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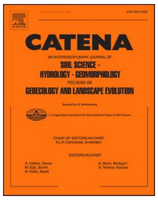

Palaeoecological and palaeoherbivory dynamics in Kaziranga National Park: Late Holocene vegetation shifts and large mammal biogeography

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ABSTRACT

This study presents an integrated palaeoecological and palaeoherbivory history of Kaziranga National Park (KNP) since the late Holocene based on biotic proxies. A 110 cm deep sedimentary profile permitted the collection of pollen and spores for analysis employing the standard acetolysis method. Around 3290–1700 years BP, the KNP consisted of a tropical dense mixed forest dominated by *Bombax*, *Cinnamomum*, *Duabanga*, and *Lagerstroemia*, with less grasslands during a period of warm and humid climatic condition with low wildlife activity compared to the present. From 1700 to 640 years BP, the evergreen taxa, *Mesua*, *Cinnamomum*, and *Litsea* decreased and with an increase in the deciduous taxa, *Bombax*, *Dillenia*, and *Careya* along with an expansion of grassland. The appearance of *Mimosa*, an invasive plant, is significant and is detrimental to the vegetation in KNP. The increase of coprophilous fungal spores, *Sporormiella*, *Saccobolus*, and *Ascodesmis*, indicates the gradual increase of wildlife in the region. During 640 years BP to present, the forest was comparatively less dense than the preceding phase with an expansion of openland areas. The significant increase of *Sporormiella*, *Saccobolus*, and *Ascodesmis* implies higher levels of the large herbivore population. We propose that the wildlife, especially rhinoceros, migrated from the western and northern part of the region into the north-eastern part of the Indian subcontinent in response to climatic amelioration and higher human activities during the late Holocene period. This study will be helpful in providing a better understanding of the palaeoecological and palaeoherbivory history of this region and can provide a greater insight into the causes of migration and subsequent extirpation of wildlife.

1. Introduction

The reduction in the geographic distribution along with extinction of many species of plants and animals during the Quaternary period is a major global ecological issue. Although the specific reasons for population declines, local extirpation or ultimately extinction of different species of plants and animals, whether due to climatic change, anthropogenic activities or both is still debated. One approach to documenting these patterns is by examining changes in pollen and fungal spore abundances preserved in sedimentary profiles with associated radiocarbon dates. This allows for a comparison of the chronology of these patterns over a wide geographic area. The study of palaeoecology in a region is essential to understanding the interactions and relationships between vegetation and wildlife of all sizes and how changes in climate impacted the vegetation which in turn influences the fauna at both regional and global levels. Accurately predicting the different impacts of climate change on biodiversity is a major scientific challenge (Pacifici et al., 2015). Palaeoecology serves as an effective tool for providing a historical baseline to better understand how different organisms responded to past environmental changes (Vegas-Vilarrúbia et al., 2011) and more accurately predicting how living representatives of various species may respond to current changes in the environment.

Extensive studies have been carried out for the reconstruction of past vegetation and climatic changes in relation to -herbivore activities

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during the Quaternary period based on both biotic and abiotic proxies in different environment all over the world especially in North America (Davis, 1987; Robinson and Burney, 2005; Gill et al., 2009), north-eastern Europe (Stivrins et al., 2019), Madagascar (Burney et al., 2003), New Zealand (Wood et al., 2011), South Africa (Ekblom and Gillson, 2010), and Australia (Rule et al., 2012). In India, extensive work has been carried out to decipher changes in palaeovegetation and palaeoclimate in relation to the seasonal monsoon in the tropical regions based on biological proxies (Singh et al., 1990; Bhattacharyya, 1989; Bhattacharya and Chanda, 1992; Chauhan and Sharma, 1996; Enzel et al., 1999; Bera and Farooqui, 2000; Sharma et al., 2004; Bhattacharyya et al., 2011a, 2011b; Dixit and Bera, 2012, 2013; Quamar and Chauhan, 2014; Trivedi et al., 2013, 2024) as well as in subtropical regions (Kotlia et al., 2000; Kar et al., 2002) and in the temperate regions (Bhattacharyya et al., 2007; Demske et al., 2009; Bali et al., 2017; Maurya et al., 2022) based on biotic and abiotic proxies. Despite the extent of previous studies very little research has been carried out on the role of palaeoherbivory and the reciprocal interaction between the impact of the herbivores on the vegetation and the impact of vegetation change on herbivore populations or diversity. Fungal spores, especially coprophilous fungal spores, from a sedimentary sequence can serve as a proxy for herbivore presence in the landscape and how it changes over time in relationship to changes in vegetation as documented by both pollen and non-pollen palynomorphs. Among the non-pollen palynomorphs, coprophilous fungal spores especially *Sporormiella*, *Sordaria*, and *Podospora* are a reliable biotic proxy to trace the past history of herbivory and grazing activities (van Geel, 1978; Davis and Shafer, 2006; van Geel et al., 2011; Van Geel et al., 2019; van Asperen et al., 2020; Lee et al., 2022) and megafaunal extinction (van Geel, 1978; Burney et al., 2003; Gill et al., 2009; Feranec et al., 2011; Wood et al., 2011; Wood and Wilmshurst, 2013). Some work has been carried out combining pollen and coprophilous fungal spores to trace vegetation dynamics in relation to pastoral activities in national parks and some archaeological sites (Graf and Chmura, 2006; Gill et al., 2012; Perrotti and van Asperen, 2019; Stahle et al., 2016; Tunno and Mensing, 2017; Loughlin et al., 2018; Birks, 2019; Stivrins et al., 2019). Various palynological studies have been carried out on surface soil and herbivore dung in relation to the existing vegetation and climate from different parts of the world to provide a baseline for comparison with the fossil record (Ebersohn and Eicker, 1992; Cugny et al., 2010; Ejarque et al., 2011; Huang et al., 2020; van Asperen et al., 2020; Wei et al., 2020, 2021; Basumatary et al., 2024).

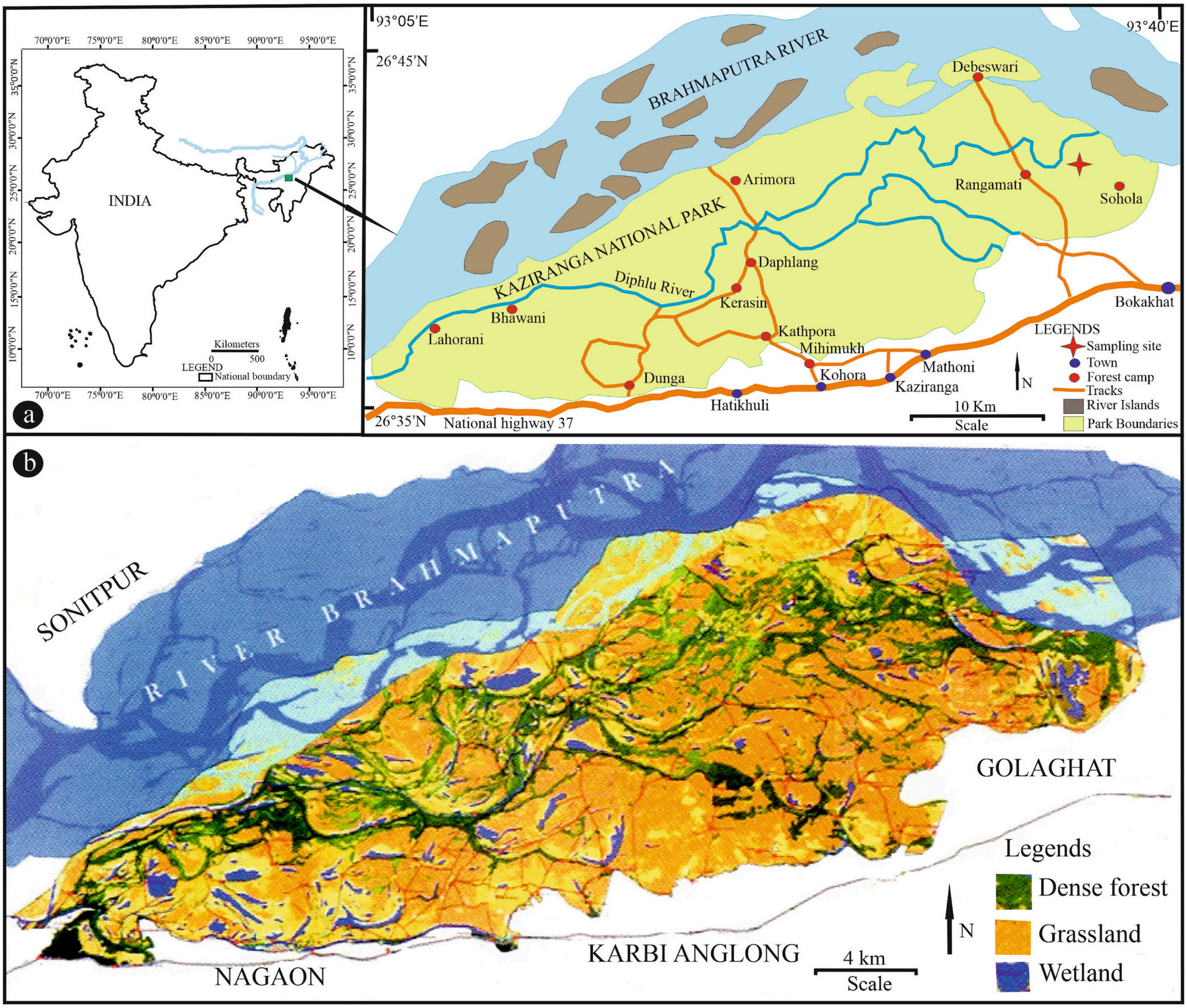

Fig. 1. a. Location map of the sampling site, b. Vegetation coverage map of the Kaziranga National Park (after Das et al., 2014).

India is considered a megadiverse country in terms of its biodiversity. While it consists only of 2.4 % of the world's land area, its biodiversity accounts for 7–8 % of the species of the world, in ten biogeographic regions. This biodiversity includes about 91,000 species of animals, 12.6 % mammals, 4.5 % birds, 45.8 % reptiles, 55.8 % amphibians, and 45,500 species of plants, of which 33 % are endemic (Vattakaven et al., 2016; Singh et al., 2022). Some limited studies have been carried out on modern wild herbivore dung from northeastern India (Basumatary et al., 2017; Basumatary and McDonald, 2017; Tripathi et al., 2019), western India (Pokharia et al., 2022) and the higher Indian Himalaya (Basumatary et al., 2019, 2021) but similar studies are lacking in many other parts of the subcontinent.

In this study, for the first time we document a palaeoecological and palaeoherbivory history of Kaziranga National Park utilizing both pollen and fungal spores from a sedimentary profile. In addition, a hypothesis is presented regarding changes in the past distribution of megaherbivores, especially one-horned rhinoceros, compared to the present distribution of these species in the other parts of the Indian subcontinent and adjoining regions.

