

The Geologic History of Plants and Climate in India

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Keywords

C₃–C₄ plants, Indian Siwaliks, Himalaya, mangrove, Thar Desert, Ganga plain, Gujarat alluvial plain, Indian lakes

Abstract

India's diverse vegetation and landscapes provide an opportunity to understand the responses of vegetation to climate change. By examining pollen and fossil records along with carbon isotopes of organic matter and leaf wax, this review uncovers the rich vegetational history of India. Notably, during the late Miocene (8 to 6 Ma), the transition from C₃ to C₄ plants in lowland regions was a pivotal ecological shift, with fluctuations in their abundance during the late Quaternary (100 ka to the present). In India, the global phenomenon of C₄ expansion was driven by the combined feedback of climate variations, changes in substrate conditions, and habitat disturbances. The Himalayan region has experienced profound transformations, including tree-line migrations, shifts in flowering and fruiting times, species loss, and

shifts in plant communities due to changing monsoons and westerlies. Coastal areas, characterized by mangroves, have been dynamically influenced by changing sea extents driven by climate changes. In arid desert regions, the interplay between summer and westerlies rainfall has shaped vegetation composition. This review explores vegetation and climate history since 14 Ma and emphasizes the need for more isotope data from contemporary plants, precise sediment dating, and a better understanding of fire's role in shaping vegetation.

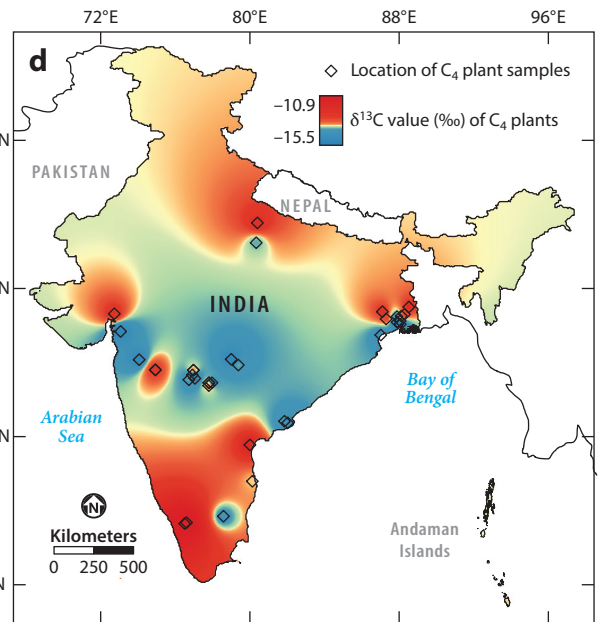
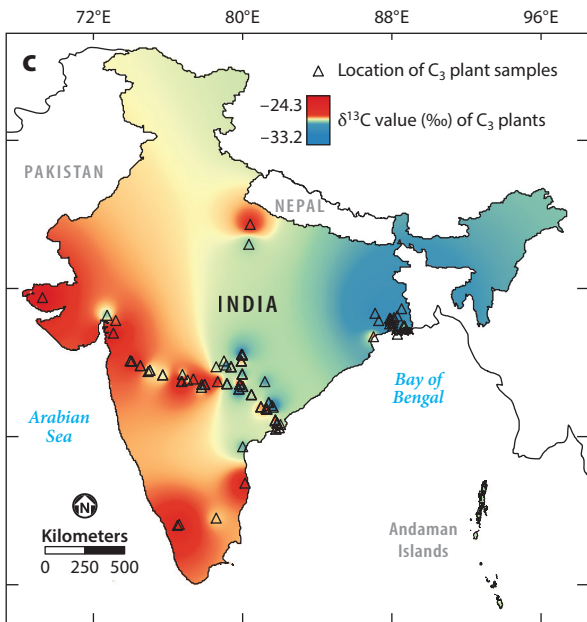
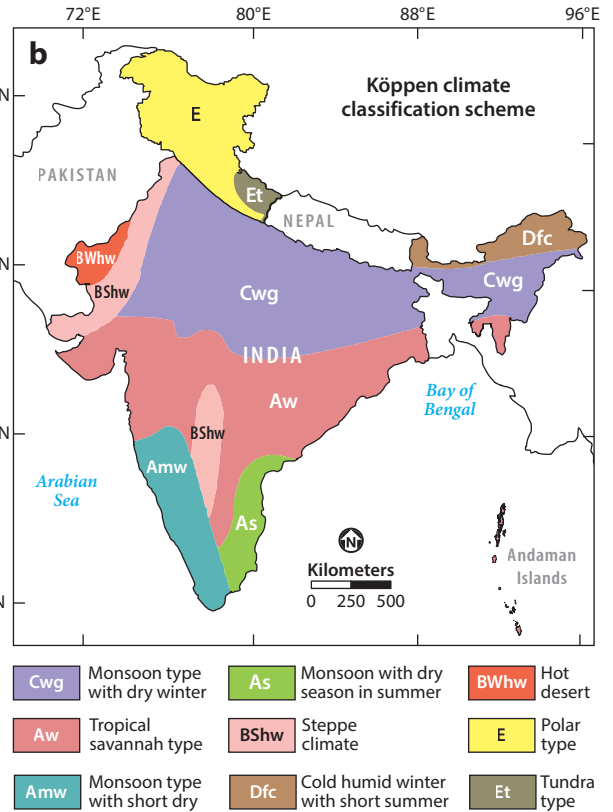
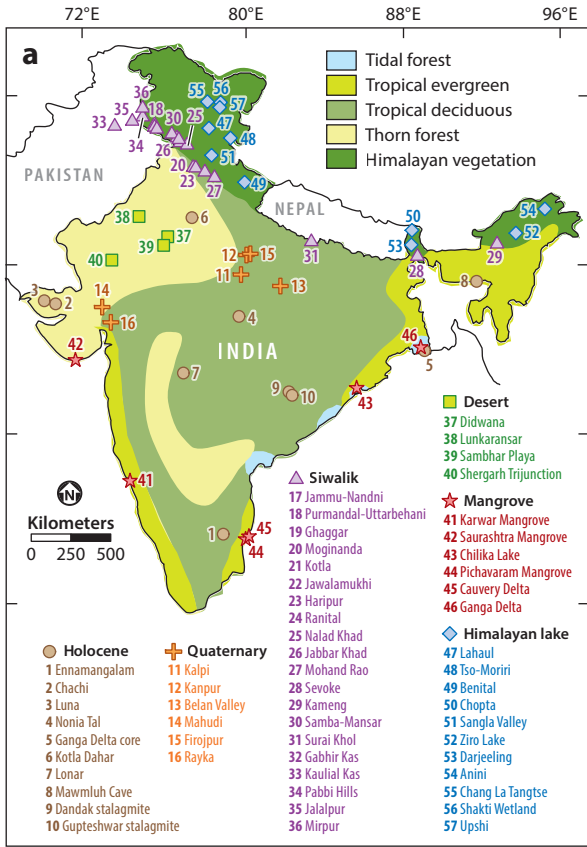
- This review highlights diverse vegetation and landscapes of India as a valuable source for understanding the vegetation-climate link during the last 14 Myr.
- A significant ecological shift occurred during 8 to 6 Ma in India, marked by the transition from C₃ to C₄ plants in the lowland regions.
- The abundance of C₃ and C₄ plants varied in India during the late Quaternary (100 ka to present).
- This review emphasizes the importance of more isotope data, precise sediment dating, and a better understanding of fire's role in shaping vegetation.

1. INTRODUCTION

One of the greatest challenges of the modern era is to mitigate the impact of climate change. Vegetation acts as both a vulnerable component, susceptible to the impacts of climate change, and a powerful ally, capable of mitigating its negative effects. By regulating energy exchange, absorbing carbon dioxide, and influencing atmospheric conditions, vegetation plays a pivotal role in stabilizing the climate and maintaining the delicate balance of our planet (Duveiller et al. 2018). Therefore, understanding the complex interplay between the vegetation mosaics and climate dynamics in past geologic history will help us to gain insights into the potential feedback loops.

