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Greening of India and revival of the South Asian summer monsoon in a warmer world

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While it is accepted that the tropical hydrological cycle has intensified during past interglacial periods due to changes in insolation, greenhouse gases and ice volume, their respective influences are uncertain. Here we present a pollen record from Bengal Bay to reconstruct vegetation changes in India's core monsoon zone during two warm periods, the current and last interglacial, comparing the data with numerical model simulations to assess the influence of different forcing mechanisms. Results show tropical forest expansion between 11.7–5 ka and 127–120 ka, defining two Indian humid periods, with the last interglacial showing the strongest monsoon activity, consistent with salinity reconstructions. Model-data comparison highlights boreal summer insolation as the primary driver of vegetation dynamics and monsoon intensity during interglacial periods, with CO₂ and ice-sheets having a limited effect. Vegetation remains unaffected by pre-industrial CO₂ variations above 250 ppmv, a threshold value that characterizes most interglacials of the last million years.

The response of the South Asian monsoon to global warming in the coming decades and centuries is a critical economic and societal issue for billions of people. Recent CMIP6 simulations point out that the global water cycle will intensify as global temperatures rise, causing monsoon systems to expand and associated rainfall to intensify^{1,2}, although there are large regional disparities in precipitation especially across India³. Interglacials are relatively short periods within glacial cycles during the Quaternary characterized by low continental ice extent, high sea level, and high atmospheric greenhouse gas content, primarily driven by variations in orbital forcing. These periods thus provide a panel of experiments to study the response of the tropical hydrological cycle under warm climates. Inconsistencies still exist in both proxy reconstructions and model simulations regarding the strength of the South Asian monsoon and its major controlling factors during the past interglacials. For example, during the last interglacial (Marine Isotope Stage (MIS) 5e), a period characterized by higher temperatures and reduced ice caps relative to the preindustrial period^{4,5}, some geological records suggest that the South Asian monsoon was the only boreal monsoon system attenuated relative to the Holocene^{6,7}, despite a larger insolation forcing. This observation contrasts with model simulations^{8–10}. Some records have shown that southern hemisphere insolation, atmospheric CO₂ and polar ice volume drive the oscillations of the

South Asian monsoon, questioning the primary role of direct northern hemisphere summer insolation forcing¹¹.

Marine pollen records integrate the signal of vegetation of large fluvial watersheds and trace past vegetation changes and climate variability, as successfully done in temperate and monsoon-sensitive domains^{12–14}. Here we present a marine pollen record, from the Integrated Ocean Discovery Program (IODP) Site U1446 which was retrieved from the Bay of Bengal off the Mahanadi River in the north-eastern Indian peninsula¹⁵. This river watershed is located in the Core Monsoon Zone (CMZ) which best represents summer monsoon rainfall variations for all of India¹⁶. This study aims to determine the response of the tropical vegetation and monsoon rainfall intensity to MIS 1 and 5e climate warming in the CMZ. We also use LOVECLIM1.3 and HadCM3 simulations to explore the relationships between the dominant forcing factors (seasonal insolation, atmospheric CO₂ concentrations and ice volume) and tropical woody cover and monsoon rainfall intensity in India during the past two interglacial periods.

IODP Site U1446 data (pollen and sea surface salinity reconstructions) as well as model simulations show that during the last two interglacial periods, i.e. MIS 1 and MIS 5e, higher summer monsoon precipitation is observed during two intervals called Indian Humid Periods (IHP) of ~7 ky duration at the beginning of each of the two interglacials, suggesting a

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northward shift of the Intertropical Convergence Zone (ITCZ) in relation to increased insolation forcing accompanied by greater moisture input over the continent. Our results suggest that, compared to the beginning of the Holocene wet period, the stronger solar forcing that characterized the last interglacial period resulted in a higher monsoon intensity that favored greater greening in the CMZ of India.

Results and discussion

Study site and modern vegetation distribution

The IODP Site U1446 was collected during the IODP expedition 353 “Indian Monsoon Rainfall” on the western margin of the Bay of Bengal (Fig. 1). This site is located off the southern part of the delta of the Mahanadi River which is one of the major rivers of the eastern Indian Peninsula (19°5′N, 85°44′E). In this area, the continental shelf is particularly narrow from 60 km to 25 km, facilitating a rapid transfer of terrestrial particles to the deep-sea. This site has been drilled at 1430 m below sea-level on a lower slope promontory, enabling to avoid turbiditic disturbances. Sediments of the IODP Site U1446 mainly consists of gray clays with nannofossils, foraminifera and biogenic silica¹⁷. Detailed drilling and site information is provided by Clemens et al.¹⁵.

The modern distribution of vegetation in India is closely related to the amount of annual rainfall, which is mainly controlled by summer monsoon rainfall and rainfall seasonality^{18,19}. Within the study area, there are four main types of potential vegetation at present-day (Fig. 1). Dry and moist deciduous forests dominate most of the Mahanadi region, with summer

rainfall ranging from 6 to 12 mm.day⁻¹, annual rainfall ranging from 1000 to 2000 mm.yr⁻¹, and with 4–8 dry months. Due to the influence of oceanic moisture, vegetation is dominated by semi-evergreen forest in the moist valleys of the lower Mahanadi watershed. Mangroves occupy most of the deltaic area. Evergreen forest is currently absent from the Mahanadi watershed, but thrives in the Western Ghats and Northeast India where annual rainfall exceeds 2300 mm.yr⁻¹ and the dry season is limited to 2–4 months or less. At Site U1446, the pollen grains in the sediment are primarily from vegetation in the Mahanadi River watershed (Supplementary Note 1). Based on the ecological requirements of the main species of the different taxa and studies on surface samples, we formed different pollen groups representing the main plant formations, i.e. tropical deciduous forest, wet evergreen forest, xerophytes and grasslands, allowing us to discriminate the different rainfall conditions (Methods)^{20–22}.

Results on vegetation and South Asian summer monsoon during MIS 1 and MIS 5e

During MIS 1 and MIS 5e interglacial stages and preceding glacial periods, vegetation dynamics show the same general trends (Fig. 2; Supplementary Fig. 1,2). Herbaceous taxa, typical of a semi-arid steppe (Amaranthaceae, Poaceae and *Artemisia*), dominate during the glacial periods of MIS 2 and 6. Although tropical forest taxa increased markedly in the early Bolling-Allerød (~14.6 ka), they become dominant in the early Holocene (11.7 ka) until 5 ka, when a minimum of semi-arid steppe (graminoid grasslands and xerophytes) is observed. For MIS 5e, tropical forest taxa show a maximum