2. Study area

Kaziranga National Park is located in northeast India along the banks of the Brahmaputra River (Fig. 1). The Park covers an area of around 430 km^2 (Basumatary et al., 2024) and is considered part of a geographical corridor for migration between the Indian subregion and the rest of Asia (Pilgrim, 1925; Chauhan, 2008). It is also an important part of the Indo-Burma biodiversity hotspot. Kaziranga National Park was declared as a reserve forest for the conservation of the Indian One-Horned Rhinoceros (*Rhinoceros unicornis*) in 1905 by Lord Curzon (the Viceroy of India at that time). In 1985, Kaziranga National Park was declared a World Heritage Site by UNESCO and is now one of the best sites to observe Indian One Horned Rhinoceros at the highest densities in their natural habitat along with the ecological interrelationship between plants and wildlife. In 2006, the role of the KNP was expanded to also serve as a tiger reserve.

3. Vegetation and wildlife

There are four different types of vegetation communities in the park; tropical evergreen forest, deciduous forest, grassland and swamp (Champion and Seth, 1968; Das et al., 2014). The evergreen forest is generally confined to the banks of the Brahmaputra River, small rivers, and streamlets within the park. The main forest elements include trees and climbers including *Cinnamomum bejolghota*, *Duabanga grandiflora*, *Mesua ferrea*, *Terminalia myriocarpa*, *Schima wallichii, Litsea monopetala*, *Calamus erectus*, *Piper longum*, and *Thunbergia grandiflora* which make this forest impenetrable. The deciduous forest occurs as isolated patches within the grasslands and along the margins of the evergreen forest. The major tree taxa are *Bombax ceiba, Dillenia indica, Albizia procera*, *Emblica officinalis*, *Careya arborea*, *Lagerstroemia parviflora, Sterculia villosa*, and *Terminalia bellerica*.

The grassland areas are scattered within KNP and the dominant tall grasses are mainly *Erianthus ravennae*, *Phragmites karka, Arundo donax*, and *Saccharum procerum*. The grasslands include some trees and shrubs such as *Bombax ceiba*, *Careya arborea*, *Dillenia indica, Butea monosperma*, and *Albizia lebbeck*.

Open land areas occur especially near the periphery of the wetland habitats. Tree taxa are almost absent, and the primary vegetation consists of shrubs such as *Melastoma malabathricum*, *Clerodendron viscosum*, and *Osbeskia nepalensis*. The ground of the open land area is covered with short grasses along with members of the Cyperaceae, Acanthaceae, Amaranthaceae, Solanaceae, Convolvulaceae, and Euphorbiaceae.

Swamp habitat is generally present in low lying areas and is occupied by water the throughout the year. The major marshy and aquatic taxa include *Polygonum orientale*, *Cyperus rotundus*, *Eichhornia crassipes*, *Trapa bispinosa*, *Nymphaea nouchali*, *Ludwigia adscendens*, *Nymphoides indica*, *Potamogeton crispus*, *Costus speciosus*, and *Alpinia nigra* which especially grow at the periphery of the swamp area.

Kaziranga National Park is primarily famous for the presence of *Rhinoceros unicornis* (Indian One Horned Rhinoceros), which is an iconic and globally threatened megaherbivore (Pant et al., 2020). Besides rhinoceros, there are 52 species of mammals including other large herbivores such as *Bubalus bubalis* (Asiatic Wild Buffalo), *Elephas maximus* (Asian Elephant), *Cervus duvauceli* (Swamp Deer), and *Axis porcinus* (Hog Deer). The Park is also very rich in other animals including 490 species of birds, 43 species of reptiles (Choudhury, 2013). Birds commonly seen in the park include *Anser erythropus* (Lesser White fronted Goose), *Aythya nyroca* (Ferruginous Pochard), *Houbaropsis bengalensis* (Bengal Florican), and *Pelecanus philippensis* (Spot billed Pelican) (Fig. 2 a-d).

4. Climate and soil

The climate of the region is controlled by the southwest and northeast monsoons and is hot and humid during the summer, and cold and dry during winter. The maximum temperature ranges from a minimum of 4 °C during winter up to 37 °C in summer. The relative humidity is very high and ranges from 75 % to 86 %. The annual rainfall ranges from 1800 mm to 2600 mm, so annual flooding is very common in the park. The soil composition varies from site to site and includes sandy loam soil in forests, sandy soil in grassland, and clayey soil in the swamp and water bodies (Das et al., 2014).

5. Material and methods

5.1. Field work

After extensive field observation of vegetation composition and wildlife activities, the first author (SKB), selected the Sohola swamp (26^{0}41′19.8“ N, 93^{0}33’58.3” E, 70 m asl) as an ideal site to study of the palaeovegetation and palaeoherbivory (Fig. 3 a-c) in Kaziranga National Park. A 110 cm deep sedimentary profile was trenched at the northwestern side of the Sohola swamp and soil samples were collected at 5 cm intervals for palynological analysis and radiocarbon dating.

5.2. Chronology of the sedimentary section

The radiocarbon dating of five carbon rich sediment samples was carried out at the radiocarbon laboratory of the Birbal Sahni Institute of Palaeosciences of India. Radiocarbon dates for the sedimentary profile were 3100 ± 30 yr BP at 105 cm; 1750 ± 50 yr BP at 80 cm; 1250 ± 40 yr BP at 50 cm; 680 ± 30 yr BP at 35 cm, and 169 ± 35 yr BP at 20 cm. The radiocarbon dates were converted into Calendric age/date (cal. BP i.e., 3290 cal. BP, 1700 cal. BP, 1130 cal. BP, 640 cal. BP and 250 cal. BP respectively) (Table 1). The entire section is bracketed to approximate 3290 cal. yr BP to the present, and all five-radiocarbon ages have been rounded to the nearest 5 or 10 years for the better representation in the text. The Bayesian age-depth model for the sedimentary profile of the KNP was constructed using the 'Bacon' package in R software (Blaauw and Christen, 2011), and the calibration curve by IntCal 20 (Reimer et al., 2020) (Fig. S1). In the sedimentary profile, the estimated sedimentation rate (SR) for the first phase (bottom of the sequence) between 3290 cal. Years and 1700 cal. Years is 0.015 cm/y. For the period between 1700 cal. Years and 1130 cal. Years, the estimated SR rises to 0.052 cm/y. Between 1130 and 640 cal. Years, the estimated SR declined to 0.030 cm/y. The SR relatively increases to 0.038 cm/y during the younger interval between 640 cal. Years to 250 cal. Years.

5.3. Sedimentary Core description

The lower part (110 cm to 85 cm) of the sedimentary profile consists of brownish clay with silt. Between 85 and 50 cm, the sediment consists

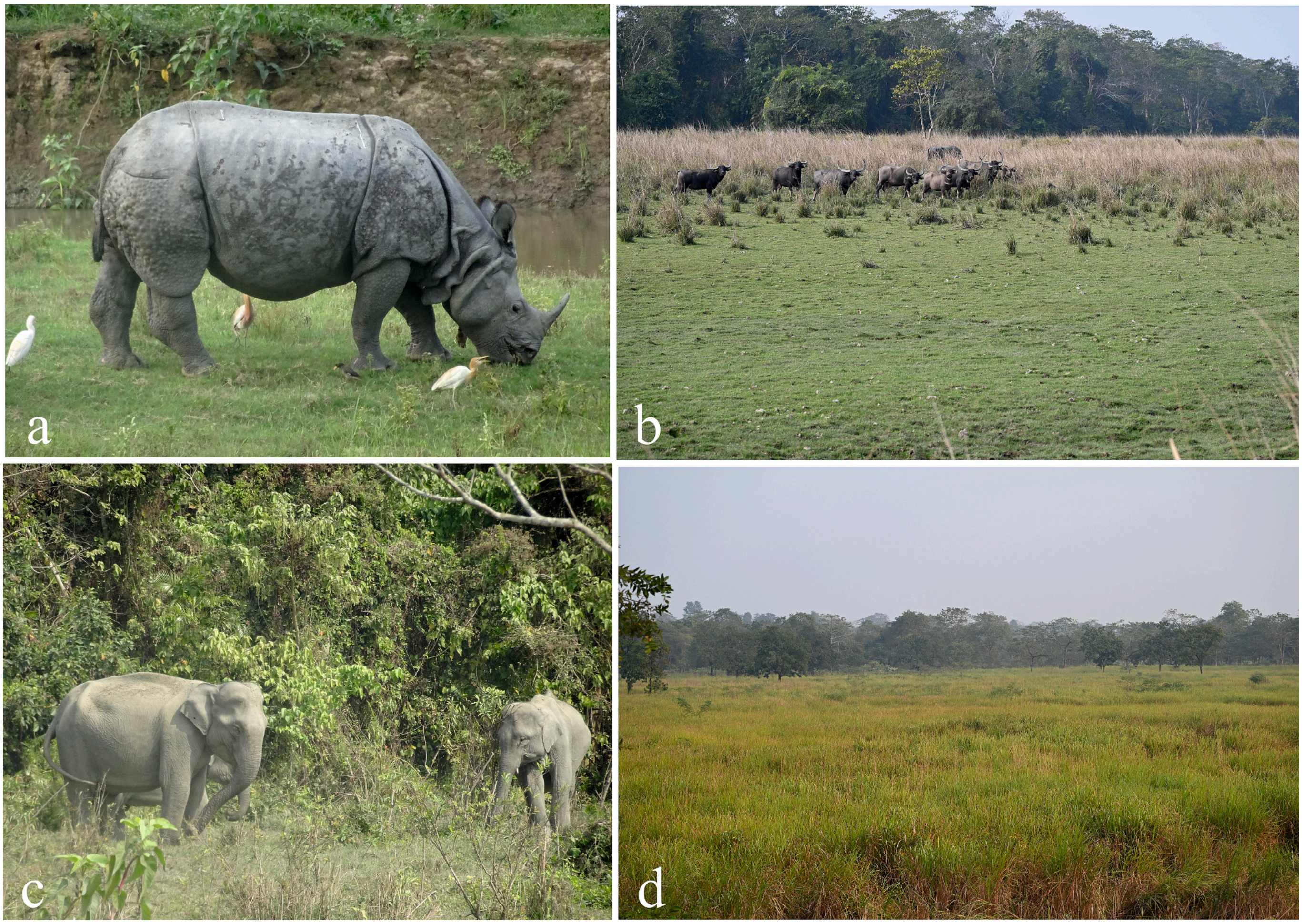

Fig. 2. a. A view of Indian One Rhinoceros in the natural habitat in KNP, b. View of Asian water Buffalo adjacent to the forestland and open land vegetation, c. Asian Elephant adjacent to the deciduous forest in natural habitat in the KNP, d. A view of grassland within KNP, photographs taken by SKB (first author).

of blackish clay with silt and rich organic matter and the top 50 cm consists of black clay with silt along with rootlets. The five radiocarbon dates were collected from the soil samples at the intervals of 105 cm, 80 cm, 45 cm, 30 cm, and 20 cm (Table 1).