India is a natural laboratory, characterized by a wide range of natural vegetation and climatic zones, and is recognized as one of the richest hotspots of biodiversity in the world (Stephen et al. 2015, Subrahmanyam 1956) (**Figure 1a,b**). The topography of India varies from high mountains to wide plains traversed by rivers to plateaus, and it is bordered by vast coastlines. The Himalayas and other high-elevation regions are characterized by dense forests, with the coexistence of angiosperms and gymnosperms (Dasgupta et al. 2022), whereas the alluvial plains are characterized by rich mosaics of deciduous and evergreen plants (Champion & Seth 1968). The coastal areas are dominated by mangrove forests consisting of salt-tolerant plants (Kathiresan 2010), in contrast to arid and desert regions, where thorny bushes represent the adaptability of plant life in such harsh environments (Bhandari 1995) (**Figure 1a**). India has a wide spectrum of climatic diversity varying from monsoonal to arid and alpine to tropical climates, where the rainfall ranges from 600 to 4,000 mm/year with an annual average of around 975 mm (Kumar et al. 2019, Subrahmanyam 1956) (**Figure 1b**). Such spatial variation in climate and vegetation provides an opportunity to understand the impact of climate on the different vegetational mosaics and their response to climate change.

The remote sensing data suggest greening in northwestern India and the central plain in the last couple of decades (Chen et al. 2019). Surprisingly, this greening phenomenon has been observed even in regions that are traditionally considered arid, which is attributed to an increase in moisture availability combined with a decrease in temperature. For the longer timescale, the relationship between the Indian climate and vegetation was studied using various proxies (Basu et al. 2019a; S. Ghosh et al. 2017, 2018; Jha et al. 2020, 2021; Roy et al. 2020; Sanyal et al. 2004, 2005a,b, 2010; Sarangi et al. 2019; Sukumar et al. 1993). Early reconstruction of vegetation in India was based



(Caption appears on following page)

(a) Distribution of modern vegetation in India and locations of the study sites. Study sites from Pakistan and Nepal were also considered for comparison. (b) Köppen climate classification scheme of India. (c) Interpolated map of $\delta^{13}\text{C}$ (VPDB) values of modern C_3 plants. (d) Interpolated map of $\delta^{13}\text{C}$ (VPDB) values of modern C_4 plants.

on pollen and fossils. However, pollen- and fossil-based reconstruction is mostly fragmentary and qualitative, and in India, quantitative analysis of vegetational change was missing until the late 1980s. Subsequently, the carbon isotopic composition ($\delta^{13}\text{C}$ value) of bulk soil organic matter (SOM), soil carbonates (SCs), and speleothems was used to reconstruct vegetation (Berkelhammer et al. 2012, Sanyal et al. 2004, Sukumar et al. 1993, Yadava & Ramesh 2005).

Based on photosynthetic pathways, nondesertic terrestrial plants are classified into C_3 and C_4 plants, and in India the $\delta^{13}\text{C}$ values of C_3 and C_4 plants range from -24.3 to -33.2% and -10.9 to -15.5% , respectively (Agrawal et al. 2012; Basu et al. 2015, 2017, 2018, 2019a; Kirkels et al. 2022; Laskar et al. 2013; Managave et al. 2023; Pradhan et al. 2014; Rajagopalan et al. 1999; Saha et al. 2022; Samantary & Sanyal 2022; Sharma et al. 2004; Sreemany & Bera 2020) (Figure 1c,d). Based on their morphology and life cycle, the C_3 plants comprise a diverse range of species, including various trees, shrubs, and some grasses. C_4 plants are primarily composed of grasses. The coastal mangroves mostly include halophytic C_3 trees, where wide $\delta^{13}\text{C}$ values (ranging from -26 to -35%) are attributed to their physiological plasticity toward the change in environmental conditions such as salinity, temperature, and rainfall (Kelleway et al. 2018, Ray et al. 2018).

In the last decade, vegetation and climate reconstruction took on a new dimension in India. Following the seminal paper by Freeman & Colarusso (2001), an effort was made to reconstruct vegetation using the isotopic composition of fossil leaf wax in paleosols and lake sediments. Although SOM is mainly contributed by plants that survived in the landscape, it can also be contributed by other sources that cannot be retrieved using the bulk isotopic composition of SOM. Paleosol-derived leaf wax long-chain *n*-alkanes (C_{29} , C_{31} , and C_{33}) and their $\delta^{13}\text{C}$ values are used to reliably reconstruct the relative abundance of C_3 and C_4 plants as they have characteristic distribution patterns for terrestrial higher plants (Eglinton & Hamilton 1967) and their isotopic compositions are less prone to alteration than other proxies (Cranwell 1981). Additionally, the hydrogen isotope composition of *n*-alkane was also used to reconstruct the hydrological conditions in the area (Ghosh et al. 2017, Jha et al. 2020, Roy et al. 2020, Sarangi et al. 2022).

India has a complex geological history spanning hundreds of millions of years, and its paleogeography has undergone significant changes due to plate tectonics and various geological processes. During the Precambrian (4.6 Ga to 538 Ma), India was a part of the supercontinent called Rodinia that was near the equator and had extensive marine environments (McMenamin & McMenamin 1990). During the Mesozoic (251 Ma), as a part of Gondwana, India was in the Southern Hemisphere and subsequently drifted toward the Northern Hemisphere and finally collided with the Eurasian Plate during the early Paleogene (~ 55 Ma) (Li et al. 2008). The collision resulted in the uplift of the Himalayan region. The Indian subcontinent began taking its present shape during the Neogene (23.03 to 2.58 Ma). During this time, the Indo-Gangetic plain and various other landforms started to take shape. Therefore, in this review, the vegetation and climate of India since the Neogene are discussed. The reconstructions of vegetation and climate are from fluvial and lake deposits. The spatial distribution of fluvial and lake deposits exhibits temporal variations. For instance, during the Neogene Period, fluvial deposits were mainly in lowland regions and occurred in the Himalayan foreland basin; they are known as Siwalik deposits. Late Quaternary deposits (100 ka to present) are found in the Ganga plain, western and northwestern regions of India. The Holocene sediments (10 ka to present) can be observed throughout

India. Therefore, the vegetation and climate reconstructions in the lowland regions of present and past have been divided into three time zones comprising primarily (a) 14 to 2 Ma (part of the Neogene), (b) 140 ka to Recent (part of the Quaternary), and (c) 10 ka to Recent (Holocene) (Figure 1). The Himalayan, desertic, and coastal vegetations are discussed separately in this review (Figure 1). Because different proxies and approaches are used in vegetation reconstruction, it is important to consolidate and summarize the existing knowledge and research. It is also important to review the strengths and limitations of each method/proxy used in the reconstruction of vegetation and climate. A comprehensive compilation will help to identify patterns, trends, and variations in vegetation dynamics over time, space, and environmental conditions. By analyzing and summarizing the collective evidence, this review aims to provide insight into the drivers of vegetation change and the potential implications for the diversity of plants.

2. THE SPATIOTEMPORAL VARIATION IN CLIMATE-VEGETATION LINK

2.1. Vegetation-Climat e Records from the Lowland Regions

Lowland regions in India are mostly in the alluvial plains formed by the major rivers such as the Ganga-Brahmaputra-Indus and its tributaries in the north and Narmada and Tapi in the west. The floodplain of these rivers and also its ancestral rivers played a significant role in India's ecosystem. The vegetation in the floodplain is subject to various environmental factors, including climate variations, which influence the ecological dynamics. The lakes that developed in the floodplain also provided archives to study the climate and vegetation link.

2.1.1. The Neogene records from the Siwalik sediments. After the collision between the Indian and Eurasian Plates, a significant portion of the former Tethys region underwent a transformation, becoming a terrestrial ecosystem that was characterized by multiple water basins as the Himalayas emerged (Acharyya 2007, Burbank et al. 1996, Kumar et al. 2011, Najman et al. 2004, Parkash et al. 1980). It is likely that these conditions closely resemble the present-day depositional characteristics of the lowland Indus and Ganga-Brahmaputra Basins. Several north-south lineaments divided the Himalayan frontal or foreland basin, known as Siwalik deposits, into multiple sub-basins. The pollen records, mostly available from the Subathu sub-basin, showed the transition from marine to terrestrial ecosystem, and subsequently vegetation changed from humid evergreen to mixed deciduous to dry to moist forest (Singh 1991).

