The Holocene

Pollen and non-pollen palynomorph depositional patterns in Kaziranga National Park, India: implications for palaeoecology and palaeoherbivory analysis

Journal:	*The Holocene*
Manuscript ID	HOL-22-0152.R1
Manuscript Type:	Paper
Date Submitted by the Author:	02-Aug-2023
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Pollen and non-pollen palynomorph depositional patterns in Kaziranga National Park, India: implications for palaeoecology and palaeoherbivory analysis

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Abstract

The main aim of this study is to produce a modern analogue for pollen and non-pollen palynomorphs (NPPs) preserved in soil in relation to the different vegetation types and herbivore impact in the Kaziranga National Park (KNP). The pollen data obtained reflects both the extant vegetation types in each habitat as well as landuse, but some site-by-site variation was observed with respect to the coprophilous fungal spores present in the palynoassemblage. Canonical correspondence analysis (CCA) analysis of pollen data reveals the presence of five significantly different vegetation types, while the non-pollen palynomorphs are relatively similar in relation to the different vegetation types. The long-term association of the wildlife and their impact on different vegetation types is one of the main reasons for the variation seen in the depositional pattern in the assemblage. The openland area is one of the most important areas for wildlife in the KNP as indicated by the presence of marker pollen and coprophilous fungal spores in the palynoassemblages. Coprophilous fungal spores were most abundant in this vegetation type reflecting the higher density of herbivores. The representation of pollen and coprophilous fungal

spores from the swamp samples reflected the overall composition of all vegetation types existing in the KNP. This data can be utilized as a baseline for the interpretation of palaeoecological and palaeoherbivory studies in other parts of the Indian subcontinent as well as its potential application at a global level.

Keywords

Coprophilous fungal spores, herbivores, palynoassemblages, pollen spectra, swamp, vegetation types.

Introduction

The study of modern pollen rain in relation to different vegetation types is a prerequisite for the interpretation of the past vegetation and climate in a region and how it has changed over time (Bent and Wright, 1963; Janssen, 1967; Wright, 1967; Overpeck et al., 1985; Prentice, 1985; Bunting et al., 2004; Wilmshurst and Mcglone, 2005; Xu et al., 2005; Deng et al., 2006; Gosling et al., 2009). The study of the modern pollen rain and extant vegetation in tropical regions is more complex and critical due to high biodiversity and heterogeneity of the pollen preservation on the forest floor and nearby areas, compared to subtropical and temperate vegetation, as documented by the presence and abundance of the major pollen taxa in the pollen assemblages (Mayle et al., 2000; Gosling et al., 2018; Bush et al., 2021). Phenological factors such as the timing of the flowering period and periods of high rainfall, along with pollen production, mode of pollination, and variation in the mode of pollen dispersal influence pollen preservation both on the landscape surface and eventual integration into soils and sediments. However, based on a knowledge of the pollen spectra and how it represents the major associated plant taxa in relation to the different vegetation types, it is possible to differentiate and distinguished the different vegetation types in a region (Gaillard et al., 1994; Guimaraes et al., 2017) and as well as the recognition of differences between modern and historic grassland uses (Hjelle, 1999).

There is an increasing global interest in palaeoherbivory and palaeodietary analysis in relation to palaeoecology during the Quaternary, particularly with respect to possible dietary changes that may have contributed to the extinction of megaherbivores (Barnosky et al., 2004; Rawlence et al., 2016). Many of these studies have been primarily based on pollen and non-pollen palynomorphs, especially changes in the relative abundance of coprophilous fungal spores, preserved in sedimentary profiles and coprolites (Burney et al., 2003; Robinson et al., 2005; Davis and Shafer, 2006; Carrión, 2007; Raper and Bush, 2009; Gill et al., 2009, 2013; Johnson et al., 2015; Graham et al., 2016; van Geel et al., 2018).

The presence of coprophilous fungi in sediments and changes in their relative abundance has been used as an indicator not only of the past presence of herbivores,but also to document changes in population sizes and in some cases the extinction of this part of the Pleistocene megafauna (van Geel, 1972, 1976, 1978; van Geel et al., 1981, 1983; Karanth and Sunquist, 1992; Feranec et al., 2011; Baker et al., 2013; Etienne et al., 2013; Lopez-Vila et al., 2014; Loughlin et al., 2018; Tunno and Mensing, 2017; van Asperen et al., 2021; Pokharia et al., 2022). More recently coprophilous fungi have increasingly been used as a proxy to address questions of pastoral and other human activities (Davis, 1987; Burney et al., 2003; van Geel et al., 2003; Gill et al., 2009; Miehe et al., 2009; Cugny et al., 2010; Feeser and O'Connell, 2010; Felauer et al., 2012; Johnson et al., 2015; Kamerling et al., 2017). When combined with the study of pollen grains, fungal spores, especially of coprophilous fungi that grow on dung of herbivorous animals can provide useful information for understanding the food habits, ecology, diversity, niche partitioning and changes in relative abundance of past herbivorous species in a region (Ebersohn and Eicker, 1992; Ekblom and Gillson, 2010; Velazquez and Burry, 2012; Basumatary et al., 2017, 2019, 2020, 2021; Tripathi et al., 2019; Pokharia et al., 2022). Previously work on the preservation of modern pollen and non-pollen palynomorphs on the modern surface soil related to highland grazing and past land use and other vegetation changes has also been investigated (Ejarque et al, 2011; Henga-Botsikabobe et al., 2020; Loughlin et al., 2021). Since both fungal spores and the pollen grains in the sediments are commonly encountered in the same palynological slide (van Geel et al., 2003), the documentation of fungal spores, especially those of coprophilous fungal spores, along with the pollen grains can be useful to interpret the impact of herbivores in relation to the different vegetation types in a region. As coprophilous fungal spores are dispersed only for a very short distance, they are local in origin (Graf and Chmura, 2006; Johnson et al., 2015) so will accumulate in sediments with pollen grains and are therefore indicators of the local presence of herbivores in relation to the existing vegetation.

While some research has been conducted to understand past vegetation and climate history in relation to the palaeoherbivory in national parks in tropical regions of the world (Burbridge et al., 2004; Ekblom and Gillson, 2010), little research has been carried out on modern pollen deposition in relation to the different vegetation types in national parks and wildlife sanctuaries in Asia (Djamali et al., 2009; Basumatary et al., 2014; Bera et al., 2014; Tripathi et al., 2016; Ghosh et al., 2017; Setyaningsih et al., 2019; Pandey and Minckley, 2019). These previous studies have often not recorded the presence ofcoprophilous fungal spores so cannot be used to determine the presence and abundance of herbivorous animals in the region. In the absence of skeletal remains of these herbivores, coprophilous fungal spores may serve as an important proxy that can be used to reconstruct the palaeoecology of a region with respect to the presence, types and abundance of herbivores and their impact on the local environment, as well as how changes in the vegetation impacts the local wildlife (Basumatary and McDonald, 2017).

The main aim of this study is to document the depositional pattern of pollen and non-pollen palynomorphs in different vegetation types in Kaziranga National Park (KNP) in relation to the types of wildlife present and their impact on the different types of habitat. Determining the degree of representation of the coprophilous fungal spores in the surface soil and sedimentary profiles serves as the primary proxy to trace the relationship between flora and fauna in the region through time. The combination of pollen and non-pollen palynomorphs, especially the abundance of coprophilous fungal spores, is taken into consideration and calibration during the analysis which permits an interpretation of palaeoherbivory and palaeoecology. Based on the changes in frequency of coprophilous fungal spores in the sedimentary profile, an analysis is possible to trace the presence, relative abundance over time and eventual decline and extinction of members of the herbivorous mammals in Kaziranga National Park and to correlate the pattern with what is observed in other national parks located in the tropical and temperate region of the globe. Based on the modern palynomorph analogues seen in different regions, the presence and absence of the local arboreal pollen taxa and coprophilous fungal spore in the pollen assemblages provides a means to distinguish the natural forest vegetation, from areas with heavy grazing or modified into cropland in both tropical and temperate regions. The resulting information can serve as a baseline to examine the influence of palaeoherbivory on vegetation in the National

Park in the past. This also provides for a better determination of the first human occupation along with their domestic livestock in the area and subsequent impact on the flora and fauna.

Study sites

Kaziranga National Park covers an area of around 430 square kilometers and is bordered on one side by the Brahmaputra River (Figure 1). In 1985, KNP was declared a UNESCO World Heritage Site in recognition of its significance as one of the best managed wildlife parks in the world. As such, KNP is one of the best sites in India and certainly for Southeast Asia to observe the long-term interrelation between plants and the indigenous wildlife, as this interrelationship has not been impacted as extensively by human activities and domesticated animals as at other sites in India. The park is within the Indo-Burmese biodiversity hotspot region, a critical corridor for immigration of members of the Indo-Malayan fauna into the Indian subregion. It is also a critical reserve for tropical species, having served as a gene reservoir for these taxa during glacial periods (Tamma and Ramakrishnan, 2015).

Climate and soil

The climate of the region is controlled by the southwest and northeast monsoons. These weather patterns result in hot, humid summers, and cold, dry winters. The temperature ranges from a minimum of 4°C during winter up to 37°C in summer. The relative humidity is very high and ranges between 75–86%. The annual rainfall ranges from 1800–2600 mm, and annual flooding is common in KNP during the summer. 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).

Vegetation and wildlife

In general, there are four main types of vegetation in the KNP; tropical evergreen forest, semi-evergreen forest, deciduous forest, grassland and swamp (Champion and Seth, 1968). Alluvial grassland is the most dominant vegetation type (50.6%), followed by woodland (21.8%), openland areas covered by short grasses and other herbaceous associates (7.7%), and eroded land caused by soil erosion and landslides during intervals of high rainfall 11.7% in the national park (Das et al., 2014).

The evergreen forest is generally confined to the areas adjacent to the Brahmaputra River, small rivers, and streamlets within the park. This vegetation remains evergreen throughout the year in the core regions and is dense and composed of forest elements including *Castanopsis indica*, *Cinnamomum bejolghota*, *Duabanga grandiflora*, *Elaeocarpus robustus*, *Toona ciliata*, *Mesua ferrea*, *Symplocos paniculata*, *Terminalia myriocarpa*, *Schima wallichii,* and *Litsea monopetala*. The common climbers are *Calamus erectus*, *Vitis latifolia, Paederia foetida, Cardiospermum halicacabum, Trichosanthes dioca, Smilax ovalifolia, Mucuna pruriens*, *Piper longum*, and *Thunbergia grandiflora*. Among the ferns, both terrestrial ferns and epiphytes such as *Lycopodium clavatum*, *Dryopteris filix-mas*, *Gleichenia dichotoma*, *Lygodium japonicum*, *Drynaria rigidula*, *Angiopteris evecta*, *Asplenium nidus*, and *Pyrrosia nummularifolia* are present (Figures 2a and 2b).

The moist deciduous forest occurs as isolated patches within grasslands and next to the evergreen forest. This forest consists of primarily deciduous trees which lose their leaves during the winter season. The major tree taxa are *Bombax ceiba, Dillenia indica, Albizia procera*, *A. lebbek, A. odoratissima, Neolamarckia cadamba, Trewia nudiflora*, *Careya arborea*, *Lagerstroemia parviflora,* and *Semicarpus anacardium*. The forest floor is covered by different species of Poaceae, Cyperaceae, Convolvulaceae, and Acanthaceae. The fern allies such as *Dryopteris filix-mas*, *Adiantum caudatum*, *Blechnum occidentale*, *Polypodium vulgare*, and *Drynaria rigidula* are the common members in this forest (Figures 2c and 2d).

The grassland areas are scattered and dominated by tall grasses mainly *Erianthus ravennae*, *Phragmites karka, Arundo donax*, *Imperata cylindrica*, and *Saccharum procerum* along with short grasses like *Hemarthria compressa*, *Microstegium ciliatum*, *Cynodon dactylon,* and *Cenchrus ciliaris*. However, some trees and shrubs such as *Bombax ceiba*, *Careya arborea*, *Dillenia indica, Butea monosperma*, and *Albizia lebbeck* also grow scattered within the grassland (Figures 3a and 3b).

The openland areas are also scattered especially near the periphery of the swamp. Tree taxa are almost absent but there are some scattered shrubs such as *Melastoma malabathricum*, *Cassia tora,* and *Clerodendron viscosum*. The openland area is covered with short grasses followed by Cyperaceae, Acanthaceae, Amaranthaceae, Solanaceae, and Convolvulaceae. *Cynodon dactylon*, *Cenchrus ciliaris*, *Chrysopogon aciculatus*, *Digitaria ciliaris*, and *Paspalum conjugatum* are the common species in short grass communities (Figure 3c).

The swamp habitat is restricted to generally low-lying areas and covers around 11.8% of the park (Das et al., 2014). It is submerged throughout the whole year but during summer (May-August) the swamp habitat may be expanded due to flooding of river channels resulting from heavy monsoonal rainfall. The major marshy and aquatic taxa include *Alpinia allughas*, *Clinogyne dichotoma*, *Calamus tenuis*, *Polygonum orientale*, *Cyperus rotundus*, *Sagittaria sagittifolia*, *Eichhornia crassipes*, *Potamogeton pectinatus*, *Nymphaea alba*, *Euryale ferox*, *Myriophyllum indicum*, *Ludwigia sedioides*, and *Nymphoides indica*. Additionally, there are some trees and shrub taxa including *Syzygium cumuni*, *Barringtonia acutangula*, *Dillenia indica*, *Bombax ceiba*, *Osbekia stellata*, and *Costus speciosus* that commonly grow on the periphery of the swamp area (Figure 3d).

With regard to wildlife, KNP is mainly famous for its *Rhinoceros unicornis* (greater one-horned rhinoceros), but the park is also very rich in other animals and birds. The fauna includes 490 species of birds, 43 species of reptiles and 52 species of mammals (Choudhury, 2003). Besides rhinoceros, other associated large and medium sized mammalian herbivores include *Bubalus arnee*, *Elephas maximus*, *Bos gaurus*, *Sus scrofa*, *Cervus unicolor*, *Cervus duvauceli*, *Axis porcinus*, *Muntiacus muntjak*, *Presbytis entellus*, *Macaca mulatta*, *Macaca assamensies*, and *Hylobates hoolock*. Birds such as *Francolinus gularis*, *Anser erythropus*, *Houbaropsis bengalensis*, *Tringa guttifer*, *Sterna acuticauda*, *Ardea insignis*, and *Pelecanus philippensis* are commonly seen in the park**.**

Materials and methods

Field work

Out of a total of 75 surface soil samples, 15 (E1-E15) were collected from the evergreen forest, 15 (D16-D30) from deciduous forest, 15 (G31-G45) from grassland, 15 (O46-O60) from openland, and 15 (S61-S75) from the swamp. In each vegetation type, the samples were procured at about 50 meter intervals.

Laboratory work

The surface soil samples were chemically processed employing the standard acetolysis method (Erdtman, 1953). The soil samples were treated with 10% aqueous KOH solution to deflocculate the pollen and spores from the soil followed by 40% hydrofluoric acid (HF) treatment to dissolve silica content. This was followed acetolysis. The samples were washed 2-3 times with glacial acetic acid and then washed 2-3 times with distilled water and sieved through a 500µm mesh. Finally, the material was kept in a 50% glycerin solution with a drop of phenol. Totals of 259-335 pollen grains per slide of each sample were counted to make the pollen spectra. The pollen taxa have been categorized into arboreal taxa, non-arboreal taxa, extra-regional taxa (highland taxa coming from the eastern Himalaya), and ferns. Similarly, a total of 225-284 fungal spores per slide were counted from the same pollen slides and were categorized into coprophilous and non-coprophilous fungal spores to make fungal spore spectra. For the precise identification of fossil palynomorphs in the sediments, the reference pollen slides available at Birbal Sahni Institute of Palaeosciences herbarium as well as pollen and fungal spore photographs in the published literature (van Geel, 2003; Basumatary et al., 2017; Basumatary and McDonald, 2017) were used. Photodocumentation of palynomorphs was made using Olympus BX-61 microscope with DP-25 digital camera under 40X magnification (Figure 4). The pollen and fungal spore spectra were made using TILIA software (Grimm, 2011) (Figures 5 and 6.).

Statistical analysis: canonical correspondence analysis

Five environmental variables were obtained from the pollen assemblages by calculating the total proportion of five vegetation type indicator assemblages in each site: (1) evergreen indicator assemblage score, (2) deciduous indicator assemblage score, (3) grassland indicator assemblage score, (4) openland indicator assemblage score, and (5) swamp indicator assemblage score (Table 1). These variables provide environmental gradients against which to assess the distribution of fungal NPPs. Pollen of wind-blown extra-regional taxa were excluded from the statistical analyses.

Many fungal NPPs have short dispersal distances, and can therefore be overrepresented in locations near fruitbodies but underrepresented at even a short distance from fruitbodies (Wilmshurst and McGlone, 2005; Van Asperen et al., 2021). A square-root transformation was applied to the fungal NPP percentage data to compensate for this effect (Legendre and Legendre, 2012; Paliy and Shankar, 2016; Borcard et al., 2018).

Canonical correspondence analysis (CCA; Ter Braak 1986; Borcard et al., 2018) was carried out on the transformed NPP data and the five environmental variables to assess the influence of the five vegetation type assemblages on the distribution of NPPs. Collinearity among the vegetation type assemblages was explored by computing Variance Inflation Factors (VIFs). Based on the results of this, CCA with forward selection of explanatory variables was carried out. Canonical axes were tested for significance by permutation ANOVA. CCA was performed in R (Version 4.0.4, R Development Core Team, 2015) using the package vegan (Oksanen et al., 2017).