5.4. *Laboratory work*

The collected soil samples were processed employing the standard acetolysis method (Erdtman, 1953). The samples were treated with 10 % aqueous KOH solution to deflocculate the pollen and spores from the sediments followed by 40 % hydrofluoric acid (HF) treatment to dissolve silica content. After that the samples were again treated with glacial acetic acid (GAA) and centrifuged and washed 2–3 times with distilled water. Thereafter, the conventional procedure of acetolysis was followed using acetolysis mixture (9:1 acetic anhydrite and concentrated H_2SO_4). After that, the samples were centrifuged twice with glacial acetic acid (GAA) and washed two times with distilled water. The samples were sieved using a 500 µm mesh and then finally the material was kept in 50 % glycerine solution with a few drops of phenol to protect microbial decomposition. Totals of 320–423 pollen grains per sample were counted to produce the pollen diagram. The frequency of the recovered pollen has been calculated in term of total pollen count. The pollen grains are categorized as arboreal (tree and shrub), non-arboreal (terrestrial, marshy and aquatics) taxa and extra-regional (conifers and other broadleaf) taxa. Plant taxa which are not naturally growing in and around the study region are considered as extra-regional taxa. Similarly, 265–270 fungal spores were counted in each sample to produce the fungal spore diagram. The recovered fungal spores were categorized as coprophilous and non-coprophilous fungi. Pollen and fungal spore zones were recognized based on the presence and abundance of the major arboreal and non-arboreal pollen taxa and the abundance of the major coprophilous and non-coprophilous fungal spore, respectively, and stratigraphically constrained hierarchical cluster analysis (CONISS). The prefix KZ is used after the name of study site from where the sedimentary profile has been collected and the zones are numbered from the bottom upwards. Pollen grains were identified to the most precise taxonomic level possible using pollen keys (Basumatary et al., 2017, 2024) and reference slides make by SKB and from the sporothek in Birbal Sahni Institute of Palaeosciences (BSIP) of India. For the identification of fungal spores, we consulted the published literature and photographs (Cugny et al., 2010; van Geel et al., 2011; Van Geel and Aptroot, 2006; Basumatary and McDonald, 2017; Basumatary et al., 2024). The pollen and fungal spore observation and microphotographs were conducted using an Olympus BX-61 microscope with Olympus DP-25 software supported digital camera under 40× magnification (Fig. S2, S3). The pollen and fungal spore diagram was produced using TILIA and modified in Coral Draw 17.

5.5. *Principal component analysis (PCA)*

The quantified frequencies of pollen and non-pollen palynomorphs from twenty-two sediment samples, obtained from a 110 cm deep sediment core in Kaziranga National Park, were statistically analyzed using Principal Component Analysis (PCA) in Canoco version 5

Fig. 3. a. A view of Sohola swamp within KNP, b. View of field observation by first author (SKB) in Sohola swamp. c. A view of sedimentary profile from Sohola swamp within KNP, Photographs taken by SKB (first author).

Table 1
Relationship of C-14 dates and their depth within the sedimentary sequence from the Sohola swamp of Kaziranga National Park.

Depth (cm)	Material	Sample and Lab ID	Raw date years	Minimum-maximum ranges	Cal BP Calibrated age (cal yr BP)
20	Soil	KZ 5; BS-5063	169 ± 35	548–692	250
35	Soil	KZ 4; BS-5062	680 ± 30	984–1266	640
50	Soil	KZ 3; BS-5060	1250 ± 40	1554–2006	1130
80	Soil	KZ 2; BS-5059	1750 ± 50	3116–3398	1700
105	Soil	KZ 1; BS-5061	3100 ± 30	–	3290

(Smilauer and Leps, 2014). Response data are compositional and have a gradient 0.8SD and 0.5 SD units for pollen and fungal spore frequencies, so linear method like PCA is recommended. The statistical significance of the data was assessed at a p-value ≤ 0.05, ensuring the reliability of the results. The PCA outputs were subsequently imported into CorelDRAW-17 for minor refinements of data labels and figure aesthetics, facilitating clearer visualization and interpretation.

6. Results

6.1. Pollen zones

Pollen zone –KZ-I (110-80 cm): *Mesua-Cinnamomum-Schima*-Arecaceae-*Litsea-Nymphaea*-Grasses-Cyperaceae assemblage: This pollen zone covers the time span of 3290 to 1700 yrs. BP (1590 years). It is characterized by the dominance of arboreal taxa with an average value of 51.4 % over non-arboreal taxa (44.6 %) followed by extra-regional taxa at 4.0 %. Among the arboreal taxa the dominant evergreen elements such as *Mesua*, *Duabanga*, *Schima*, *Cinnamomum*, and Arecaceae are recorded at 2.1 %–4.7 %. The deciduous taxa *Bombax*, *Albizia*, *Dillenia*, and *Lagerstroemia* are also consistently represented with ranges of 0.7 %–2.4 %. The extra-regional taxa in the pollen assemblage include *Pinus*, *Abies*, *Betula*, and *Rhododendron* which are present with ranges of 0.3 %–1.4 %. Among non-arboreal taxa, the grasses are dominant with an average value of 9.0 %. The other associated herbaceous taxa such as Asteroideae, Convolvulaceae, *Justicia*, Euphorbiaceae, and Piperaceae are regularly recorded with ranges of 0.7 %–3.1 %. Among marshy and aquatic taxa, the Cyperaceae, Onagraceae, *Nymphaea*, and *Potamogeton* are represented between 0.3 %–5.2 % (Fig. 4).

Pollen zone –KZ-II (80-45 cm): *Mesua-Schima-Duabanga-Litsea-Nymphoides*-Grasses-Cyperaceae-Onagraceae assemblage: This pollen zone covering the time span of 1700 to 640 yr BP (1060 years) is characterized by an increase in non-arboreal taxa that average 52.9 % over arboreal taxa (42.0 %) followed by extra-regional taxa with the value of 5.1 %. Among the arboreal taxa the evergreen elements such as *Mesua*, *Schima*, *Cinnamomum*, *Litsea*, and Arecaceae significantly decrease with values of 2.1 %–4.7 %. The deciduous taxa *Bombax*, *Albizia*, *Dillenia*, and *Lagerstroemia* increase with ranges of 0.7 %–2.4 %. The extra-regional taxa *Pinus*, *Abies*, *Betula*, and *Rhododendron* are slightly more common with ranges of 0.3 %–1.4 %. Among non-arboreal taxa, the grasses are dominant with an average value of 9.0 %. The other associated herbaceous taxa include Asteroideae, Convolvulaceae, Euphorbiaceae, *Justicia*, and Piperaceae with ranges of 0.7 %–3.1 %. Among marshy and aquatic taxa Cyperaceae, *Polygonum*, Onagraceae, *Nymphaea*, and *Potamogeton* are represented between 0.3 %–5.2 % (Fig. 4).

Pollen zone –KZ-III (45-0 cm): *Bombax-Dillenia-Careya-Terminalia-Albizia-Syzygium-Nymphaea*-Grasses-Onagraceae assemblage: This pollen zone which covers the time span of 640 yrs. BP to the present is characterized by the increasing dominance of non-arboreal taxa with an average value of 59.3 % over arboreal taxa (35.8 %) followed by extra-regional taxa with the value of 4.9 %. Among the arboreal taxa, the evergreen elements chiefly *Mesua*, *Schima*, *Syzygium*, *Cinnamomum*, Arecaceae, and *Litsea* continue to decrease, with values of 2.1 %–4.7 %. The deciduous taxa *Bombax*, *Emblica*, *Albizia*, *Dillenia*, *Lagerstroemia*, and *Melastoma* in the pollen assemblages increase somewhat with ranges of 0.7 %–2.4 %. The extra-regional taxa *Pinus*, *Abies*, *Betula*, and *Rhododendron* are fairly constant with ranges of 0.3 %–1.4 %. Among non-arboreal taxa, the grasses are dominant with an average value of 9.0 %. The other associated herbaceous taxa such as Asteroideae, Convolvulaceae, *Justicia*, and Piperaceae are regularly recorded at the ranges of 0.7 %–3.1 % in the pollen assemblages. Marshy and aquatic taxa such as the Cyperaceae, Onagraceae, *Nymphaea*, and *Potamogeton* have increased with values between 0.3 %–5.2 % (Fig. 4).

6.2. Fungal spore zones

Fungal zone –KZ-I (110–80 cm): *Tetrploa*-Microthyriaceae-*Meliola-Bipolaris-Sporormiella-Saccobolus* assemblage: This zone covering the time span of 3290 to 1700 yrs. BP is characterized by the dominance of non-coprophilous fungal spores at an average value of 71.9 % over coprophilous fungal spore (28.1 %). Among non-coprophilous fungal spores, Microtyriaceae, *Meliola*, and *Tetraploa* have ranges of 2.4 %–11.2 %. The coprophilous fungal taxon *Sporormiella* is recorded at values of 6.0 % to 9.1 %. The other fungal spores such as *Saccobolus*,

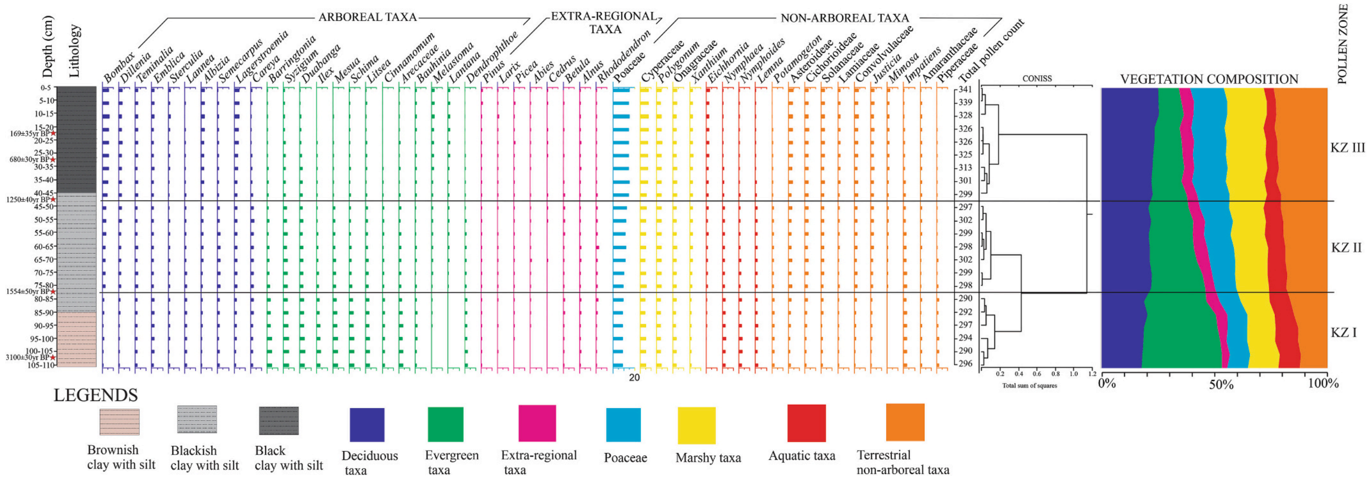

Fig. 4. Pollen diagram of a sedimentary profile in the Sohola swamp from the KNP.