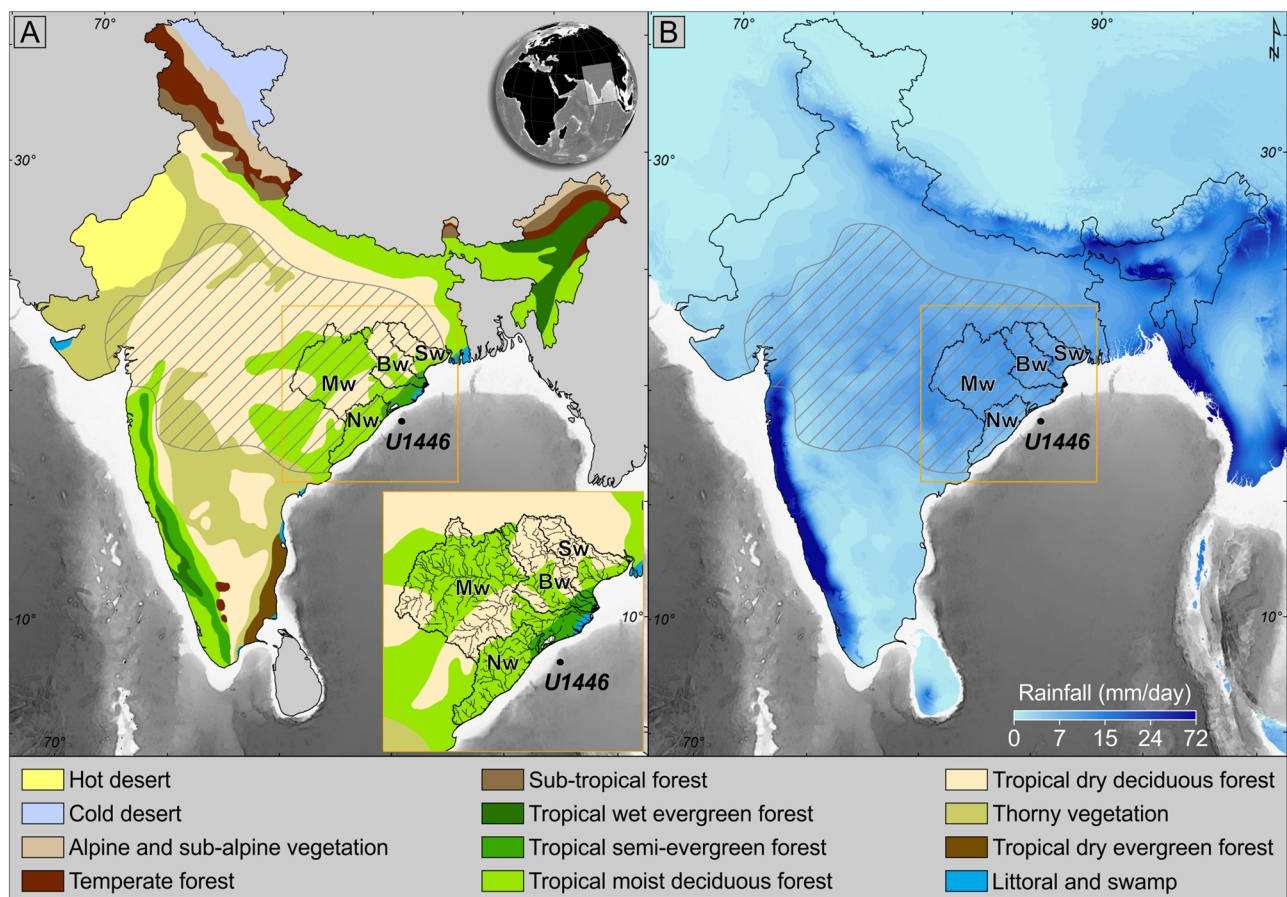
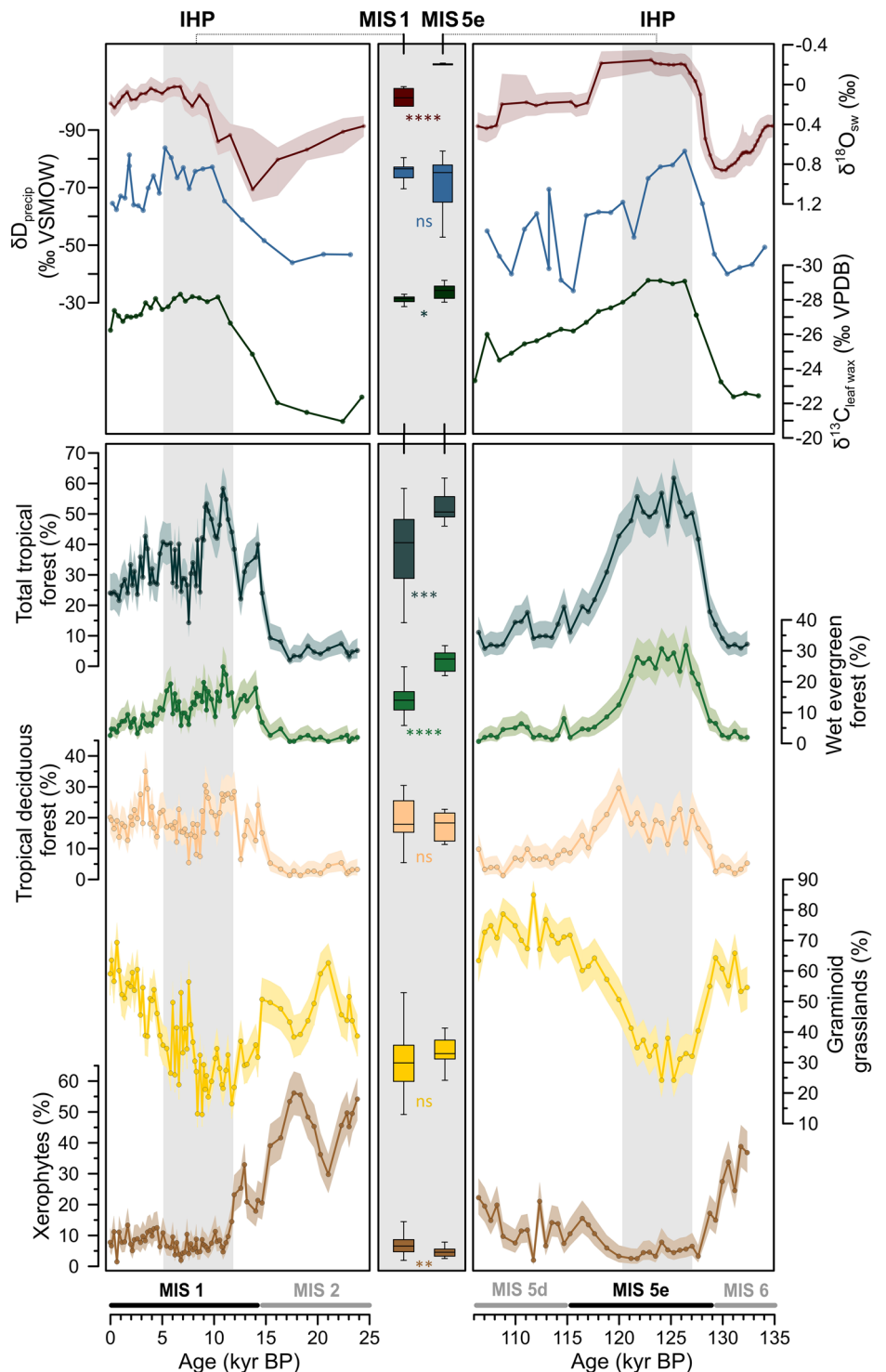


Fig. 1 | Distribution of potential vegetation and JJA mean precipitation in the Indian Peninsula. **A** Distribution of potential vegetation in the Indian Peninsula; vegetation data are derived from Champion and Seth¹⁹; inset shows the main river network for the Brahmani (Bw), Mahanadi (Mw), Navgati (Nw) and Subarnarekha (Sw) watersheds; gray hatched area corresponds to CMZ. **B** June to August average daily precipitations in the Indian Peninsula during the 1970 to 2020 period

calculated from the WorldClim Historical climate database¹⁰⁶. Bathymetry is taken from the General Bathymetric Chart of the Oceans (GEBCO). The Central Monsoon Zone (CMZ) is taken from Rajeevan et al.¹⁰⁷. The watershed and hydrographic network are derived from Shuttle Radar Topography Mission (SRTM) data using hydrological modeling with ArcGIS Desktop 10.8 software (Environmental Systems Research Institute, ESRI).