Results

The presence and abundance of major pollen taxa, which serve as marker taxa and their ecological significance in KNP are listed in Table 2. Diagrams of the pollen and fungal spore spectra are presented in Figures 5 and 6 respectively.

Evergreen forest: The surface soil samples (E1-E15) are characterized by the dominance of the major evergreen taxa *Mesua*, *Schima*, Arecaceae, *Symplocos*, and *Litsea* with values of 1.6-4.9% each followed by deciduous elements at values of 1.0-3.0%. Among non-arboreal taxa, Poaceae is recorded with values of 6.0-8.2% and other herb taxa are also consistently encountered with values of 3.3-3.8% in the pollen assemblages. Extra-regional taxa are consistently present but with low values. Ferns, both monolete and trilete, are encounteredwith ranges of 4.5-8.0% (Figure5). The most common coprophilous fungal spores are of the taxa *Sporormiella*, *Saccobolus*, and *Ascodesmis* with values of 0.8-5.6%. *Podospora, Sordaria, Arnium* and *Cercophora* were also encountered at low values. Non-coprophilous fungal spores are consistently represented at the ranges of 0.8-14.1% , with *Glomus, Meliola* and Microthyriaceae the most common taxa.

Deciduous forest: The samples from the deciduous forest (D16-D30) are characterized by the dominance of deciduous taxa with the ranges of 0.3-4.7% each, compared with evergreen taxa at values of 0.3-1.6%. Among non-arboreal taxa, Poaceae is dominant and varies from 6.5-9.4% and the other associated terrestrial and aquatic herbs are also recorded with values of 0.3-4.6%. Extra-regional taxa are represented with maximum values upto 2.1% in the pollen assemblages. Fern spores are also consistently present with maximum ranges of 4.5% and 5.8% respectively.

The coprophilous fungal spores occur with values from 0.9-4.9%. Non-coprophilous fungal spores are dominated by *Meliola*, *Glomus*, and Mycrothyriaceae as in the Evergreen forest, with ranges from 0.8-15.5%.

Grassland: The surface soil samples (G31-G45) from the grassland habitat are characterized by the dominance of Poaceae with an average value of 30.7%. Other associated terrestrial and aquatic taxa occur with maximum ranges upto 9.7%. Arboreal taxa, both evergreen and deciduous elements, namely *Mesua*, *Bombax*, and *Careya* are regularly encountered at low values. The extra-regional taxa are also consistently recorded with maximum values of 2.6%. The monolete and trilete ferns are represented with ranges of 1.9-5.6% in the pollen assemblages (Figure5). Coprophilous fungal spores are dominated by *Sporormiella*. *Saccobolus*, and *Ascodesmis* with ranges of 1.0-6.9%, with other coprophilous taxa reaching 6.2%. Among the non-coprophilous fungal spores, *Helmithosporium* is abundant with values up to 11.5%. *Meliola* and *Glomus* are regularly recorded with values of 0.5%-11.8%.

Openland: The samples (O46-O60) from the openland located adjacent to the swamp are characterized by the dominance of non-arboreal taxa with an average value of 58.9% compared to arboreal taxa at 27.3%, followed by extra-regional taxa (7.7%) and ferns (6.1%). Among arboreal taxa, both evergreen and deciduous elements are regularly encountered at ranges of 0.3-4.9%. Among non-arboreal taxa Poaceae is dominant with an average value of 19.8% and the other herb taxa are consistently represented by values of 0.3-6.1% in the pollen assemblages. The extra-regional taxa are regularly encountered at the ranges of 0.4-3.2%. The ferns, both monolete and trilete, are recorded by ranges of 2.1-4.3% (Figure5).The coprophilous fungal spores are much more abundant than in the evergreen and deciduous forest and the grassland. They are dominated by *Sporormiella*, *Saccobolus*, and *Ascodesmis* which are recorded at the values of 1.0-20.0% each. The non-coprophilous fungal spores are less abundant that in the forest and grassland areas, with values of 0.7-8.0%.

Swamp: The mud samples (S61-S75) from the swamp habitat are characterized by the dominance of non-arboreal taxa with an average value of 51.5% over arboreal taxa (30.7%). The ferns and extra-regional taxa are also recorded with average values of 9.2% and 8.6% respectively. Among arboreal taxa both evergreen and deciduous taxa are consistently encountered at the values of 0.3-3.9%. Among non-arboreal taxa, Poaceae is dominant with an average value of 15.6%. The marshy and aquatic taxa are consistently recorded with ranges of 0.6-4.5%. The extra-regional taxa are consistently encountered at the values of 0.3- 2.9%. The fern spores, both monolete and trilete, are represented by values of 3.2-5.8% in the pollen assemblages (Figure5). Among fungal spores, the coprophilous fungal spores are similarly abundant as in the openland samples, and are dominated by *Sporormiella*, *Saccobolus*, and *Ascodesmis* which are represented in the range of 1.8-19.2% each. The non-coprophilous fungal spores are present at similarly lower ranges as in the openland samples of 0.4-7.8% .

Statistical analysis of NPPs frequencies

VIFs based on an initial CCA indicated significant collinearity was present among the environmental variables. Therefore, CCA with forward selection was carried out. Four environmental variables were selected for inclusion in the CCA: Deciduous forest, Grassland, Openland and Swamp (Figure 7). The environmental variables account for 92.4% (constrained inertia = 0.22728, total inertia = 0.24572) of the variance in the fungal NPP data. The first two CCA axes (eigenvalues: CCA1 = 0.2066, CCA2 = 0.01577) explain 90.4% of the variance.The permutation tests show that both the CCA as a whole (p = 0.001) and each CCA axis (each p = 0.001) are significant and VIFs indicate collinearity among the vegetation type assemblages is low in this analysis.CCA1 is closely related to the openland pollen taxa (positive side) and deciduous pollen taxa (negative side), indicating an inverse relationship between forest pollen taxa and taxa typical of open environments. CCA2 is closely related to grassland pollen taxa on the negative side. Swamp pollen taxa have a positive relationship with both CCA1 and CCA2. Sites located in the different vegetation types cluster closely, with sites from deciduous and evergreen forest fairly well-differentiated in the upper left-hand quarter of the graph and sites in grassland habitats in the lower left-hand quarter of the graph, while sites from openland and swamp areas cluster together in the upper right-hand quarter.

NPPs cluster into four main groups (Figure 7). The coprophilous fungal spores, *Ascodesmis, Podospora, Sordaria, Sporormiella*, and *Saccobolus*, covary with the openland gradient. While, also present in relatively high numbers in the other vegetation types, they are most abundant in the openland and swamp habitats. *Helminthosporium* is the only type that covaries with the grassland gradient, which is unsurprising as this taxon consists mainly of molds that grow on grasses. Fungal NPPs that plot in the center of the graph, such as *Alternaria, Arnium, Helicoon, Tetraploa, Valsaria*, Type1, and Type2, are not strongly controlled by any of the environmental variables and occur at relatively similar proportions throughout the samples.

Some of these represent ubiquitous plant pathogens and decomposers (van Geel et al., 2003). All other fungal NPPs (*Bipolaris, Cookeina, Dictyosporium, Glomus, Meliola,* Microthyriaceae, Teleutospores) most strongly covary with the forest gradient. This group includes a number of species that grow on woody debris (*Cookeina, Dictyosporium*), as well as plant pathogens and decomposers, and the mycorrhizal fungus *Glomus*, which is well-known to form associations with tree roots (van Geel et al., 2003), though it occurs in a wide variety of environments.

Discussion

The modern pollen study of the different vegetation types and areas of different land-use in KNP reveals a good agreement with the extant vegetation. However, some site by site variation has been recorded in the fungal spores in the assemblages. A composite diagram shows the relationship between, the vegetation types and wildlife in KNP based on the abundance of local arboreal and non-arboreal pollen taxa and coprophilous fungal spores in the palynoassemblages (Figure 8). The evergreen forest is characterized by the high abundance of evergreen arboreal pollen taxa (31.3%). The high abundance of deciduous arboreal pollen taxa (32.6%) in the palynoassemblages signifies the deciduous forest. The grassland is characterized by the abundance of Poaceae pollen (30.6%). Similarly, the openland area is characterized by the abundance of both Poaceae (20.6%) and other associated non-arboreal pollen (20.2%). The swamp area is characterized by the high abundance of marshy and aquatic pollen (21.9%) followed by deciduous (20.1%), evergreen (10.6%) and Poaceae (15.6%) pollen. The abundance of the coprophilous fungal spores in the openland (60.7%), swamp (59.3%), and grassland (23.9%) are exhibited in the palynoassemblages which indicates that these sites are highly impacted by the herbivores. The evergreen and deciduous forest can be characterized as moderately impacted sites as indicated by the relatively lower abundance of coprophilous fungal spores with average values of 16.4% and 16.3%, respectively in the palynoassemblages.

The samples taken from the evergreen forest reveals *Mesua-Schima-Duabanga-Cinnamomum*-Arecaceae-*Litsea* assemblage, showing a good relationship between the pollen and extant vegetation. The abundance of evergreen taxa, especially *Mesua*, *Duabanga*, and *Syzygium* in the pollen assemblage is significant (maximum value up to 4.9%) and is indicative of high rainfall activity in the region, as these taxa are high rainfall indicators (>2500 mm/y; Singh et al., 1990; Barboni and Bonnefille, 2001). The evergreen forest was evident in the KNP by the presence of *Mesua* and *Duabanga* pollen in the rhino dung samples (Basumatary et al., 2017), as these aforesaid taxa are dominant in the evergreen forest of the KNP. The presence of marshy and aquatic taxa, such as Cyperaceae, *Polygonum*, *Nymphoides*, and *Nymphaea* pollen, which could have been transported by wild herbivores and birds, indicate natural perennial water bodies in and around the study area (Ekblom and Gillson, 2010; Basumatary et al., 2017; Stivrins et al., 2019). During the daytime after feeding in the swamp areas these animals move towards the surrounding forests for rest, shelter or to forage in the forest.

Among the fungal spore assemblages, the presence of non-coprophilous fungal spores, Microthyriaceae, *Glomus*, and *Meliola* was marked. These taxa are characteristic of dense forest vegetation under warm and humid climatic conditions in response to the high rainfall in the region. Specifically, the abundance of Microthyriaceae, *Glomus*, and *Meliola* is considered to be indicative of the presence of dense forest vegetation (Musotto et al., 2012, 2017; Cookson, 1947; Selkirk, 1975; Johnson and Sutton, 2000; Hofmann, 2010; Medeanic and Silva, 2010; Loughlin et al., 2017), and this is reflected in the studied samples from KNP. In the palaeoecological literature, *Glomus* is often seen as an indicator of erosion (Shumilovskikh et al., 2021). However, since this fungus is an endomycorrhiza and often associates with trees, in this case the abundance of its spores is due to its abundance in the forest soil (Kołaczek et al., 2013).

The presence of coprophilous fungal spores was marked in the studied samples and the relatively high percentages are indicative of the presence of wildlife. The coprophilous fungal spores may be limited to specific locations frequented by herbivores so can be considered local in origin since they can only actively disperse a short distance which restricts their presence to near to where sporulation took place (Davis et al., 1977; Parker, 1979; Wicklow, 1992; Richardson, 2001; Malloch and Blackwell, 1992; van Geel et al., 2003, 2008; van Geel and Aptroot, 2006; Ekblom and Gillson, 2010; Parker and Williams, 2011; van Asperen et al., 2021). The frequency of *Sporormiella*, *Ascodesmis*, and *Saccobolus* was relatively higher in openland and swamp areas as compared to the dense forest. In our study, the moderately high value of coprophilous fungal spores (5.6%) was observed in the palynoassemblage which is quite higher than the 2%, considered as a 'background' level (Davis, 1987; Gill et al., 2013; Baker et al., 2016; Raczka et al., 2016). These spores can therefore be inferred to reflect local abundance of the herbivore fauna. The forest area is generally dark, windless, cooler and more humid than outside the forest; conditions that are favorable for fungal growth (Musotto et al., 2017; Promis et al., 2010; Godeas and Arumbarri, 2007). Monkeys, gibbons, birds, and other arboreal animals are common, and their excreta regularly falls to the forest floor. The diversity of the fungal remains especially the non-coprophilous fungal spores is high in all samples.

The *Salmalia*-*Dillenia*-*Lagerstroemia*-*Semecarpus*-*Careya* pollen assemblage was in agreement with the extant deciduous forest vegetation in KNP. The *Dillenia*-*Terminalia*-*Careya* assemblage is significant as it is characteristic of the preferred habitat of wildlife in the Balpakram valley in the Garo hills of Meghalaya (Basumatary et al., 2014) which coincided with the pollen assemblages in KNP. These plants are utilized as the primary food plants preferred by many herbivorous mammals including elephant and deer species (Odden et al., 2005; Steinheim et al., 2005; Neupane et al., 2019; Devi et al., 2022). The consistent abundance of *Bombax* pollen in the palynoassemblage which is recorded upto 4.7% was marked in comparison to the other associated arboreal taxa. *Bombax* is a fire resistant plant (Troth, 1976) which is one of the reasons for its abundance in the palynoassemblage. Forest fires during winter are an important part of the ecology for the wildlife of KNP. Herbivory is an important driver of vegetation structure in the region (Ekblom and Gillson, 2010), so the large herbivores may have played a significant role in shaping the structure of plant communities in the KNP. The coprophilous fungi, *Sporormiella*, *Saccobolus*, and *Ascodesmis* are represented consistently in the studied samples and their abundance closely resembles that in the evergreen forest samples and is also indicative of the presence of wildlife habitation in the deciduous forest. These fungi are also present at relatively higher abundances than in the evergreen forest, indicative of the higher impact of herbivores on the deciduous forest.

The percentages of Poaceae pollen are relatively high in the grassland samples (average 30.7%) and the *Salmalia*-*Dillenia*-*Emblica*-*Butea*-*Careya*-Poaceae pollen assemblage was identified as characteristic of this habitat. The presence of some arboreal taxa, especially *Mesua*, *Duabanga*, and *Symplocos,* is significant as these taxa do not usually occur in this vegetation type. Given that these taxa are insect-pollinated, they most likely have been secondarily deposited through animal dung where the herbivores ingested the plant parts elsewhere and were subsequently defecated in and around the grassland areas. The presence of arboreal pollen taxa, both evergreen and deciduous, was recorded from the midden dung of rhinoceros from forested and grassland regions of KNP (Hazarika and Saikia, 2010; Basumatary et al., 2018). The pollen clumping in grasses and *Bombax*, is marked and indicative of their local origin. The presence of pollen grain clumps is a characteristic feature of entomophilous plants whose pollen disperses shorter distances than wind-dispersed pollen grains (Faegri and Van Der Pijl, 1966; Martin et al., 2009). Since the Kaziranga National Park is enriched with swampy areas, the aquatic vegetation need to be included in the pollen spectra for monitoring the status of water level through pollen records in relation to the monsoonal activities. Moreover, the dung of the megaherbivores like one horn rhino also include aquatic pollen and thus, the modern aquatic pollen preservation could act as a baseline for the coprolite studies for tracing the megafaunal extinction during the Quaternary (Basumatary et al., 2017). The generated pollen data would assist in distinguishing the natural forest vegetation from areas impacted by human activities in the region, based on the fossil marker pollen taxa like Poaceae and Brassicaceae (Basumatary et al., 2018; Tripathi et al., 2021).

Among the fungal spores, coprophilous fungi such as *Sporormiella*, *Saccobolus*, *Podospora*, and *Ascodesmis* are dominant and represented consistently in the palynoassemblages. Herbivorous animals, especially rhinoceros and elephant, feed and defecate in the grassland, dispersing coprophilous fungal spores with their dung. However, although they are more common than in the forest assemblages, coprophilous fungal spores are less common in the grassland than in the openland and swamps. This may be due to the midden behaviour of some of the large mammals, especially the rhinoceros, which tends to defecate in specific areas, so the spores are not distributed uniformly on the landscape. The *Sporormiella*-*Saccobolus*-*Ascodesmis* assemblage was present in the midden dung of rhinoceros from grassland areas (Basumatary and McDonald, 2017) from the KNP. Among the non-coprophilous fungi, *Helminthosporium* and *Alternaria* are especially dominant. Both taxa are common pathogens of herbaceous plants, particularly grasses. Other fungal spores such as *Glomus*, Microthyriaceae, and *Tetraploa* are also present in lower values in the assemblages. However, grasses have a high resistivity to fungal infection due to their silica content (Park et al., 2006, 2010; Hayasaka et al., 2008) which is the main reason for the low fungal diversity exhibited in the grassland.

The palynological study in the openland area identified some distinguishing features of this habitat within the park, as it is characterized by the *Salmalia*-*Dillenia*-*Mesua*-*Barringtonia*-*Litsea*-*Melastoma*-Poaceae-*Mimosa* pollen assemblage. Grasses are dominant and recorded a maximum value upto 19.8%. However, the arboreal, marshy, and aquatic taxa, *Mesua*, *Bombax*, *Lagerstroemia*, *Syzygium*, Onagraceae, and *Nymphaea* are also consistently present in the pollen assemblages. This reflects the excreted dung of herbivorous animals and birds which incorporated these tree taxa through their ingestion in and around the openland areas. Pollen clumping of Poaceae, Cyperaceae, and *Polygonum* is very common in the palynoassemblages indicating they originate from local sources (Faegri and van der Pijl, 1966; Martin et al., 2009). Among the fungal spores the coprophilous fungal spores *Sporormiella-Saccobolus-Ascodesmis* are dominant in the assemblage and confirmed that the openland habitat can be considered to function as a corridor for wildlife. The abundance of coprophilous fungal spores in the openland areas suggests a direct link of abundance of wildlife and higher amount of decomposed organic matter derived from dung.

