orbital acceleration. *Geosci. Model Dev.* **9**, 3859–3873 (2016).
14. Barker, S. et al. Early interglacial legacy of deglacial climate instability. *Paleoceanogr. Paleoclimatol.* **34**, 1455–1475 (2019).
15. Capron, E. et al. Temporal and spatial structure of multi-millennial temperature changes at high latitudes during the Last Interglacial. *Quat. Sci. Rev.* **103**, 116–133 (2014).
16. The NCAR Command Language (NCL) v.6.62, https://doi.org/10.5065/D6WD3XH5 (UCAR/NCAR/CISL/TDD, 2019).

Acknowledgements We acknowledge instructive comments by P. Bakker to improve this study. We also thank Y. Sun and Z. Fu for preparing the figures, and E. J. Gowan, X. Xiao and W. Xiao for helpful discussions. This study is supported by the Basic Science Center for Tibetan Plateau Earth System (BSCTPES, NSFC project No. 41988101) and the National Science Foundation of China (no. 42075047).

Author contributions X.Z. initiated and developed this study by pointing out roles of sea ice change in global mean annual temperature. X.Z. and F.C. contributed equally to the writing of the Comment.

Competing interests The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to Xu Zhang.

Matters arising

Reply to: Non-trivial role of internal climate feedback on interglacial temperature evolution

https://doi.org/10.1038/s41586-021-03931-3

Published online: 1 December 2021

Check for updates

Samantha Bova[1,7]✉, Yair Rosenthal[1,2], Zhengyu Liu[3], Mi Yan[4,5], Anthony J. Broccoli[6], Shital P. Godad[1,8] & Cheng Zeng[4,5]

REPLYING TO X. Zhang and F. Chen *Nature* https://doi.org/10.1038/s41586-021-03930-4 (2021)

The accompanying Comment[1] questions various aspects of the seasonal to annual mean transformation (SAT) method proposed in our original study[2], suggesting that the final results are predetermined by its underlying assumptions[1]. The primary critique raised relates to the assumed dominance of external insolation over internal feedbacks in shaping the evolution of interglacial temperatures, at least in the low to mid-latitudes. While the issue as it relates to feedbacks arising from slow components of the climate system needs to be further explored, the role of feedbacks from fast processes, such as sea ice, should not affect our conclusions qualitatively. The consistency of our trends with fully coupled model simulations supports the suggested evolution of mean annual temperatures throughout the Holocene epoch.

The SAT method offers a possible solution to the apparent discrepancy between proxy records showing long-term cooling[3,4] and models, which show long-term warming across the Holocene, known as the Holocene temperature conundrum[5,6]. Importantly, it also offers a solution to the observed discrepancies between proxy archives; alkenone and *Globigerinoides ruber*-Mg/Ca sea surface temperature (SST) reconstructions exhibit a systematic divergence in Holocene SST trends with the former often indicating warming and the latter indicating cooling across the Holocene, even at adjacent core locations[7,8]. It is therefore not possible for both alkenone and *G. ruber*-Mg/Ca SST reconstructions to record mean annual SSTs at a majority of low- to mid-latitude locations. Nevertheless, they are largely considered to be mean annual records when integrated into global reconstructions[3,4], probably because there has been no systematic approach for assessing proxy seasonal biases. We remind the readers of this issue, as it must be addressed in any proposed solution to the Holocene conundrum. Model deficiencies, as suggested in the accompanying Comment[1], therefore may contribute to the conundrum, but they are not a sufficient explanation.

The fact that the corrected records, generated by the SAT method, are consistent with the trends suggested by state-of-the-art climate models supports our argument that seasonal biases in proxy data are a major reason for the disparity with models. Although seasonal biases have previously been discussed, owing to the low eccentricity of Earth's orbit and the resulting low seasonal contrast in insolation, it is difficult if not impossible to detect proxy seasonal biases in the modern ocean, especially in the low latitudes, owing to the low signal-to-noise ratio. As an illustration, despite a majority of sediment trap studies indicating a greater flux of *G. ruber* and alkenone biomarkers in boreal summer and autumn (including sites in the western tropical Pacific[9,10], eastern tropical Pacific[11,12] and northwest Pacific[13] and south of the subtropical front on the Chatham Rise[14]; note an austral summer bias was observed north of the front), an often observed 'warm bias' in SST estimates[15,16] and discrepancies between the two SST proxies seen in many sites that can be explained only if their carriers have different seasonal biases[8], measurements of *G. ruber* shell Mg/Ca and the alkenone unsaturation index are interpreted and calibrated as reflecting mean annual surface conditions. A mean annual interpretation is usually justified because the correlation with both mean annual SST and boreal summer SSTs is statistically indistinguishable[8,9,15]. Thus, seasonal biases in marine SST proxies cannot directly be addressed in calibration studies, leading us to 'calibrate' the SAT method using records from the last interglaciation (LIG), when seasonality was at its maximum.