Fig. 2 | Downcore pollen data from Site U1446 during the time intervals 0–25 ka and 107–135 ka compared to other monsoon proxies from the same site. Bottom panels: Pollen abundances of the main vegetation groups. Colored shaded areas represent the 0.90 confidence interval on pollen percentages. Top panels: Site U1446 $\delta^{13}\text{C}_{\text{wax}}$ and $\delta\text{D}_{\text{precip}}$ results^{11,69,101} and $\delta^{18}\text{O}_{\text{seawater}}$ estimates^{6,11,56} (Methods). Colored shaded area for $\delta^{18}\text{O}_{\text{seawater}}$ estimates represents the confidence interval (1 σ error). The gray bands represent the Indian Humid Periods (IHP) of both interglacials identified from pollen assemblages. The colored box-and-whisker plots show the distribution of each proxy data during the IHP of MIS 1 and MIS 5e (center line: median; box limits: upper and lower quartiles; whiskers: 1.5x interquartile range). Symbols (stars) denote the significance level of the Wilcoxon rank sum tests (two-sided) indicating that the median of the parameter considered between the two IHP differs significantly (significance levels: ns (non significant) for a p -value > 0.05; * for a p -value < 0.05; ** for a p -value < 0.01; *** for a p -value < 0.001; **** for a p -value < 0.0001). This non-parametric test was used because some data sets are not normally distributed as determined by the Shapiro-Wilk test.



over a similar time interval between 127 and 120 ka. After these maxima, an opening of the tropical forest is observed, giving way to a savannah type vegetation including more xerophytic elements (Amaranthaceae) and graminoid grasslands (Cyperaceae, Poaceae) during the last millennia of the two interglacials. Given the strong dependency of modern vegetation on rainfall amount and seasonality in India (Fig. 1), the periods of maximal expansion of total tropical forest (Fig. 2; 11.7–5 and 127–120 ka) are interpreted as the wettest intervals of the current and last interglacials due to intensified summer monsoon precipitation, called hereafter Indian Humid Periods (IHP).

Although tropical forest taxa reach similar maximum values during both IHPs, forest expansion is on average over the wet interval (IHP) significantly greater during MIS 5e (cf. box-plots in Fig. 2). In addition, forest composition is significantly different between these two intervals (Fig. 2), as demonstrated by multi-dimensional scaling with a permutational analysis of variance (Supplementary Fig. 3). The wet evergreen forest, mainly composed of *Mallotus*, *Olea paniculata*, *Trema* and *Moraceae/Urticaceae*, is on average ~40% higher during the last interglacial IHP than during the Holocene IHP, clearly suggesting greater magnitude of summer monsoon precipitation during MIS 5e humid interval (Fig. 2). This is clearly supported

by the ratio of evergreen forest to xerophyte and graminoid grassland taxa (Supplementary Fig. 4). In addition, *Alchornea*, a taxa often identified in marine sediments off equatorial Africa and sporadically found in the wettest regions of northern India^{23–25}, is exclusively detected during MIS 5e IHP. Finally, a lower expansion of the drier (deciduous) forest type, primarily represented by Combretaceae/Melastomataceae, *Haldina*, and *Glochidion*, during the MIS 5e IHP relative to that of the MIS 1 IHP, at least during the early part (8–11.7 ka), is consistent with higher precipitation and a shorter dry season during the last interglacial. Although anthropogenic activity may have contributed to the decline of the tropical forest over the past few millennia, it is unlikely to have affected the pollen signal during the early and mid Holocene²⁶.

Mechanisms contributing to vegetation changes and interglacial humid periods in India

In addition to precipitation which is the main driver of vegetation distribution in the tropics^{27,28}, vegetation changes indicated by the pollen record from Site U1446 may have been influenced by variations in past atmospheric CO₂ concentrations. It has been suggested that atmospheric CO₂, through its physiological effects, may have played a role in vegetation changes at both tectonic and orbital timescales^{29–32}. The C₄ pathway allows high photosynthetic rates with low stomatal conductance, even at low CO₂ concentrations, allowing C₄ plants to achieve greater water use efficiency and to dominate in more arid environments³³. Pollen and $\delta^{13}\text{C}_{\text{wax}}$ data from Site U1446 reveal a higher cover of C₄ herbaceous plants than C₃ trees and shrubs during glacial MIS 2 and 6, compared with interglacials MIS 5 and 1 (Fig. 2). These orbital-scale C isotopic variations in leaf waxes have been linked to variations in atmospheric CO₂, with a minor influence from precipitation³⁴, based on sensitivity experiments with nine General Circulation Models (GCM) and a complex Dynamic General Vegetation Model (DGVM). While a 100 ppmv decrease in CO₂ between the pre-industrial period (PI, 285 ppmv) and the last glacial period (LGM, 185 ppmv) induces a 15% increase in C₄ vegetation cover, a simulated 9% ($\pm 23\%$) decrease of mean precipitation between the same two periods induces an increase in C₄ of 2% only³⁴. This lack of change in vegetation reflects the small change in mean precipitation simulated by the models, but it is not representative of the high standard deviation of precipitation change ($\pm 23\%$)³⁴, which may reflect the difficulty of GCM models in simulating key hydrological processes at low latitudes^{35,36}. The respective roles of CO₂ and precipitation in the development of C₄ plants, and thus the C₃/C₄ ratio in tropical and subtropical regions, are still widely debated. For example, the expected replacement of C₄ plants by C₃ plants during the last glacial termination is not systematically observed, as in Central and North America where C₄ expanded during the Holocene despite high atmospheric CO₂ concentrations^{37,38}. In contrast, C₃ plants dominated glacial landscapes in Indonesia, Central America and Africa when CO₂ concentrations were low^{12,37,39,40}. A number of studies emphasize that regional climatic factors, particularly precipitation during the growing season, exert essential control over vegetation changes on an ecosystem scale^{38,41,42}. On shorter time scales, over the past 30 to 150 years, stimulation of plant growth by CO₂ is also challenged^{13,44}, temperature, water availability and nutrients being identified as drivers of the carbon demand⁴⁵. Atmospheric CO₂ may also affect the sensitivity of tropical vegetation to rainfall, in particular a better water-use efficiency of C₃ plants under increased CO₂ concentrations, according to simulations with DGVM representing complex eco-physiological processes^{30,46}. A comparison between simulations and observations over the recent period indicate that most DGVM largely overestimate the impact of CO₂ fertilization on tropical forest productivity, possibly because they do not take nutrient limitation into account⁴⁷. The CO₂ effect on vegetation at the ecosystem scale on modern and paleoclimatic timescales involves definitively complex mechanisms and interactions that remain debated.