An isotopic analysis of SOM, SCs, and leaf wax from the paleosols of the Siwalik deposits has been done to provide a continuous record and to understand the vegetation mosaics, their evolution, and their relation to climate in different sub-basins developing adjacent to the Himalayas. The $\delta^{13}\text{C}$ values of SC ($\delta^{13}\text{C}_{\text{SC}}$) and bulk organic matter (OM) ($\delta^{13}\text{C}_{\text{OM}}$) available across the Siwaliks showed a spatially nonuniform distribution pattern of C_3 and C_4 plants. Due to the absence of SC in the eastern Siwalik deposits, the majority of the paleorecords used the $\delta^{13}\text{C}$ value of bulk OM and leaf waxes. The oldest reported $\delta^{13}\text{C}_{\text{OM}}$ values from the Upper Dharamshala group of rocks (Kangra sub-basin) suggested that the vegetation was mostly dominated by C_3 -type plants (Vögeli et al. 2017). A spread of $\sim 4\text{‰}$ in the $\delta^{13}\text{C}_{\text{OM}}$ values has been observed in the paleosols between 20 and 12 Ma, which is similar to the variation observed in the $\delta^{13}\text{C}_{\text{SC}}$ values. The $\sim 4\text{‰}$ variation in the $\delta^{13}\text{C}$ values cannot be accounted for solely by the variability in $\delta^{13}\text{C}$ values of C_3 plants and the influence of climate. Therefore, such variation implied the presence of C_4 plants in the lowland areas of rivers before 12 Ma (Basu et al. 2015, 2019b, 2021; Diefendorf et al. 2010; Kohn 2010). The presence of grass-like leaf imprints in rocks older than 12 Ma also supports the presence or restricted growth of C_4 plants, which led to the 4‰ variation in the $^{13}\text{C}/^{12}\text{C}$ ratios of SOM and SC.

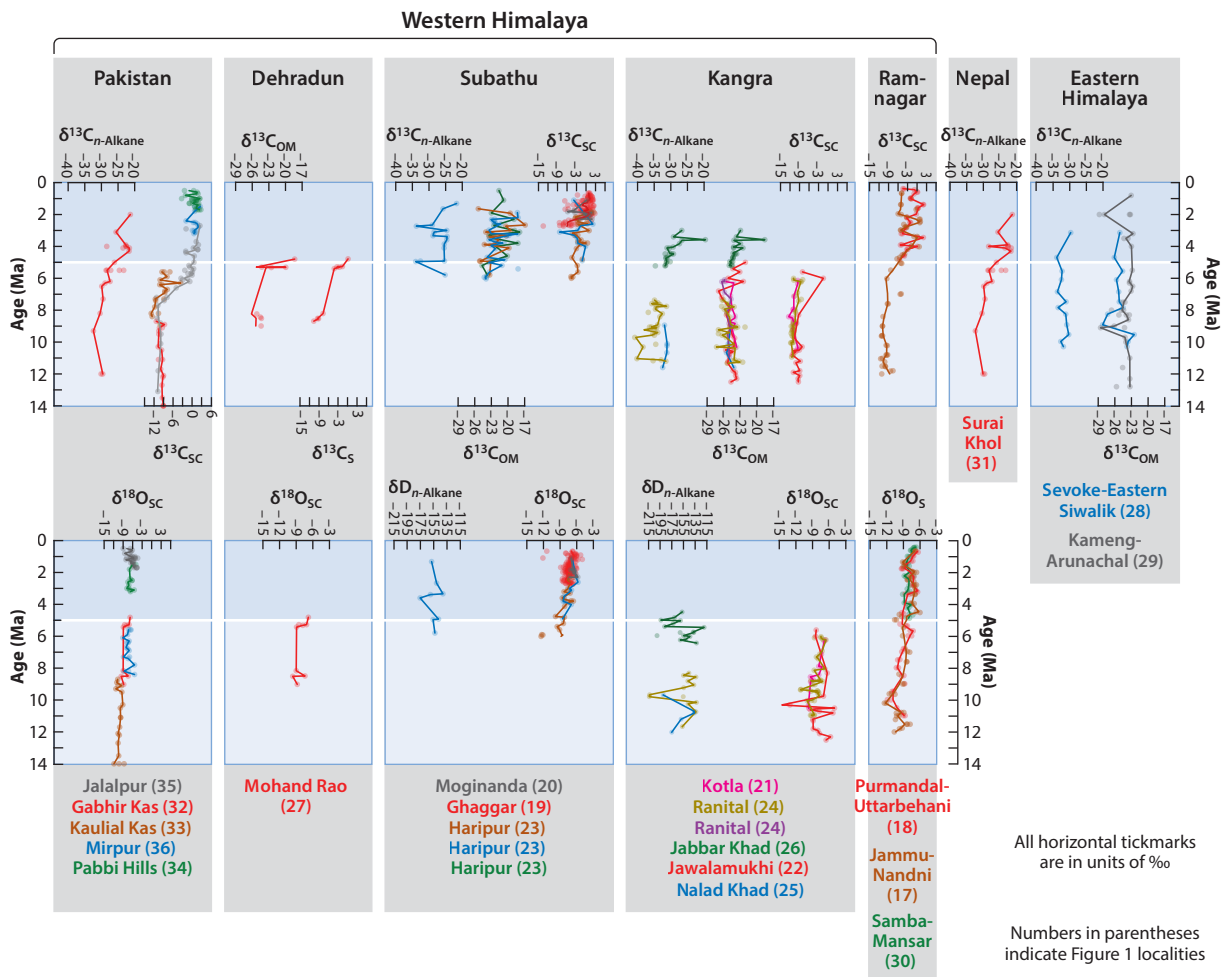


Figure 2

The top panel shows the variations in the $\delta^{13}C$ (VPDB) values of vegetation proxies. The lower panel shows the δD (VSMOW) and $\delta^{18}O$ (VPDB) values of monsoonal rainfall proxies from the Siwaliks. The Dehradun, Subathu, Kangra, Ramnagar, and Eastern Himalaya are from the Indian Siwaliks. The lighter and darker blue shaded areas represent the nature of the expansion of C_4 plants (*top panel*) and contemporaneous rainfall conditions (*lower panel*) for pre 5 Ma and post 5 Ma, respectively.

The $\delta^{13}C_{SC}$, $\delta^{13}C_{OM}$, $\delta^{13}C_{n\text{-alkane}}$, $\delta^{18}O_{SC}$, and $\delta D_{n\text{-alkane}}$ values younger than 12 Ma provided an important time window to examine the spatial variability of the C_4 vegetation across the Indian, Pakistan, and Nepal Siwaliks and its relation to climate (**Figure 2; Supplemental Figure 1**). The prevalence of mostly C_3 -type vegetation with limited occurrence of C_4 vegetation was observed across different Siwalik sub-basins (Behrensmeier et al. 2007; Ghosh et al. 2017; Quade et al. 1989; Roy et al. 2020; Sanyal et al. 2004, 2005a; Vögeli et al. 2017) (**Figure 3**). Within a sub-basin, different locations also showed variation in the abundance of C_3 and C_4 vegetation (**Figure 2**). The corresponding $\delta^{18}O_{SC}$ and $\delta D_{n\text{-alkane}}$ values showed fluctuations, implying change in the monsoonal rainfall. The comparison of vegetation and climate proxies suggested that not only monsoonal rainfall but also the geomorphic features, substrate condition, and habitat disturbance controlled the vegetation mosaic. During this time, while western to central Siwaliks

