

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

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Keywords:	Coprophilous fungal spores,, herbivores,, palynoassemblages,, pollen spectra,, swamp,, vegetation types
Abstract:	<p><b>Abstract</b></p> <p>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.</p>

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4 1 **Pollen and non-pollen palynomorph depositional patterns in Kaziranga**  
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6 2 **National Park, India: implications for palaeoecology and palaeoherbivory**  
7  
8 3 **analysis**

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33 18 **Abstract**

34 19 The main aim of this study is to produce a modern analogue for pollen and non-pollen  
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4 33 in the KNP. This data can be utilized as a baseline for the interpretation of palaeoecological and  
5 34 palaeoherbivory studies in other parts of the Indian subcontinent as well as its potential  
6 35 application at a global level.  
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### 11 37 **Keywords**

12 38 Coprophilous fungal spores, herbivores, palynoassemblages, pollen spectra, swamp, vegetation  
13 39 types.  
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### 18 41 **Introduction**

19 42 The study of modern pollen rain in relation to different vegetation types is a prerequisite  
20 43 for the interpretation of the past vegetation and climate in a region and how it has changed over  
21 44 time (Bent and Wright, 1963; Janssen, 1967; Wright, 1967; Overpeck et al., 1985; Prentice,  
22 45 1985; Bunting et al., 2004; Wilmshurst and Mcglone, 2005; Xu et al., 2005; Deng et al., 2006;  
23 46 Gosling et al., 2009). The study of the modern pollen rain and extant vegetation in tropical  
24 47 regions is more complex and critical due to high biodiversity and heterogeneity of the pollen  
25 48 preservation on the forest floor and nearby areas, compared to subtropical and temperate  
26 49 vegetation, as documented by the presence and abundance of the major pollen taxa in the pollen  
27 50 assemblages (Mayle et al., 2000; Gosling et al., 2018; Bush et al., 2021). Phenological factors  
28 51 such as the timing of the flowering period and periods of high rainfall, along with pollen  
29 52 production, mode of pollination, and variation in the mode of pollen dispersal influence pollen  
30 53 preservation both on the landscape surface and eventual integration into soils and sediments.  
31 54 However, based on a knowledge of the pollen spectra and how it represents the major associated  
32 55 plant taxa in relation to the different vegetation types, it is possible to differentiate and  
33 56 distinguished the different vegetation types in a region (Gaillard et al., 1994; Guimaraes et al.,  
34 57 2017) and as well as the recognition of differences between modern and historic grassland uses  
35 58 (Hjelle, 1999).

36 59 There is an increasing global interest in palaeoherbivory and palaeodietary analysis in  
37 60 relation to palaeoecology during the Quaternary, particularly with respect to possible dietary  
38 61 changes that may have contributed to the extinction of megaherbivores (Barnosky et al., 2004;  
39 62 Rawlence et al., 2016). Many of these studies have been primarily based on pollen and non-

63 pollen palynomorphs, especially changes in the relative abundance of coprophilous fungal  
64 spores, preserved in sedimentary profiles and coprolites (Burney et al., 2003; Robinson et al.,  
65 2005; Davis and Shafer, 2006; Carrión, 2007; Raper and Bush, 2009; Gill et al., 2009, 2013;  
66 Johnson et al., 2015; Graham et al., 2016; van Geel et al., 2018).

67         The presence of coprophilous fungi in sediments and changes in their relative abundance  
68 has been used as an indicator not only of the past presence of herbivores, but also to document  
69 changes in population sizes and in some cases the extinction of this part of the Pleistocene  
70 megafauna (van Geel, 1972, 1976, 1978; van Geel et al., 1981, 1983; Karanth and Sunquist,  
71 1992; Feranec et al., 2011; Baker et al., 2013; Etienne et al., 2013; Lopez-Vila et al., 2014;  
72 Loughlin et al., 2018; Tunno and Mensing, 2017; van Asperen et al., 2021; Pokharia et al.,  
73 2022). More recently coprophilous fungi have increasingly been used as a proxy to address  
74 questions of pastoral and other human activities (Davis, 1987; Burney et al., 2003; van Geel et  
75 al., 2003; Gill et al., 2009; Miede et al., 2009; Cugny et al., 2010; Feeser and O'Connell, 2010;  
76 Felauer et al., 2012; Johnson et al., 2015; Kamerling et al., 2017). When combined with the  
77 study of pollen grains, fungal spores, especially of coprophilous fungi that grow on dung of  
78 herbivorous animals can provide useful information for understanding the food habits, ecology,  
79 diversity, niche partitioning and changes in relative abundance of past herbivorous species in a  
80 region (Ebersohn and Eicker, 1992; Ekblom and Gillson, 2010; Velazquez and Burry, 2012;  
81 Basumatary et al., 2017, 2019, 2020, 2021; Tripathi et al., 2019; Pokharia et al., 2022).