Over the narrow range of CO₂ (260–285 ppmv) that characterizes the last and current interglacial periods, excluding the “industrial” era, the pollen percentages of the major ecological groups at Site U1446 vary considerably from 10 to 70% for the total tropical forest and 5–30% for the wet

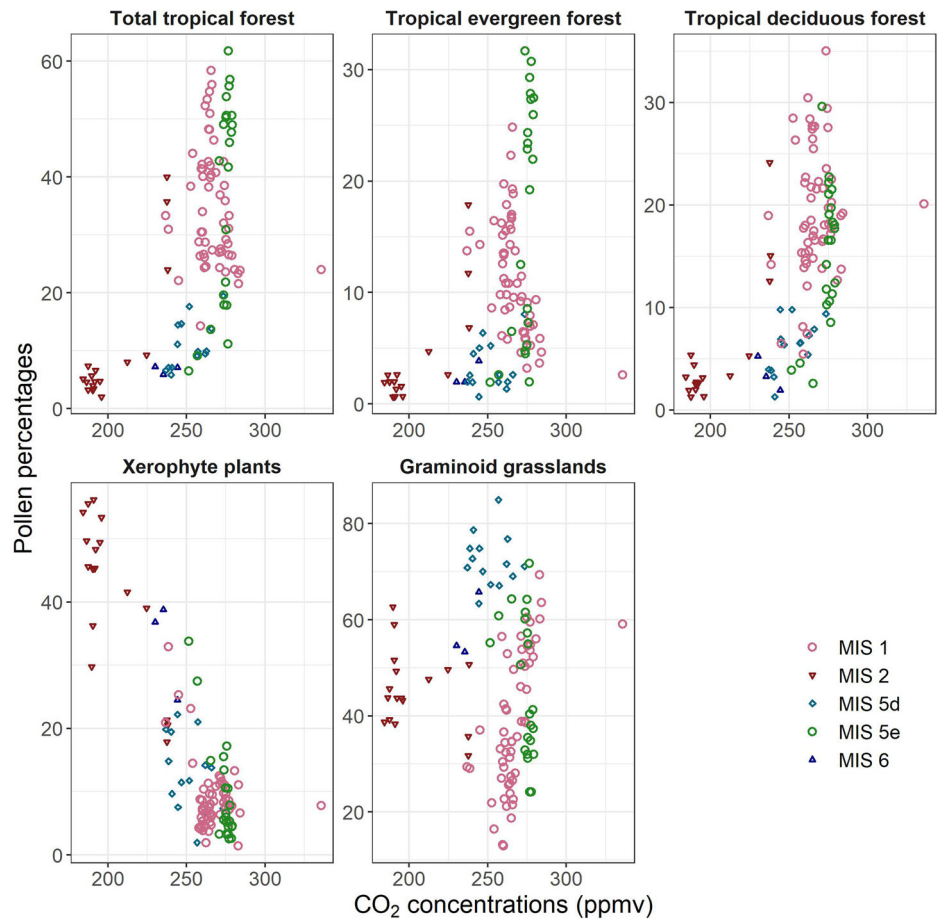
evergreen or deciduous forests (Fig. 3). There is no apparent relationship between changes in forest extent and composition as seen by pollen assemblages and interglacial CO₂ concentrations below industrial levels. Although high interglacial CO₂ concentrations may have had a greater fertilizing effect on vegetation than low glacial values, the similar CO₂ levels of MIS 1 and 5e cannot explain the vegetation differences, i.e. tropical forest composition and extent of the different forest types, between the two IHPs. While during the last 5 kyr, the increase in CO₂ and concomitant growth of Indian savannahs can be linked to anthropogenic activity^{26,48}, similar savannah expansion independent of anthropogenic impact is observed during MIS 5e while CO₂ remains very high. Therefore, the amount and seasonal distribution of precipitation is most likely the main driver explaining the difference in vegetation observed between the IHP of MIS 1 and MIS 5e, consistently with the expansion or even appearance of the wettest taxa during the IHP of the last interglacial.

Variations in tropical forest during MIS 1 and MIS 5e are strongly correlated with variations in local summer insolation (JJA) (Fig. 4), forest expansion (contraction) during deglaciations (end of interglacials) corresponding to increasing (decreasing) insolation. Strikingly, the IHPs of the two interglacials correspond well to summer insolation maxima, the more intense IHP of MIS 5e coinciding with its much higher summer insolation. This would suggest that local summer insolation is an important driver of humidity and vegetation variations in India during interglacials. In addition, the radiative effect of atmospheric CO₂ concentrations and the ice volume effect also varied significantly over the two study intervals (Fig. 4). Both play a role in the atmospheric water vapor content that feeds the monsoon system⁴⁹ and thereby influences vegetation in South Asia, but their respective contributions remain unclear.

To investigate the individual effects of insolation, CO₂ and ice sheets, simulation results from two models, LOVECLIM1.3 and HadCM3 (Methods), are analyzed and compared with the pollen record from Site U1446. During MIS 1, the summer precipitation simulated by both models corresponds well with local summer insolation (Fig. 4). The LOVECLIM1.3 Orb simulation, in which only insolation change is considered, shows that precession plays a dominant role on summer precipitation, leading to an early peak at 12 ka BP corresponding to a precession minimum. The OrbGHG and OrbGHGIce simulations of LOVECLIM1.3 and HadCM3, which additionally consider the effects of CO₂ and ice-sheets respectively, show that neither modifies the major effect of insolation, but that they play a non-negligible role in reducing summer precipitation before 10 ka BP. This leads to a peak in precipitation and in simulated tree fraction occurring at 10 ka BP in the full forcing simulation, in agreement with the timing of the forest peak in the pollen record. During MIS 5e, the simulated summer precipitation and tree fraction are also primarily driven by precession like during MIS 1, peaking at 128 ka BP in the Orb simulation. As CO₂ and sea level reach their highest interglacial level at the start of MIS 5e (~128–129 ka) in contrast to MIS 1, precipitation and the tree fraction peaks at 128 ka in the full forcing simulation, both being only slightly reduced before this date. Although both the simulated precipitation/tree fraction and the reconstructed forest are primarily driven by insolation, the simulated results systematically lead the pollen record by ~3 ka, which could be related to the age uncertainty of the pollen record and or to abrupt cold events. Indeed, such abrupt climatic events (e.g., Heinrich Stadials 11 between 129 and 135 ka) leading to weak monsoon intervals are not taken into account by the models used in this study, although they have been proposed to explain the reduced intensity of the monsoon despite the increase in insolation^{50,51}. Interestingly, both simulations and pollen records show a stronger IHP during MIS 5e than during MIS 1. As compared to MIS 1, under the much higher summer insolation of MIS 5e, the model simulates a much warmer Asian continent in summer, an increase in moisture over India carried by stronger summer monsoon winds (Fig. 5).

