



# The crucial role of soil moisture in the evolution of forest cover in Asia since the Last Glacial Maximum

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## THE DEGLACIAL FOREST CONUNDRUM IN THE NORTHERN HEMISPHERE (NH)

Forest cover plays a pivotal role in facilitating ecosystem services and climate regulation. In recent decades, much concern has been raised regarding the extent to which forest cover tracks past climate change. Studies at different spatiotemporal scales have revealed significant temporal lags, ranging from decades to millennia, with no consensus reached on this issue.<sup>1</sup>

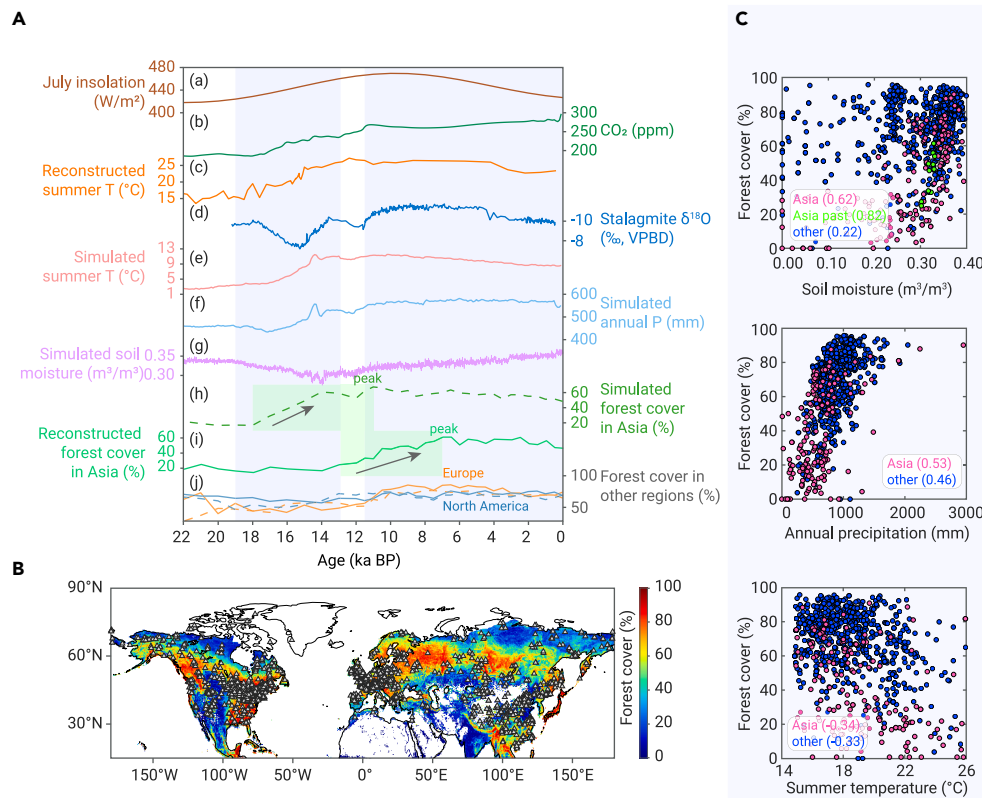
Recently, a new issue regarding the deglacial forest conundrum was identified.<sup>1</sup> It was demonstrated that the simulated expansion of deglacial forest in the NH occurred approximately 4,000 years earlier than the pollen-based reconstruction suggests, even when accounting for the climate change that has occurred over this time period. The climate during the last glacial maximum period (22–19 ka BP [thousands of years before present]) was cold, followed by a significant warming from 19 to 12.9 ka BP, after which the cold period of the Younger Dryas (12.9–11.5 ka BP) occurred (Figures 1Aa–1Ag). Consequently, the simulated forest cover in the NH responded rapidly, experiencing a sharp increase from 18 ka and peaking at approximately 11 ka BP, albeit with a temporary decline during the cold Younger Dryas event. Subsequently, forest cover continuously declined throughout the Holocene (11.5 ka BP to present) (Figure 1Ah). In comparison, the pollen-based reconstructions of forest cover in the NH exhibited a notably different pattern. There was minimal discernible change during 19–12.9 ka BP, followed by a gradual and sustained increase culminating around 7 ka BP, with a gradual decline from 2 ka BP onwards