The palynological study of the swamp sediments reveals that the *Salmalia-Dillenia-Syzygium-Mesua-Duabanga-Litsea-Melastoma*-Poaceae-*Mimosa* pollen assemblage indicates different types of forest vegetation in and around the swamp area of the national park. The riparian forest taxa, *Lagerstroemia*, *Barringtonia*, and *Duabanga* grow luxuriantly along the periphery of the wetland area. Among non-arboreal taxa, the marshy and aquatic taxa are local in source. The other terrestrial non-arboreal taxa, chiefly Asteroideae, Convolvulaceae, and *Mimosa*, were deposited in and around the areas by the inwash of rainwater. The presence of *Rhododendron* pollen (a flood marker taxon; Basumatary et al., 2019) indicates flood activity in the region.

Among the fungal spores the non-coprophilous fungal spores predominate but coprophilous fungal spores, especially *Sporormiella*, *Podospora*, and *Saccobolus*, are still comparatively abundant in comparison to the other studied sites. The preserved fungal spores may have originated from surrounding areas and subsequently transported and deposited through rainwater and slopewash. Furthermore, the swamp serves as a focal point for mammals and birds for their food and especially drinking water. The amount of dung, especially the midden dung of rhinoceros, is large. Water availability is an important factor for the germination and sporulation of coprophilous fungi (Austin, 1958; Ingold and Marshall, 1962; Kuthubutheen and Webster, 1986a, 1986b), and dung deposited in the swamp can be expected to remain wet longer than in the other vegetation types and thus enhance the potential for germination.

Among the non-coprophilous fungi *Tetraploa* was more abundant than in the other vegetation types, which reflects its ecology as a saprophytic fungus of Poaceae and Cyperaceae, both of which are major wetland taxa. The abundance of *Glomus* in the palynoassemblage might be the result of transport directly from the surrounding forest, as *Glomus* is indicative of soil erosion (van Geel et al., 2003; Kiage and Liu, 2009). The diversity of the coprophilous fungal spores is similar to that of the openland samples with abundant spores of *Sporormiella*, *Saccobolus*, and *Ascodesmis*. This pattern is also seen in the rhinoceros dung midden samples (Basumatary et al., 2017).

The presence of the extra-regional taxa, *Pinus*, *Abies*, *Picea*, and *Larix* in samples from all vegetation types is significant and indicative of strong wind activity from the higher Himalaya but might also be introduced by migratory Siberian birds (Barua and Sharma, 1999), when they fly through pollen-laden environments. The bird diversity documented in KNP is over 521 species of which more than 200 are residents while the rest are migrants, including local migrants (Rahmani et. al., 2022). Pollen may adhere to their body and feathers of migratory species and then subsequently be dislodged during grooming while they are in KNP, especially from species that may overwinter in the park.

Studies of modern analogues based on the pollen and fern spore assemblages have shown it is possible to distinguish agricultural land from the fallow and salt marsh grassland (Graf and Chmura, 2006). The presence of coprophilous fungal spores can aid in distinguishing grazed or manured land use from natural vegetation. Similarly, this study can serve as a guideline to differentiate and distinguish the different vegetation types and the presence and impact of herbivores based on the presence and absence of local arboreal pollen taxa along with coprophilous fungal spores especially *Sporormiella*, *Sodaria*, and *Ascodesmis* in the palynoassemblages. Vegetation structure is mainly controlled by herbivores density (Bell, 1982) in African savannah and the woody cover reduction is directly linked to the concentration of herbivores (Dublin et al., 1990), their presence or absence can be documented by the presence of coprophilus fungal spores in the palynological studies of soil sediments. In order to understand the actual reason of decline and extinction of megaherbivores whether by human activities or due to climate-induced environment change (Wroe et al., 2013) documentation of their presence, either directly by skeletal remains or indirectly via proxy such as coprophilous fungal spores is critical. Other evidence for human impact can be the ability to recognize former cropland whether manured or unmanured based on the representation of local arboreal pollen taxa and coprophilous fungal spores in the palynoassemblages preserved in sediments.

Comparison of pollen spectra with canonical correspondence analysis

The CCA confirms that the five vegetation types present in KNP are significantly different in their taxonomic composition and this is reflected in both the vegetation and pollen assemblages. While the fungal NPP assemblages are relatively similar in overall composition between the different vegetation types, there are some differences in abundance of the taxa recovered reflecting the populations levels of herbivores Coprophilous fungal spores are present in significant numbers in all vegetation types, but the concentration is greater in the openland and swamp areas, where herbivores are more abundant than in the forested areas. The other vegetation types are dominated by mycorrhizal fungi, pathogens and decomposers of the plant species common in these vegetation types.

Interaction between vegetation and herbivores

Demonstrating the strong relationship between pollen types and vegetation in an area provides an opportunity to infer changes in wildlife habitat at both a temporal and spatial scale. Complementing the pollen record is the associated coprophilous fungal spore record which can provide an indication of the presence of herbivore populations utilizing the different vegetation types in these habitats and thus responding to their expansion or reduction over time (Ekblom and Gillson, 2010). Integrating ecological studies of all herbivores in the park and their preferred habitats is critical to integrate with the documentation of the association of pollen and vegetation types to better understand how the vegetation and fauna interact through time (Table 3). Equally important is the documentation of the abundance and types of coprophilous fungal spores associated with each species' dung (Basumatary and McDonald, 2017; Basumatary et al., 2019; Basumatary et al., 2021) to provide more refined information on what species of herbivores were present and their association with specific habitats and recognize their heterogenous distribution on the landscape rather than just rough estimates of the increase or decrease in herbivore populations through time.

Conclusions

This study demonstrates that the depositional pattern of pollen and NPP and their relative abundance in different vegetation types in KNP parallels the vegetation present in each type of habit and the impact of herbivores that utilize them. The pollen data from the different vegetation types in KNP reveals a strong relationship with the extant vegetation. In contrast, the depositional pattern of fungal spores varies from site to site due to different levels of wildlife impact and seasonal differences in their presence and utilization of the different vegetation types in the national park. Our study is in close agreement with the vegetation survey and existing forest types in KNP (Champion and Seth, 1968; Das et al., 2014).

As such, the data will be helpful in providing a foundation to differentiate and distinguish the natural forest vegetation from areas impacted by human activities in the region, based on the fossil pollen record given the potential for misidentification of conserved landscapes such as national parks and wildlife sanctuaries and areas that are not set aside or protected and have been heavily impacted by human activity, such as deforestation, farming, and pastoral practices. This may be indicated by the presence and abundance of local arboreal pollen or the relative abundance of coprophilous fungi since unmanured soil has significantly less coprophilous fungi than manured soil (Graf and Chmura, 2006). The openland area is also an important place for wildlife survival as indicated by the presence of marker pollen taxa and the abundance of coprophilous fungal spores. The overall palynological analysis of the swamp sediments could be a reliable and complementary data for the representation of the vegetation types and abundances of herbivores both of which can contribute to palaeoecological and palaeoherbivory analysis.

Acknowledgements

We thank Director, Birbal Sahni Institute of Palaeosciences, India for laboratory facilities to carry out this research. First author is very much grateful to Department of Science and Technology, New Delhi for funding (DST No: EEQ-2021/000846 (SERB) the research work. First author is also thankful to the forest department, Govt. of Assam for permission to work and necessary help during field visit.

Declaration of conflicting interests

The authors declared that they have no conflict of interest.

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905 **LEGENDS**

906 **Table 1:**Taxa included in each environmental variable for the Canonical correspondence analysis (CCA).

908 **Table 2:**Characterization of marker pollen taxa recovered from the surface soil samples in relation to the different vegetation and landuse from Kaziranga National Park.

910 **Table 3:**Association between major mammalian herbivores and vegetation types in Kaziranga National Park.

912 **Figure 1.**a. Map showing the study areas; b. Vegetation coverage map of Kaziranga National Park (modified after Das et al., 2014).

914 **Figure2.**a.Thick evergreen forest within Kaziranga National Park, b. *Buceros bicornis* (Hornbills) sitting on the tree within the evergreen forest, c. Group of *Elephas maximus* (Asian Elephant) in deciduous forest in Kaziranga National Park, d. *Rhinoceros unicornis* grazing in the periphery near swamp.

918 **Figure 3.**a. Grassland and grazing by *Rhinoceros unicornis* b. A view of grassland during winter, c. A view of openland showing *Bubalus arnee* (Asian Buffalo) and numbers of

migratory birds, d. A view of swamp showing numbers of *Cervus duvauceli* (Swamp Deer) in the center.

Figure 4. Palynoassemblages recovered from the surface soil samples from the Kaziranga National Park.

Explanation of palynomorphs

a. *Bombax ceiba*, b. *Duabanga* in cluster, c. *Cinnamomum*, d. *Litsea*, e. *Terminalia*, f. *Lagerstroemia*, h. *Shorea robusta*, i. *Schima*, j. *Semecarpus*, k. *Syzygium*, l. Arecaceae, m. *Albizia*, n. *Lantana*, o. *Pinus*, p. *Rhododendron*, q. Asteroideae, r. Chinoroideae, s. *Impatiens*, t. Convolvulaceae, u. Cyperaceae, v. Poaceae in cluster, w. *Polygonum*, x. *Nymphaea*, y. *Typha*, z. Monolete, aa. Trilete, ab. *Sporormiella*, ac. *Sordaria*, ad. *Meliola*, ae. *Tetraploa*, af. *Glomus*.

Figure 5. Comparative pollen spectra in relation to the different vegetation types from Kaziranga National Park.

Figure 6. Comparative fungal spores spectra in relation to the different vegetation types and herbivores impact from the Kaziranga National Park.

Figure 7. Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types and environmental variables. NPP types (red) and samples (dark green: evergreen forest; light green: deciduous forest; yellow: grassland; orange: openland; light blue: swamp) are plotted against vegetation type indicator assemblages (blue arrows).

Figure 8. Composite pollen and fungal spore diagram in relation to the different vegetation types from Kaziranga National Park.

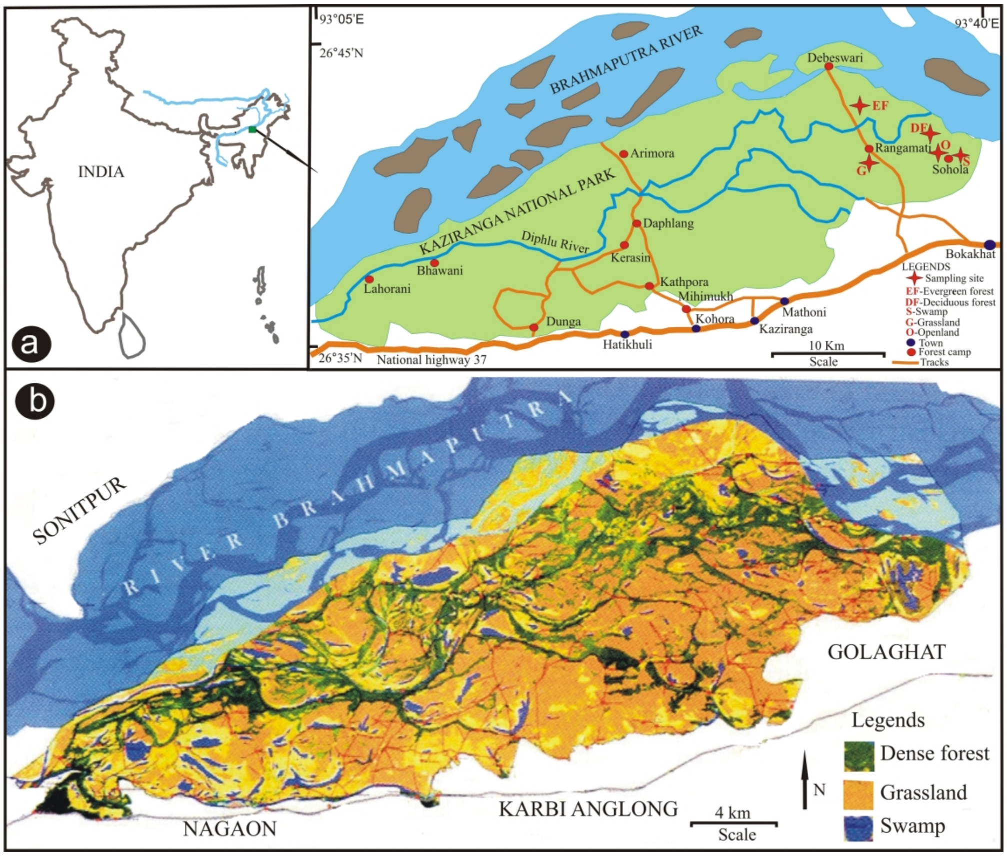


Figure 1. a. Map showing the study areas; b. Vegetation coverage map of Kaziranga National Park (modified after Das et al., 2014).

244x207mm (300 x 300 DPI)

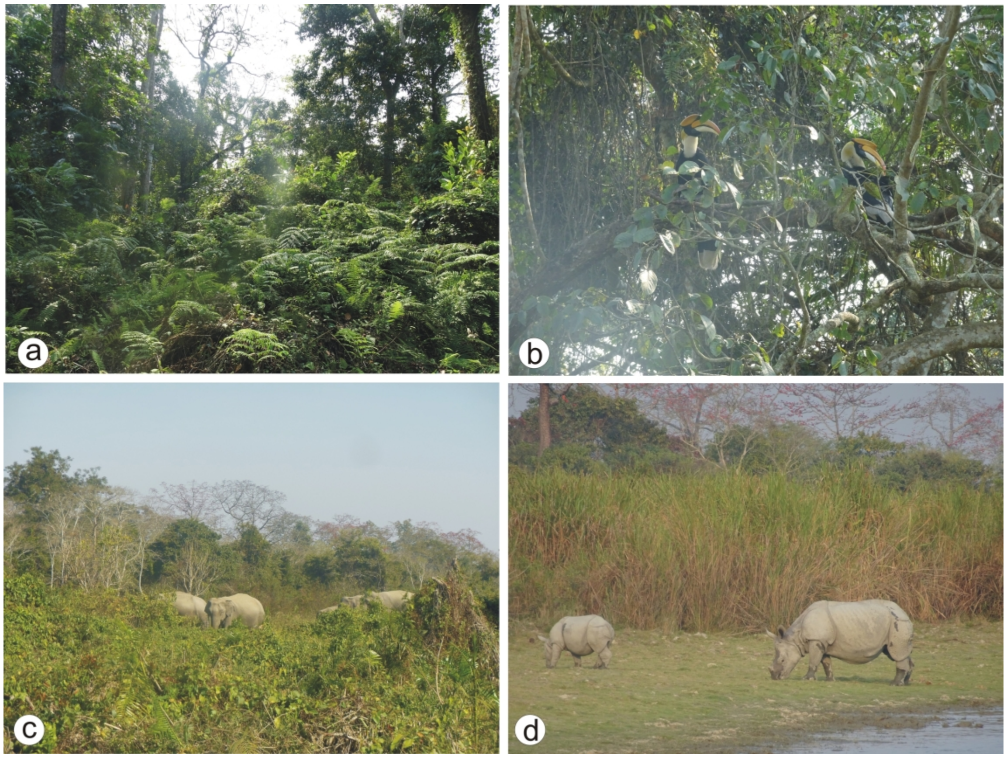


Figure 2. a. Thick evergreen forest within Kaziranga National Park, b. Buceros bicornis (Hornbills) sitting on the tree within the evergreen forest, c. Group of Elephas maximus (Asian Elephant) in deciduous forest in Kaziranga National Park, d. Rhinoceros unicornis grazing in the periphery near swamp.

266x200mm (300 x 300 DPI)

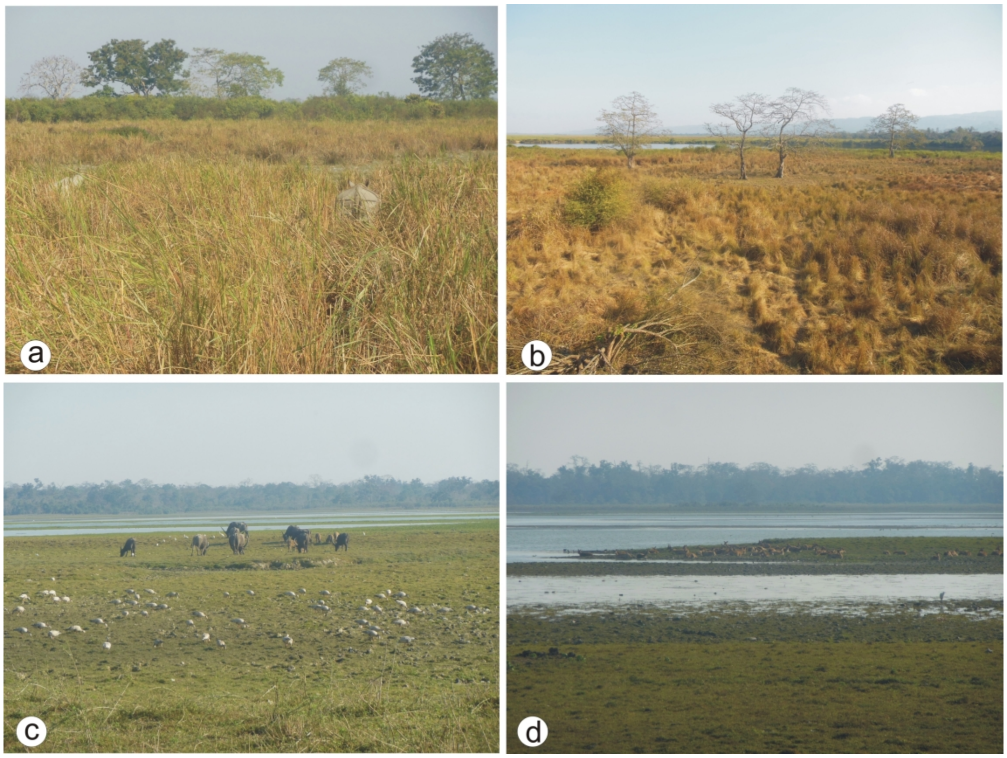


Figure 3. a. Grassland and show grazing of Rhinoceros unicornis b. A view of grassland during winter, c. A view of openland showing Bubalus arnee (Asian Buffalo) and numbers of migratory birds, d. A view of swamp showing numbers of Cervus duvauceli (Swamp Deer) in the center.