One can also notice from the LoveCLIM1.3 simulations (OrbGHGIce) that at the beginning of the Holocene the residual polar ice sheets tend to increase the simulated tree fraction in the CMZ. The largest increase occurs

Fig. 3 | Vegetation and atmospheric CO₂ relationships. Scatterplot comparing vegetation changes (total tropical forest; tropical evergreen forest; tropical deciduous forest; grassland; arid and semi-arid plants) as a function of atmospheric CO₂ concentrations¹⁰⁸ over the entire record. The different climatic periods are distinguished by different symbols.



at ~10 ka, which explains the forest peak at ~10 ka observed in both the simulation and the pollen record. On the contrary, the ice sheets between 118–110 ka BP considerably reduce the tree fraction. This shows that the relationship between ice-sheets and the CMZ vegetation is not constant. In LOVECLIM1.3, the main factor that limits forest growth in a warm low-latitude climate is annual precipitation. Our further analysis shows that the ice-sheets in both the early Holocene and 118–110 ka interval cool the Indian continent, but the relatively small ice-sheets under a relatively high summer insolation during the early Holocene increase the annual precipitation in the CMZ, while the large ice-sheets under the very low insolation during 118–110 ka reduce the annual precipitation. Therefore, the effect of ice-sheets on the CMZ annual precipitation and thus vegetation depends on the ice-sheet size and background insolation, but it does not alter the dominant role of insolation as seen in both the simulations and the pollen record during interglacial periods.

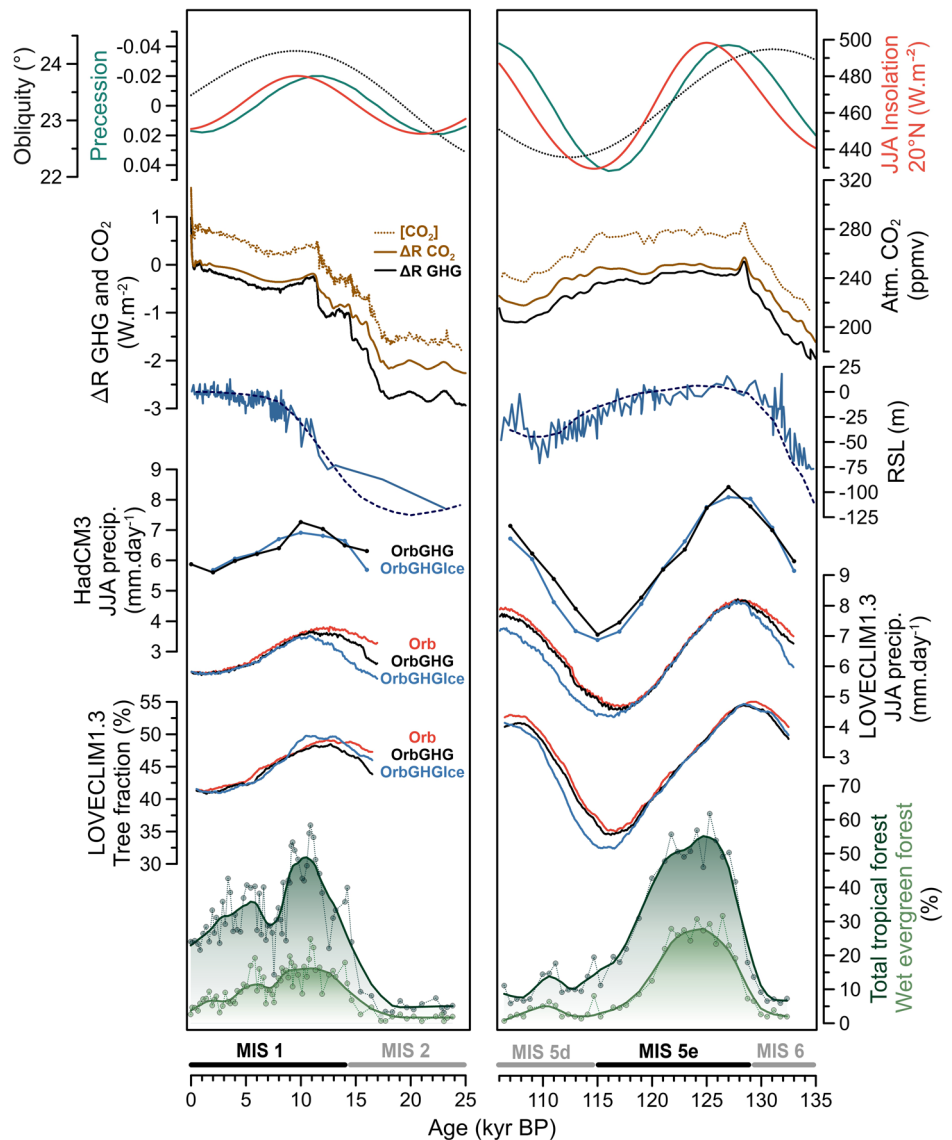
Cross-spectral analysis between precipitation proxies from Site U1446 and both external (insolation) and internal (CO₂, ice volume) forcing factors has highlighted that the pacing of monsoon rains in India followed ice-sheet melting and CO₂ increase during the glacial-interglacial oscillations of the last million years¹¹. This may seem contradictory to our results. Since in the precession band, the Arabian Sea wind proxies vary in phase with the Bay of Bengal monsoon proxies¹¹, and since the Arabian Sea wind is under the control of the inter-hemispheric pressure and temperature gradient, it has been suggested that the moisture feeding the Indian monsoon came from cross-equatorial moisture transfer¹¹. Comparison of the Indian summer monsoon stack from the northern Arabian Sea⁵² with our data (Supplementary Fig. 5) shows effectively that winds in the Arabian Sea are more intense and forest in India is more developed during interglacials 1 and 5 than during previous ice ages. However, if the wind strength in the Arabian Sea starts to increase at the beginning of the two interglacial periods MIS 1

and 5 at the same time as the rainforest develops in our study area, the wind maximum is clearly reached ~4 ky after the end of each of the two IHP. In other words, the most intense winds and thus cross equatorial humidity transport are observed at the end of the interglacials when forest is greatly reduced and a savannah maximum is reached. These differences are not attributable to chronological discrepancies, given that both the stack and our record are based on the timing of rapid events, with a potential difference of 1 to 2 ky. Thus, these observations together with simulation results show that the contribution of external and internal forcing factors likely varies with boundary climate conditions⁵³. During ice age, low CO₂ and high ice volume would contribute more significantly to monsoon variability, which could explain the predominance of these forcings, particularly when long time series are taken into account. Model simulations show effectively that the latitudinal migration of the intertropical convergence zone (ITCZ) caused by large northern hemisphere ice sheets is much larger than the one caused by insolation change⁵⁴. During interglacial conditions when ice-sheets are reduced, the intensity of solar radiation is the main driver controlling the amplitude of the ITCZ migration and the amount of water vapor in the atmosphere transported landward by winds^{8–10,49,55}.