Ascodesmis, and *Podospora* are also consistently present with ranges of 0.4 %–5.5 % (Fig. 5).

Fungal zone –KZ-II (80–45 cm): *Tetrploa*-Microthyriaceae-*Glomus*-*Helminthosporium*-*Sporormiella*-*Saccobolus* assemblage: This zone covering the time span of 1700 to 640 yrs. BP is characterized by a reduced dominance of non-coprophilous fungal spores with an average value of 50.6 % over coprophilous fungal spore (49.4 %). Among non-coprophilous fungal spores, *Tetraploa* is still the most common taxa with ranges of 5.5–9.0 %. Microtyriaceae and *Meliola* decrease to values of 2.7–6.6 %, whilst *Helminthosporium* maintains similar values. *Glomus* increases to values of 5.7–6.5 %. The coprophilous fungal spore *Sporormiella* increases significantly to values of 15.1–17.7 %. The other coprophilous fungal spores, *Saccobolus*, *Ascodesmis*, and *Podospora*, increase more slowly, with ranges of 0.8 % to 10.2 % (Fig. 5).

Fungal zone –KZ-III (45-0 cm): *Glomus*-Microthyriaceae-*Meliola*-*Helminthosporium*-*Sporormiella*-*Ascodesmis*-*Saccobolus* assemblage: This zone covering the time span of 640 yr BP to the present is characterized by the dominance of coprophilous fungal spores at the average value of 67.0 % over non-coprophilous fungal spores (33.0 %). Among coprophilous fungal spores *Sporormiella* further increases to values of 18.9 %–20.9 %. The other coprophilous fungal spores *Saccobolus*, *Ascodesmis*, *Sodaria*, and *Podospora* also increase somewhat with ranges of 1.0 %–15.6 %. Among the non-coprophilous fungal spores *Glomus* continues to increase to values of 6.3–7.2 %. *Helmithosporium* also increases somewhat, with values of 4.5–5.5 %. Microtyriaceae, *Meliola*, and *Tetraploa* all decrease, with ranges of 0.7 %–5.6 % (Fig. 5).

6.3. Principal component analysis (PCA) for pollen and fungal spore frequency of the sedimentary profile

The PCA score plot revealed Eigenvalues of 0.9262 (Axis 1) and 0.0344 (Axis 2), with the cumulative explained variation being 92.62 % for Axis 1 and 96.06 % for Axis 2. Overall, 66.09 % of the total variance could be explained by the distribution of pollen taxa across the sediment samples of the core. Examination of the PCA score plot indicates that the pollen taxa contributing to the similarity among sediment samples1–9 (0–45 cm) include *Terminalia*, *Emblica*, *Lagerstroemia*, *Syzygium*, *Bombax*, *Dillenia*, *Albizia*, *Melastoma*, Amaranthaceae, Poaceae, Asteroideae, Cichorioideae, Solanaceae, Convolvulaceae, and *Polygonum*, which cluster within the left quadrant. In contrast, the taxa primarily associated with sediment samples 10–16 (45–80 cm) are *Rhododendron* and *Betula*. The lower section, represented by sediment samples 17–22 (80–110 cm), is characterized by taxa such as Arecaceae, *Schima*, *Mesua*, *Litsea*, *Duabanga*, *Impatiens*, and *Cinnamomum*, which fall within the same quadrant (Fig. S4).

Similarly, the PCA score plot for fungal spore had illustrated Eigenvalues of 0.8771 (Axis 1) and 0.0532 (Axis 2), with a cumulative explained variation of 87.71 % for Axis 1 and 93.03 % for Axis 2. The PCA 1 and PCA 2 explains 93 % of the total variation while all four eigen axes cover 96 % of the variance. The analysis shows that the fungal spores driving the similarity between sediment samples 1–9(0–45 cm) are *Sporormiella*, *Saccobolus*, *Ascodesmis*, *Sordaria, Podospora*, *Arnium*, *Glomus*, and *Helminthosporium*, clustering within the right quadrant. The fungal spore, *Gelasinospora* occurs exclusively and consistently in sediment samples 10–16 (45–80 cm). Meanwhile, the deeper samples 17–22 (80–110 cm) share common NPP taxa such as *Tetraploa*, *Bipolaris*, *Alternaria*, *Helicoon*, *Meliola*, *Cookeina*, *Dictyospora*, Microthyriaceae, *Valsaria*, and *Pleospora*, which group in close proximity on the plot (Fig. S5).

7. Discussion

The studied profile indicated three phases of palaeoecological and palaeoherbivore activities in KNP based on the pollen and coprophilous fungal spores recovered from the sedimentary profile.

7.1. First phase of palaeovegetation and palaeoherbivory history

From 3290 to 1700 yrs. BP, a period of 1590 years, the arboreal pollen taxa dominated the pollen record, and their composition indicates that there was a tropical mixed dense forest primarily composed of *Mesua*, *Cinnamomum*, *Bombax*, *Lagerstroemia*, *Albizia*, and *Dillenia* under warm and humid climatic conditions in the KNP. The consistent presence of *Duabanga*, *Barringtonia*, and *Syzygium* in the pollen assemblages is observed and indicative of evergreen forest with riparian habitat in and around the study area. The recovery of *Mesua*, *Duabanga*,

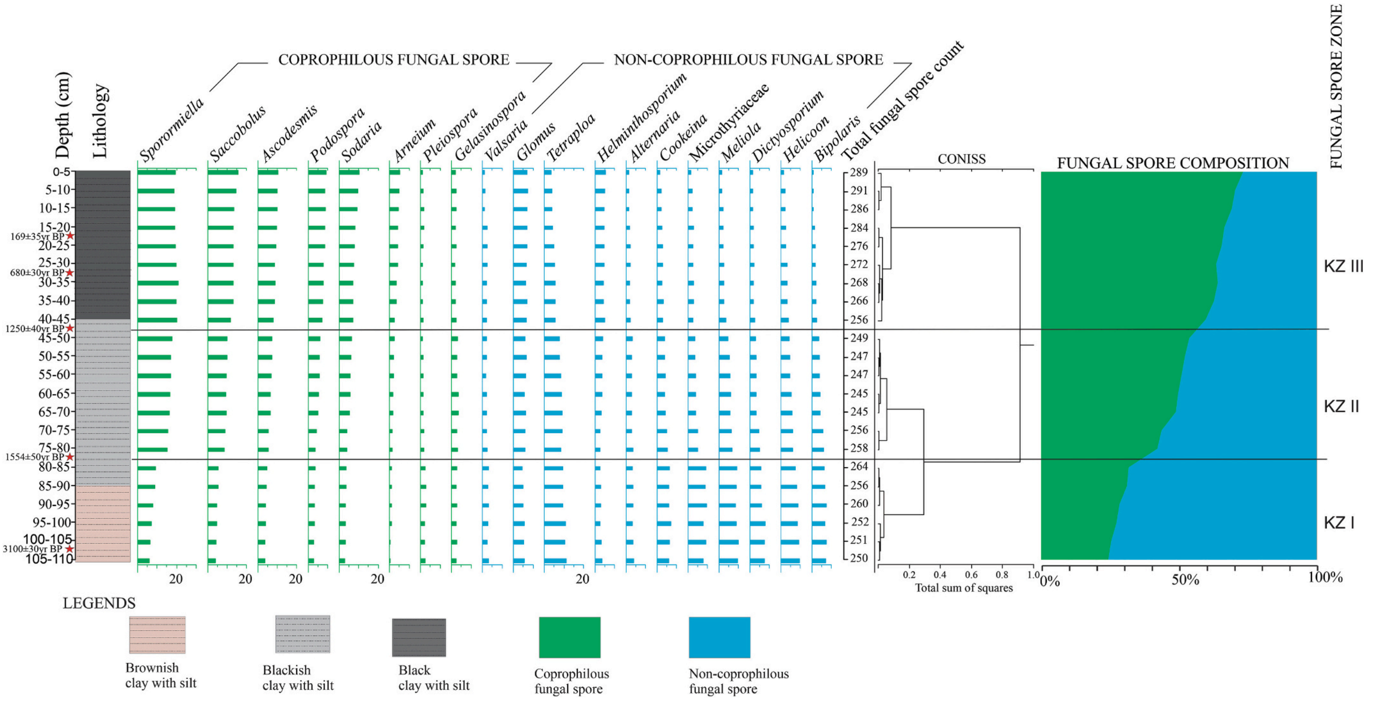

Fig. 5. Fungal spore diagram of a sedimentary profile in the Sohola swamp from the KNP.

and *Syzygium* up to 4.9 % in the evergreen forest samples is strongly indicative of the high rainfall activities in the region (Basumatary et al., 2024) as well as the presence of *Syzygium* pollen in the sediments, a taxa characteristic of high rainfall (>2500 mm/y; Barboni and Bonnefille, 2001; Singh et al., 1990). Clumping of the *Duabanga* pollen in the pollen assemblages was observed which is suggestive of a local origin within in the park as the recovery of pollen clumping in the sediment is characteristic of local sources and a shorter dispersal distance than solitary pollen and spores (Faegri and Van Der Pijl, 1966; Martin et al., 2009). The presence of Poaceae pollen (7.9 %) shows that some grassland was also present in and around the study area. The other associated annual and perennial herbs including Asteroideae, Euphorbiaceae, Piperaceae, Convolvulaceae, and *Justicia* are suggestive of open land habitat in and around the study areas. The abundance of the aquatic taxa *Nymphaea*, *Potamogeton*, and *Trapa* in the pollen assemblage is indicative of the presence of a wider and deeper perennially waterlogged condition in the Sohola swamp and adjacent areas. The low values of marshy taxa such as, Cyperaceae, *Polygonum*, and Onagraceae is marked and is indicative of the low marshy land area in and around of the Sohola swamp. The evergreen and riparian taxa such as *Mesua*, *Cinnamomum*, *Syzygium*, *Barringtonia*, and *Duabanga* along with aquatic taxa *Nymphaea*, *Potamogeton*, and *Nymphoides* in the pollen assemblages are indicative of the high monsoonal activity during this period in the region. The evergreen taxa, especially *Mesua*, *Schima*, *Duabanga*, and *Litsea*, along with *Dendrophthoe* are high rainfall indicator taxa (Singh et al., 1990; Barboni and Bonnefille, 2001; Basumatary et al., 2024). The presence of *Rhododendron* pollen in the pollen assemblage is marked and strongly indicative of the annual flood activity in the region as *Rhododendron* is considered an indicator taxa of seasonal flooding (Basumatary et al., 2019). *Rhododendron* is totally entemophilous (Stephenson et al., 2007) and naturally grows only in the higher Himalaya which is at least 500 kms from the study areas. The extra-regional taxa, especially *Larix* and *Abies*, are considered indicative of the seasonal presence of migratory birds from Siberia and Europe.