266x200mm (300 x 300 DPI)

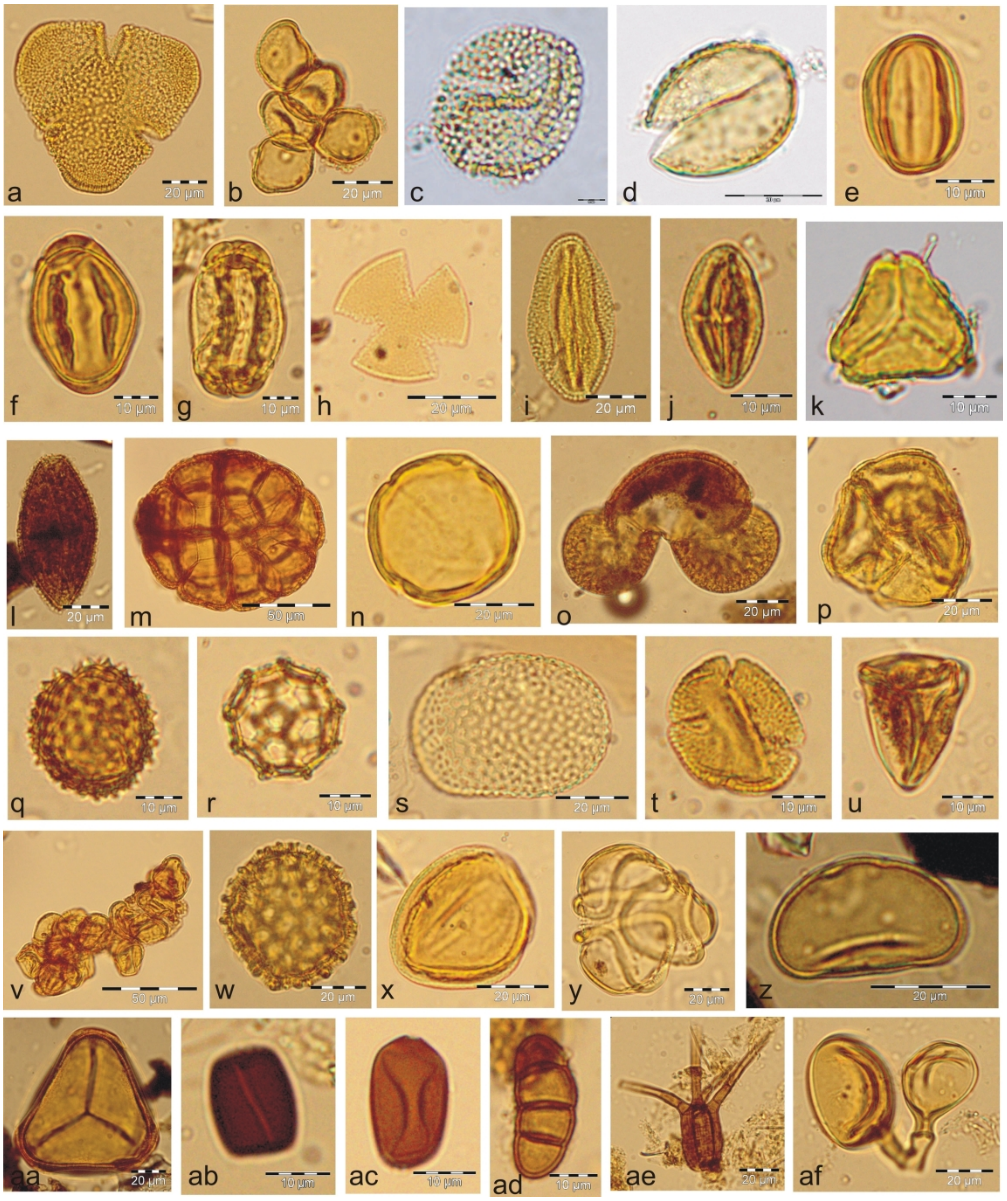
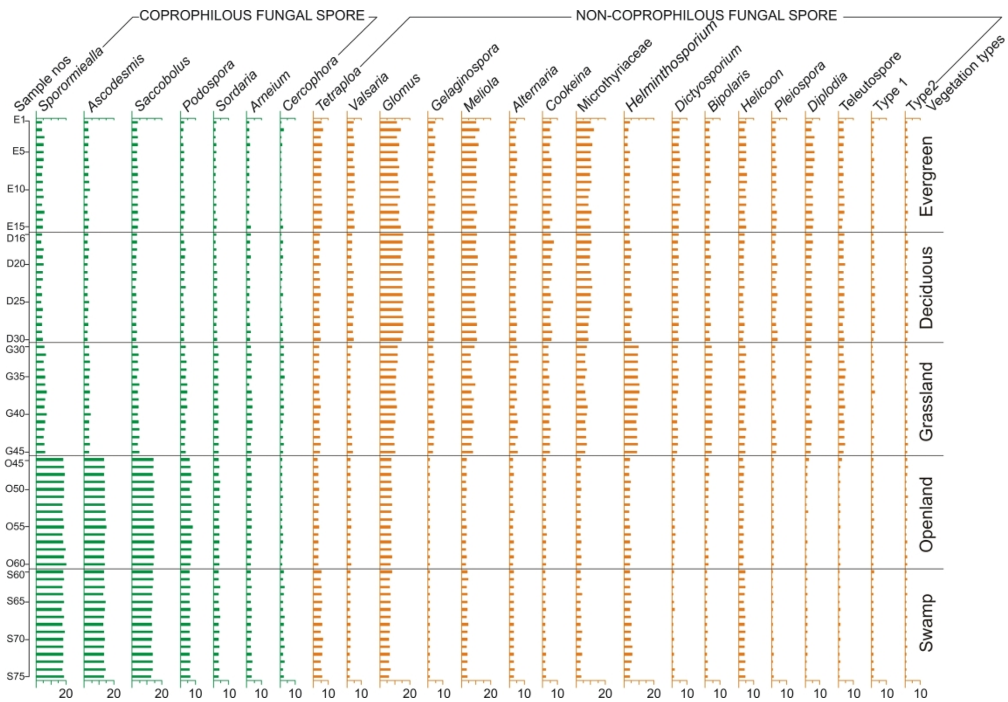


Figure 4. Palynoassemblages recovered from the surface soil samples from the Kaziranga National Park. Explanation of palynomorphs
a. Bombax ceiba, b. Duabanga in cluster, c. Cinnamomum, d. Litsea, e. Terminalia, f. Lagerstroemia, h. Shorea robusta, i. Schima, j. Semecarpus, k. Syzygium, l. Arecaceae, m. Albizia, n. Lantana, o. Pinus, p. Rhododendron, q. Asteroideae, r. Chinoroideae, s. Impatiens, t. Convolvulaceae, u. Cyperaceae, v. Poaceae in cluster, w. Polygonum, x. Nymphaea, y. Typha, z. Monolete, aa. Trilete, ab. Sporormiella, ac. Sordaria, ad. Meliola, ae. Tetraploa, af. Glomus.

198x236mm (300 x 300 DPI)

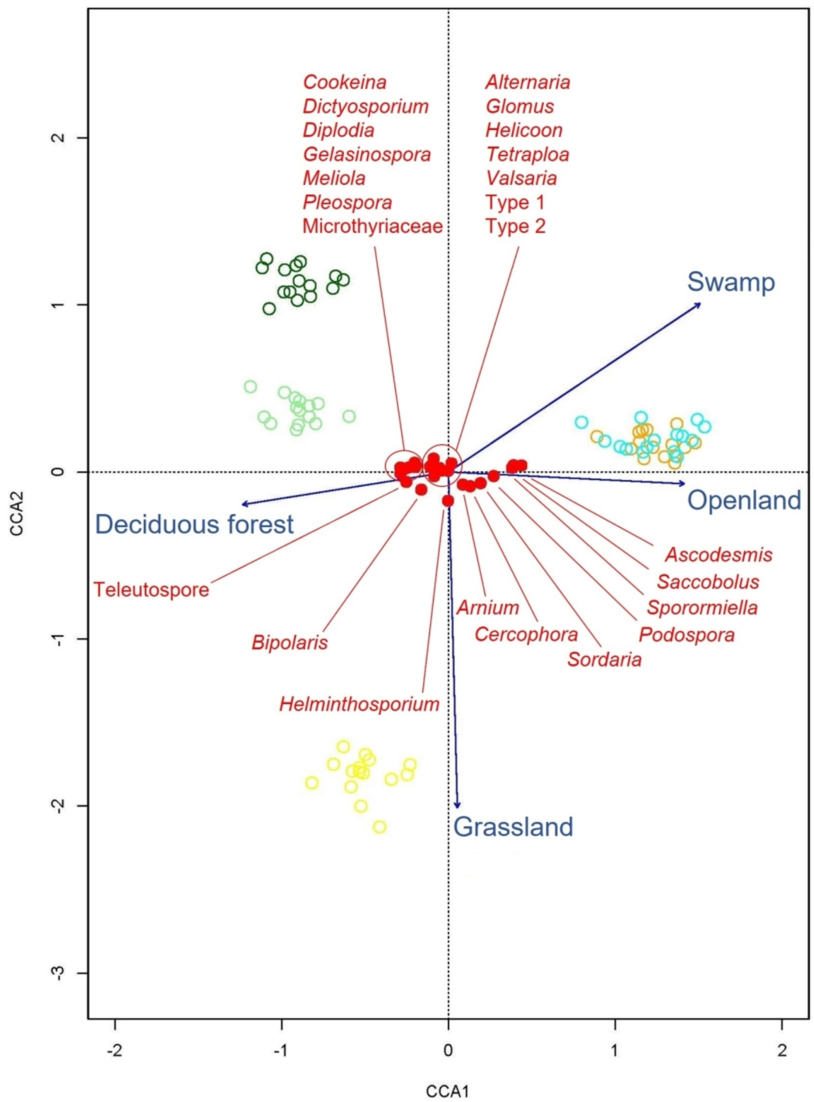
Comparative pollen spectra in relation to the different vegetation types from Kaziranga National Park.

290x144mm (300 x 300 DPI)



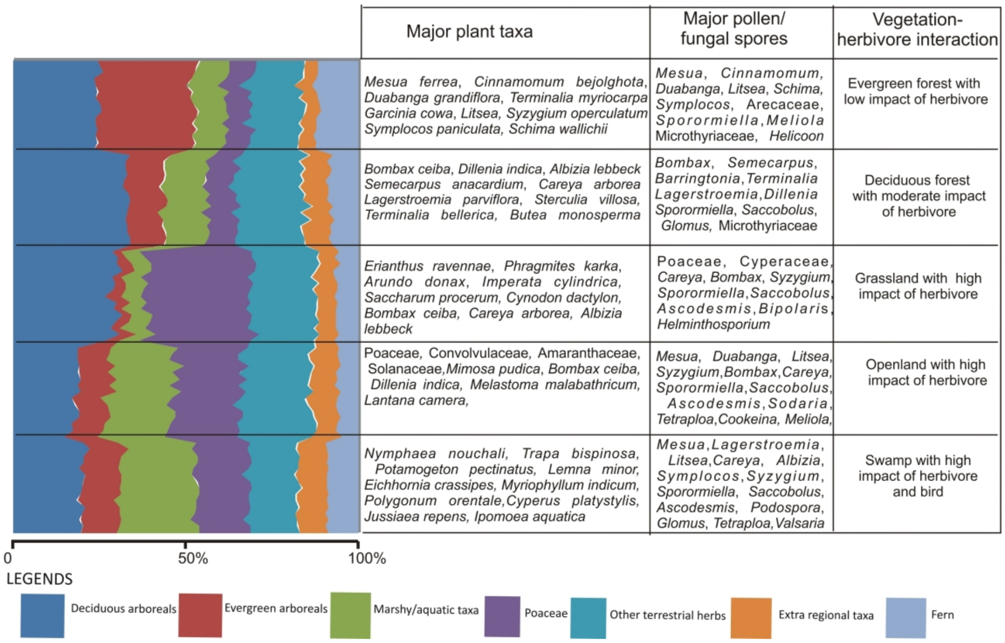
Comparative fungal spores spectra in relation to the different vegetation types and herbivores impact from the Kaziranga National Park.

279x192mm (300 x 300 DPI)



Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types and environmental variables. NPP types (red) and samples (dark green: evergreen forest; light green: deciduous forest; yellow: grassland; orange: openland; light blue: swamp) are plotted against vegetation type indicator assemblages (blue arrows).

134x190mm (300 x 300 DPI)



Composite pollen and fungal spore diagram in relation to the different vegetation types from Kaziranga National Park.

284x180mm (300 x 300 DPI)

Table 1. Taxa included in each indicator assemblage score

Vegetation type	Major taxa included
Evergreen (EV)	*Cinnamomum, Duabanga, Litsea, Mesua, Schima, Symplocos,* Arecaceae, Dipterocarpaceae, Oleaceae, *Impatiens,* Piperaceae
Deciduous (DC)	*Albizia, Careya, Dillenia, Emblica, Lagerstroemia, Lannea, Bombax, Semicarpus, Sterculia, Terminalia*, Convolvulaceae, Cyperaceae, Lamiaceae
Grassland (GL)	*Butea, Bauhinia, Dillenia, Bombax*, Asteroideae, Chinoriideae, Poaceae
Openland (OL)	*Barringtonia, Bombax, Clerodendron, Lantana, Melastoma, Bombax, Justicia, Mimosa, Xanthium,* Amaranthaceae, Convolvulaceae, Cyperaceae, Euphorbiaceae, Onagraceae, Solanaceae
Swamp (SW)	*Syzigium, Eichhornia, Lemna, Myriophyllum, Nymphoides, Polygonum, Potamogeton, Typha, Nymphaea*, Onagraceae

Table 2: Characterization of marker pollen taxa recovered from the surface soil samples in relation to the different vegetation and landuse from Kaziranga National Park.

Marker pollen taxa	Vegetation type/Ecological significance/Indicator
1. *Mesua*	Evergreen/High rainfall/Forestland
2. *Schima*	Evergreen/High rainfall/Forestland
3. *Litsea*	Evergreen/High rainfall/Forestland
4. *Cinnamomum*	Evergreen/High rainfall/Forestland
5. *Duabanga*	Evergreen/High rainfall/Swamp
6. Dipterocarpaceae	Deciduous/High rainfall/Forestland
7. *Bombax*	Deciduous/Forestland/Openland
8. *Syzygium*	Deciduous/High rainfall/Forestland
9. *Albizia*	Deciduous/Forestland
10. *Semecarpus*	Deciduous/forestland
11. *Sterculia*	Deciduous/Forestland
12. *Lagerstroemia*	Deciduous/Riparian/Forestland
13. *Barringtonia*	Riparian/Swamp/Forestland
14. *Careya*	Deciduous/Swamp/Forestland
15. *Melastoma*	Deciduous/Swamp/Openland
16. *Dendropthae*	Evergreen/Deciduous/High rainfall
17. *Impatiens*	Riparian/High rainfall/Forestland
18. Poaceae	Perennial herb/Grassland/Openland
19. Cyperaceae	Marshy/Swamp
20. Onagaraceae	Marshy/Aquatic/Swamp
21. *Eichhornia*	Marshy/Aquatic/Swamp
22. *Polygonum*	Marshy/Swamp
23. *Xanthium*	Marshy/Swamp
24. *Nymphoides*	Aquatic/High rainfall/Swamp
25. *Nymphaea*	Aquatic/High rainfall/Swamp
26. *Potamogeton*	Aquatic/High rainfall/Swamp
27. *Typha*	Aquatic/High rainfall/Swamp
28. *Justicia*	Perennial herb/Openland
29. Convolvulaceae	Perennial herb/Openland
30. *Mimosa*	Perennial herb/Openland

Table 3. Association between major mammalian herbivores and vegetation types in Kaziranga National Park.