A humid period of greater magnitude over the last interglacial period in India

At Site U1446, the only available site to track Indian summer monsoon variations in the CMZ prior to the last ice age, Holocene¹¹ and MIS 5e^{5,56} $\delta^{18}\text{O}_{\text{sw}}$ values calculated using the same method for both intervals (Methods) indicate significantly lower salinity during the last interglacial IHP compared to the Holocene IHP (Fig. 2; cf. box-plots). Therefore, pollen and $\delta^{18}\text{O}_{\text{sw}}$ records indicate a more intense monsoon rainfall in the CMZ during the IHP of MIS 5e. In contrast, a recent compilation of distributed records over tropical monsoon systems coupled with a

Fig. 4 | Data-model comparison with driving factors. From bottom to top: Total tropical forest and wet evergreen forest percentages from pollen data (dotted curves) and LOWESS curves (bold curves) (this study); Simulated summer precipitation using LOVECLIM1.3 and HadCM3 (red curves: orbital forcing only = Orb; black curves: orbital and GHG forcing = OrbGHG; blue curves: orbital, GHG and ice volume forcing = OrbGHGIce) and tree fraction simulated with LOVECLIM1.3; Sea-level reconstructions from Rohling et al.¹⁰⁹ (blue curve) and Waelbroeck et al.¹¹⁰ (blue dashed curve); Total radiative forcing (ΔR GHG, black curve) calculated from greenhouse gases (CO_2 , CH_4 and N_2O) and CO_2 radiative forcing (ΔR CO_2 , solid brown curve) calculated from atmospheric CO_2 concentrations⁷⁷; since the contribution of CH_4 and N_2O to ΔR GHG is small compared with that of CO_2 at orbital scales, the radiative forcing of GHG on the monsoon is mainly exerted by CO_2 ; Atmospheric CO_2 concentrations from Antarctic ice-core EPICA Dome C¹⁰⁸ (dotted brown curve); Orbital forcing expressed by mean June-July-August insolation at 20°N (red curve), precession (green curve) and obliquity (dotted gray curve)¹¹¹.

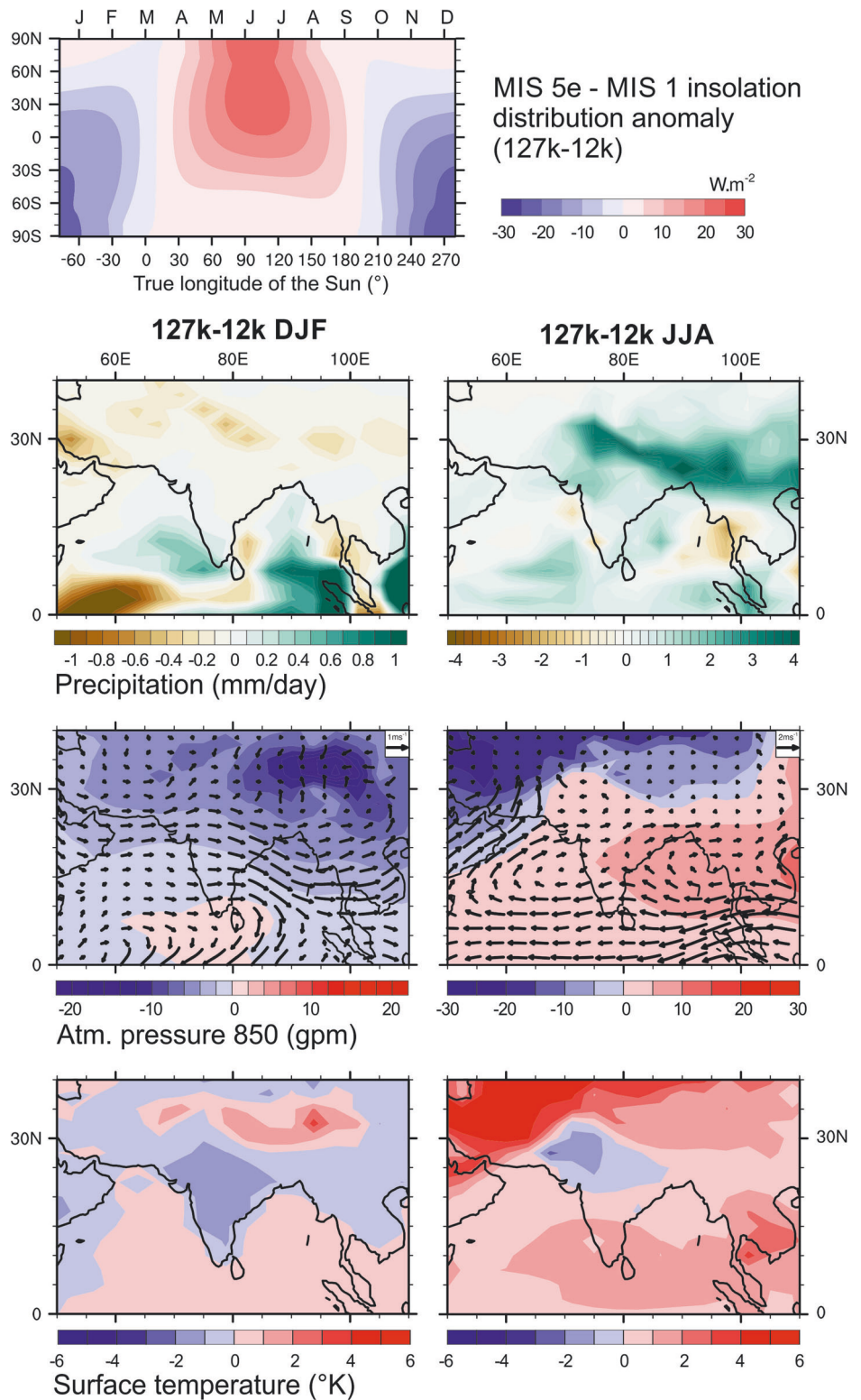


modeling experiment has suggested an intensification of summer precipitation during the MIS 5e relative to the Holocene⁶ in all monsoon systems, except the Indian monsoon. This is mainly inferred from model simulations, whereas the data compilation⁶ shows strong spatial heterogeneity in Asia. For instance, speleothem $\delta^{18}\text{O}$ records from Mawmluh and Tianmen show wetter conditions during MIS 5e whereas Bittoo Cave speleothem $\delta^{18}\text{O}$ indicates drier conditions^{57–60}. $\delta^{18}\text{O}_{\text{sw-ivc}}$ from core SO188-17286^{7,61} located in the northern part of the Bay of Bengal under the influence of the Ganges-Brahmaputra-Meghna river discharge does not show significant differences between the two IHP as identified at Site U1446 (Supplementary Fig. 4). Spatial heterogeneity may be related to regional hydroclimatic differences in India, as modeled and observed in recent data covering the last century^{62,63}. Orbital-scale simulated changes in Indian monsoon precipitation show significant regional differences, both at the scale of the Indian peninsula and more broadly across Southeast Asia^{9,64,65}, although large spread of summer precipitation changes among models is often observed in this tropical region^{66–68}. Observed differences in speleothem isotopic data^{57–60} could also arise due to distinct isotopic controls modulated by large-scale circulation features over Asia, as opposed to local precipitation amount alone⁶.