Supplemental Material >

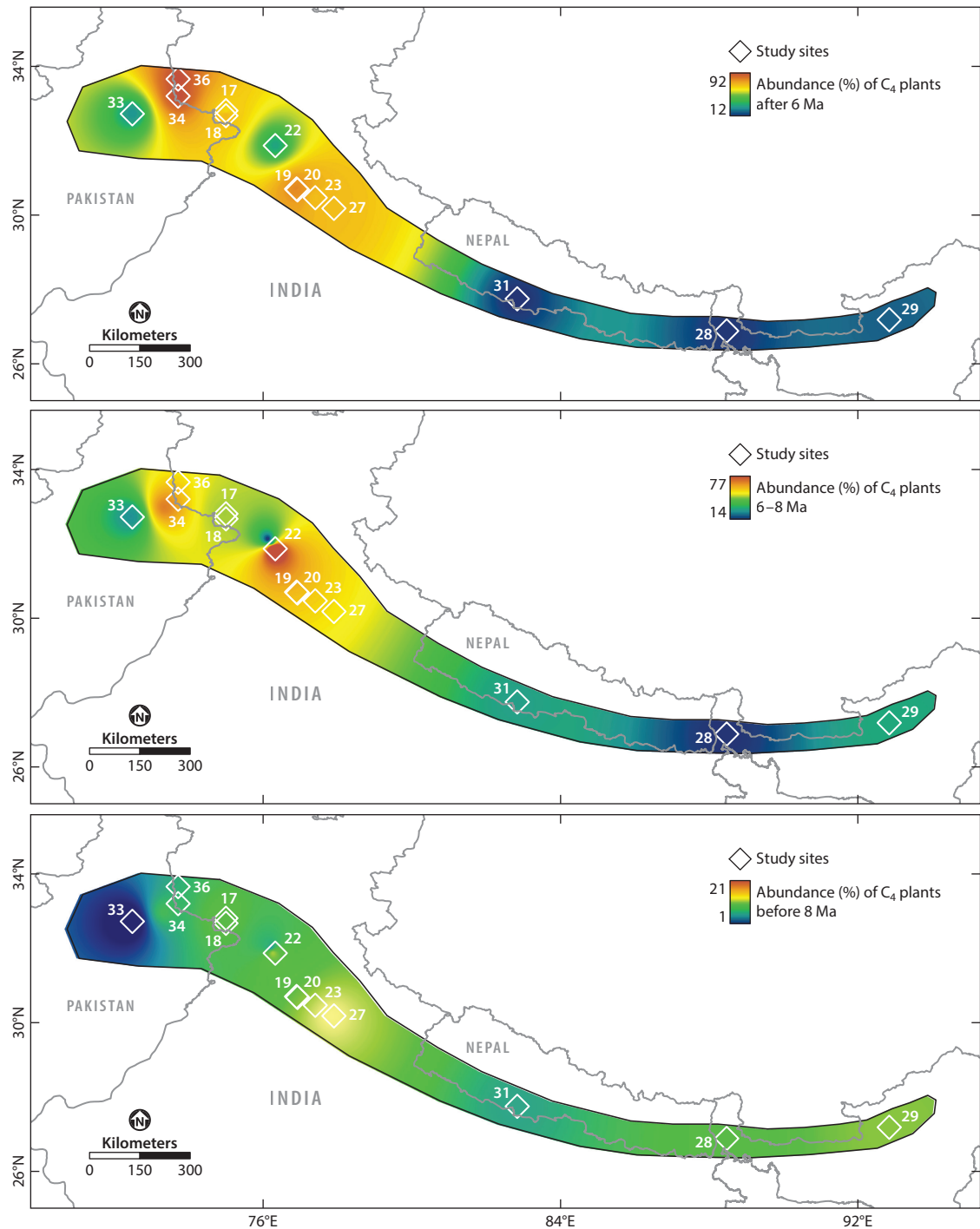


Figure 3

Spatiotemporal variations in abundance of C₄ plants in the Siwaliks. The northwest Siwaliks were characterized by a higher abundance of C₄ plants compared to the central and eastern Siwaliks. Note that the width of Siwalik exposure is a little exaggerated to help visualize the spatial variation in abundance of C₄ plants.

witnessed a fluvial environment, the eastern part of the foreland experienced a marine or estuarine environment that led to higher $\delta^{13}\text{C}$ value in OM (Coutand et al. 2016, Roy et al. 2021) (Figures 2, 3).

A significant increase in the $\delta^{13}\text{C}$ values of different proxies between 8 and 6 Ma has been observed from different sub-basins in the northwest Siwaliks compared to the eastern part (Figures 2, 3). The increase in $\delta^{13}\text{C}$ values suggested the possible time window of expansion of C_4 plants in the Siwaliks. The increase in the $\delta^{13}\text{C}$ values across different sub-basins was asynchronous and nonuniform, being gradual at some sub-basins while showing rapid expansion in others. Within the given time frame, variations in the abundance of C_4 plants in different areas/sections suggest the influence of multiple factors on their abundance. Through comparison of the paleovegetation records among different northwest Siwalik deposits, it becomes evident that the evolution and expansion patterns of C_4 plants varied across different areas (Figure 3). The asynchronous emergence of C_4 plants in different parts of foreland deposits was due to a combined effect of microclimate such as varying monsoon intensity, habitat disturbance such as forest fires, decrease in the influence of the westerlies, and changes in substrates (Behrensmeyer et al. 2007; Ghosh et al. 2017; Karp et al. 2018; Quade & Cerling 1995; Quade et al. 1989, 1995; Sanyal et al. 2005a,b, 2010; Vögeli et al. 2017) (Figure 2). The expansion of the C_4 grassland in the Siwaliks was also recorded in the late Miocene sedimentary archives of the Bengal and Indus Fans (Feakins et al. 2020, Freeman & Colarusso 2001, Polissar et al. 2021), which received sediments from the foreland region through the paleo-Ganga-Brahmaputra and Indus drainage systems. The $\delta^{13}\text{C}$ values from both the submarine fan sediments suggested a possible expansion of C_4 grassland between 7.5 and 6 Ma, supporting the time-equivalent change in vegetation mosaics across the Siwaliks. The appearance and expansion of C_4 plants have been observed globally including in Asia, North and South America, Africa, and Australia, which was asynchronous. Increasing aridity, low atmospheric carbon dioxide levels, and changes in temperature patterns have been attributed to the global expansion of C_4 plants (Andrae et al. 2018, Hoetzel et al. 2013, Loughney et al. 2023, Lu et al. 2020, Pagani et al. 1999).

Although post 5 Ma, a dominance of C_4 vegetation was observed across the northwest sub-basins, few areas recorded lowering in the $\delta^{13}\text{C}$ values post 2 Ma. The lowering of the $\delta^{13}\text{C}$ record from the younger foreland deposits has been advocated as the possible resurgence of C_3 vegetation (Kotla et al. 2018, Roy et al. 2021). The prevalence of cool and dry climatic conditions due to the onset of the Northern Hemisphere glaciation has been thought to be the possible reason for the increase and reappearance of the C_3 plants, which was favored due to the excess water availability in the conglomerate-dominated substrates of younger Siwalik deposits.

2.1.2. Quaternary records from the Ganga, Gujarat, and Ghaggar alluvial plains. In the Indian subcontinent, thick Quaternary deposits are exposed in North-Central India along the Ganga and Yamuna Rivers and the Narmada and Tapi Valleys, in parts of Rajasthan and Gujarat, and on the Ghaggar alluvial plain (Figure 1). Despite a large extent of Quaternary deposits in India, most of the available records of past climate and vegetation are limited to the Ganga, Gujarat, and Ghaggar alluvial deposits. The paleovegetation records from the Ganga plain are available from the fluvial sequence of the Belan River, sediment cores from the Ganga and Yamuna interfluvial region (Agrawal et al. 2012, 2013, 2014; Rahaman et al. 2011; Sarangi et al. 2021; Sinha et al. 2006). In western India, the Quaternary deposits are exposed along the banks of the Mahi and Sabarmati Rivers (Basu et al. 2019a), and in northwestern India, samples were collected from the drill core raised from the Ghaggar plain (Singh et al. 2016). Initial paleovegetational investigations from the Indian Quaternary deposits were mostly qualitative and often fragmented in nature. For instance, changes in vegetation composition in the past were reconstructed using pollen and plant fossils preserved within the sedimentary deposits (Trivedi et al. 2013). Similarly, sedimentary

textural attributes and changes in depositional environment were used to derive qualitative information on past rainfall variations. To provide continuous records, rainfall and vegetation-specific stable isotope-based proxies such as $\delta^{13}\text{C}_{\text{COM}}$, $\delta^{13}\text{C}_{\text{SC}}$, $\delta^{18}\text{O}_{\text{SC}}$, $\delta^{13}\text{C}_{n\text{-alkane}}$, $\delta\text{D}_{n\text{-alkane}}$, $\delta^{13}\text{C}$ value of fatty acids ($\delta^{13}\text{C}_{\text{FAME}}$), and $\delta^{13}\text{C}$ value of OM occluded in carbonate nodules ($\delta^{13}\text{C}_{\text{NOM}}$) were used (Agrawal et al. 2012, 2013, 2014; Basu et al. 2018, 2019a; S. Ghosh et al. 2017, 2018, 2020; Jha et al. 2020; Singh et al. 2016).