Mammalian Taxon	Evergreen Forest	Deciduous Forest	Grassland	Open Land	Swamp	Reference
Rhinoceros unicornis	++	+++	+++	++	+++	Gurung and Chalise, 2015; pers. Comn. Local community
Elephas maximus	+++	+++	+++	+	+++	Neupane et al., 2019; pers. Comn. Local community
Bubalus bubalis	++	+++	+++	+++	+++	pers. Comn. Local community
Bos gaurus	+++	+++	+	++	+++	Imama and Kushwaha, 2013; pers. Comn. Local community
Cervus unicolor	++	+++	+++	+++	+++	pers. Comn. Local community
Cervus duvauceli	++	+++	+++	++	++	pers. Comn. Local community
Axis porcinus	+	+++	+++	+++	+++	Biswas 2004; Odden et al,

						2005; Peacock 1933; Johnsingh et al. 2004
Muntiacus muntjak	++	+++	+++	+++	+++	pers. Comn. Local community
Presbytis entellus	+++	+++	+	+	+	pers. Comn. Local community
Macaca mulatta	+++	+++	+	+	+	pers. Comn. Local community
Macaca assamensies	+++	+++	+	+	+	pers. Comn. Local community
Hylobates hoolock	+++	+++	+	+	+	pers. Comn. Local community

Legends

+-Low associated; ++-Moderate associated; +++-Highly associated

Pollen and non-pollen palynomorph depositional patterns in Kaziranga National Park, India: implications ~~to~~for ~~P~~palaeoecology and palaeoherbivory analysis

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Abstract

The main aim of this study is to produce a modern analogue for pollen and non-pollen palynomorphs (NPPs) preserved in soil in relation to the different vegetation types and herbivore impact in the Kaziranga National Park (KNP). The pollen data obtained reflects both the extant vegetation types in each habitat as well as landuse, but some ~~site by site~~site-by-site variation was observed with respect to the coprophilous fungal spores present in the palynoassemblage. Canonical correspondence analysis (CCA) analysis of pollen data reveals the presence of five significantly different vegetation types~~ and~~are~~significantly different~~, while the non-pollen palynomorphs are relatively similar in relation to the different vegetation types. ~~The *Sporormiella-Saccobolus-Ascodesmis* assemblage was marked and abundant in the openland and swamp habitat.~~The long-term association ~~impact~~ of the wildlife and their impact ~~i~~on different vegetation types ~~and theirhabitat~~with ~~long-term association~~ is one of the main reasons for the variation~~s~~ seen in ~~of~~the depositional pattern in the assemblage. ~~It is observed that t~~The openland

area is one of the most important ~~and impactful~~areas for ~~the~~ wildlife in the ~~National Park~~ KNP as indicated ~~evidenced~~by the presence of marker pollen and coprophilous fungal spores in the palynoassemblages. Coprophilous fungal spores were most abundant in this vegetation type reflecting the higher density of herbivores. The representation of pollen and coprophilous fungal spores from the swamp samples reflected the overall ~~a~~ composition of all vegetation types existing in the KNP. ~~and wildlife.which is considered as reliable palynodata and~~ This data c~~ould~~an be utilized as a baseline for the interpretation of palaeoecological and palaeoherbivory studies ~~analysis and to correlate it to~~ in other parts of the Indian subcontinent as well as its potential application at a global level.

Keywords

Coprophilous fungal spores, herbivores, palynoassemblages, pollen spectra, swamp, vegetation types.

Introduction

The study of modern pollen rain in relation to different vegetation types is a prerequisite for the interpretation of the past vegetation and climate in a region and how it has changed over time (Bent and Wright,1963; Janssen, 1967; Wright,1967; Overpeck et al., 1985; Prentice, 1985; Bunting et al., 2004; Wilmshurst and Mcglone, 2005; Xu et al., 2005; Deng et al., 2006; Gosling et al., 2009). ~~However, it is observed that, t~~The study of the modern pollen rain and extant ~~of~~ vegetation in ~~the~~ tropical regions ~~vegetation~~ is more complex and critical due to high biodiversity and ~~heterogenecity~~ heterogeneity of the pollen preservation ~~i~~on the forest floor and nearby areas, compared to ~~than the~~subtropical and temperate vegetation, as ~~is shown~~ documented by the presence and abundance of the major pollen taxa in the pollen assemblages (Mayle et al., 2000; Gosling et al., 2018; Bush et al., 2021). ~~It is identified that, the f~~ Phenological factors such as the timing of the flowering period and periods of high rainfall, along with pollen production, ~~high rainfall,~~ mode of pollination, and variation in the mode of pollen dispersal ~~variation~~ ~~al~~influence ~~during the~~ pollen preservation both ~~o~~in the landscape surface and eventual integration into soils and sediments. ~~soil.~~However, based on a knowledge of the pollen spectra and how it ~~the~~ represents ~~ation of~~ the major associated plant taxa in relation to the different vegetation types, it is possible to differentiate and distinguished ~~to~~ the different vegetation types in a region (Gaillard et al., 1994; Guimaraes et al., 2017) and as well as ~~allowing~~ the recognition of differences ~~also~~ between ~~the~~ modern and historic grassland uses (Hjelle, 1999).

There is an increasing global interest in palaeoherbivory and palaeodietary analysis in relation to palaeoecology during the Quaternary, particularly with respect to possible dietary changes that may have contributed to the extinction of megaherbivores (Barnosky et al., 2004; Rawlence et al., 2016). Many of these studies have been primarily based on pollen and non-pollen palynomorphs, especially changes in the relative abundance of coprophilous fungal spores, preserved in sedimentary ~~soil~~ profiles and coprolites (Burney et al., 2003; Robinson et al., 2005; Davis and Shafer, 2006; Carrión, 2007; Raper and Bush, 2009; Gill et al., 2009, 2013; Johnson et al., 2015; Graham et al., 2016; van Geel et al., 2018).~~).~~

The presence of coprophilous fungi in sediments and changes in their relative abundance has been used as an indicator not only of the past presence of herbivores,~~and changes in their relative abundance~~ but also to document changes in population sizes and in some cases the extinction of this part of the Pleistocene megafauna (van Geel, 1972, 1976, 1978; van Geel et al., 1981, 1983; Karanth and Sunquist, 1992; ~~Kuhry, 1985;~~ Feranec et al., 2011; Baker et al., 2013; Etienne et al., 2013; Lopez-~~V~~Vila et al., 2014; Loughlin et al., 2018~~7~~; Tunno and Mensing, 2017; van Asperen et al., 2021; Pokharia et al., 2022). More recently coprophilous fungi have increasingly been used as a proxy to address questions of pastoral and other human activities (Davis, 1987; Burney et al., 2003; van Geel et al., 2003; Gill et al., 2009; Miehe et al., 2009; Cugny et al., 2010; Feeser and O'Connell, 2010; Felauer et al., 2012; Johnson et al., 2015; Kamerling et al., 2017). When combined with the study of pollen grains, ~~and~~ fungal spores, especially of coprophilous fungi that grow on dung of herbivorous animals ~~,~~can provide useful information for understanding the food habit~~ats~~, ecology, diversity, niche partitioning and changes in relative abundance of past herbivorous species in a region (Ebersohn and Eicker, 1992; Ekblom and Gillson, 2010; Velazquez and Burry, 2012; Basumatary et al., 2017, ~~2018,~~ 2019, 2020, 2021~~2~~; Tripathi et al., 2019; Pokharia et al., 2022). ~~However,~~Previously~~some~~ work ~~have been carried out~~ on ~~the~~ the preservation of modern pollen and non-pollen palynomorphs ~~preservation~~ on the modern surface soil related to ~~in~~ highland grazing and past land use and other vegetation changes has also been investigated (Ejarque et al, 2011; Henga-Botsikabobe et al., 2020; Loughlin et al., 2021). Since both ~~The~~ fungal spores and the pollen grains in the sediments are commonly encountered in the same palynological slide (van Geel et al., 2003), the documentation of ~~and obviously, the combination~~ fungal spores, especially those of coprophilous fungal spores, along with the ~~and~~pollen grains can ~~will~~ be useful to interpret ~~of~~the impact of herbivores ~~impact~~ in relation to the different vegetation types in a region. ~~Since~~ As coprophilous fungal spores are dispersed only for a~~in~~ very short distance, they are ~~and~~ local in origin (Graf and Chmura, 2006; Johnson et al., 2015) so will ~~and~~ accumulate in sediments with pollen grains and are therefore indicators ~~es~~ of the local presence of ~~local~~ herbivores in relation to the existing vegetation.

~~However, some works~~While some research has ~~have~~ been conducted ~~carried out~~to understand ~~the~~ past vegetation and climate history in relation to the palaeoherbivory~~analysis~~ in ~~then~~National parks in ~~the~~ tropical regions of the world (Burbridge et al., 2004; Ekblom and Gillson, 2010), l~~. L~~ittle research has been carried out on modern pollen deposition in relation to the different vegetation types in n~~N~~ational p~~P~~arks and w~~W~~ildlife s~~S~~anctuaries in Asia (Djamali et al., 2009; Basumatary et al., 2014;Bera et al., 2014; Tripathi et al., 2016; Ghosh et al., 2017; Setyaningsih et al.,2019; Pandey and Minckley, 2019).~~These p~~ These p~~P~~revious studies have often not recorded ~~recorded~~ the presence ofcoprophilous fungal spores so cannot be used to determine~~in relation to~~ the presence and abundance of herbivorous animals in the region. In the absence of skeletal remains of these herbivores, ~~Since~~ coprophilous fungal spores may serve as an important proxy that can be used ~~be preserved in situations when skeletal remains of the herbivores are not preserved~~absent ~~such studies are important in order~~to reconstruct the palaeoecology of a region ~~in relation~~ with respect to the presence, types and abundance of herbivores and their impact on the local environment,~~including their diet,~~as well as how changes in the vegetation impacts the local wildlife (Basumatary and McDonald, 2017).~~**However, some works have been carried outto understand the past vegetation and climate history in relation to the palaeoherbivory analysis in the National parks in the tropical region of the world (Burbridge et al., 2004; Ekblom and Gillson, 2010).**~~

The main aim of this study is to document the depositional pattern of pollen and non-pollen palynomorphs in different vegetation types in Kaziranga National Park (KNP) in relation to the types of wildlife present and their impact on the different types of habitat. Determining the degree of representation of the coprophilous fungal spores in the surface soil and sedimentary profiles serves as the primary proxy to trace the relationship between flora and fauna in the region through time. So, tThe combination of pollen and non-pollen palynomorphs, especially the abundance of coprophilous fungal spores,are to be taken into consideration and calibration during the analysis which permits an interpretation of palaeoherbivory and palaeoecology analysis. However, bBased on the changes increase and decreasein frequency of coprophilous fungal spores in the sedimentary profile, an analysis is could be possible to trace the presence, relative abundance over time and eventual declined and extinction of members of the herbivorous mammals in theKazirangaNnational Ppark and to correlate the pattern with what is observed in other national parks located in the tropical and temperate region of the globe. So, bBased on the modern palynomorph analogues seen in different regions, it can cleared that the presence and absence of the local arboreal pollen taxa and coprophilous fungal spore in the pollen assemblages provides a means can possible to distinguish among the natural forest vegetation, from areas with heavy grazing or modified into and cropland in both tropical and temperate regions. in the globe The resulting information can serve as a baseline to examine the influence of palaeoherbivory in relation to theon vegetation palaeoecology in the National Park in the past. This also provides for a better determination of the first human occupation along with their domestic livestock in the area and subsequent impact on the flora and fauna.

Study sites

Kaziranga National Park covers an areaarea of around 430 square kilometers and is bordered on one side by the Brahmaputra River (Figure 1). In 1985, KNP was declared a UNESCO World Heritage Site in recognition of its significance aas one of the best managed wildlife parks in the world. As such,,KNP is one of the best sites in India and certainly for southeastAsia to observe the long-term interrelation between plants and the indigenous wildlife,as this interrelationship has not been as impacted as extensively by human activities and domesticated animals as at other sites in India. The park is within the Indo-Burmese biodiversity hotspot region, a critical corridor for immigration of members of the Indo-Malayan fauna into the Indian subregion. -It is also a critical reserve for tropical species, having served as a gene reservoir for these taxa during glacial periods (Tamma and Ramakrishnan, 2015).

Climate and soil

The climate of the region is controlled by the southwest and northeast monsoons. These weather patterns result in ~~hot,humid~~hot, humid summers, and cold, dry winters. The temperature ranges from a minimum of 4°C during winter up to 37°C in summer. The relative humidity is very high and ranges between ~~from~~ 75–86%. The annual rainfall ranges from 1800–2600 mm, and annual flooding is common in KNP during the summer. 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).

Vegetation and wildlife

In general, there are four main types of vegetation in the KNP; tropical evergreen forest, semi-evergreen forest, deciduous forest, grassland and swamp (Champion and Seth, 1968~~;~~ ~~Alfred, 1989~~). Alluvial grassland is the most dominant ~~covering~~ vegetation type (50.6%), followed by woodland (21.8%), openland areas covered by ~~ing~~ short grasses and other herbaceous associates (7.7%), and eroded land caused by ~~due to~~ soil erosion and land slides during intervals of high rainfall ~~activities and occupies (~~11.7%~~)~~ in the national park (Das et al., 2014).

The evergreen forest is generally confined to the areas adjacentto the Brahmaputra River, small rivers, and streamlets within the park. This vegetation remains evergreen throughout the year in the core regions and is dense and composed of forest elements including *Castanopsis indica*, *Cinnamomum bejolghota*, *Duabanga grandiflora*, *Elaeocarpus robustus*, *Toona ciliata*, *Mesua ferrea*, *Symplocos paniculata*, *Terminalia myriocarpa*, *Schima wallichii,* and *Litsea monopetala*. The common climbers are *Calamus erectus*, *Vitis latifolia, Paederia foetida, Cardiospermum halicacabum, Trichosanthes dioca, Smilax ovalifolia, Mucuna pruriens*, *Piper longum*, and *Thunbergia grandiflora*. Among the ferns, both terrestrial ferns and epiphytes such as *Lycopodium clavatum*, *Dryopteris filix-mas*, *Gleichenia dichotoma*, *Lygodium japonicum*, *Drynaria rigidula*, *Angiopteris evecta*, *Asplenium nidus*, and *Pyrrosia nummularifolia* are present (Figures 2a and2b).

The moist deciduous forest occurs as isolated patches within grasslands andnext to the evergreen forest. This forest consists of primarily deciduous trees which lose their leaves duringthe winter season. The major tree taxa are*Bombax ceiba, Dillenia indica, Albizia procera*, *A. lebbek, A. odoratissima,*Neolamarckia *cadamba, Trewia nudiflora*, *Careya arborea*, *Lagerstroemia parviflora,* and *Semicarpus anacardium*. The forest floor is covered by different species of Poaceae, Cyperaceae, Convolvulaceae, and Acanthaceae. The fern allies such as *Dryopteris filix-mas*, *Adiantum caudatum*, *Blechnum occidentale*,*Polypodium vulgare*, and *Drynaria rigidula* are the common membersin this forest (Figures 2c and2d).

The grassland areas are scattered and dominated by ~~nt of~~tall grasses ~~are~~mainly *Erianthus ravennae*, *Phragmites karka, Arundo donax*, *Imperata cylindrica*, and *Saccharum procerum* along with short grasses like *Hemarthria compressa*, *Microstegium ciliatum*, *Cynodon dactylon,* and *Cenchrus ciliaris*.However, some trees and shrubs such as *Bombax ceiba*, *Careya arborea*, *Dillenia indica, Butea monosperma*, and *Albizia lebbeck* also grow scattered within the grassland (Figures 3a and 3b).

The openland areas are also scattered especially near the periphery of the swamp. Tree taxa are almost absent ~~and~~ but there are some scattered shrubs such as *Melastoma malabathricum*, *Cassia tora,* and*Clerodendron viscosum*. The openland area is covered with short grasses followed by Cyperaceae, Acanthaceae, Amaranthaceae, Solanaceae, and Convolvulaceae. *Cynodon dactylon*, *Cenchrus ciliaris*, *Chrysopogon aciculatus*, *Digitaria ciliaris*, and *Paspalum conjugatum* are the common species in short grass communities (Figure 3c).

The swamp habitat is restricted to generally ~~low lying~~low-lying areas and covers around 11.8% of the p~~P~~ark (Das et al., 2014). It is submerged ~~underwater~~ throughout the whole year but during summer (May-August) the swamp habitat may be expanded due to flooding of river channels resulting from heavy monsoonal rainfall. The major marshy and aquatic taxa include *Alpinia allughas*, *Clinogyne dichotoma*, *Calamus tenuis*, *Polygonum orientale*, *Cyperus rotundus*, *Sagittaria sagittifolia*, *Eichhornia crassipes*, *Potamogeton pectinatus*, *Nymphaea alba*, *Euryale ferox*, *Myriophyllum indicum*, *Ludwigia sedioides*, and *Nymphoides indica*. Additionally, there are some trees and shrub~~s~~ taxa including *Syzygium cumuni*, *Barringtonia acutangula*, *Dillenia indica*, *Bombax ceiba*, *Osbekia stellata*, and *Costus speciosus*that commonly grow on the periphery of the swamp area (Figure 3d).

With regard to wildlife, KNP is mainly famous for ~~the~~its *Rhinoceros unicornis* (greater one-horned rhinoceros), but the park is also very rich in other animals and birds. The fauna includes 490 species of birds, 43 species of reptiles and 52 species of mammals (Choudhury, 2003). Besides rhinoceros, other associated large and medium sized mammalian herbivores include *Bubalus arnee*, *Elephas maximus*,*Bos gaurus*, *Sus scrofa*, *Cervus unicolor*, *Cervus duvauceli*, *Axis porcinus*, *Muntiacus muntjak*, *Presbytis entellus*, *Macaca mulatta*, *Macaca assamensies*, and *Hylobates hoolock*. Birds such as *Francolinus gularis*, *Anser erythropus*, *Houbaropsis bengalensis*, *Tringaguttifer*, *Sterna acuticauda*, *Ardea insignis*, and *Pelecanus philippensis* are commonly seen in the park.