Leaf wax δD is another widely used indicator for reconstructing the hydrologic cycle, e.g. African or Indian^{7,66–68}. Based on this proxy measured

on core SO-17286-1 from the northern Bay of Bengal, it is argued that conditions were drier during the entire MIS 5e than during the entire Holocene⁷. However, particularly during the two IHP intervals defined in this work, the δD of leaf wax from site SO-17286-1 does not differ significantly between them as observed for leaf wax $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{seawater}}$. This suggests that in the vast watershed of Ganges-Brahmaputra-Meghna rivers, the average precipitation signal and C_3/C_4 ratio are similar between the two IHP (Supplementary Fig. 4). At Site U1446, the $\delta\text{D}_{\text{precip}}$ values of the two IHP are not significantly different, within the uncertainty of error⁶⁹, while vegetation is different. In the CMZ, the difference between $\delta\text{D}_{\text{precip}}$ signals and both vegetation and $\delta^{18}\text{O}_{\text{sw}}$ data could be related to the multiple processes that affect δD of plant leaf waxes such as different potential moisture sources and the associated transport pathways^{69,70}. A hydroclimatic parameter, namely recycled rainfall, which is not often considered in paleoclimatic studies⁷¹ could potentially reconcile hydrogen isotopic data with pollen data in the CMZ. During MIS 5e, the development of wet evergreen forest generated by a large input of oceanic moisture probably led to an amplification of the magnitude of this recycled precipitation compared to MIS 1. Thus, vegetation must have played a positive feedback role by feeding the monsoon rains through the evapotranspiration mechanism (up to 25% of current precipitation) and in particular by lengthening the duration of the wet season^{72,73}. Such a prolonged rainy season during MIS 5e is supported by

Fig. 5 | Maps extracted from the OrbGHGIce experiment using HadCM3. Maps illustrating anomalies in seasonal insolation distribution (top), JJA (June–July–August) and DJF (December–January–February) anomalies in precipitation, atmospheric pressure (color) and surface wind speed (black arrows), and surface temperature between 127 and 12 ka, each of these ages representing a precessional minimum situation at MIS 5e and MIS 1 respectively.



geochemical and isotopic data from the Mawmluh cave speleothem⁵⁷. Moisture formed from plant transpiration leads to relatively enriched values of δD precipitation in subsequent rainfall^{74,75}. Therefore, this mechanism may have altered the hydrogen isotopic signal of lipids in the CMZ.

Conclusion

The Indian peninsula, like northern tropical Africa, has experienced periods of higher humidity (Indian Humid Periods, IHP) than at present, associated

with an intensification of the South Asian monsoon during recent interglacial periods. These conditions allowed the expansion of wet evergreen forests in the northeastern Indian peninsula. Our study shows that MIS 5e IHP conditions were wetter than those of the current interglacial and that summer insolation is the dominant factor controlling the Indian summer monsoon precipitation and vegetation during interglacial periods. Vegetation does not appear to be sensitive anymore to CO_2 when CO_2 concentration is above ~ 250 ppmv (before industrial era), a value characterizing

most if not all the interglacials of the last one million years⁷⁶. At the present-day and the end of the century, summer insolation is and will remain significantly lower than the early Holocene and much lower than the last interglacial. According to our results, this is not favorable to the greening of savannah or even semi-desert regions of India as compared to the current and last warm interglacials. However, our results are obtained under natural climate condition with a maximum interglacial CO₂ concentration of ~280 ppmv while the present CO₂ concentration already reached 420 ppmv and is predicted to continue to increase in the future (e.g. most pessimistic SSP5-8.5, ~1100 ppmv of CO₂, additional 7.35 W.m⁻² relatively to pre-industrial radiative forcing^{77,78}). Whether this exceptionally high CO₂ concentration would fundamentally alter the climate-vegetation relationship as observed during the past interglacials and whether it would be able to counteract the effect of low summer insolation are unclear. These important questions remain to be investigated, given that tropical forests represent the main carbon reservoir in continental ecosystems that can in turn help mitigate anthropogenic carbon emissions^{79,80}.

Methods

Pollen analysis

Hole C of the IODP site U1446 was subsampled for pollen analysis every 1–11 cm over the upper 7.47 m CCSF-A. A total of 74 samples was analyzed in this interval. 39 samples between 26.37 m and 32.96 m CCSF-A were taken from Hole A and C every 14 to 30 cm. Samples of 1–5 g of dry sediment were processed using standard palynological techniques (detailed extraction protocol available at https://www.epoc.u-bordeaux.fr/index.php?lang=en&page=eq_paleo_pollens). A tablet of marker grains including a known number of *Lycopodium* was added to each sample to estimate pollen concentrations. Extraction of pollen and spores consists of successive chemical treatments on the sediment fraction inferior to 150 µm with cold HCl and cold HF and sieving through a 5-µm nylon mesh screen. The residue was mounted unstained in a mobile media (glycerol) to allow polar and equatorial observations of pollen grains.

Counting was performed using a light microscope at 400 and 1000 (oil immersion) magnifications. On average 185 pollen grains and spores were counted in each sample. Pollen percentages for each identified morphotypes are based on the total pollen and spore sum excluding undeterminable, aquatic plants and pteridophyte spores. Values for these groups were obtained from the total sum. A total of 145 pollen morphotypes have been identified. Identification is based on the reference collections of the French Institute of Pondicherry (India), MNHN (France) and OSU OREME (France) as well as diverse atlases of tropical flora^{81–85}.

At Site U1446, based on the ecological requirements of the major species of the different arboreal taxa, pollen taxa can be separated in two different groups of forest type. Some taxa, such as Combretaceae/Melastomataceae, *Haldina* and *Glochidion*, are important constituents of two dominant plant formations in the present-day Mahanadi watershed, namely the dry and moist deciduous forests^{19,86,87}. The pollen rain of these two forest types cannot be differentiated^{21,22} and the corresponding taxa are grouped here under the term tropical deciduous forest. Other taxa, such as *Mallotus*, *Olea paniculata*, *Trema* and Moraceae/Urticaceae, currently thrive preferentially in wetter forest formations of India^{18,19,88}. Although these taxa can be found in moist deciduous to evergreen forests, they have been identified as pollen markers of the modern pollen rain of the western Ghats evergreen forest^{20–22}. Thus, when taxa from this group are well represented in the sediments of Site U1446, it therefore indicates that evergreen forest is developing in the Mahanadi Basin and thus that monsoon rainfalls reach the highest intensity. These two forest groups, namely evergreen forest and tropical deciduous forest, also aggregate minor taxa such as *Elaeocarpus*, *Celtis/Cannabis*, *Macaranga*, *Eurya*, *Gnetum* for the former and *Shleichera*, *Cassia*, *Holoptelea*, *Hardwickia*, *Tectona* for the latter. We also formed a group of graminoid grassland consisting of Poaceae and Cyperaceae and a group of xerophyte plants (semi-arid and arid plants) constituted of Amaranthaceae, *Ephedra distachya* type, *Ephedra major* type and *Artemisia*.