At present, monsoonal rainfall in eastern and Central India is dominantly contributed by the vapor derived from the Bay of Bengal, but in western India, moisture is mostly sourced from the Arabian Sea, and northwestern India receives rainfall from westerlies in addition to monsoonal rainfall. The available $\delta^{13}\text{C}$ values of modern plants in the Ganga and Gujarat alluvial plains are distinctly different (Basu et al. 2015, 2018, 2019a,b; Managave et al. 2023; Saha et al. 2022) (**Figure 1c,d**). For the Quaternary time, response of vegetation and climate in the Ganga, Gujarat, and Ghaggar plains has been compared with the glacial (cold and dry) and interglacial (warm and humid) periods, which are based on the marine isotope stages (MISs) (**Figure 4; Supplemental Figure 2**). During MIS-5, the lower $\delta^{18}\text{O}_{\text{SC}}$ values remained mostly unchanged, whereas the $\delta\text{D}_{n\text{-alkane}}$ values implied an increase in the rainfall in the Ganga plain (Jha et al. 2020). The warm and humid conditions prevailing during the latter part of MIS-5 (~79 ka) led to the proliferation of C_3 plants as suggested by the lowering of $\delta^{13}\text{C}_{\text{COM}}$, $\delta^{13}\text{C}_{\text{NOM}}$, and $\delta^{13}\text{C}_{n\text{-alkane}}$ values (Agrawal et al. 2012, 2013, 2014; Sarangi et al. 2021). In contrast, the $\delta^{13}\text{C}_{\text{SC}}$ and $\delta^{13}\text{C}_{\text{FAME}}$ values showed a dominance of C_4 plants. The observed disparity among the vegetational proxies has been linked to the isotopic fractionation associated with the decomposition and incorporation of OM in the soil (Sarangi et al. 2021). During MIS-4, the paleoclimatic proxies in the Ganga plain did not fluctuate much. In contrast, the $\delta^{18}\text{O}_{\text{SC}}$ values showed increasing rainfall between ~72 and 60 ka in the Gujarat and Ghaggar alluvial plains (Basu et al. 2018, Singh et al. 2016). The humid condition prevailing during this period was reciprocated with an increase in the abundance of C_3 plants as suggested by the $\delta^{13}\text{C}_{\text{SC}}$ and $\delta^{13}\text{C}_{n\text{-alkane}}$ values (Jha et al. 2020). The advent of MIS-3 marked a decrease in the rainfall in both the Ganga and Gujarat alluvial plains. The prevailing cold and dry phase was characterized by a dominance of C_4 plants as suggested by the $\delta^{13}\text{C}_{\text{SC}}$, $\delta^{13}\text{C}_{\text{COM}}$, $\delta^{13}\text{C}_{\text{NOM}}$, $\delta^{13}\text{C}_{n\text{-alkane}}$, and $\delta^{13}\text{C}_{\text{FAME}}$ values (Agrawal et al. 2012, 2014; Basu et al. 2018). The latter part of MIS-3 witnessed an increase in rainfall, with the warm and humid phase favoring the proliferation of C_3 plants (Sarangi et al. 2021). The $\delta^{13}\text{C}_{\text{SC}}$, $\delta^{13}\text{C}_{\text{COM}}$, $\delta^{13}\text{C}_{\text{NOM}}$, $\delta^{13}\text{C}_{n\text{-alkane}}$, and $\delta^{13}\text{C}_{\text{FAME}}$ values suggested that the Ganga, Gujarat, and Ghaggar alluvial plains were characterized by a dominance of C_4 vegetation during the early phase of MIS-2, which was also supported by the vegetation record from the Bengal Fan (Agrawal et al. 2012, 2014; Basu et al. 2018; Galy et al. 2008; Jha et al. 2020; Sarangi et al. 2021). Increase in C_4 plants during Last Glacial Maxima (LGM) was also observed in the Nilgiri basin (altitude 2 km), Western Ghats (Sukumar et al. 1993). A comparison among Ganga, Gujarat, and Ghaggar alluvial data suggests climate was more stable in the Ganga plain. Within the Gujarat alluvial plain, the lowering in rainfall observed toward the northwest direction in modern time also prevailed during Quaternary time. Comparison of vegetation suggests that abundance of C_4 plants was higher in the Gujarat plain than the Ganga plain during the dry periods (Basu et al. 2018) (**Supplemental Figure 5**).

2.1.3. Holocene vegetation and climate records from the lowland areas. There are more climate records for the Holocene in India compared to the other time periods. The climate and vegetation records have been reconstructed from the lake and fluvial sediments as well as from speleothem. A recent review by Misra et al. (2019) reported that more than 70 lakes were studied from different regions of India; however, most of them lack chronological constraints. Only a few records have temporal constraints and provide environmental conditions for the entire Holocene. The climate during the Holocene showed significant fluctuations that were controlled by regional

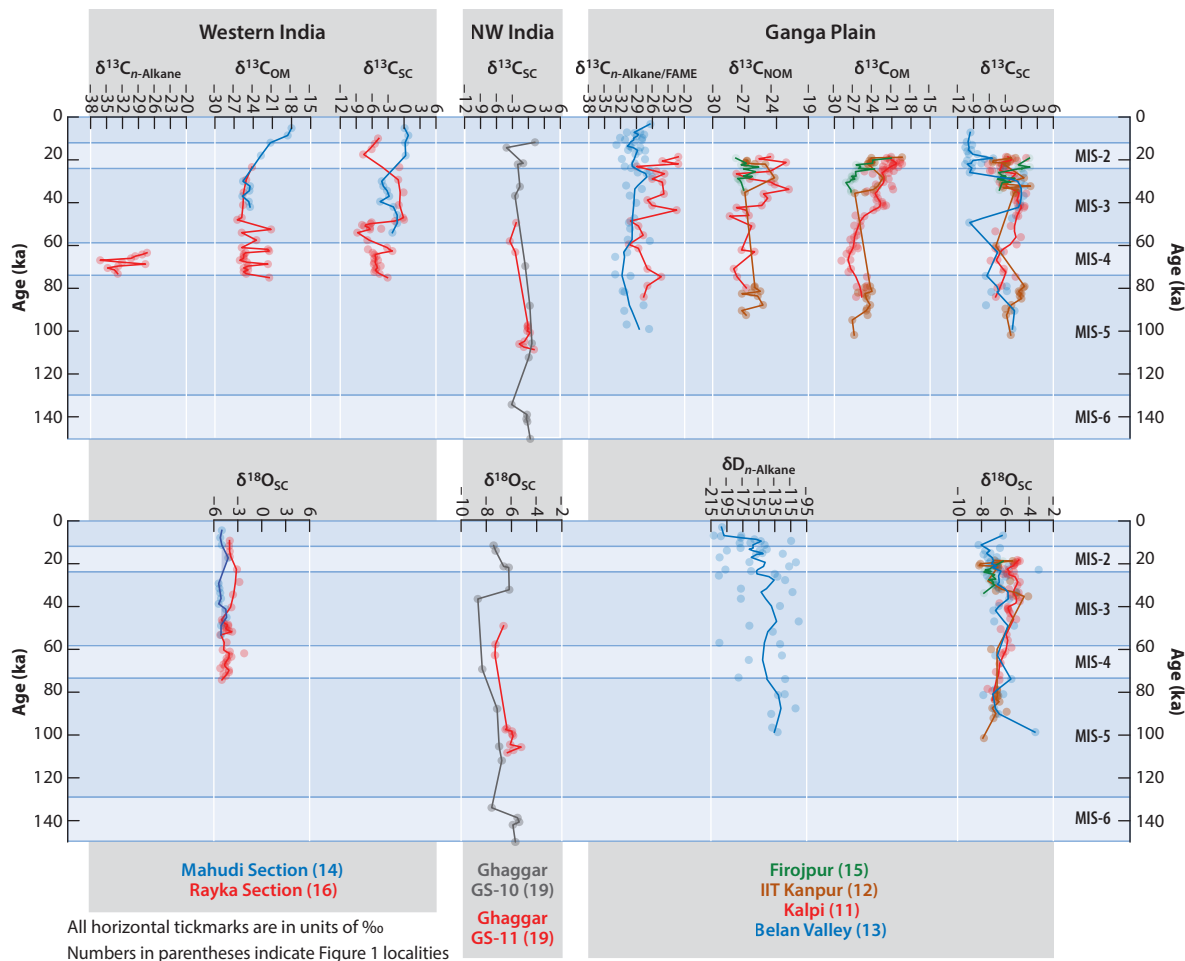


Figure 4

The top panel shows the variations in the $\delta^{13}\text{C}$ (VPDB) values of vegetation proxies. The lower panel shows the δD (VSMOW) and $\delta^{18}\text{O}$ (VPDB) values of monsoonal rainfall proxies from the Quaternary sediments. The shades represent marine isotope stages (MISs).