Among the fungal spores, both coprophilous and non-coprophilous fungal spores are observed. The coprophilous fungal spores, especially *Sporormiella*, *Ascodesmis*, *Saccobolus*, and *Podospora* are recorded upto 9.1 % which is indicative of the presence of herbivores in small numbers in the KNP. A similar *Sporormiella-Saccobolus-Ascodesmis-Sodaria* assemblage was recorded from a modern rhinoceros midden dung and surface soil samples from the KNP (Basumatary and McDonald, 2017; Basumatary et al., 2024). The composition of the coprophilous fungal spore assemblages may therefore indicate the presence of rhinoceros and other large mammals at this time. However, non-coprophilous fungal spores such as *Meliola*, *Tetraploa*, *Glomus*, and Microthyriaceae dominate the fungal spore assemblage which is indicative of the warm and humid depositional environment in the region. The abundance of Microthyriaceae, *Glomus*, and *Meliola* is considered indicative of the presence of dense forest vegetation (Johnson and Sutton, 2000; Medeanic and Silva, 2010; Musotto et al., 2017; Loughlin et al., 2018) which could be deposited in the sedimentary profile through in wash rain water from the surrounding forest vegetation. It is observed that, the high value of evergreen pollen taxa (4.7 %) and non-coprophilous fungal spore up to 11.2 % are indicative of the dense forest vegetation. Similarly, these fungal spore taxa also dominated in the fungal spore assemblages from soil samples in the evergreen and deciduous forest in the Kaziranga National Park (Basumatary et al., 2024). The dominance of this dense forest vegetation may also explain the low abundance of herbivores (Fig. 9a).

7.2. Second phase of palaeovegetation and palaeoherbivory history

During the interval 1700–640 yrs. BP (1060 years), the pollen diversity dominated by *Mesua*, *Schima*, *Duabanga*, *Syzygium*, *Bombax*, *Lagerstroemia*, *Litsea*, and *Dillenia* in the assemblage is similar to the previous phase, but with comparatively lower values for arboreal taxa (42.0 %), especially the evergreen taxa *Mesua*, *Duabanga*, *Schima*, *Cinnamomum*, *Ilex*, and Arecaceae which indicates the relative decrease in evergreen forest in the KNP. The decrease in values of evergreen taxa is indicative of the deterioration of the natural forest vegetation under warm and relatively less humid conditions. The relative increase in values of deciduous open land arboreal taxa, chiefly *Bombax*, *Dillenia*, *Albizia*, *Lagerstroemia*, and *Melastoma* is highly significant as these taxa are preferred dietary plants for many herbivores (Basumatary et al., 2024). The presence of *Melastoma* and *Clerodendron* along with *Mimosa* is suggestive of forest deterioration in the KNP. The recovery of the *Mimosa* pollen is marked, which is an exotic species and indicative of the initial invasion in the KNP. The relative increase in values of Poaceae along with other non-arboreal pollen taxa, especially Asteroideae, Convolvulaceae, and *Justicia* in the pollen assemblage compared to the preceding phase is indicative of the expansion of the grassland and open land vegetation in and around the study area. The relative decrease in values of core aquatic taxa, *Nymphaea* and *Potamogeton* and increased values of marshy taxa chiefly *Polygonum*, Onagraceae, and Cyperaceae are indicative of the wider extent of marshy land in the region, and the shallowing of deeper water bodies. The slightly increased values of the extra-regional taxa, *Larix* and *Abies* are indicative of an increase of the migratory birds and wind activity in the region. The continuous presence of *Rhododendron* pollen in the pollen assemblages is indicative of the consistent occurrence of regular flood activity in the region.

Among the fungal spores, the relative increase in the values of coprophilous fungal spores, especially *Sporormiella*, *Ascodesmis*, *Saccobolus*, and *Podospora,* is suggestive of an increase in the wildlife population in the KNP over that of the preceding period. Non-coprophilous fungal spores, especially *Meliola*, *Helminthosporium*, Microthyriaceae, and *Tetraploa,* are also consistently present but at relative lower values compared to the previous phase. This is indicative of the relative decrease in forest density in and around the study area. The increased value of *Helminthosporium* in the assemblage is indicative of the expansion of the grassland in the KNP as it is a pathogen of grasses (Fig. 6b). In a study of soil samples from the KNP, this fungal spore type was particularly abundant in grassland (Basumatary et al., 2024). In comparison, the deciduous elements, mainly *Bombax*, *Lagerstroemia*, *Albizia*, and *Dillenia* and coprophilous fungal spores *Sporormiella*, *Saccobolus*, and *Ascodesmis*, increase significantly which is directly indicative of the increased herbivore activity in the KNP.

7.3. Third phase of palaeovegetation and palaeoherbivory history

During the interval from 640 cal yrs. BP-present, the frequency of arboreal taxa is even lower than in the second phase. The continuously decreasing value of arboreal evergreen taxa, chiefly *Mesua*, *Ilex*, *Schima*, *Cinnamomum*, Arecaceae, and *Litsea,* is suggestive of the contraction of the evergreen forest vegetation in the KNP. However, the increased values of deciduous arboreal taxa *Bombax*, *Dillenia*, *Emblica*, *Albizia*, and *Melastoma* indicates the conversion of forest to open land. *Bombax ceiba* is a fire-resistant tree (Troth, 1976) and a major deciduous taxon in the national park. Deterioration of the forest is also indicated by the decreased values of core forest taxa and increased values of pollen of secondary vegetation especially *Melastoma*, *Clerodendron*, and *Lantana*. Furthermore, the increased abundance of *Eichhornia* and *Xanthium* pollen strongly indicative of the lower water level and reduction in waterlogged condition in the KNP. Accordingly, in this phase, the expansion of grassland and openland is indicated by the significant increase in values of Poaceae (cereal pollen <45 μm) and other non-arboreal taxa. Herbivore activities increased significantly as indicated by increased values of coprophilous fungal spore especially *Sporormiella*, *Ascodesmis*, *Saccobolus*, and *Sodaria*. The high impact of herbivores activities was recorded in both the openland and swamp areas of the KNP (Basumatary et al., 2024). A continuous increase in *Mimosa* is indicative of the invasion of this exotic plant and deterioration of the local vegetation in the region. The abundance of *Dillenia* pollen is significant as it is

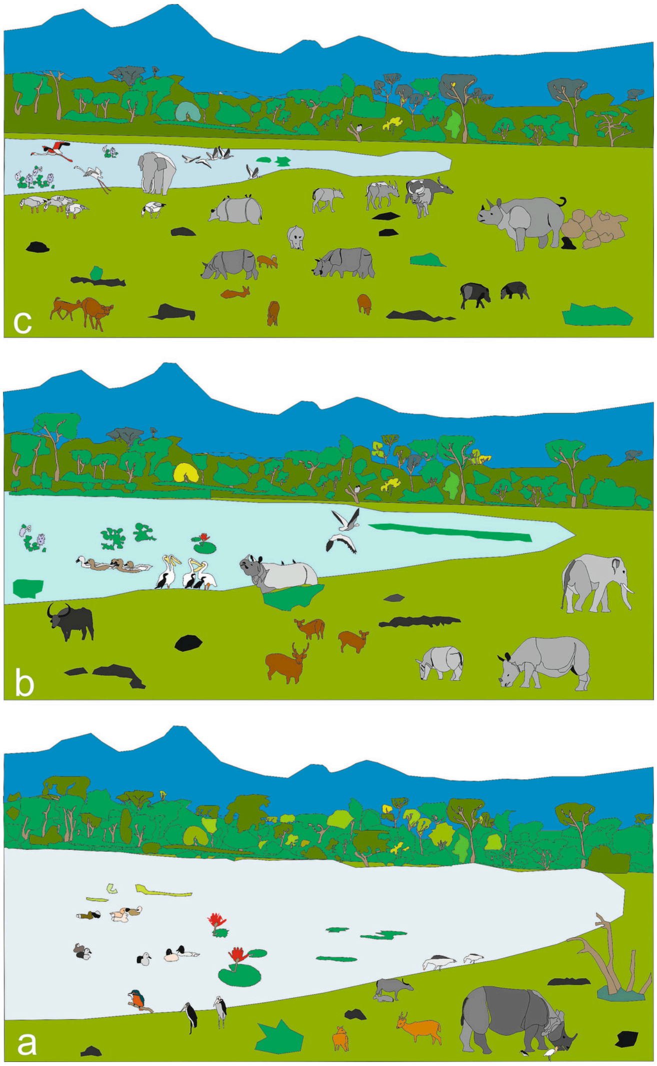

Fig. 6. A model (schematic view) of palaeovegetation and palaeoherbivory activities in the KNP, a. Dense forest with wider and swamp condition with low wildlife activities, b. Relatively less dense and less deep water with increased wildlife activities, c. Comparatively more less dense forest and less deep swamp with more increased wildlife activities within KNP.

one of the primary dietary plants favoured by elephants.

The abundance of Poaceae pollen is indicative of the expansion of grassland in the region. Besides Poaceae, the increased values of other non-arboreal terrestrial pollen taxa such as Asteroideae, Convolvulaceae, *Justicia*, *Mimosa*, Solanaceae, and Amaranthaceae are strongly indicative of the expansion of open land areas in and around the study area. The increased values of Asteroideae and Cichorioideae is indicative of heavily grazed open area (Kar et al., 2002; Ejarque et al., 2011) as can be observed in our pollen assemblages. The significantly increased values of coprophilous fungal spores especially *Sporormiella*, *Ascodesmis*, and *Saccobolus* in the assemblages during this period is strongly suggestive of the significant increase in herbivore activity in the KNP. In addition, the increased value of *Glomus* is marked during this period and the presence of this taxa is directly linked with soil erosion in and around the area (van Geel et al., 1989). So, the abundance of *Glomus* is directly indicative of the expansion of the openland with high grazing activities within the national park due to uprooting of the dietary plant and ultimately transported by runoff to the swamp sediment. Similarly, the increased value of *Helminthosporium* is marked at the value of 4.9 %, compared to the preceding period and strongly suggestive of the expansion of the grassland in the KNP as this fungus is one of the major grass pathogenic species and also has been recorded present in high abundance in the rhinoceros midden dung analysis (Basumatary and McDonald, 2017). In contrast the values of aquatic taxa such as *Nymphaea*, *Potamogeton*, and *Lemna* are continuously decreasing and so is indicative of the expansion of marshyland and relatively less humid condition in the KNP. The increased values of the extra-regional taxa *Picea* and *Larix* are suggestive of an increased presence of migratory birds coming from Siberian and Mongolian region via crossing the Himalayas (Barua and Sharma, 1999; Basumatary et al., 2024). Pollen that accumulates on the bird's feathers and other body parts during the flight through the pollen laden environment are subsequently dislodged during grooming while in Kaziranga National Park.