Statistics on pollen data

Statistical analyzes were conducted on the pollen abundance data in the R environment⁸⁹ using the *rioja* and *vegan* packages^{90,91}. Constrained hierarchical cluster analysis was performed to define the pollen zones. We used multidimensional scaling (MDS) ordination with a permutational analysis of variance (PERMANOVA) to compare pollen assemblages from the studied intervals and evaluate the closeness of the pollen assemblages of the most humid periods. We performed these analyzes on pollen data from the periods 11.7–5 ka ($n = 31$ samples) and 127–120 ka ($n = 12$ samples). Clustering and ordination were applied to a dissimilarity matrix based on the Bray–Curtis distance. To highlight trends in the data we modeled the tropical forest evolution thought time for both intervals using a local regression smoother (LOWESS) performed in the R environment. The smoother span was chosen to remove millennial-scale variability. Confidence interval on pollen relative abundances were estimated with the R package *binom* using the ‘exact’ Clopper–Pearson method⁹².

Chronological framework

Chronology of the upper section (from 0 to 7.47 m CCSF-A) is derived from published Bayesian age-depth modeling based on 14 radiocarbon datings⁹³ (Supplementary Table 1). As in Nilsson-Kerr et al.⁶, the age-depth model of the interval 32.96–26.37 m CCSF-A is derived from the AICC2012 chronology. However, we used a different methodology based on evidence of northern hemisphere high latitude to tropical coupling at the millennial timescale⁹⁴. In Zorzi et al.⁹³, which presented the analysis of the last glacial section from site U1446, we observed a marked response of the Indian vegetation and summer monsoon to the most drastic millennial-scale climatic changes in the North Atlantic, i.e. Heinrich events. Here, we assume that the coupling observed between Greenland warming and Asian monsoon intensification⁹⁴, in particular for the warming episode after an ice drifting event, persisted over the last climatic cycles. The ODP Site 983 and associated G_{LT-syn_hi} signal which reflect the northern millennial-scale climatic variability on the AICC2012 chronology⁹⁵ were used as tuning target. We tuned increases in Rb/Ca ratio from Site U1446 interpreted as enhancement of runoff on adjacent continent and induced marine stratification¹¹ to abrupt increases in synthetic Greenland temperature linked to reductions in *Neogloboquadrina pachyderma* s. and IRD contents from Site 983 marking abrupt warming after major millennial-scale events associated to ice-sheet calving (Supplementary Fig. 6). The tie-point at 32.1 m CCSF-A links the start of the increase in U1446 Rb/Ca and the decrease in *N. pachyderma* s. and IRD content in ODP 983 at 128.9 ka. Concomitant increase in arboreal pollen taxa in IODP Site U1446 confirms Indian monsoon rainfall intensification. This follows the sequence of climatic events established for Termination II showing an increase in Asian monsoon dated at ~129 ka in Chinese speleothems which occurs subsequently to the North Atlantic event HS 11^{96,97}. Two other control points link the increases in the ratio Rb/Ca at 24.5 and 26.3 m CCSF-A to the northern high latitude warming associated to the end of the events C24 and C23. Ages in our chronology are 1.77 ± 0.6 ky younger than in Nilsson-Kerr et al.⁶.

Simulations with LOVECLIM and HadCM3

LOVECLIM1.3 is an atmosphere-ocean-sea ice-vegetation coupled model. Three transient simulations are performed for each of MIS 1 and MIS 5e with LOVECLIM1.3. In the first simulation, the model is driven only by changes in insolation (the Orb experiment) with CO₂ being fixed to 280 ppmv. In the second simulation, the model is driven by changes in insolation and greenhouse gas concentrations (the OrbGHG experiment). These two simulations have been used and presented in Yin et al.⁹⁸ and detailed model and experiment design can be found there. In the third simulation, ice sheets changes in the Northern Hemisphere, which are simulated by Ganopolski and Calov⁹⁹, are additionally considered (the OrbGHGIce experiment), but the associated sea level change is not.

HadCM3 is an atmosphere-ocean coupled general circulation model. Two sets of snapshot simulations are performed with HadCM3 with a time interval of 2 ka for each of MIS 1 and MIS 5. In the first set of simulations,

The model is driven by changes in insolation and greenhouse gas concentrations (the OrbGHG experiment). In the second set of simulations, like in LOVECLIM 1.3, the changes of the Northern Hemisphere ice sheets are additionally considered (the OrbGHGice experiment), but not the sea level. The detailed description of the HadCM3 model and the experiment setup of the two set of simulations are provided in Lyu and Yin¹⁰⁰.

$\delta^{18}\text{O}$ seawater estimates

We used the Mg/Ca and $\delta^{18}\text{O}$ analyzes on *G. ruber* published previously in Clemens et al.^{11,101} for section 0–7.47 m CCSF-A and in Nilsson Kerr et al.^{6,56,102} for section 32.96–26.37 m CCSF-A. Since the $\delta^{18}\text{O}$ sea-water reconstructions presented in these works were obtained using different Mg/Ca corrections and calibrations, we re-generated estimates of $\delta^{18}\text{O}_{\text{sw}}$ following a single method, as described in Clemens et al.¹¹ using the Matlab toolkit PSU Solver¹⁰³. The procedure uses: (1) the calibration of Tierney et al.¹⁰⁴ applied to Mg/Ca data corrected by 6% to account for the effect of reductive cleaning to estimate SST (Sea Surface Temperature), (2) the equation of Bemis et al.¹⁰⁵ describing the relationship between seawater $\delta^{18}\text{O}$ and temperature (low light), (3) Sea-level data extracted from U1446 smooth benthic $\delta^{18}\text{O}$ (lowess smoothing with a span f of 0.15) using the conversion factor (-0.01068‰/m). A 2 ky time uncertainty and a 2 m mean sea-level uncertainty were used. For all sections, we used levels with paired Mg/Ca and $\delta^{18}\text{O}$ data only, meaning that we retrieving all $\delta^{18}\text{O}$ on *G. ruber* data without corresponding Mg/Ca measurement in the same level. Note that it produces a lower time resolution record over the end of MIS 5e in comparison with that published in Nilsson Kerr^{6,56}.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data generated for this study are available online in the FigShare Repository <https://doi.org/10.6084/m9.figshare.26335576>. It includes a file with source data used for the main figures: pollen percentage data of the main ecological groups as well as estimations of Site U1446 $\delta^{18}\text{O}_{\text{sw}}$. In addition, detailed pollen percentage data shown in Supplementary Figs. 1, 2 are stored in a separate file.

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Author contributions

S.D. and P.M. conceived the study. S.D. and P.M. wrote the manuscript with contributions from C.C., Q.Y., S.C. and K.T. C.C. undertook the pollen analyses with the help of S.D., S.P. and K.A. while Q.S., A.S. and Q.Y. performed the climate-model experiments. C.C. performed the statistical analyses with the help of A.G., and designed the figures. All authors contributed to the ideas in this paper.

Competing interests

The authors declare no competing interests.

Additional information

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