Materials and methods

Field work

~~The collection of palynological samples from the KNPis challenging due to danger from attack bywildlife. A total of 75 surface soil samples were procured at about 50 meter intervals for pollenand non-pollen palynomorphs fromeach of the different vegetation types.~~ Out of ~~the~~ atotal of 75 surface soil samples, 15 (E1-E15) were collected from the evergreen forest, 15 (D16-D30) from deciduous forest, 15 (G31-G45) from grassland, 15 (O46-O60) from openland, and 15 (S61-S75) from the swamp. In each vegetation type, the samples were procured at about 50 meter intervals.

Laboratory work

The surface soil samples were chemically processed employing the standard acetolysis method (Erdtman, 1953). The soil samples were treated with 10% aqueous KOH solution to deflocculate the pollen and spores from the soil followed by 40% hydrofluoric acid (HF) treatment to dissolve silica content. This was followed ~~with treatment with an~~acetolysis ~~mixture (9:1 acetic anhydride $(CH_3 CO)_2 O$)and concentratedsulfuric acid (H_2SO_4))~~. The samples were washed 2-3 times with glacial acetic acid and then washed 2-3 times with distilled water and sieved through a 500µm mesh. Finally, the material was kept in a 50% glycerin solution with a drop of phenol. Totals of 259-335 pollen grains per slide of each ~~per~~ sample were counted to make the pollen spectra. The pollen taxa have been categorized into arboreal taxa, non-arboreal taxa, extra-regional taxa (highland taxa coming from the eastern Himalaya), and ferns. Similarly, a total of 225-284 fungal spores per slide were counted from the same pollen slides and ~~the fungal spores~~these were categorized into coprophilous and non-coprophilous fungal spores to make fungal spore spectra. For the precise identification of fossil palynomorphs in the sediments, the reference pollen slides available at Birbal Sahni Institute of Palaeosciences herbarium as well as ~~the~~ pollen and fungal spore photographs in the published literature (van Geel, 2003; Basumatary et al., 2017;

Basumatary and McDonald, 2017) were used. Photodocumentation of palynomorphs was made using Olympus BX-61 microscope with DP-25 digital camera under 40X magnification (Figure 4). The pollen and fungal spore ~~spectra~~ ~~diagrams~~spectra were madeusing TILIA software (Grimm, 2011) (Figures 5 and 6.). ~~Thepercentages of the recovered non-pollen palynomorphs (NPPs) have been calculated based on the total sum of pollen, including aquatic taxa.~~

~~3.2~~ *Statistical analysis: canonical correspondence analysis*

Five environmental variables were obtained from the pollen assemblages by calculating the total proportion of five vegetation type indicator assemblages in each site: (1) evergreen indicator assemblage score, (2) deciduous indicator assemblage score, (3) grassland indicator assemblage score, (4) openland indicator assemblage score, and (5) swamp indicator assemblage score (Table 1). These variables provide environmental gradients against which to assess the distribution of fungal NPPs. Pollen of wind-blown extra-regional taxa were excluded from the statistical analyses.

Many fungal NPPs have short dispersal distances, and can therefore be overrepresented in locations near fruitbodies but underrepresented at even a short distance from fruitbodies (Wilmshurst and McGlone, 2005; Van Asperen et al., 2021). A square-root transformation was applied to the fungal NPP percentage data to compensate for this effect (Legendre and~~&~~ Legendre, 2012; Paliy and Shankar, 2016; Borcard et al., 2018).

Canonical correspondence analysis (CCA; Ter Braak 1986; Borcard et al., 2018) was carried out on the transformed NPP data and the five environmental variables to assess the influence of the five vegetation type assemblages on the distribution of NPPs. Collinearity among the vegetation type assemblages was explored by computing Variance Inflation Factors (VIFs). Based on the results of this, CCA with forward selection of explanatory variables was carried out. Canonical axes were tested for significance by permutation ANOVA. CCA was performed in R (Version 4.0.4, R Development Core Team, 2015) using the package vegan (Oksanen et al., 2017).

Results

The presence and abundance of major pollen taxa, which serve as marker taxa and their ecological significance in KNP are listed in Table 2. Diagrams of the pollen and fungal spore spectra are presented in Figures 5 and 6 respectively.

Evergreen forest: The surface soil samples (E1-E15) are characterized by the dominance of the major evergreen taxa ~~namely~~*Mesua, Schima,* Arecaceae, *Symplocos*, and *Litsea* with values of 1.6~~%~~-4.9% each followed by deciduous elements at values of 1.0~~%~~-3.0%. Among non-arboreal taxa, Poaceae is recorded with values of 6.0~~%~~-8.2% and other ~~terrestrial,~~~~aquatic and~~ herb taxa are also consistently encountered with values of 3.3~~%~~-3.8% in the pollen assemblages. Extra-regional taxa are consistently present but with ~~sporadic~~low values. ~~The f~~Ferns, both monolete and trilete, are encounteredwith ranges of 4.5~~%~~-8.0% (Figure5). The most common ~~C~~coprophilous fungal spores ~~include~~ are of the taxa*Sporormiella*, *Saccobolus*, and *Ascodesmis* with values of 0.8~~%~~-5.6%. *Podospora, Sordaria, Arnium* and *Cercophora* were also encountered at low values. Non-coprophilous fungal spores ~~, includingMicrothyriaceae, *Meliola*, and *Glomus*~~are ~~also~~ consistently represented at the ranges of 0.8~~%~~-14.1% ~~in the assemblages(Figure6)~~, with *Glomus, Meliola* and Microthyriaceae the most common taxa.

Deciduous forest: The ~~palynological analyses~~samples from the deciduous forest (D16-D30) are characterized by the dominance of deciduous taxa with the ranges of 0.3~~%~~-4.7% each,~~over~~ compared with evergreen taxa at ~~the~~ values of 0.3~~%~~-1.6%. Among non-arboreal taxa, Poaceae is dominant and varies from 6.5-~~ is dominant with a maximum value of~~ 9.4% and the other associated terrestrial and aquatic herbs are also recorded with values of 0.3~~%~~-4.6%. Extra-regional taxa are ~~primarily~~ represented with maximum values upto 2.1% in the pollen assemblages. Fern spores ~~,both monolete and trilete,~~ are also consistently present with maximum ranges of 4.5% and 5.8% respectively~~(Figure5)~~.

The coprophilous fungal spores ~~include *Sporormiella, Saccobolus*, and*Ascodesmis*~~occur with values from 0.9~~%~~-4.9%. Non-coprophilous fungal spores are dominated by~~include*Tetraploa*,~~ *Meliola*, *Glomus*, and ~~*Helminthosporium*~~Mycrothyriaceae as in the Evergreen forest, ~~are consistently recorded~~with ranges from 0.8~~%~~-15.5%~~(Figure6)~~.

Grassland: The ~~palynological study of~~ surface soil samples (G31-G45) from the grassland habitat ~~is~~are characterized by the dominance of Poaceae with an average value of 30.7%. ~~over o~~Other associated terrestrial and aquatic taxa occur with maximum ranges upto 9.7%~~ in the pollen assemblages~~. Arboreal taxa, both evergreen and deciduous elements, namely *Mesua, Bombax* and *Careya* are ~~also~~ regularly encountered ~~in sporadic~~ at low values. The extra-regional taxa are also consistently recorded with maximum values of ~~upto~~ 2.6%. The monolete and trilete ferns are ~~also~~ represented with ranges of 1.9~~%~~-5.6% in the pollen assemblages (Figure5). Coprophilous fungal spores ~~including~~are dominated by *Sporormiella*. ~~,~~*Saccobolus*, and *Ascodesmis* ~~are present at the~~ with ranges of 1.0~~%~~-6.9%, with other coprophilous taxa reaching 6.2~~xx~~%. Among the ~~N~~non-coprophilous fungal spores, *Helmithosporium* is abundant with values up to 11.5~~xx~~%. *Meliola*~~, *Helminthosporium*, *Alternaria*,~~ and *Glomus* are regularly recorded with values of 0.5%-11.8%~~(Figure6)~~.

Openland: ~~The palynological analysisof t~~The samples (O46-O60) from the openland located adjacent to the swamp are characterized by the dominance of non-arboreal taxa with an average value of 58.9% compared to arboreal taxa at 27.3%, followed by extra-regional taxa (7.7%) and ferns (6.1%). Among arboreal taxa, both evergreen and deciduous elements are regularly encountered at ~~the~~ ranges of 0.3~~%~~-4.9%. Among non-arboreal taxa Poaceae is dominant with an average value of 19.8% and the other ~~associated~~ herb taxa are consistently represented by values of 0.3~~%~~-6.1% in the pollen assemblages. The extra-regional taxa are regularly encountered at the ranges of 0.4~~%~~-3.2%. The ferns, both monolete and trilete, are recorded by ranges of 2.1~~%~~-4.3% (Figure5).The coprophilous fungal spores are much more abundant than in the e~~E~~vergreen and d~~D~~eciduous forest and the g~~G~~rassland. They are dominated by ~~include~~*Sporormiella*, *Saccobolus*, and *Ascodesmis* which are recorded at the values of 1.0~~%~~-20.0% each. The non-coprophilous fungal spores~~, *Helminthosporium*, *Bipolaris*, *Cookeina*, and *Glomus*~~ are less abundant that in the f~~F~~orest and g~~G~~rassland areas, ~~consistently encountered~~with values of 0.7~~%~~-8.0%~~(Figure6)~~.

Swamp: The ~~palynological analysis of the~~ mud samples (S61-S75) from the swamp habitat are characterized by the dominance of non-arboreal taxa with an average value of 51.5% over arboreal taxa (30.7%). The ferns and extra-regional taxa are also recorded with average values of 9.2% and 8.6% respectively. Among arboreal taxa both evergreen and deciduous taxa are consistently encountered at the values of 0.3~~%~~-3.9%. Among non-arboreal taxa Poaceae is dominant with an average value of 15.6%. The marshy and aquatic taxa are consistently recorded with~~the~~ranges of 0.6~~%~~-4.5%. The extra-regional taxa are consistently encountered at the values of 0.3~~%~~- 2.9%. The fern spores, both monolete and trilete, are represented by values of 3.2~~%~~-

5.8% in the pollen assemblages (Figure5). Among fungal spores, the coprophilous fungal spores are similarly abundant as in the o~~O~~penland samples, and are dominated by ~~include~~*Sporormiella*, *Saccobolus*, and *Ascodesmis* which are represented in the range of 1.8~~%~~-19.2% each. The non-coprophilous fungal spores~~, Microthyriaceae, *Helminthosporium*, *Bipolaris*, and *Glomus*~~ are present ~~but~~ at ~~much~~ similarly lower ranges as in the o~~O~~penland samples of 0.4~~%~~-7.8~~%~~ %~~in the assemblages(Figure 6)~~.

Statistical analysis of NPPs frequencies

VIFs based on an initial CCA indicated significant collinearity was present among the environmental variables. Therefore, CCA with forward selection was carried out. Four environmental variables were selected for inclusion in the CCA: Deciduous forest, Grassland, Openland and Swamp (Figure 7). The environmental variables account for 92.4% (constrained inertia = 0.22728, total inertia = 0.24572) of the variance in the fungal NPP data. The first two CCA axes (eigenvalues: CCA1 = 0.2066, CCA2 = 0.01577) explain 90.4% of the variance.The permutation tests show that both the CCA as a whole (p = 0.001) and each CCA axis (each p = 0.001) are significant and VIFs indicate collinearity among the vegetation type assemblages is low in this analysis.CCA1 is closely related to the openland pollen taxa (positive side) and deciduous pollen taxa (negative side), indicating an inverse relationship between forest pollen taxa and taxa typical of open environments. CCA2 is closely related to grassland pollen taxa on the negative side. Swamp pollen taxa have a positive relationship with both CCA1 and CCA2. Sites located in the different vegetation types cluster closely, with sites from deciduous and evergreen forest fairly well-differentiated in the upper left-hand quarter of the graph and sites in grassland habitats in the lower left-hand quarter of the graph, while sites from openland and swamp areas cluster together in the upper right-hand quarter.

NPPs cluster into four main groups (Figure 7). The coprophilous ~~types~~ fungal spores, *Ascodesmis,Podospora, Sordaria, Sporormiella*, and *Saccobolus*, covary with the openland gradient. While, ~~they are~~ also present in relatively high numbers in the other vegetation types, they are most abundant in the openland and swamp habitats. *Helminthosporium* is the only type that covaries with the grassland gradient, which is unsurprising as this taxon consists mainly of molds that grow on grasses. Fungal NPPs that plot in the center of the graph, such as *Alternaria, Arnium, Helicoon, Tetraploa, Valsaria*, Type1, and Type 2, are not strongly controlled by any of the environmental variables and occur at relatively similar proportions throughout the samples. Some of these represent ubiquitous plant pathogens and decomposers (van Geel et al., 2003). All other fungal NPPs (*Bipolaris, Cookeina, Dictyosporium, Glomus, Meliola,* Microthyriaceae, Teleutospores) most strongly covary with the forest gradient. This group includes a number of species that grow on woody debris (*Cookeina, Dictyosporium*), as well as plant pathogens and decomposers, and the mycorrhizal fungus *Glomus*, which is well-known to form associations with tree roots (van Geel et al., 2003), though it occurs in a wide variety of environments.

Discussion

The modern pollen study of the different vegetation types and areas of different land use in KNP reveals a good agreement with the extant vegetation. However, some site by site variation has been recorded in the fungal spores in the assemblages. A composite diagram shows the relationship between, the vegetation types and wildlife in KNP based on the abundance of local arboreal and non-arboreal pollen taxa and coprophilous fungal spores in the palynoassemblages (Figure 8). The evergreen forest is characterized by the high abundance of evergreen arboreal pollen taxa (31.3%). The high abundance of deciduous arboreal pollen taxa (32.6%) in the palynoassemblages signifies the deciduous forest. The grassland is characterized by the abundance of Poaceae pollen (30.6%). Similarly, the openland area is characterized by the abundance of both Poaceae (20.6%) and other associated non-arboreal pollen (20.2%). The swamp area is characterized by the high abundance of marshy and aquatic pollen (21.9%) followed by deciduous (20.1%), evergreen (10.6%) and Poaceae (15.6%) pollen. The abundance of the coprophilous fungal spores in the openland (60.7%), swamp (59.3%), and grassland (23.9%) are exhibited in the palynoassemblages which indicates that these sites are highly impacted by the herbivores. The evergreen and deciduous forest can be characterized as moderately impacted sites as indicated by the relatively lower abundance of coprophilous fungal spores with average values of 16.4% and 16.3%, respectively in the palynoassemblages.

~~A composite diagram was made in relation to the vegetation and wildlife interaction based on the abundance of marker pollen and fungal spores (Figure 8).~~

The ~~palynological study in~~samples taken from the evergreen forest reveals ~~s that the~~a *Mesua-Schima-Duabanga-Cinnamomum*-Arecaceae-*Litsea* assemblage~~, was recorded and~~ showing ~~s~~a good relationship between the pollen and~~with the~~ extant ~~scenario~~vegetation. The abundance of evergreen taxa, especially *Mesua*, *Duabanga*, and *Syzygium* ~~pollen~~ in the pollen assemblage is ~~marked~~ significant (maximum value up to 4.9%) and is indicative of high rainfall activity in the region, as these taxa are high rainfall indicators (>2500 mm/y; Singh et al., 1990; Barboni and Bonnefille, 2001). The ~~presence of~~ evergreen forest was evident in the KNP by the presence of *Mesua* and *Duabanga* pollen in the ~~palynoassemblage of~~ rhino dung samples (Basumatary et al., 2017), as these evergreen taxa ~~dominanted~~ ~~that~~ are dominant in the evergreen forest of~~in~~ the KNP.~~Our study is in close agreement with the vegetation survey and existing forest types in KNP (Champion and Seth, 1968;Das et al., 2014).~~The presence of marshy and aquatic taxa, such as Cyperaceae, *Polygonum*, *Nymphoides*, and *Nymphaea* pollen, which could have been transported by wild herbivores and birds, indicate natural perennial water bodies in and around the study area (Ekblom and Gillson, 2010; Basumatary et al., 2017; Stivrins et al., 2019). During the daytime after feeding in the swamp areas these animals move towards the surrounding forests for rest, shelter or to forage ~~search~~ ~~fordietary plants~~ in the forest.

Among the fungal spore assemblages, the presence of ~~the~~ non-coprophilous fungal spores, Microthyriaceae, *Glomus*, and *Meliola*~~, and *Dictyosporium*~~ was marked. These taxa are~~is~~ ~~is~~ characteristic of dense forest vegetation under warm and humid conditionsin response to the high rainfall in the region. Specifically, the abundance of Microthyriaceae, *Glomus*, and *Meliola* is considered to be indicative of the presence of dense forest vegetation (Musotto et al., 2012, 2017; Cookson, 1947; Selkirk, 1975; Johnson and Sutton, 2000; Hofmann, 2010; Medeanic and Silva, 2010; Loughlin et al., 2017), and this is reflected in the studied samples from KNP. In the palaeoecological literature, *Glomus* is often seen as an indicator of erosion (Shumilovskikh et al., 2021). However, since this fungus is an endomycorrhiza and often associates with trees, in this case the abundance of its spores is due to its abundance in the forest soil (Kołaczek et al., 2013).