Among the fungal spores, the increased values of coprophilous fungal spores, especially *Sporormiella*, *Ascodesmis*, *Saccobolus*, and *Podospora* are suggestive of the significantly increased herbivore activities compared to the second phase. The clumping of coprophilous fungal spores especially *Sporormiella*, *Saccobolus*, and *Ascodesmis* in the assemblages was recorded and indicative of the high herbivore activity in the KNP as this clumping was observed in the rhinoceros midden dung (Basumatary and McDonald, 2017). *Sporormiella* spores are also commonly associated with the droppings of herbivorous birds (Wood et al., 2011) as well as large herbivores, which suggests increasing bird activities in the KNP. Large animals play an important role for maintaining biodiversity and ecosystem complexity (Estes et al., 2011; Galetti et al., 2018; Enquist et al., 2020). With the decreasing trend in the forest vegetation and expansion of grassland and open land, the herbivore populations seem to have significantly increased (Fig. 6c). Elephants sometimes damage tender leaves of *Shorea robusta*, will consume fruits of *Dillenia pentagyna* and *Dillenia indica,* tender bamboos and natural *Musa* spp. Rodents, monkeys, and pigs can cause damage to plants by uprooting the tender seedling, tubers of *Dioscorea pentaphylla* and *Dioscorea bulbifera* or damaging the roots. The correlations of the decline of forest habitat with the increase in herbivore populations suggests this is one of the main causes for the forest deterioration in this national park. Secondarily, the development of urbanization, road construction and continuous forest deterioration by human activity in other parts of the state and the hilly terrain in the adjoining state has a negative impact on wildlife habitat, resulting in higher than normal densities of wildlife and the greater impact on the vegetation in the current KNP.

7.4. KNP and comparative palaeoclimate records in the western and northern region of the Indian sub-continent

We compare the recorded of KNP based on our study with other palaeoclimate records from the western and northern region of the Indian subcontinent to trace the vegetation dynamics and climate variability in relation to past rhinoceros habitat (Fig. 7). In the Wadhwana of Gujarat during 6795–5565 yrs. BP, the climate was warm and humid followed by a relatively less humid condition from 5560 to 4255 yrs. BP, followed by a weak monsoon between 3238 and 2709 yrs. BP and a climate similar to the present day from 2709 yrs. BP onwards (Prasad et al., 2014). In the Banni of Gujarat region, a warm and moist climatic condition is recorded from 4600 to 2500 yrs. BP, with a high abundance of arboreal taxa especially *Syzygium* in response to the high rainfall. From 2500 yrs. BP onwards the vegetation was changing in response to increased aridity as indicated by the replacement of the arid adapted arboreal taxa, *Acacia*, *Prosopis*, and *Ephedra* in relation to the weaken monsoonal activities under semiarid to arid climatic condition at present (Pillai et al., 2018). Further, in the Karela lake of Ganga plain, during 4800–2000 yrs. BP, the deterioration of natural forest was observed under warm and relatively less humid climatic conditions followed by an amelioration of climate from 2000 yrs. BP to present (Chauhan et al., 2015; Tripathi et al., 2018). In the Lahuradewa lake, where the first agricultural activity was recorded in the Ganga plain region there was an amelioration of climate with dry phases, e.g. 5300–4100 yrs. BP, 1650–1200 cal yrs. BP and 950–700 yrs. BP in relation to the weak

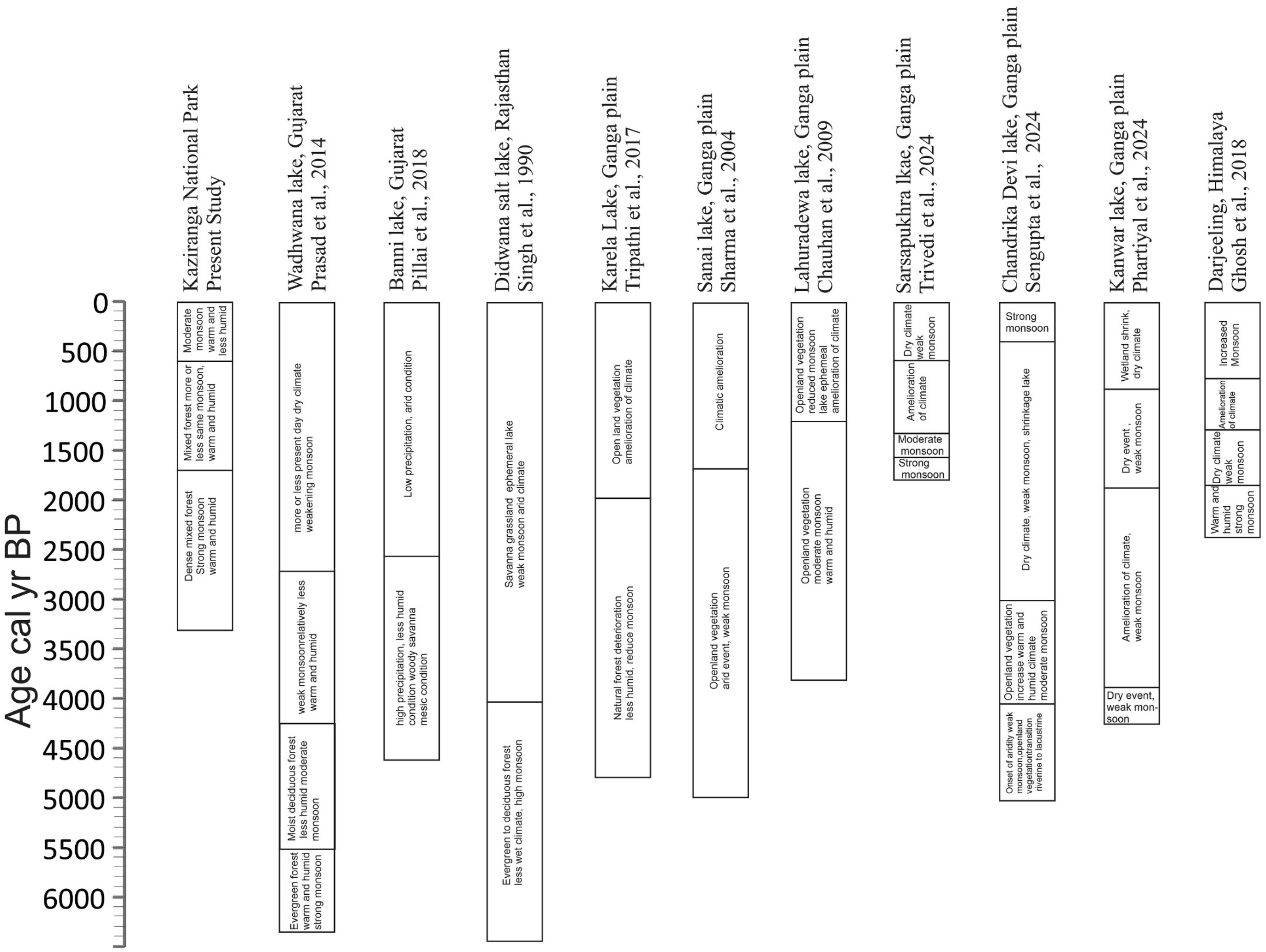

Fig. 7. A palaeoclimatic record diagram of the Kaziranga National Park and its comparison with the other western and northern parts of the Indian sub-continent.

monsoonal activities in the Ganga plain (Chauhan et al., 2009). In the Sanai lake, during 5000 yrs. BP to 2000 yrs. BP, arid climate was observed followed by the amelioration of climate from 1700 yrs. BP to the present (Sharma et al., 2004). In the Chandrika Devi lake, between 5063 yrs. BP and 4117 yrs. BP, the onset of aridity was observed with an increase in openland and a transition of riverine to lacustrine conditions in response to weak monsoon followed by moderate monsoonal activities under arid condition during 4117 yrs. BP to 3060 yrs. BP. From 3060 yrs. BP to 1511 yrs. BP, an amelioration of climate was followed by weak monsoonal variability and shrinkage of the lake with dry climate conditions from 1511 cal yrs. BP to 697 cal yrs. BP. From 697 yrs. BP to 75 yrs. BP, a strong monsoon is observed (Sengupta et al., 2024). In the Sarsapukra lake of central Ganga plain a strong summer monsoon occurred from 1800 cal yrs. BP to 1600 yrs. BP followed by a moderate Indian Summer Monsoon from 1600 cal yrs. BP to 1350 cal yrs. BP, while from 1350 yrs. BP to 1200 yrs. BP weak Indian Summer Monsoon was found. Short term warm and humid condition are observed from 1200 cal yrs. BP to 1030 cal yrs. BP followed by weak monsoon from 1030 yrs. BP to 620 yrs. BP with a relatively dry climate. Lastly, from 450 cal yrs. BP to the present a weak monsoon and acute dry climate was observed (Trivedi et al., 2024). A high resolution multiproxy analysis of the Kanwar wetland from Ganga plain recorded, multiple distinct dry events at 4300–4200, 3800, 1800–900 and 300 cal yr BP, with high anthropogenic activities along with shrinkage of many natural wetland areas in the regions (Phartiyal et al., 2024) in relation to the increased aridity due to the weak Indian summer monsoon in the Ganga plain (Fig. 7. Similarly, in the Darjeeling Himalaya, during 2400 cal yrs. BP to 1819 cal yrs. BP, the climate was warm and humid in response to strong monsoon followed by weak monsoon from 1819 yrs. BP to 1326 yrs. BP with a dry climate. From 832 yrs. BP to 583 yrs. BP, strengthening of Indian Summer Monsoon was followed by drier climate with a weakened Indian Summer Monsoon (Ghosh et al., 2018a, 2018b). In the Didwana of Rajasthan from 7500 yrs. BP to 4000 yrs. BP, the evergreen forest flourished and replacing deciduous taxa with less wet followed by forest was deteriorated and become semi-arid savanna grassland due to weaken monsoon with arid climate and the lake become ephemeral (Singh et al., 1990).

7.5. KNP and palaeoclimatic variability in Northeast India

Understanding the climate of northeastern India is very critical due to the high variation of topography, altitudinal variations, and rainfall. The palaeoclimatic analysis in northeastern India is mainly based on biotic proxies where the rainfall activity is taken as playing a key role in controlling vegetation dynamics and past climatic changes at a regional level.