(Figure 1Ai). Forest cover from model simulations and pollen reconstructions do not align with the climate change, and this phenomenon is referred to as the “deglacial forest conundrum.”<sup>1</sup>

Interestingly, this asynchronous NH forest cover change has mainly been observed in Asia (Figures 1Ah and 1Ai), with no significant differences in the changes of forest cover in Europe or North America (Figure 1Aj).<sup>1</sup> Factors such as solar radiation, ice cover, and atmospheric carbon dioxide levels have been identified as the primary influencers of temperature and precipitation fluctuations in the NH, which, in turn, have a substantial influence on large-scale forest cover dynamics. However, they are insufficient to interpret the continental difference raised above. The underlying drivers responsible for this intriguing divergence in the response patterns of forest cover across individual continents remain a challenging scientific inquiry that warrants a thorough investigation.

## SOIL MOISTURE LIMITS THE EVOLUTION OF FOREST COVER IN ASIA SINCE THE LAST GLACIAL MAXIMUM

Here, we investigated soil moisture as a potential solution to the deglacial forest conundrum. The establishment and growth of forest are more sensitive to soil moisture than precipitation, especially in drought-restricted areas. Based on the high-resolution global woody cover data obtained from Earth observation satellite products, we found that forest cover had a much stronger correlation with soil moisture over Asia than over Europe and North America (Figures 1B and 1C), particularly for sites where the climate conditions are similar to those



**Figure 1. The relationship between forest cover and soil moisture** (A) Climate change and the evolution of forest cover since the Last Glacial Maximum. (a) July insolation at  $65^{\circ}N$  ([https://doi.org/10.1016/0277-3791\(91\)90033-0](https://doi.org/10.1016/0277-3791(91)90033-0)). (b) The changes in global atmospheric  $CO_2$  concentration (<https://doi.org/10.5194/essd-9-363-2017>). (c) The reconstructed continental summer air temperature in Asia (<https://doi.org/10.1016/j.epsl.2010.11.010>). (d) Precipitation changes based on the Sanbao cave stalagmite  $\delta^{18}O$  in Asia (<https://doi.org/10.1038/nature06692>). (e–g) The simulated summer temperature, annual precipitation, and volumetric soil water in Asia from the TraCE-21 ka dataset, respectively (<https://www.earthsystemgrid.org/project/trace.html>). (h) The simulated forest cover in Asia based on the MPI-ESM simulation.<sup>1</sup> (i) The reconstructed forest cover based on pollen records in Asia (<https://doi.org/10.1016/j.quascirev.2019.07.034>). (j) The reconstructed (solid lines) and simulated forest cover (dashed lines) over Europe (orange) and North America (blue). The spatial coverage was the same for the model simulation and reconstructed forest cover. The light blue background represents the phase of deglacial and Holocene climate change, respectively. The green shaded areas indicate the asynchronous pace of forest cover between model simulations and pollen reconstructions. (B) Modern spatial distribution of forest cover for the NH. The forest cover was obtained from <https://doi.org/10.1126/science.1244693>. The gray triangles represent the pollen records for the forest cover reconstruction in Asia, Europe, and North America that were obtained in this study.<sup>2</sup> (C) Dependence of modern forest cover on soil moisture, annual precipitation, and summer temperature, respectively. The modern meteorological data were obtained from the ERA5 dataset. Multi-year average values from 1960 to 2020 with a spatial resolution of  $0.25^{\circ} \times 0.25^{\circ}$  were used. The forest cover data were collected over the sites

shown in (B). To assimilate modern data with the past climate, we only show the results for sites with a summer temperature between  $15^{\circ}C$  and  $26^{\circ}C$  (the range of reconstructed temperature for the whole period, see Ac). For comparison, we also show the change between 12.9 and 7 ka BP (Asia past) in Ag and Ai.

of the past (i.e., temperatures between 15°C and 26°C, as suggested by Figure 1Ac). Such a relationship is also supported by the modeled soil moisture and reconstructed forest cover for the period of 12.9–7 ka BP, when there was a rapid increase in reconstructed forest cover (Figures 1Ag, 1Ai, and 1C). Although soil moisture can be affected by precipitation, we observed a slightly weaker correlation between forest cover and precipitation compared to the relationship with soil moisture (Figure 1C). There was a much weaker correlation for temperature (Figure 1C). These differences in the strengths of correlations were not observed in Europe or North America.