The presence of coprophilous fungal spores ~~, *Sporormiella-Saccobolus-Ascodesmis*assemblage~~was marked in the studied samples and the relatively high percentages are indicative of the presence of wildlife. The coprophilous fungal spores may be limited to specific locations frequented by herbivores so can be considered local in origin since they can only actively disperse ~~over~~a short distance which restricts their presence to near to where sporulation took place (Davis et al., 1977; Parker, 1979; Wicklow, 1992; Richardson, 2001; Malloch and Blackwell, 1992; van Geel et al., 2003, 2008; van Geel and Aptroot, 2006; Ekblom and Gillson, 2010; Parker and Williams, 2011; van Asperen et al., 2021). The frequency of *Sporormiella*, *Ascodesmis*, and *Saccobolus* was ~~relatively~~ relatively higher ~~high~~in ~~, though lower than in the~~ openland and swamp areas as compared to the dense forest. In our study, ~~and is considered significant with a maximum value upto~~the moderately high value of coprophilous fungal spores (5.6%) was observed in the palynoassemblage ~~5.6% in the assemblages,~~ which is quite higher than the 2%, considered as a 'background' level (Davis, 1987; Gill et al., 2013; Baker et al., 2016; Raczka et al., 2016). These spores can therefore be inferred to reflect local abundance of the herbivore fauna. The forest area is generally dark, windless, cooler and more humid than outside the forest; conditions that are favorable for fungal growth (Musotto et al., 2017; Promis et al., 2010; Godeas and Arumbarri, 2007). Monkeys, gibbons,birds, and other arboreal animals are common, and their excreta regularly falls ~~down~~to the forest floor. The diversity of the fungal remains especially the non-coprophilous fungal spores is high in all samples.

The *Salmalia-Dillenia-Lagerstroemia-Semecarpus-Careya* pollen assemblage was in agreement with the extant deciduous forest vegetation in ~~this national park~~KNP. The ~~subassemblageof~~ *Dillenia-Terminalia-Careya* assemblage is significant as it is characteristic of the preferred habitat of wildlifein the Balpakram valley in the Garo hills of Meghalaya (Basumatary et al., 2014) which coincided with the pollen assemblages in KNP. These plants are utilized as the primary food plants preferred by many herbivorous mammals including elephant and deer species (Odden et al., 2005; Steinheim et al., 2005; Neupane et al., 2019; Devi et al., 2022). The consistent abundance of *Bombax* pollen in the palynoassemblage which is recorded upto 4.7% was marked in comparison to the other associated arboreal taxa. *Bombax* is a fire resistant plant (Troth, 1976) which is one of the reasons for its abundance in the palynoassemblage. Forest fires during winter are an important part of the ecology for the wildlife of KNP. Herbivory is an important driver of vegetation structure in the region (Ekblom and Gillson, 2010), so the large herbivores may have played a significant role in shaping the structure of plant communities in the KNP. The coprophilous fungi, *Sporormiella*, *Saccobolus*, and *Ascodesmis* are represented consistently in the studied samples and their abundance closely resembles that in~~ose of~~ the evergreen forest samples and are also indicative of the presence of wildlife habitation in the deciduous forest. These fungi are also present at relatively higher abundances than in the evergreen forest, indicative of the higher impact of herbivores on the deciduous forest.

The percentages of Poaceae pollen are relatively high in the grassland samples (average 30.7%) and the *Salmalia-Dillenia-Emblica-Butea-Careya*-Poaceae pollen assemblage was identified as characteristic of this habitat. The presence of some arboreal taxa, especially *Mesua*, *Duabanga*, and *Symplocos,* is significant as these taxa do not usually occur in this vegetation type. Given that these taxa are insect-pollinated, they most likely have been secondarily deposited through animal dung where the herbivores ingested the plant parts elsewhere and were subsequently defecated in and around the grassland areas. The presence of arboreal pollen taxa, both evergreen and deciduous, was recorded from the midden dung of rhinoceros from forested and grassland regions of KNP (Hazarika and Saikia, 2010; Basumatary et al., 2018). The pollen clumping in grasses and *Bombax*, is marked and indicative of their local origin. The presence of pollen grain clumps is a characteristic feature of entomophilous plants whose pollen disperses shorter distances than wind-dispersed pollen grains (Faegri and Van Der Pijl, 1966; Martin et al., 2009). Since the Kaziranga National Park is enriched with swampy areas, the aquatic vegetation need to be included in the pollen spectra for monitoring the status of water level through pollen records in relation to the monsoonal activities. Moreover, the dung of the megaherbivores like one horn rhino also include aquatic pollen and thus, the modern aquatic pollen preservation could act as a baseline for the coprolite studies for tracing the megafaunal extinction during the Quaternary (Basumatary et al. 2017). The generated pollen data would assist in distinguishing the natural forest vegetation from areas impacted by human activities in the region, based on the fossil marker pollen taxa like Poaceae and Brassicaceae (Basumatary et al., 2018; Tripathi et al., 2021).

Among the fungal spores, coprophilous fungi such as *Sporormiella*, *Saccobolus*, *Podospora*, and *Ascodesmis* are dominant and represented consistently in the palynoassemblages. Herbivorous animals, especially rhinoceros and elephant, feed and defecate in the grassland, dispersing coprophilous fungal spores with their dung. However, although they are more common than in the forest assemblages, coprophilous fungal spores are less common in the grassland than in the openland and swamps. This may be due to the midden behaviour of some of the large mammals, especially the rhinoceros, which tends to defecate in specific areas, so the spores are not distributed uniformly on the landscape. The *Sporormiella-Saccobolus-Ascodesmis* assemblage was present in the midden dung of rhinoceros from grassland areas (Basumatary and McDonald, 2017) from the KNP. Among the non-coprophilous fungi, ~~especially~~ *Helminthosporium* and *Alternaria* ~~,~~are especially dominant. Both taxa are common pathogens of herbaceous plants, particularly grasses. Other fungal spores such as *Glomus*, Microthyriaceae, and *Tetraploa* are also present in ~~sporadic~~ lower values in the assemblages. However, grasses have a high resistivity to fungal infection due to their silica content~~s~~ (Park et al., 2006, 2010; Hayasaka et al., 2008) which is the main reason for the low fungal diversity exhibited in the grassland.

The palynological study in the openland area identified some distinguishing features of this habitat within the p~~P~~ark~~.~~, as it ~~which~~ is characterized by ~~T~~the *Salmalia-Dillenia-Mesua-Barringtonia-Litsea-Melastoma*-Poaceae-*Mimosa* pollen assemblage. ~~was marked and significant.~~~~The g~~Grasses are dominant and recorded a maximum value upto 19.8%. ~~.~~However, the arboreal, marshy, and aquatic taxa, *Mesua*, *Bombax*, *Lagerstroemia*, *Syzygium*, Onagraceae, and *Nymphaea* are also consistently present in the pollen assemblages. This reflects the excreted dung of herbivorous animals and birds which incorporated these tree taxa through their ingestion in and around the openland areas. Pollen clumping of Poaceae, Cyperaceae and *Polygonum*is very common in the palynoassemblages indicating they originate from local sources (Faegri and van der Pijl, 1966; Martin et al., 2009). Among the fungal spores the coprophilous fungal spores *Sporormiella-Saccobolus-Ascodesmis* are dominant in the assemblage and confirmed that the openland habitat can be considered to function as a corridor for wildlife. The abundance of coprophilous fungal spores in the openland areas suggests a direct link of abundance of wildlife and higher amount of decomposed organic matter derived from dung.

The palynological study of the swamp sediments reveals that the *Salmalia-Dillenia-Syzygium-Mesua-Duabanga-Litsea-Melastoma*-Poaceae-*Mimosa* pollen assemblage indicates ~~a composition of~~ different types of forest vegetation in and around the swamp area of the n~~N~~ational p~~P~~ark. The riparian forest taxa, *Lagerstroemia*, *Barringtonia*, and *Duabanga* ~~are~~grow luxuriantly ~~growing~~ along the periphery of the wetland area. Among non-arboreal taxa, the marshy and aquatic taxa are local in source. The other terrestrial non-arboreal taxa, chiefly Asteroideae, Convolvulaceae, and *Mimosa*, were deposited in and around the areas by the inwash of rainwater. The presence of *Rhododendron* pollen (a flood marker taxona~~a~~; Basumatary et al., 2019) indicates flood activity in the region.

Among the fungal spores the non-coprophilous fungal spores predominate but coprophilous fungal spores, especially *Sporormiella*, *Podospora*, and *Saccobolus*, are still comparatively abundant in comparison to the other studied sites. The preserved fungal spores may have originated from surrounding areas and were subsequently transported and deposited through rainwater and slopewash. Furthermore, the swamp is serve as theafocal point for mammals and birds for their food and especially drinking water. The amount of dung, especially the midden dung of rhinoceros, is large. Water availability is an important factor for the germination and sporulation of coprophilous fungi (Austin, 1958; Ingold and Marshall, 1962; Kuthubutheen and Webster, 1986a, 1986b), and dung deposited in the swamp can be expected to remain wet longer than in the other vegetation types and thus enhance the potential for germination.

Among the non-coprophilous fungi the presence of *Tetraploa* was markedmore abundant than in the other vegetation types, which might reflects its ecology as a saprophytic fungus of Poaceae and Cyperaceae, both of which are major wetland taxa. The abundance of *Glomus* in the palynoassemblage might be the result of transport directly from the surrounding forest, as *Glomus* is indicative of soil erosion (van Geel et al., 2003; Kiage and Liu, 2009). The fungal diversity observed in the samples may be due to herbivores feeding habits and food choice (Ebersohn and Eicker, 1992; Feranec et al., 2011).The diversity of the coprophilous fungal spores is similar in all the studied surface soil samplesto that of the openland samples with abundant spores of *Sporormiella*, *Saccobolus*, and *Ascodesmis*. This pattern is also seen in the rhinoceros dung midden samples (Basumatary et al., 2017).

The presence of the extra-regional taxa, *Pinus*, *Abies*, *Picea*, and *Larix* in samples from all vegetation types is significant and indicative of strong wind activity from the higher Himalaya and but might also be introduced by migratory Siberian birds (Barua and Sharma, 1999), when they fly through pollen-laden environments. The bird diversity documented in KNP is over 521 species of which more than 200 are residents while the rest are migrants, including local migrants (Rahmani et. al., 2022). and the pPollen may adheres to their body and feathers of migratory species and then subsequently be dislodged which may be lost during grooming while they are in KNP., especially from species that may overwinter in the park.

Studies of It is recorded that, the modern analogues based on the pollen and fern spore assemblages have shown it is possible to , it could be distinguished the agricultural land from the fallow and salt marsh grassland (Graf and Chmura, 2006). , but tThe presence of coprophilous fungal spores can aid in distinguishing grazed or manured land use from natural vegetation.and other. Similarly, this study can serve as , it will be a guideline and applicable to differentiate and distinguish the different vegetation types and the presence and ~~ir~~ impact of herbivores based on the presence and absence of local arboreal pollen taxa along with coprophilous fungal spores especially *Sporormiella*, *Sodaria*, and *Ascodesmis* in the palynoassemblages. ~~The~~ V~~As~~egetation structure is mainly controlled by herbivores density (Bell, 1982) in African savannah and the woody cover reduction is directly linked to the concentration of herbivores (Dublin et al., 1990), their presence or absence can be documented by the presence of coprophilus fungal spores in the palynological~~ollen~~ studies of soil sediments. In order t~~T~~o understand the actual reason of decline and extinction of megaherbivores ~~is very difficult and controversial and the two view always come into account,~~ whether by ~~the~~ human activities~~both on continent and large Island (Johnson et al. 2015)and other view~~ or due to climate-induced environment change (Wroe et al. 2013) documentation of their presence, either directly by skeletal remains or indirectly via proxy such as coprophilous fungal spores is critical. Other evidence for human impact can be the ability to recognize former ~~However, this data also helpful for the differentiation of the~~ cropland whether ~~using the dung~~ manured or unmanured based on the representation of local arboreal pollen taxa and coprophilous fungal spores in the palynoassemblages preserved in sediments.

Comparison of pollen spectra with canonical correspondence analysis

The CCA confirms that the five vegetation types present in KNP are significantly different in their taxonomic composition and this is reflected in both the vegetation and pollen assemblages. While the fungal NPP assemblages are relatively similar in overall composition between the different vegetation types, there are some differences in abundance of the taxa recovered reflecting the populations levels of herbivores~~.~~ Coprophilous fungal spores are present in significant numbers in all vegetation types, but the concentration is greater in the openland and swamp areas, where herbivores are more abundant than in the forested areas. The other vegetation types are dominated by mycorrhizal fungi, pathogens and decomposers of the plant species common in these vegetation types.

Interaction between vegetation and herbivores

Demonstrating the strong relationship between pollen types and vegetation in an area provides an opportunity to infer ~~document~~ changes in wildlife habitat at both a temporal and spatial scale. Complementing the pollen record is the associated coprophilous fungal spore~~s~~ record which can provide ~~estimates of the size~~an indication~~s~~ of the presence of herbivore populations utilizing the different vegetation types in these habitats and thus responding to their expansion or reduction over time (EkblomandGillson, 2010). Integrating ecological studies of all herbivores in the park and their preferred habitats is critical to integrate with the documentation of the association of pollen and vegetation types to better understand how the vegetation and fauna interact through time (Table 3). Equally important is the documentation of the ~~value~~ abundance and types of coprophilous fungal spores associated with each species' dung (Basumatary and McDonald, 2017; Basumatary et al., 2019; Basumatary et al., 2021) ~~is needed~~to provide more refined information on what species of herbivores were present and their associat~~ed~~ion with specific habitats and recognize their heterogenous distribution on the landscape rather than just rough estimates of the increase or decrease in herbivore populations through time.

Conclusions

This study demonstrates that the depositional pattern of pollen and NPP and their relative abundance ~~s~~in different vegetation types in KNP parallels the vegetation present ~~is dependent on differences~~ in each ~~the~~type of habit and the impact of ~~wild~~herbivores that utilize them .The pollen data from the different ~~study sites~~vegetation~~s~~ types in KNP ~~r~~reveals a strong relationship with the extant vegetation. In contrast, the depositional pattern of fungal spores varies from site to site due to different levels of wildlife impact and seasonal differences in their presence and utilization of ~~migration in different times on~~ the different vegetation types in the n~~N~~ational p~~P~~ark. ~~The relative representation of the fungal spores, especially those of coprophilous fungal spores is closely correlated with the wildlife while those of non-coprophilous fungi are linked to specific plant types with which they form a symbiotic relationship such as mycorrhizae on plant roots and parasites on plants.~~Our study is in close agreement with the vegetation survey and existing forest types in KNP (Champion and Seth, 1968; Das et al., 2014).

As such, the data will be helpful in providing a foundation to differentiate and distinguish the natural forest vegetation from areas ~~and the~~ impacted by ~~of~~ human activities in the region, based on the fossil pollen record given ~~,as there is~~ the potential for misidentification of ~~between~~ conserved landscapes such as ~~(~~national parks and wildlife ~~sanctuary~~sanctuaries ~~)~~and areas that are not set aside ~~unconserved~~or protected and have been ~~and~~ heavily impacted by human activity, such as deforestation, farming, and pastoral practices. ~~, timber harvest or simply due to the building of infrastructure such as roads or housing and other buildings.The presence and abundance of local arboreal pollen taxa in the recovered pollen assemblages may play an important role for the differentiation and identification between natural vegetation coverage and areas of high human activity.~~ This may ~~also~~ be indicated by the presence and abundance of local arboreal pollen or the relative abundance of coprophilous fungi since unmanured soil has significantly less coprophilous fungi than manured soil (Graf and Chmura, 2006). The openland area is also an important place for ~~the~~wildlife ~~for their~~ survival as indicated by the presence of marker pollen taxa and the abundance of coprophilous fungal spores. ~~Lastly, t~~The overall palynological analysis of the swamp sediments could be a reliable and complementary data for the representation of the vegetation types and abundances of herbivores both of which can contribute to ~~both~~palaeoecological and palaeoherbivory analysis.

Acknowledgements

We thank ~~Dr. Vandana Prasad,~~ Director, Birbal Sahni Institute of Palaeosciences, India for laboratory facilities to carry out this research. First author is very much grateful to Department of Science and Technology, New Delhi for funding (DST No: EEQ-2021/000846 (SERB) the research work. First author is also thankful to the forest department, Govt. of Assam for permission to work and necessary help during field visit.

Declaration of conflicting interests

The authors declared that they have no conflict of interest.

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LEGENDS

Table 1: Taxa included in each environmental variable for the Canonical correspondence analysis (CCA).

Table 2: Characterization of marker pollen taxa recovered from the surface soil samples in relation to the different vegetation and landuse from ~~the~~Kaziranga National Park.

Table 3: Association between major mammalian herbivores and vegetation types in Kaziranga National Park.

Figure 1.a. Map showing the study areas; b. Vegetation coverage map of Kaziranga National Park (modified after Das et al., 2014).

Figure2.a.Thick evergreen forest within Kaziranga National Park, b. *Buceros bicornis* (Hornbills) sitting on the tree within the evergreen forest, c. Group of *Elephas maximus* (Asian Elephant) in deciduous forest in Kaziranga National Park, d. *Rhinoceros unicornis* grazing in the periphery near swamp.

Figure 3.a. Grassland and ~~show~~ grazing by ~~of~~*Rhinoceros unicornis* b. A view of grassland during winter, c. A view of openland showing *Bubalus arnee* (Asian Buffalo) and numbers of migratory birds, d. A view of swamp showing numbers of *Cervus duvauceli* (Swamp Deer) in the center.

Figure 4. Palynoassemblages recovered from the surface soil samples from the Kaziranga National Park.

Explanation of palynomorphs

a. *Bombax ceiba*, b. *Duabanga* in cluster, c. *Cinnamomum*, d. *Litsea*, e. *Terminalia*, f. *Lagerstroemia*, h. *Shorea robusta*, i. *Schima*, j. *Semecarpus*, k. *Syzygium*, l. Arecaceae, m. *Albizia*, n. *Lantana*, o. *Pinus*, p. *Rhododendron*, q. Asteroideae, r. Chinoroideae, s. *Impatiens*, t. Convolvulaceae, u. Cyperaceae, v. Poaceae in cluster, w. *Polygonum*, x. *Nymphaea*, y. *Typha*, z. Monolete, aa. Trilete, ab. *Sporormiella*, ac. *Sordaria*, ad. *Meliola*, ae. *Tetraploa*, af. *Glomus*.