In this study we have observed that, between 3290 and 1700 cal yrs. BP, warm and humid climatic conditions existed in response to high monsoonal activity in the KNP, as indicated by the abundance of arboreal evergreen taxa. In contrast only moderate rainfall activity is observed from 1700 cal yrs. BP -present, under warm and a relatively less humid condition in the region based on the increased values of deciduous arboreal taxa. However, between 580 CE to760 CE, a weak southwest monsoon was observed in the Barak valley region of Assam followed by enhanced monsoonal variability (538–1875 mm) during 760–940 CE (1190–1000 cal yrs. BP) and continued between 940 and 1220 CE (1000–730 cal yrs. BP) owing to the intense southwest monsoon (upto-2250 mm) (Tripathi et al., 2021). Accordingly, in the Chaygaon swamp of lower Assam, during 6780–1950 cal yrs. BP, a warm and humid climate with moderate monsoonal activity was recorded. Between 1950 yrs. BP -989 yrs. BP this changed to an increasing by warmer and more humid climate with strengthened monsoonal activity and a warm and relatively dry climate recorded between 989 yrs. BP to present (Dixit and Bera, 2013). Further, in the Meer beel (swamp) of upper Assam region, during 3000 yrs. BP to 2000 yrs. BP, there was a semi-evergreen forest under a warm and humid climate with high monsoonal activity followed by 2000 yrs. BP to 859 yrs. BP, and 859 yrs. BP to onwards resulting in the conversion to mixed deciduous forest under a relatively less warm and humid climate (Bera and Dixit, 2011).

Based on pollen, phytolith and stable carbon isotope ($\delta^{13}C$) analysis, between 3.8 and 1.2 ka BP, high monsoonal activity (1867 ± 33.4 mm) was recorded in the Ziro lake basin of the Arunachal Pradesh followed by a gradual decline of monsoonal activity from 1.2 ka to present (Ghosh et al., 2014). Further, based on the pollen and carbon isotope data ($\delta^{13}C_{org}$), from 3150 cal yrs. BP-2300 cal yrs. BP, there was a comparatively low rainfall in the Dzuko valley of the Nagaland region followed by increased monsoonal activity from 2300 cal yrs. BP to 1000 cal yrs. BP, while from 1000 cal yrs. BP the precipitation again declined resulting in a relatively dry climate (Misra et al., 2020). Similarly, in the Loktak lake of Manipur, from 2330 cal yrs. BP to 1460 cal yrs. BP moderate monsoonal activity occurred under a warm and relatively dry climate followed by a warm and humid climate in response to higher monsoonal activities from 1460 cal yrs. BP to 560 cal yrs. BP. From 560 cal yrs. BP to the present a relatively less warm and humid climate occured with a reduction of the southwest monsoon (Tripathi et al., 2018) (Fig. 8).

In the Demagiri wetland of Mizoram, a warm and humid climate prevailed between 850 and 450 yrs. BP, driven by intensified monsoonal activity. This phase was subsequently followed by relatively less warm and less humid conditions, corresponding to a weakening of the southwest monsoon in the region (Chauhan and Mandaokar, 2006). In Tripura, climatic conditions from ~6800 yrs. BP to the present show variability linked to monsoonal fluctuations, shifting from warm and humid to warm and relatively less humid climate (Bhattacharyya et al., 2011). Furthermore, a pronounced dry event between 4.2 and 3.9 ka BP, corresponding to the Meghalayan age, has been documented from high-

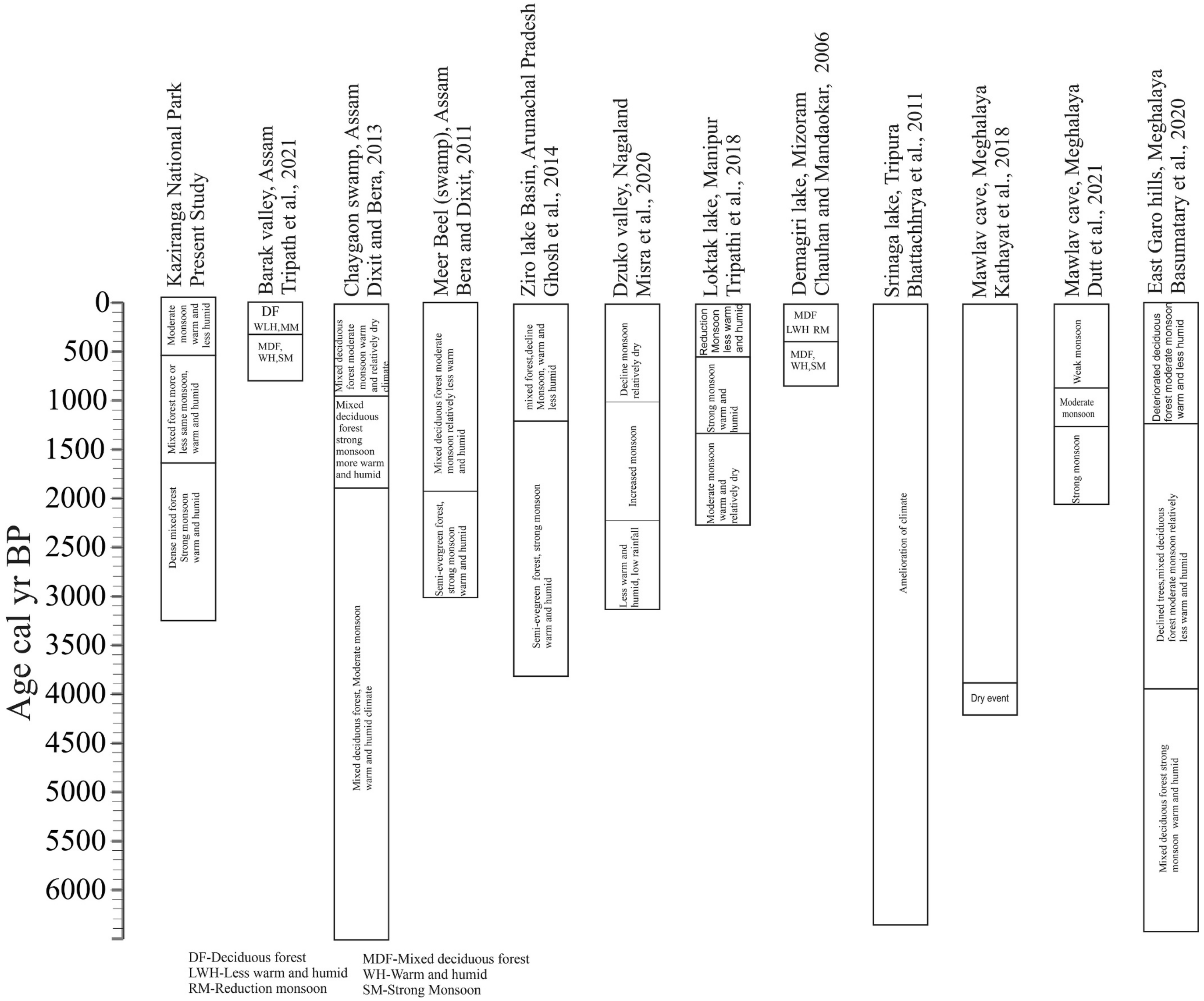

Fig. 8. A palaeoclimatic record diagram of the Kaziranga National Park and its comparison with the other regions of the northestern India.

resolution $\delta^{18}O$ records of speleothems from Mawmluh Cave (Berkelhammer et al., 2012; Kathayat et al., 2018).

Similarly, high Indian summer monsoonal variability has been recorded for the last two millennia based on a ($\delta^{18}O$) proxy record from a stalagmite from the Mawmluh cave. Here the monsoon was strong from 212 BCE to 1986 CE. A moderate Indian Summer Monsoon is recorded between 212 BCE and 400 CE followed by a strong Indian Summer Monsoon during 400–500 CE and 640–1060 CE and a weak Indian Summer Monsoon, between 520 and 540 CE, 820–850 CE, 940–980 CE and after 1060 CE (Fig. 8). Multiple phases of strong and weak Indian Summer Monsoon were observed during the Medieval climate anomaly and Little Ice Age (Dutt et al., 2021). In the East Garo hills of Meghalaya, from 7540 cal yrs. BP to 3590 cal yrs. BP, there was a dense mixed deciduous forest under warm and humid climate in response to high followed by from 3590 to 1120 cal yrs. BP, the forest gradually declines due to moderate monsoonal activity under a warm and relatively dry climate. Further, from 1120 cal yrs. BP to the present the deteriorated forest with a warm and less humid climate existed with a reduction of the southwest monsoon (Basumatary et al., 2020).

Based on the palaeoclimatic records of western, northern, and northeastern part of Indian sub-continent, we observed that, there is no such climatic amelioration and monsoonal variabilities in KNP during the late Holocene period, comparable to the western and Ganga plain region of Indian subcontinent. No agricultural activities were observed in the KNP based on the absence of cereal and other cultural pollen (*Brassica* and *Coriandrum*), while high agricultural activities have been recorded in the western and Ganga plain region of Indian subcontinent. Furthermore, the high wildlife activities in the KNP are the strong driver of the current vegetation shifting from evergreen to deciduous with expanding grassland and openland.

We hypothesize that, many megaherbivores, especially rhinoceros were gradually migrating from western India and the Ganga plain region towards the northeastern part of the Indian subcontinent.

Rhinoceros are presently found in natural habitat in restricted pockets of the Brahmaputra valley of Assam state, especially KNP (Fig. 9a, b), Pobitora Wildlife Sanctuary, Manas National Park, and Orang Wildlife Sanctuary, and part of south Nepal. During the middle to late Holocene, the distribution of Indian One-Horned rhinoceros was greater than at present (Fig. 10) based on the distribution of skeletal fossil remains (Banerjee and Chakraborty, 1973; Momin et al., 1973; Roberts, 1977; Rookmaaker, 1983, 2002; Blanford, 1888). Historically, during the Indus valley civilization of Harappa and Mohenjo-Daro, objects such as seals and pottery represented rhinoceros, Asian elephants, and other species (Marshall, 1931; Pounds et al., 1936; Rao, 1957; Rookmaaker, 1999, 2000). The presence of rock paintings of Indian One Horned Rhinoceros and their hunting is known in the north-western Indian region during the fifteenth and sixteenth century of the Mughal Period (Ali, 1927; Rookmaaker, 2000), indicating their occurrence in these regions.