Notably, this 'calibration' method enables SAT to be applied widely, overcoming the limitations of modern field studies. However, we caution that the SAT method cannot be applied blindly. For effective application of SAT, two key assumptions that underpin the method must be upheld: the SST responds approximately linearly to local insolation, or to insolation that is highly correlated with the local insolation; multi-millennial trends in LIG SST at the location are forced dominantly by orbitally driven changes in local insolation or insolation that is highly correlated with the local insolation. If either of these assumptions is violated, SAT will not work and should not be applied.

We openly acknowledge that these assumptions will not be satisfied in all locations. For example, there may be locations where feedback processes responding to remote climate forcing uncorrelated to the site local insolation overwhelm the response to changes in local insolation, leading to changes uncorrelated with local insolation. In our compilation, we were therefore selective of the records included, limiting the records included to low- to mid-latitude regions where SST is most likely to respond linearly to the local insolation. Even within this region, we were critical of the records used, excluding sites in proximity to oceanographic fronts where SST can be strongly affected by nonlinear dynamics as seen, for example, in a previous reconstruction[4].

Nevertheless, in the accompanying Comment, Zhang and Chen[1] question whether these assumptions can be reasonably upheld even in the selected locations. While they agree that land ice and greenhouse gases (GHGs) probably had a limited impact, the authors assert that changes in polar sea ice may have had a non-trivial impact on SSTs at

[1]Department of Marine and Coastal Sciences, Rutgers, State University of New Jersey, New Brunswick, NJ, USA. [2]Department of Earth and Planetary Sciences, Rutgers, State University of New Jersey, New Brunswick, NJ, USA. [3]Atmospheric Science Program, Department of Geography, The Ohio State University, Columbus, OH, USA. [4]School of Geography, Nanjing Normal University, Nanjing, China. [5]Open Studio for Ocean-Climate-Isotope Modeling, Pilot National Laboratory for Marine Science and Technology, Qingdao, China. [6]Department of Environmental Sciences, Rutgers, State University of New Jersey, New Brunswick, NJ, USA. [7]Present address: Department of Geological Sciences, San Diego State University, San Diego, USA. [8]Present address: Department of Geosciences, National Taiwan University, Taipei, Taiwan. ✉e-mail: sbova@sdsu.edu

the locations studied, thereby violating the second assumption, and invalidating the use of SAT. Sea ice, which is the focus of the Comment[1], is one possible mechanism that could induce a nonlinear response to local insolation forcing. Furthermore, its impact can extend from high to low latitudes via atmospheric and oceanic transport. Feedbacks involving vegetation and clouds have also been suggested.

We do not dispute the possible and, in fact, likely influence of sea-ice variations and other internal feedbacks on tropical and mid-latitude SSTs, but it is not yet clear that their impact is sufficient to alter the SST response such that it would be uncorrelated with local insolation, and thereby invalidate the SAT method. Sea-ice feedback is a fast feedback, similar to, for example, cloud feedbacks at high latitudes. Therefore, unless its response to high-latitude insolation or other climate forcing significantly differs in phase from tropical insolation, it will not affect the tropical SST evolution. Reconstructions of variations in sea-ice extent in the LIG[17,18] and the impacts of sea ice on low- and mid-latitude SSTs[19] appear to follow the same phase to the insolation forcing as the seasonally unadjusted proxy SSTs in most reconstructions, and will therefore affect the amplitude of the overall response to the external forcing (June–August insolation) but not the phase. As discussed in the supplementary methods of our original study, the SAT method is insensitive to the amplitude of variations, and therefore, the calculated MASSTs would not be compromised by sea-ice feedbacks.

Nevertheless, even if the sea-ice feedback has an effect, it is far from clear whether its remote impact is strong enough to overwhelm the local insolation effect quantitatively. Moreover, these feedbacks, to the best of our knowledge, have been included in all current generation climate models. As far as the global mean is concerned, these feedbacks have apparently been seen to be far too weak to substantially change the global mean trends[5,19]. In fact, despite continued increases in complexity, the sign and magnitude of the mid- to late Holocene global mean temperature evolution has changed very little[5,6]. In fact, the latest mid-Holocene simulations (Paleoclimate Modelling Intercomparison Project Phase 4–Coupled Model Intercomparison Project Phase 6), including all known feedback processes, suggest even greater Holocene warming than previous versions[6], thereby doubling down on the Holocene temperature conundrum.