as well as global forcing factors. As the studied regions in India are distributed in different climatic zones, the climate reconstruction captured the spatiotemporal variability (**Figure 1a,b**). Although the lake records provided significant information about the Holocene, in many cases observed records are influenced by the size of the lake or selection of proxies. For example, the reconstruction of climate was done based on endogenic carbonates. The response of isotopic composition of such carbonates depends on the size of the lake and the volume of the water present in the lake. For vegetation reconstruction, the $\delta^{13}\text{C}$ value of OM was used except in a few cases (Basu et al. 2017, 2019b). Bulk OM can have various sources such as catchment vegetation and in situ production in lakes, making it not so useful for vegetation reconstruction. In such a situation, the isotopic composition of *n*-alkyl compounds of lake sediments should be used as it not only helps to understand sources of OM but also provides clues about the preservation of organic compounds in the lake sediments (Ghosh et al. 2020).

Even with the uncertainties within the proxies and size of study sites, comparison of all the Holocene records shows broad agreements (**Figure 5**; **Supplemental Figure 3**). In the

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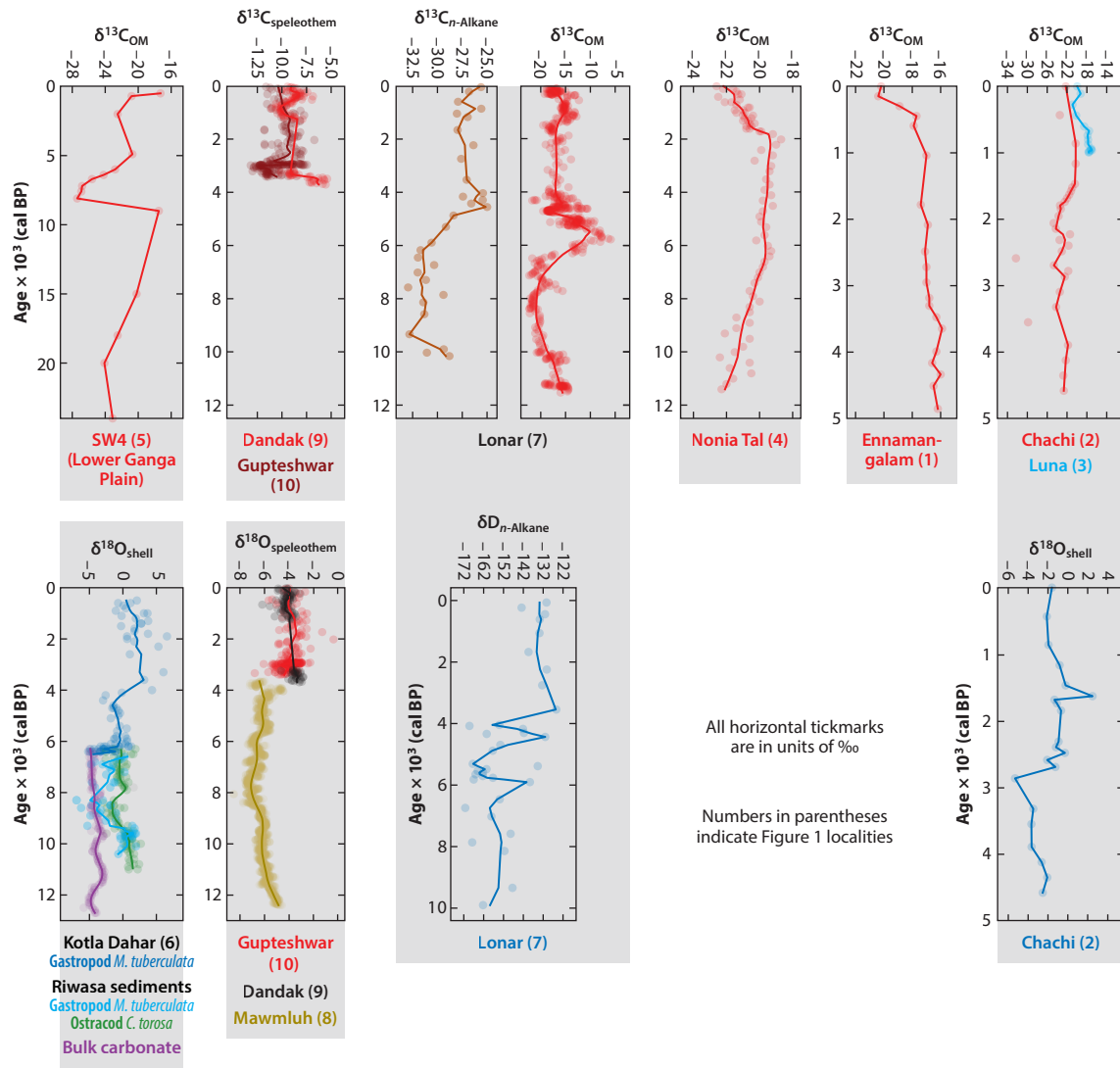


Figure 5

The top panel shows the variations in the $\delta^{13}\text{C}$ (VPDB) values of vegetation proxies. The lower panel shows the δD (VSMOW) and $\delta^{18}\text{O}$ (VPDB) values of monsoonal rainfall proxies from the Holocene sediments of lowland areas.

post-LGM, the climate was humid and subsequent aridity at around 12 ka cal BP coincided with the globally recognized Younger Dryas event. The post-10 ka cal BP witnessed high monsoonal rainfall. However, the response of different proxies varied spatially. The climate record from northwestern India suggested weak summer monsoons during pre-11 ka cal BP, and subsequently monsoonal rainfall increased at around 9.4 ka cal BP. An abrupt decrease in rainfall was observed around 8.3 ka cal BP. Rainfall increased again with an abrupt drier event around 4.1 ka cal BP, following which the lakes ceased to exist (Dixit et al. 2014a,b). In the central part of India, which falls in the core monsoon zone, the hydrological behaviors of the lakes were different. The Lonar lake, which is one of the most well-studied lakes for the Holocene, is still active (Prasad et al. 2014,

S. Sarkar et al. 2015). The Lonar lake records suggest that from 10.1 to 6 ka cal BP, the climate was humid but witnessed the driest conditions around 4.8 to 4 ka cal BP, which transformed it into a saline lake. The humid period was characterized by the woody C₃ plants, which thrived in more than 200 cm of rainfall. During the dry period, moist arboreal C₃ vegetation changed to C₄ grasses as suggested by the $\delta^{13}\text{C}_{n\text{-alkane}}$ values. The significant correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ value of speleothem from Central India also suggests rainfall control on isotopic composition of vegetation during the late Holocene (Yadava & Ramesh 2005). The pollen-based vegetation records from the Ganga plain suggested that at ~ 12 ka cal BP, there was a prevalence of open grassland. The vegetation was primarily composed of ferns, sedges, and other herbaceous plants that thrived in cooler and drier conditions (Chauhan et al. 2015, Sharma et al. 2004, Trivedi et al. 2013). Isotopic records from the lower Ganga plain and Nonia Tal from Central India (**Figure 5**) suggested that the abundance of C₃ and C₄ plants was modulated by changes in depositional environment, specific ecological niches, and climate rather than atmospheric CO₂ (Kumar et al. 2019, Sarkar et al. 2009). The western part of India showed continuous decrease in rainfall since the early Holocene that culminated at peaks around 4.2 and 2.5 ka cal BP, a time also marked by an expansion of C₄ plants in the area (Basu et al. 2019b, Sengupta et al. 2020). In the southern part of India, the bulk $\delta^{13}\text{C}_{\text{OM}}$ and other biomarker indices from the Ennamangalam lake, which receives rainfall from both the summer and winter monsoons, showed that an increase in winter rainfall led to higher abundance of C₃ plants in the catchment area (Basu et al. 2017). Overall, the 4.2 ka cal BP [Mawmluh Cave (Berkelhammer et al. 2012)] event is observed in all climatic records in India, unlike the 8.2 ka cal BP event, which is mostly observed in northwestern India.