Figure 5. Comparative pollen spectra in relation to the different vegetation types from ~~the~~Kaziranga National Park.

Figure 6. Comparative fungal spores spectra in relation to the different vegetation types and herbivores impact from the Kaziranga National Park.

Figure 7. Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types and environmental variables. NPP types (red) and samples (dark green: evergreen forest; light green: deciduous forest; yellow: grassland; orange: openland; light blue: swamp) are plotted against vegetation type indicator assemblages (blue arrows). ~~Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types and environmental variables. NPPtypes (red) and samples (green) are plotted against vegetation type indicator assemblages (blue arrows).~~

Figure 8. Composite pollen and fungal spore diagram in relation to the different vegetation types from ~~the~~Kaziranga National Park.

Response to the editors and reviewers comments

Manuscript ID HOL-22-0152 entitled "Pollen and non-pollen palynomorph depositional pattern in Kaziranga National Park, India: implications to Palaeoecology and palaeoherbivory analysis"

Editor words and comments

Comment 1: I agree with most of the comments of reviewer 1, although I think the standard of English is good overall, and just needs some minor polishing in places. I think you provide important new modern pollen and NPP data from a part of the world that remains under-studied compared with other temperate, mid-latitude regions. However, although you present high-quality data, which is an important pre-requisite for palaeoecological study, I think you need to flesh out your introduction section to provide a stronger rationale for your study, placing it in a broader global context; e.g. the lack of modern pollen studies in the tropics; their importance as a basis for interpreting fossil pollen data; the need to combine pollen with NPP studies to explore past changes in mega-herbivores; the types of research question that can be tackled by combining pollen and NPP -- e.g. changes in mega-herbivore population through time, Pleistocene mega-herbivore extinctions etc.

Reply 1: Thank you very much for your appreciation and valuable comments. As per your suggestions, we have included the stronger rationale with significant points of our study in the Introduction section in relation to the modern pollen rain in tropics including additional references (Line nos. 51-64). This includes the importance of pollen and non-pollen palynomorph studies in the analysis of present and past herbivore dung in both the regional and global context (Line nos. 125-140). The manuscript was reviewed and revised thoroughly for the English grammar and spelling. In addition, we have deleted the unnecessary sentences from the introduction which are not required. Please see the text in the manuscript.

Comment 2. In the Discussion section you should also expand on the wider implications and significance of your findings; i.e. are they just relevant for understanding the history of your specific national park, or are there broader implications? As The Holocene is an international journal, its important to scale up the significance/implications of your findings to a broader audience, and explain how your findings constitute a significant advance in our understanding of modern pollen/NPP relationships with tropical veg and mega-fauna.

Reply 2: Sir you are right but for your information, in 1985, Kaziranga National Park of Assam (northeast India) was declared a UNESCO World Heritage Site in recognition of its significance as one of the best managed wildlife parks in the world. The KNP has a unique vegetation setup with the combination of tropical evergreen, deciduous and grassland, and therefore understanding the interplay between modern pollen and vegetation in this national park will provide an overview of pollen-vegetation association at varied vegetation setup.,which will be globally significant especially in tropical and subtropical regions of the globe. As per your suggestion, we have now included the importance of our findings in the formulation of modern pollen deposition and megafaunal extinction at the global scale (Line nos. 553-572). Kindly see in the revised discussion part in the text of the manuscript.

Comment 3.

Furthermore, there is a disconnect between some of what you say in your Conclusions section and the rest of the paper. In your Conclusions you refer to human-impacted landscapes, but your dataset instead relates to different veg types in relation to differing abundance of mega-fauna, so this needs to be revised.

To sum up, you have produced a valuable and important dataset, but you need to improve the rationale (intro) and wider significance/implications (Discussion). If you can make these revisions, as well as address the other comments and edits of reviewer 1, I would be happy to receive a revised ms.

Reply 3: Sir, as per your suggestion, we have now discussed the issues related to human-impacted landscapes in the 'Discussion section' as provided in the conclusion section (Line nos. 482-484). We have now pointed out in the conclusion section that, our generated data could be possibly utilized to identify and differentiate between the human-impacted landscapes and natural landscapes based on the presence and absence of local arboreal pollen and coprophilous fungal spore in the pollen assemblages (Line nos. 617-633). Moreover, as per your suggestion, we have now included the importance of our findings in the formulation of modern pollen deposition and megafaunal extinction at the global level in the 'discusssion section' (Line nos. 553-572). We have now included the stronger rationale with significant points of our study in the 'introduction section' (Line nos. 51-64).

Response to the reviewer's comments
Reviewer: 1

Comments to the Author
General comments

The analysis of pollen and non-pollen palynomorphs from Kaziranga National Park shows interesting points, but there are some considerations that need to be assessed prior to publication

First, an English revision of the text is needed. There are problems with punctuation and choice of words that make the text very incoherent in some parts. This would make clearer the message the authors want to pass to the readers.

Reply: First of all, thank you very much Sir, for your appreciation of our research study. As per your suggestions we have gone through the whole manuscript with regard to the English (grammar, punctuation and spellings) and have revised accordingly.

Comment 1:

Figures:
The resolution of the figures needs improvement. Also, it is necessary to redo some labels to make them readable. The axis in some of the graphs also makes it difficult to interpret the figures.

Reply 1: Thank you very much for your suggestions, based on that, we have revised the figures and related labels for more clear resolution. Kindly look after.

Comment 2:

Results:
The results are described in sections, such as Evergreen forest, Deciduous forest and so on, however, the sections look incomplete. Sometimes the values are presented in a range, and sometimes only the average or the maximum values of a taxon is presented. Also, in some parts, only a handful of what is on the figure is described in the results. I think it would be good to restructure the way the results are presented. Avoid some terms like "associated taxa" and "sporadic values" because they could complicate the interpretation of the data.

Reply 2: Sir, as per your suggestions, I have gone through the result section of the manuscript and presented the values and revised accordingly. Also, we have revised the interpretation parts, avoiding the term associated taxa and sporadic values. Please see the revised text (marked copy) of the manuscript (Line nos. 277-346).

Comment 3:

Discussion:
Figure 8, which is part of the discussion, is difficult to interpret. Also, when there is a link in the text with this figure, they don't match because the information is incomplete. I would suggest presenting the data in Figure 8 in a different way.

Reply 3: As per your suggestions, we have revised and cleared the description of Fig. 8 (Line nos. 384-398). Kindly see in the text of the manuscript.

Comment 4: There are many parts of the discussion that reference is needed.

Reply 4: As per your and second reviewers' suggestions, we have revised the discussion part and also included some more significant points in relation to our results and have included some additional references (Line nos. 414; 452-453; 484 and more). Kindly see the discussion part of the marked copy).

Comment 5:

More importantly, I miss the debate on how the findings of the research can serve as a baseline to examine the influence of palaeoherbivory in relation to palaeoecology in the National Park, a point that was made in the introduction.

References:
There were some references in the bibliography that were not cited in the text, such as Karanth KU and Sunquist ME (1992), these references should help clarify this issue, on the preferential relationship between herbivores and different types of vegetation and habitats..
Detailed comments were made on the pdf file of the manuscript

Reply 5: As per your point and comment, we have now added the reference 'Karanth and Sunquist (1992)' (Line no. 77) and added the debate on 'how the findings of the research can serve as a baseline to examine the influence of palaeoherbivory in relation to palaeoecology in the National Park' in the introduction part including some references (Line nos. 125-140). Kindly see the marked manuscript.

The replies from the comments in the PDF file are also responded separately below.

<u>Response to the reviewer Comments made on the pdf file of the manuscript</u>

Comment 1: Line no.-63-68 (This whole sentence is a little confusing. Try to rephrase it).

Reply 1: The same has been revised, please see in the text of the manuscript (Line nos. 83-88).

Comment 2: Line no-114 (openland, What is this type of vegetation? Is it similar to grassland? and eroded land, Is this eroded land a human related? Deforestation?).

Reply 2: In the Kaziranga National Park, openland areas (Fig. 3c) are those which are generally located in near proximity or surrounding the swamp area (Fig. 3d). These areas are not exactly grassland because this area is generally covered by short grasses and associated herbs with no trees and shrubs. This openland area is not similar in the composition of plant taxa as what is we consider grassland of Kaziranga National Park because the grassland of the Kaziranaga National Park is dominated by the tall grasses (Fig. 3 a & b) with scattered trees and shrubs such as *Bombax ceiba*, *Careya arborea*, *Melastoma malabathricum*, etc.

The eroded land is not related to the human activities like deforestation, but is due to heavy rainfall activities and sometimes by annual floods so it becomes a barren/eroded land.

Comment 3: Line no-169-171 (This part is a little confusing?, were the samples collected in a 50 m interval from each other)

Reply 3: Yes, I agree with your point, we have revised this sentence in the text of the manuscript (Line nos. 228-232). During the field work, in each of the vegetation types, the samples were collected at about 50 m intervals within the Kaziranga National Park.

Comment 4: Line no-180-185 (can you explain why 259-335 pollen grains? Is there any particular reason for that? What do you mean by extra-regional taxa?)

Reply 4: We have counted these pollen grains covering the whole pollen slide covered by cover glass (22 X 40 mm). So, based on the availability of the pollen grains in each studied slide, the total number of pollen grains were counted which varies from 259-335 (pls. see Fig. 5). We maintained a minimum of 150 pollen grains for the total pollen count, for a satisfactory representation of the vegetation composition and to make pollen spectra.

We considered highland taxa such as *Pinus*, *Betula*, *Alnus*, *Rhododendron* which are not growing in and around the Kaziranga National Park as the "extra-regional taxa" that grows in the higher Himalaya (Line nos. 242-243).

Comment 5: Line no-193-194 (what is the reason for including the aquatic taxa in the total sum?)

Reply 5: Sir, we have now included the discussion on the importance of incorporating aquatic pollen in the total pollen sum (Line nos. 477-482). We have added the reference pertinent to this. Since the Kaziranga National Park is enriched with swampy areas, the aquatic vegetation need to be included in the pollen spectra (Fig. 5) for monitoring the status of water level through pollen records in relation to the monsoonal activities. Moreover, the dung of the megaherbivores like one horn rhino also include aquatic pollen and thus, the modern aquatic pollen preservation could act as a baseline for the coprolite studies for tracing the megafaunal extinction during the Quaternary.

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Comment 6: Line no-220-221 (It would be nice if you include the names of each taxon you are referring to here?).

Reply 6: As per your suggestion, I have included the major evergreen taxa (*Mesua, Schima*, Arecaceae, *Symplocos*, and *Litsea*). Please see the same in the text of the manuscript (Line no. 281).

Comment 7: Line no-221 (values of 1.6%-4.9%; When I look at the figure, I cannot see this values. You should work on the scale of the figure).

Reply 7: As per your suggestion the scale has been revised. Kindly see Fig. 5.

Comment 8: Line no-223 (What "other terrestrial" means ?).

Reply 8: Sir, We have revised the term "other terrestrial" which is used for the herbs growing in the land in association with the grasses (Line nos. 283-284).

Comment 9: Line no-226-227 (How about the other coprophilous types?).

Reply 9: Yes, we have revised the sentence (Line nos. 286-287). The coprophilous fungal spore is the standard term used in the previous published records. Kindly refer the marked copy of manuscript.

Comment 10: Line no-231-232, (This part is confusing?).

Reply 10: Yes Sir and I have revised the same in the text (Line nos. 293-295). Please see the same.

Comment 11: Line no-233 (maximum value of 9.4%); You should follow the same pattern as in the previous section and cite the range, not only the maximum value)

Reply 11: The same has been done (Line nos. 293-295). Kindly see the same in the manuscript.

Comment 12: Line no-237-238 (see the comment in the previous section for this group?).

Reply 12: Yes Sir, the same has been done. Kindly see the same.

Comment 13: Line no-238-239 (Also check the comment about this group in the previous section?).

Reply 13: The same has been done. Please see the result section in the marked copy.

Comment 14: Line no-244-245 (sporadic values is too vague, You should describe the arboreal elements with more detail ?).

Reply 14: Yes Sir, we have revised the same including the name of some taxa (Line nos. 309-310). Kindly see the same in the marked copy of the manuscript.

Comment 15: Line no- 247-250 (*Helminthosporium*, this spore has very different values from the previous zone. You should be more detailed in describing this vegetation types).

Reply 15: As per your suggestion, we have revised the same (Line nos. 315-317). Kindly see the same in the marked copy.

Comment 16: Line no-252-255 (Not sure if this part is informative because you are describing each category below).

Reply 16: I have deleted the repeated text and revised the sentence as per your suggestion (Line no. 319). Kindly see in the marked manuscript.

Comment 17: Line no-260-263 (Check previous comments about these groups).

Reply 17: Sir, as per your suggestion, we have revised the same. Kindly see the same in the marked manuscript.

Comment 18: Line no-301-312 (Check previous comments and apply where necessary in this section).

Reply 18: As per your suggestion, we have revised the same accordingly. Please see the same.

Comment 19: Line no-281 (Figure-7, It would be good to work on the labels of this figure. The way it is now is impossible to read the name of the fungal types. You could re do the names in graphic software or something similar).

Reply 19: Honestly, I agreed your point, and as per your suggestion, the figure 7 has been revised. Kindly see the same in the figure no 7.

Comment 20: Line no-294-297 (Which ones? Direct what you want to say to the figure the reader should look. Is it figure 8? ; I think it would be good if you give an explanation on why this is the case).

Reply 20: No sir, this is not figure 8, this is figure 7 and I have included Fig. 7 under the heading '**Statistical analysis of NPPs frequencies**' (Line no. 366). Accordingly, we have already explained this matter in the Discussion part of the manuscript (Openland and Swamp samples discussion part). Please see the same in the text of the manuscript.

Comment 21: Line no-339 (I think a reference is needed here).

Reply 21: The same has been given in the text (Line no. 374). Please see in the manuscript.

Comment 22: Line no-320-322 (This is confusing may be rewrite this part or give some more explanation on this?).

Reply 22: Sir, as per your suggestions, I have revised the sentence (Line nos. 407-411). Kindly see the same.

Comment 23: Line no-324-328 (Any references to support this?).

Reply 23: Yes Sir, I have given references in relation to this point (Line nos. 414-415). Besides, as per my field observation and forest people after grazing in swamp and surrounding areas, the herbivores and other animals then move towards the core forests for their rest and other needs which are supported by our pollen data.

Comment 24: Line no-329-330 (Are you still referring to the evergreen ?).

Reply 24: Yes, it refers to the evergreen forest.

Comment 25: Line no-343-346 (why 5.6% is considered significant? What are the implications of finding higher values of coprophilous fungal spores in the dense forest than in the cropland and swamp areas? What does this indicates?).

Reply 25: Sir, as per your comments, I have reframed and revised these sentences (Line nos. 434-440). Given their limited dispersal ability as discussed in the text, the presence of coprophilous fungal spores in the palyassemblage are indicative of the immediate presence of the herbivorous animals. However, the values of coprophilous fungal spores in the palynoassemblages of forest samples are lower than openland and swamp samples, which is now well expressed in the reframed sentences.

Comment 26: Line no-353-354 (Is this assemblage in Figure 8? May be it is the case to rethink how to graphically display this information Figure 8 is very confusing and does not match with the text?).

Reply 26: No this is not the assemblage of Fig. 8. I have now revised and clarify the Fig. 8 and included its detailed description in the first paragraph of the 'discussion section' (Line nos. 384-398). Kindly refer the marked copy.

Comment 27: Line no-356-358 (Reference is needed here).

Reply 27: The same has been done. Kindly see the same (Line nos. 452-453).

Comment 28: Line no-458 (How can you estimate the size of the population with abundance of spores?)

Reply 28: Sir, as per your comment, I have revised this line (Line nos. 590-592). Please see in the text of the manuscript.

Comment 29: Line no-475-478 (This conclusion does not bring a new finding. I think has been establish by multiple studies.

Reply 29: Sir, as per your comments, we have revised the conclusion section (Line nos. 605-627). Kindly see.

Comment 30: Line no-479-483 (I think the important/impact of human activity is missing in the discussion). .

Reply 30: Yes Sir, It has now been added in the discussion section (Line nos. 482-484).

Comment 31: Line no-484-486 (This is indeed very important but it was not explored previously?).

Reply 31: Sir, as per our recorded data, based on the presence and abundance of the local arboreal pollen taxa it could be possible to distinguish and characterize among the natural forest, cropland and other land-use form in the regional and global level. So, this data will be useful as a baseline for the identification and differentiation between natural vegetation and human activities areas (Cropland, farmland, etc.). The same has been added in the discussion section. Kindly see (Line nos. 482-484); Line nos. 553-572).

Comment 32: Figure 5 and Figure 6 (Align the vegetation types label?).

Reply 32: The same has been corrected. Please see Figure 5 and Figure 6.

All the corrections in the manuscript have been made under the guidance of reviewer's and Editor's suggestions. Revisions like inclusion and deletion of references, deletion and reframing of sentences, etc., have been done in the text of the manuscript and related line numbers have been provided with each response (pls. refer marked copy). The figures have been revised as per suggestion for more clearance. We are extremely thankful to editor and anonymous reviewer's for such a valuable suggestions which helped a lot in the improvement of the manuscript.

Dr. Sadhan K. Basumatary
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