The key takeaway here is that the efficacy of the SAT method is not hindered by sea-ice feedback, or any other fast feedback process, so long as their impacts either do not alter the phase of the identified apparent seasonality of the SST record or are small relative to those imparted by the local insolation forcing. The same is not true of slow feedback processes, such as ice sheets and GHGs (associated with the global carbon cycle), which have much longer timescales. Therefore, they can be effectively considered as forcing 'external' to the coupled ocean–atmosphere system, causing the phase of the response to deviate from that of the seasonal insolation. As neither land-ice volume nor GHG concentrations vary substantially across the LIG, the only relevant external forcing to consider during this period is insolation.

Although Zhang and Chen[1] do not explicitly question the models, they note that using an accelerated simulation may underestimate polar warming as a consequence of not fully representing the nonlinear feedbacks associated with millennial-scale climate variability during termination 2. We note that in a 100× simulation there is ample opportunity for the near surface to respond to the forcing. This assertion is supported by the fact that the 100× simulation gives the same results as the nonaccelerated TraCE (Transient Climate Evolution) results for the Holocene. Furthermore, even if early interglacial warmth was underestimated in the accelerated simulation, this would affect only the amplitude of the cooling observed in SST records, not the phase.

Given the complexity of the feedbacks and the transport processes, the net effects of all the feedbacks and local insolation are difficult to assess. Our model test of SAT is a first attempt in this direction. We show that a simple linear response of SST to local insolation produces SST estimates consistent with climate models that include feedbacks and nonlinear dependencies, thereby resolving the Holocene temperature conundrum. Furthermore, seasonal biases detected using SAT can resolve the second conundrum (that is, proxy–proxy discrepancies). In our opinion, these results provide strong support for the hypothesis that the SST response to local insolation and/or insolation that is highly correlated with the local insolation is dominant, at least over much of the low to mid-latitudes. Nevertheless, this hypothesis requires further testing, and we encourage continued investigation.

Several lines of evidence including the benthic $\delta^{18}O$ stack[20] (where $\delta^{18}O$ represents the $^{18}O/^{16}O$ composition), deep and intermediate ocean cooling, ice-core noble gas records of mean ocean temperature[21,22] and direct proxy records of subsurface temperatures from the Pacific[23] suggest cooling across the last and current interglacials apparently at odds with our compilation. However, we remind the readers that our compilation is restricted to the low to mid-latitudes (40° N–40° S), and does not reflect changes in the high latitudes. Deep and intermediate waters, which make up more than 90% of the volume of the oceans, form at the high latitudes at the coldest season of the year, and thus, arguably the evolution of deep ocean temperature may be biased towards the high-latitude winter temperature rather than reflecting annually averaged global mean temperatures at the surface at orbital timescales. In fact, if less heat is being sequestered in the deep ocean, more heat will remain at the surface, potentially amplifying surface warming trends across past interglacial periods as suggested by the SAT and model results.