2.2. Vegetation and Climate Records from the Himalayas

The Indian Himalayan Region (IHR) supports more than 18,440 species of flowering plants, 25% of which are endemic to the area (Samant et al. 1998, Singh & Hajra 1996). There are six main forest types: subtropical dry evergreen, subtropical pine, Himalayan moist temperate, Himalayan dry temperate, subalpine, and alpine (Champion & Seth 1968). Despite gymnosperms' numeric dominance in the western IHR, the central and eastern regions exhibit noticeably higher species- and genus-level diversity (Singh & Pusalkar 2020). The eastern IHR is referred to as the cradle of angiosperms because it is home to several primitive flowering plant species. Among the several elements that work together to produce disparities in habitat, climate, and flora, elevation is thought to be the most crucial (Polunin & Stainton 1984). This is because elevation is the primary driver for the climatic (rainfall and temperature) gradient observed in the montane ecosystems.

Climate change has significant impacts on the distribution of Himalayan flora, with some species losing their potential habitat and others colonizing new areas (Wambulwa et al. 2021). The flowering cycle and altitude distribution have shifted due to changes in the environment. The biological cycles of the species are changing as a result of such shifts in phenology, which has an impact on the pollination of many cross-pollinated species. Pests and diseases are moving up and down in altitude due to an increase in the maximum and minimum temperatures and a decrease in rainfall and snowfall (Devi et al. 2019, Lal & Samant 2019, Singh & Samant 2020).

In the Himalayas, vegetation and climate records are available from lakes at different altitudes. Some of these records are continuous while others are fragmentary (**Figures 1a, 6**). Mostly $\delta^{13}\text{C}$ values of bulk OM were measured to retrieve environmental conditions except the Benital lake (**Figure 6**). Understanding the variation in abundance of angiosperm and gymnosperm based on the bulk $\delta^{13}\text{C}_{\text{OM}}$ value poses a challenge because their end-member isotopic compositions from the Himalayas are not well constrained and the bulk OM can have multiple sources in addition to the vegetation (Jha et al. 2024). Although the bulk OM and $\delta^{13}\text{C}_{\text{OM}}$ values are influenced by both

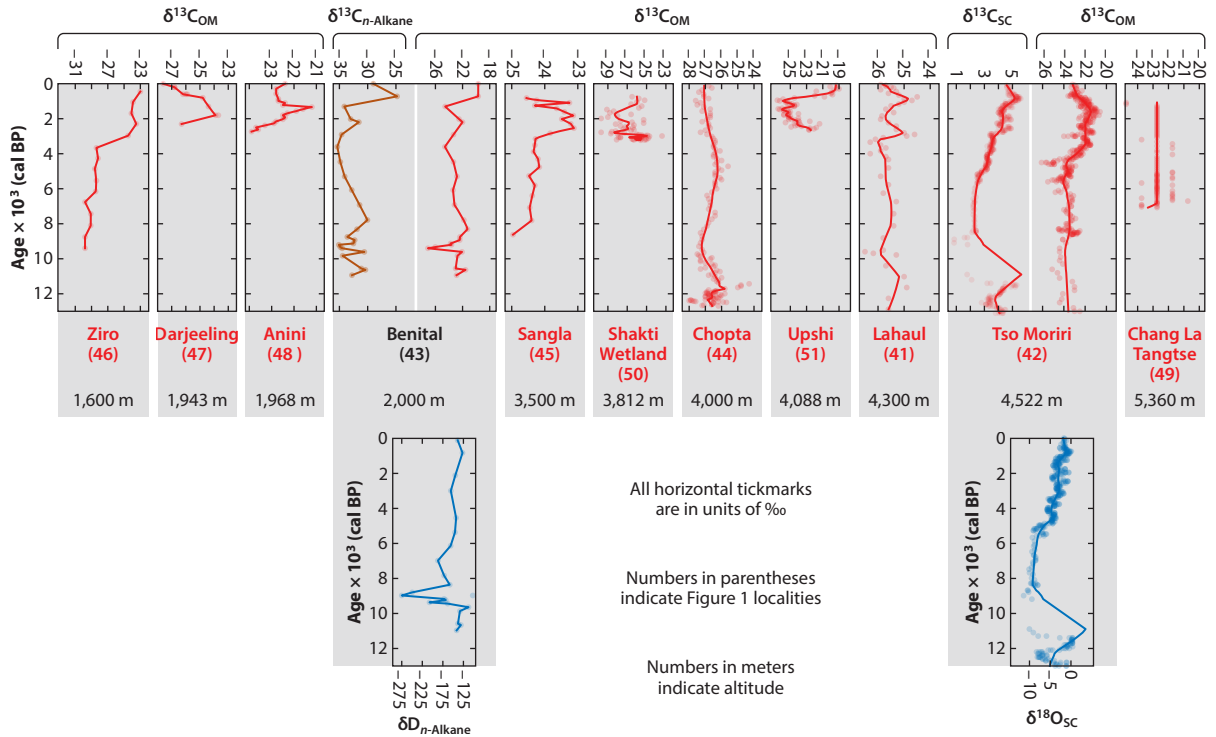


Figure 6

The top panel shows the variations in the $\delta^{13}\text{C}$ (VPDB) values of vegetation proxies. The lower panel shows the δD (VSMOW) and $\delta^{18}\text{O}$ (VPDB) values of rainfall proxies from the Himalayan lakes.

in situ production in the lake and vegetation in the catchment area, these values were interpreted in conjunction with other geochemical indicators.

Most of the lake records show evidence of monsoon intensification during the beginning of the Holocene (**Figure 6**). In the central Himalayas, the $\delta\text{D}_{n\text{-alkane}}$ values from the Benital lake suggest that the early Holocene was characterized by a wet phase at ca. 9 ka cal BP with 25% higher rainfall compared to present while the middle–late Holocene was relatively arid (Ghosh et al. 2020), which is similar to the records observed in other parts of the Himalayas. The $\delta^{13}\text{C}_{n\text{-alkane}}$ values of the lake sediments suggest a transition from woody to nonwoody plant assemblages at 7 ka. The poor correlation between $\delta\text{D}_{n\text{-alkane}}$ and $\delta^{13}\text{C}_{n\text{-alkane}}$ values suggests that at higher rainfall, the $\delta^{13}\text{C}_{n\text{-alkane}}$ values of catchment vegetation were less responsive, which is in agreement with the carbon isotopic response of C_3 plants in high rainfall (Basu et al. 2019a).

However, in the regions dominated by the westerly rainfall such as Chang La Tangtse basin (altitude 5,360 m), the climate was stable but arid during the early Holocene, and vegetation was characterized by both C_3 and C_4 plants (Joshi et al. 2023). The climate began to change around 6040 cal BP, with the onset of the Mid-Holocene Thermal Maxima (MHTM). During the MHTM, the climate became warmer and wetter, leading to an increase in the $\delta^{13}\text{C}_{\text{OM}}$ values in the lake sediments. The MHTM ended around 3.4 ka cal BP, and the climate subsequently became cooler and drier. Subsequent to the MHTM, the climate was fluctuating with higher aridity at 4.5 to 4.3 ka BP. During the arid conditions vegetation was characterized by steppe and desert taxa, and warm and wet conditions witnessed alpine meadow and marshy taxa (Agrawal et al.

2015; Ali et al. 2018, 2020; Chakraborty et al. 2006; R. Ghosh et al. 2014, 2018; S. Ghosh et al. 2020; Joshi et al. 2023; Leipe et al. 2014; Maurya et al. 2022; Mishra et al. 2015; Phadtare 2000; Rawat et al. 2015; Sharma et al. 2020) (**Figure 6; Supplemental Figure 4**).