Soil moisture could buffer or decrease the forest cover under the dramatic climate change since the Last Glacial Maximum (Figures 1Ag and Ai). Evidently, many of the pollen-based forest reconstructions did not show a rapid response to the deglacial climate change (Figures 1Aa–1Af and 1Ai). This phenomenon possibly resulted from the soil moisture-temperature relationship, with an increase in temperature intensifying evaporation, ultimately promoting evapotranspiration and leading to a decrease in soil moisture (Figures 1Ac, 1Ae, and 1Ag). Hence, during the deglacial period, climate warming failed to trigger a substantial increase in forest cover during 19–12.9 ka BP due to the soil-regulating effect (Figures 1Ac, 1Ae, 1Ag, and 1Ai). This phenomenon was particularly pronounced during the rapid warming period between 15 and 12.9 ka BP. During the Holocene, temperature decreased from 11.5 ka BP onwards, while reconstructed forest cover peaked around 7 ka BP and then gradually decreased. These unsynchronized changes in temperature and forest cover imply that the increasing precipitation and soil moisture might co-determine the changes in forest cover during the Holocene (Figures 1Ac–1Ag and 1Ai). In contrast, the simulated forest cover kept almost the same pace as the changes in temperature and precipitation from 19 ka BP onwards (Figures 1Ac–1Af and 1Ah). Therefore, soil moisture could be the underlying factor controlling the evolution of forest cover in Asia since the Last Glacial Maximum.

#### THE MECHANISM BY WHICH SOIL MOISTURE REGULATES THE EVOLUTION OF FOREST COVER IN ASIA

Forest cover is highly dependent on soil moisture. The root system of trees must absorb soil water, which is the most direct and fundamental water source for forest growth and distribution.<sup>2,3</sup> Moreover, recent studies have shown that stomatal closure depends on soil moisture.<sup>4</sup> Low soil moisture may reduce, or even reverse, the potential benefits of a warming climate on photosynthesis because warming may reduce light-saturated net photosynthesis during the growing season.<sup>4</sup> Insufficient soil moisture supplies are considered to pose a huge threat to forest cover and cause widespread tree mortality. Such an impact is more pronounced in more arid areas, as indicated by the much higher correlation coefficient between forest cover and soil moisture over arid areas (up to 0.83 for sites with annual precipitation <400–500 mm) compared to humid areas

(0.4–0.5 for sites with annual precipitation >500 mm), as shown in the Asian data in Figure 1C.

Our findings suggest that by using modern data to interpret past climate-forest interactions, it is possible to understand the paleo forest dynamics, although there are still some limitations. The consideration of soil moisture as a potential factor influencing forest cover has not been fully considered in attempts to understand the deglacial forest conundrum in Asia. Indeed, soil moisture has been overlooked when modeling the interactions between deglacial climate change and forest dynamics. Therefore, we highlighted the significance of soil moisture as a factor affecting the evolution of forest cover in Asia. There is an urgent need for future models and even most climate-forest relationship interpretations to comprehensively incorporate the dynamics of soil water and the resulting impacts, which will advance our understanding of the changes in forest cover. However, the coupling of the soil-plant-atmosphere is complex and might be affected by other environmental factors (e.g., groundwater) than those discussed here.<sup>2,5</sup> The integration of these important factors and processes would greatly enhance our understanding of the “deglacial forest conundrum” and contribute to more reliable modeling of the evolution of forest cover.

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#### DECLARATION OF INTERESTS

The authors declare no competing interests.