1. Zhang, X. & Chen, F. Non-trivial role of internal climate feedback on interglacial temperature evolution. *Nature* https://doi.org/10.1038/s41586-021-03930-4 (2021).
2. Bova, S., Rosenthal, Y., Liu, Z., Godad, S. P. & Yan, M. Seasonal origin of the thermal maxima at the Holocene and the last interglacial. *Nature* **589**, 548–553 (2021).
3. Kaufman, D. et al. Holocene global mean surface temperature, a multi-method reconstruction approach. *Sci. Data* **7**, 201 (2020).
4. Marcott, S. A., Shakun, J. D., Clark, P. U. & Mix, A. C. A reconstruction of regional and global temperature for the past 11,300 years. *Science* **339**, 1198–1201 (2013).
5. Liu, Z. et al. The Holocene temperature conundrum. *Proc. Natl Acad. Sci. USA* **111**, E3501–E3505 (2014).
6. Brierley, C. M. et al. Large-scale features and evaluation of the PMIP4-CMIP6 *midHolocene* simulations. *Clim. Past* https://doi.org/10.5194/cp-2019-168 (2020).
7. Leduc, G., Schneider, R., Kim, J.-H. & Lohmann, G. Holocene and Eemian sea surface temperature trends as revealed by alkenone and Mg/Ca paleothermometry. *Quat. Sci. Rev.* **29**, 989–1004 (2010).
8. Timmermann, A., Sachs, J. & Timm, O. E. Assessing divergent SST behavior during the last 21 ka derived from alkenones and *G. ruber*-Mg/Ca in the equatorial Pacific. *Paleoceanogr. Paleoclimatol.* **29**, 680–696 (2014).
9. Mohtadi, M. et al. Low-latitude control on seasonal and interannual changes in planktonic foraminiferal flux and shell geochemistry off south Java: a sediment trap study. *Paleoceanogr. Paleoclimatol.* https://doi.org/10.1029/2008PA001636 (2009).
10. Lin, H.-L., Wang, W.-C. & Hung, G.-W. Seasonal variation of planktonic foraminiferal isotopic composition from sediment traps in the South China Sea. *Mar. Micropaleontol.* **53**, 447–460 (2004).
11. Sautter, L. R. & Thunell, R. C. Seasonal variability in the $\delta^{18}O$ and $\delta^{13}C$ of planktonic foraminifera from an upwelling environment: sediment trap results from the San Pedro Basin, Southern California Bight. *Paleoceanogr. Paleoclimatol.* **6**, 307–334 (1991).
12. Thunell, R. C. & Reynolds, L. A. Sedimentation of planktonic foraminifera: seasonal changes in species flux in the Panama Basin. *Micropaleontology* **30**, 243–262 (1984).
13. Sawada, K., Handa, N. & Nakatsuka, T. Production and transport of long-chain alkenones and alkyl alkenoates in a sea water column in the northwestern Pacific off central Japan. *Mar. Chem.* **59**, 219–234 (1998).
14. Sikes, E. L., O'Leary, T., Nodder, S. D. & Volkman, J. K. Alkenone temperature records and biomarker flux at the subtropical front on the chatham rise, SW Pacific Ocean. *Deep Sea Res. I* **52**, 721–748 (2005).
15. Kienast, M. et al. Alkenone unsaturation in surface sediments from the eastern equatorial Pacific: implications for SST reconstructions. *Paleoceanogr. Paleoclimatol.* https://doi.org/10.1029/2011PA002254 (2012).
16. Hertzberg, J. E. & Schmidt, M. W. Refining *Globigerinoides ruber* Mg/Ca paleothermometry in the Atlantic Ocean. *Earth Planet. Sci. Lett.* **383**, 123–133 (2013).
17. Wolff, E. W. et al. Southern Ocean sea-ice extent, productivity and iron flux over the past eight glacial cycles. *Nature* **440**, 491–496 (2006).
18. Malmierca-Vallet, I. et al. Simulating the Last Interglacial Greenland stable water isotope peak: the role of Arctic sea ice changes. *Quat. Sci. Rev.* **198**, 1–14 (2018).
19. Bader, J. et al. Global temperature modes shed light on the Holocene temperature conundrum. *Nat. Commun.* **11**, 4726 (2020).
20. Lisiecki, L. E. & Raymo, M. E. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanogr. Paleoclimatol.* https://doi.org/10.1029/2004pa001071 (2005).
21. Shackleton, S. et al. Global ocean heat content in the Last Interglacial. *Nat. Geosci.* **13**, 77–81 (2020).

22. Bereiter, B., Shackleton, S., Baggenstos, D., Kawamura, K. & Severinghaus, J. Mean global ocean temperatures during the last glacial transition. *Nature* **553**, 39–44 (2018).
23. Rosenthal, Y., Linsley, B. K. & Oppo, D. W. Pacific Ocean heat content during the past 10,000 years. *Science* **342**, 617–621 (2013).

Acknowledgements Funding for this research was provided by the NSF grants OCE-1834208 and OCE-1810681, the NSF-sponsored US Science Support Program for IODP, the Institute of Earth, Ocean, and Atmospheric Sciences at Rutgers University, the Chinese NSF (41630527), the School of Geography, Nanjing Normal University, and the USIEF-Fulbright Program.

Author contributions All authors contributed to conception of the presented ideas. S.B. wrote the first manuscript draft. All authors provided review and editing. Two authors not on the original paper were added to the author list. C.Z. provided additional analysis of model results. A.J.B. provided critical feedback and discussion.

Competing interests The authors declare no competing interests.

Additional information
Correspondence and requests for materials should be addressed to Samantha Bova.