It is interesting to compare the Holocene Himalayan lake records with the lowland records. The intensity of monsoonal rainfall decreases from the eastern to the western regions of the Indian subcontinent, but in the Himalayas, rainfall increases from the northern to the southern areas of the Southern Himalayan Front (Bookhagen & Burbank 2006). Analysis of Tropical Rainfall Measuring Mission data from the years 1998 to 2005 reveals two distinct bands of maximum rainfall: one at an altitude of approximately 1 km across the entire Himalaya region and another at an altitude of around 2 km in the central Himalayan range. This could explain the greater intensity of early Holocene monsoonal rainfall in areas near the Himalayas (such as the Benital lake) compared to regions located in central peninsular India (Lonar lake). Marine archives, such as the Bay of Bengal and Arabian Sea, receive sediments from rivers that drain the Indian landmass and represent averaged-out continental records. Consequently, paleoclimate data from marine archives indicate a lower intensity of early Holocene monsoonal rainfall when compared to the Himalayan records (Ghosh et al. 2020).

2.3. Vegetation and Climate Records from the Thar Desert

Qualitative information about climate and vegetation from the Thar Desert is available from pedogenic calcretes and dunes. Such records suggest that between 1600 and 600 ka and between 650 and 350 ka, the climate was semiarid (Dhir et al. 2010, Kailath et al. 2000), and the sand dunes suggest stability in climate. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of calcretes (age around 200 ka) of the 16R Dune are available from the eastern margin of the Thar Desert (Achyuthan et al. 2007) (**Figure 7**). It was observed that warm, wetter summer monsoons favored C_4 plants, while winter rain (westerlies) and low temperature favored C_3 plants. In contrast, Andrews et al. (1998) observed C_4 plants in glacial periods, a time with low $p\text{CO}_2$ (**Figure 7**).

The high-resolution climatic and vegetation records from the Thar Desert are obtained from lake records. There are a number of salt lakes in and around the Thar Desert such as Sambhar, Kuchaman, Didwana, Lunkaransar, and Kharaghoda (Bryson & Swain 1981, Enzel et al. 1999). Stable isotope studies showed these lakes are meteoric water in origin, which is against the hypothesis of their origin as relict lakes from the Tethys Sea. The salt is locally derived by the weathering of rocks from the catchment area (Ramesh et al. 1993). During 20000 and 13000 cal BP, the presence of steppe vegetation, mainly of Chenopodiaceae/Amaranthaceae, grasses, *Artemisia*, *Aerva*, and *Ephedra*, implied weakened summer monsoons and a higher winter rainfall than at present (Singh et al. 1990). The early Holocene was less dry; the vegetation was characterized by open land steppes that were rich in grasses, *Artemisia*, and sedges and poor in halophytes. The species *Artemisia*, *Typha angustata*, *Mimosa rubicaulis*, and *Oldenlandia* were observed in the lake sediments that now grow under areas of comparatively higher average annual rainfall more than 50 cm. During ca. 3000 to ca. 1000 BC, rainfall increased as suggested by the presence of swamp vegetation. Subsequently, aridity continued as evidenced by desiccation (Singh et al. 1972, 1974) (**Figure 7**). The Sambhar lake did not show any evidence of desiccation, which suggests spatial variation in climatic condition in the Thar Desert (Sinha et al. 2006).

2.4. Mangrove in the Past and Contemporaneous Climate

The mangrove vegetation in the eastern and western parts of India has undergone significant changes (**Figure 8**). The sediment records of the Ganga plain and Chilika lagoon suggest limited mangroves on the east coast of India during the late-glacial period because of the freshwater conditions. On the west coast of India, the oldest record of mangrove vegetation dates back to

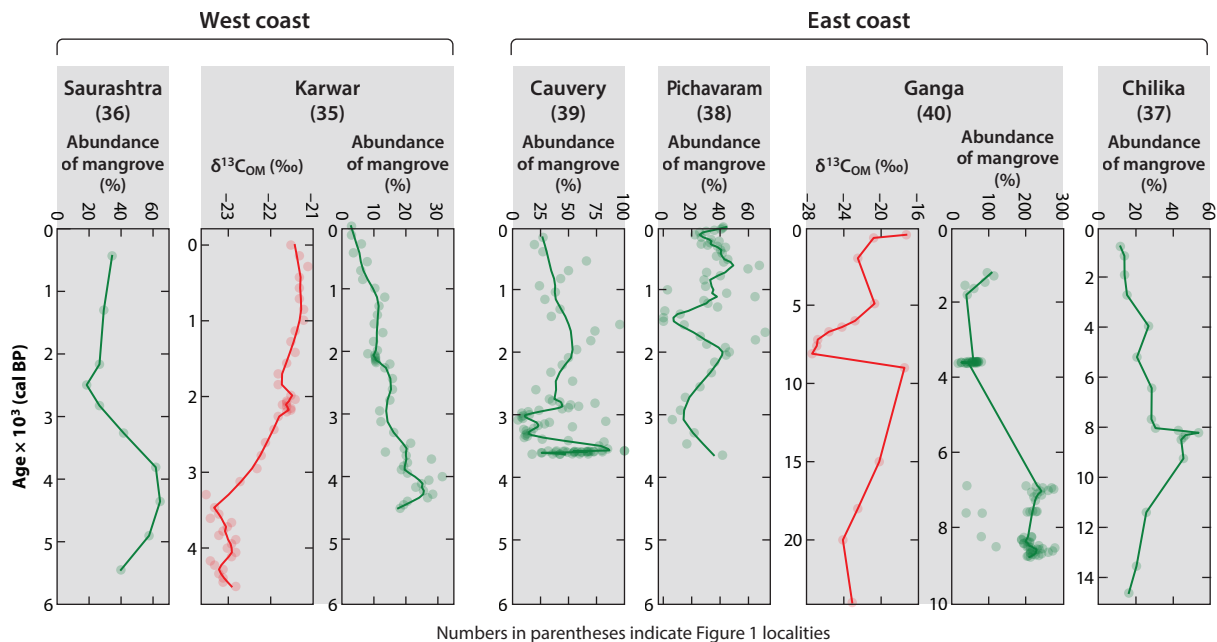


Figure 8

Shown are the variations in the abundance of mangroves based on pollen and $\delta^{13}\text{C}$ (VPDB) values from the east and west coasts of India.

mangrove ecosystem on both the east and west coasts due to high monsoon rainfall, which led to the lower $\delta^{13}\text{C}$ values of OM in sediments (Banerji et al. 2015, Sridhar et al. 2015). After 2600 BP, the climate transitioned from warm and humid to cold and dry, and marginal sea-level regression led to a decline in mangrove populations and an increase in salt-tolerant species on both the east and west coasts of India (Farooqui & Vaz 2000, Limaye & Kumaran 2012, Pandey et al. 2014, Samal et al. 2023, Sridhar et al. 2015). Overall, mangrove vegetation in the eastern and western peninsulas of India has been influenced by monsoon and sea-level fluctuations.

3. SUMMARY

In India, the major vegetational change from C_3 dominant to mixed C_3 and C_4 vegetation happened during the late Miocene. The expansion of the C_4 plants was asynchronous in the different Siwalik sub-basins, albeit in the eastern part, C_4 did not make a significant component in the vegetation mosaic. During the late Quaternary and Holocene, the abundance of C_3 and C_4 plants varied depending mostly on the climatic conditions. The mangrove vegetation is one of the sensitive components of Indian vegetation whose spatial extent in the coastal area changed mostly by climate and sea level. The Thar Desert plants and the Himalayan plants responded to changes in rainfall from both summer monsoons and westerlies.

FUTURE ISSUES

1. There is a need for more isotope data from modern plants to understand the relation between isotopic composition of plant biomolecules and climate.

2. Study of the polyaromatic hydrocarbon molecules is required to understand the impact of forest fire in controlling the vegetation mosaic.
3. We also need more absolute ages to constrain the climatic events better.
4. We require biomarker-based study of the lake sediments so that in situ and catchment productivity can be separated out.
5. Finally, we need to incorporate sedimentological aspects with the isotope data while comparing the spatiotemporal variation in isotope records.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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