Today, the rhinoceros has disappeared from these regions and the exact reasons for this are still controversial and require considerable additional investigation to determine whether the decrease in the range of the rhinoceros was primarily due to ecological change or to anthropogenic activities. A dry climatic event between 4.0 ka BP to 3.2 ka BP has been recorded in north-western and northern India reflecting a drastic reduction in precipitation (Staubwasser et al., 2003; Madella and Fuller, 2006; McDonald, 2011) which may be one of the causes for the habitat loss and disappearance of rhinoceros from these regions. Multiproxy studies suggest that the western Indian region had become increasingly arid due to weakening rainfall during the mid-Holocene (Singh et al., 1990; Bryson and Swain, 1981; Swain et al., 1983; Enzel et al., 1999; Singh et al., 2007; Dixit et al., 2014; Prasad et al., 2014; Kumari et al., 2025). Similarly, the high impact of anthropogenic activities (Chauhan et al., 2015) coupled with the severe climatic fluctuations of the Medieval Warm Period followed by the Little Ice Age in the central Ganga plain, central India, and the Himalayas, affected both ecological and social stability of the region (Quamar and Chauhan, 2014; Singh et al., 2015; Saxena and Singh, 2017; Mohanty et al., 2024). During this period, the Little Ice Age, which locally was a very extreme climatic event in north-west and Ganga plain region resulted in the deterioration of the tropical forest affecting the natural habitat of many flora and fauna and would have had a great impact on the megafauna, especially Rhinoceros, Elephant, and Asian Buffalo. Rhinoceros prefer different types of forest vegetation and a perennial water logged condition (Fig. 9a, b) as part of their habitat (Basumatary et al., 2017) which reflected in the rhinoceros midden dung and surface soil analysis in the KNP (Basumatary et al., 2017, 2024). Alternating climate change between warm and cold episodes impacted both vegetation composition and human civilization (Trivedi et al., 2019, 2024) and the resulting change impacted wildlife, especially megaherbivores, causing their migration from the north-western to the north eastern region of the Indian subcontinent (Fig. 10). Recent studies suggest that the worldwide expansion of *Homo sapiens* is the responsible for the decrease or extinction of megaherbivores rather than the rapid climate changes during the Quaternary period (Bergman et al., 2023). Historical records suggest that during the late eighteenth to early nineteenth century

Fig. 9. a. View of Rhinoceros and elephant grazing in together in natural habitat within KNP, b. Indian One Horned Rhinoceros and deers are grazing in together in natural habitat in KNP. Photographs taken by SKB (first author).

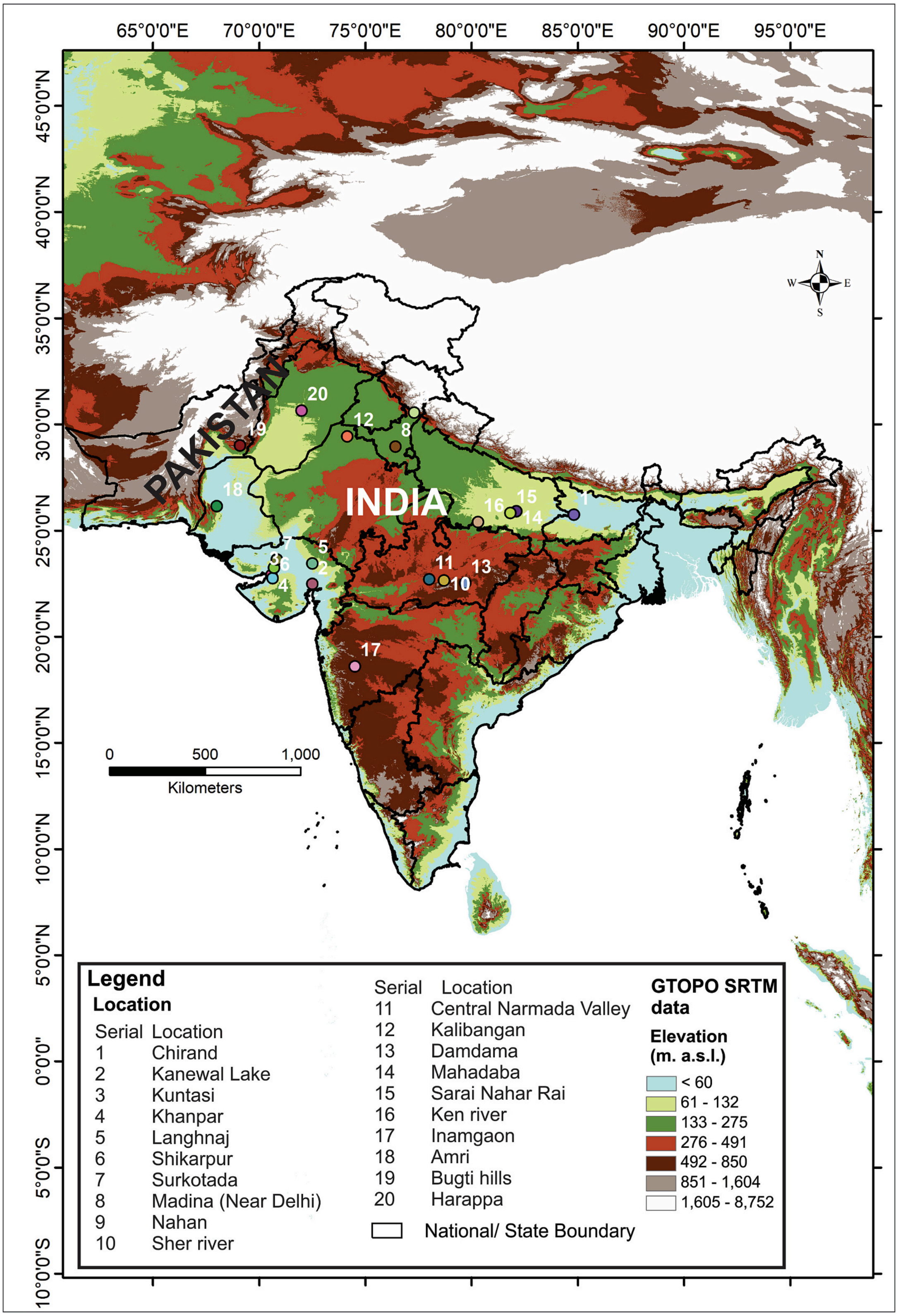

Fig. 10. A map showing of the *Rhinoceros unicornis* fossil distribution during the Holocene period.

rhinoceros are present all over the Assam flood plain areas (Rookmaan, 2000). Recently due to the loss of habitat and human activities this natural habitat has become compressed towards the reserve forests where national parks and wildlife sanctuaries were established. In comparison, it is observed that, during the middle Holocene to the present, the northeastern part of India experienced comparatively less climatic deterioration with a lower impact of anthropogenic activities than the north-western and Ganga plain regions of India (Bhattacharyya et al., 2007, 2011; Dixit and Bera, 2012, 2013; Bhattacharryya and Chanda, 1992; Basumatary et al., 2018) as the *Rhinoceros unicornis* rarely inhabits mountainous and hilly areas (Choudhury, 2022), so that conditions in the other states of northeastern India are not favourable for their survival.

7.6. Multivariate analysis (PCA) of pollen and fungal spore data in relation to climate and herbivores activity

According to the PCA plot, samples 17–22, representing the period from 3290 yrs. BP to 1700 yrs. BP, exhibit a high abundance of evergreen taxa such as *Mesua*, *Schima*, *Cinnamomum*, *Syzygium*, *Duabanga*, Arecaceae, and *Litsea*. This assemblage indicates high rainfall and warm, humid climatic conditions. In contrast, tropical deciduous taxa, including *Bombax*, *Terminalia*, *Dillenia,* and *Albizia,* show comparatively lower abundances during this interval (Fig. S4). In the subsequent period represented by samples 10–16, corresponding to 1700 yrs. BP to 640 yrs. BP, the second PCA cluster shows a relative decline in evergreen elements along with higher frequencies of *Rhododendron* and *Betula*. This shift suggests the sparsening of previously dense evergreen forest cover.

Further, based on the PCA loading plot, the period from 640 yrs. BP to the present (samples 1–9), corresponding to the third pollen cluster, is dominated by deciduous taxa such as *Bombax*, *Terminalia*, *Dillenia*, *Albizia*, and *Melastoma*. This reflects a significant decline in evergreen vegetation and the establishment of less warm and humid conditions. Among nonarboreal taxa the terrestrial, marshy, and aquatic elements, including Poaceae, Cyperaceae, *Polygonum*, *Xanthium*, Asteroideae, *Justicia*, and *Mimosa*, also occur abundantly, indicating increased forest opening and expansion of open-land habitats. The PCA score plot for fungal spores shows that samples 17–22, corresponding to 3290 yrs. BP to 1700 yrs. BP contain high abundances of *Tetraploa*, *Bipolaris*, *Alternaria*, *Helicoon*, *Meliola*, *Cookeina*, *Dictyospora,* and Microthyriaceae, collectively supporting the presence of dense forest vegetation during the earlier phase. Between 1700 yrs. BP and 640 yrs. BP, coprophilous fungal taxa such as *Sporormiella*, *Saccobolus*, *Ascodesmis*, *Podospora*, and *Gelasinospora* display comparatively higher abundances, suggesting increased herbivore activity within a partially open landscape. Further, during 640 yrs. BP to present, coprophilous fungal spores, including *Sporormiella*, *Saccobolus*, *Ascodesmis*, *Sordaria,* and *Podospora,* show markedly high abundances, reflecting intensified herbivore activity in the KNP (Fig. S5).

8. Conclusions

For the first time, three distinct palaeoecology and palaeoherbivory phases have been identified and distinguished in the KNP extending back to 3290 yr BP.

1. During 3290 yrs. BP to 1700 yrs. BP, a tropical dense mixed forest was present under warm and humid climatic condition in response to the high rainfall activities with comparatively low wildlife habitation than today in the KNP.
2. Subsequently, between 1700 yrs. BP to 640 yrs. BP, the forest vegetation especially evergreen forest taxa declined and there was expansion of grassland in relation to the increased of herbivore activities in the KNP. The invasion by *Mimosa* (an exotic plant) is observed over 1700 years and with a continuously increasing trend is identified and characterized which may be critical for the wildlife habitation in near future.
3. Around 640 yrs. BP to present, the decline of evergreen taxa continued and the grassland and openland continued expanding in relation to the increased wildlife density in the KNP.
4. The absence of agricultural activities in the KNP is indicated by the absence of Poaceae (cereal >45 μm) and other cultural pollen (*Brassica* and *Coriandrum*) in the sedimentary profile.
5. A systematic analysis on coprophilous fungal spores, especially *Sporomiella-Ascodesmis-Saccobolus* assemblage is needed when analysing sediment from fossil sites in and around the north-western, and Ganga plain region of Indian subcontinent to trace rhinoceros and other megaherbivores presence and their cause of extinction on the regional level during the Holocene period. Additionally an ancient DNA analysis of the recoded rhinoceros bone fossils could be helpful for the accurate confirmation of their extinction.
6. Based on the comparative analysis of vegetation dynamics and climatic variabilities along with earlier recorded of rhinoceros bone fossils and historical records, we hypothesize that, rhinoceros occurred in western and the northern and its adjoining regions in the Indian subcontinent, and due to the deterioration of natural vegetation and climatic amelioration along with high human activities, preferred rhinoceros habited decreased resulting in a translocation towards the north eastern region of the Indian subcontinent during the mid to late Holocene.
7. Our data provides a baseline to understand the dynamic interaction between climate change, the response of vegetation to this change and ultimately how this impacts the long-term survival of the wildlife within a physically restricted habitat. Such data could be helpful to make decisions for the long-term survival, conservation, and wildlife management plan by Governmental and other non-governmental organizations (NGOs)agencies.

CRediT authorship contribution statement

Sadhan K. Basumatary: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Eline N. van Asperen:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Formal analysis. **Siddhant Vaish:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Swati Tripathi:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Data curation. **H. Gregory McDonald:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Rajib Gogoi:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Ajay Kumar Arya:** Writing – review & editing, Supervision, Methodology, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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