82 Previously work on the preservation of modern pollen and non-pollen palynomorphs on the  
83 modern surface soil related to highland grazing and past land use and other vegetation changes  
84 has also been investigated (Ejarque et al, 2011; Henga-Botsikabobe et al., 2020; Loughlin et al.,  
85 2021). Since both fungal spores and the pollen grains in the sediments are commonly  
86 encountered in the same palynological slide (van Geel et al., 2003), the documentation of fungal  
87 spores, especially those of coprophilous fungal spores, along with the pollen grains can be useful  
88 to interpret the impact of herbivores in relation to the different vegetation types in a region. As  
89 coprophilous fungal spores are dispersed only for a very short distance, they are local in origin  
90 (Graf and Chmura, 2006; Johnson et al., 2015) so will accumulate in sediments with pollen  
91 grains and are therefore indicators of the local presence of herbivores in relation to the existing  
92 vegetation.

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3 93 While some research has been conducted to understand past vegetation and climate  
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5 94 history in relation to the palaeoherbivory in national parks in tropical regions of the world  
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7 95 (Burbridge et al., 2004; Ekblom and Gillson, 2010), little research has been carried out on  
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9 96 modern pollen deposition in relation to the different vegetation types in national parks and  
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11 97 wildlife sanctuaries in Asia (Djamali et al., 2009; Basumatary et al., 2014; Bera et al., 2014;  
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13 98 Tripathi et al., 2016; Ghosh et al., 2017; Setyaningsih et al., 2019; Pandey and Minckley, 2019).  
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15 99 These previous studies have often not recorded the presence of coprophilous fungal spores so  
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17 100 cannot be used to determine the presence and abundance of herbivorous animals in the region.  
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19 101 In the absence of skeletal remains of these herbivores, coprophilous fungal spores may serve as  
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21 102 an important proxy that can be used to reconstruct the palaeoecology of a region with respect to  
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23 103 the presence, types and abundance of herbivores and their impact on the local environment, as  
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25 104 well as how changes in the vegetation impacts the local wildlife (Basumatary and McDonald,  
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27 105 2017).

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29 106 The main aim of this study is to document the depositional pattern of pollen and non-  
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31 107 pollen palynomorphs in different vegetation types in Kaziranga National Park (KNP) in relation  
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33 108 to the types of wildlife present and their impact on the different types of habitat. Determining the  
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35 109 degree of representation of the coprophilous fungal spores in the surface soil and sedimentary  
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37 110 profiles serves as the primary proxy to trace the relationship between flora and fauna in the  
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39 111 region through time. The combination of pollen and non-pollen palynomorphs, especially the  
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41 112 abundance of coprophilous fungal spores, is taken into consideration and calibration during the  
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43 113 analysis which permits an interpretation of palaeoherbivory and palaeoecology. Based on the  
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45 114 changes in frequency of coprophilous fungal spores in the sedimentary profile, an analysis is  
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47 115 possible to trace the presence, relative abundance over time and eventual decline and extinction  
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49 116 of members of the herbivorous mammals in Kaziranga National Park and to correlate the pattern  
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51 117 with what is observed in other national parks located in the tropical and temperate region of the  
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53 118 globe. Based on the modern palynomorph analogues seen in different regions, the presence and  
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55 119 absence of the local arboreal pollen taxa and coprophilous fungal spore in the pollen assemblages  
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57 120 provides a means to distinguish the natural forest vegetation, from areas with heavy grazing or  
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59 121 modified into cropland in both tropical and temperate regions. The resulting information can  
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122 serve as a baseline to examine the influence of palaeoherbivory on vegetation in the National

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3 123 Park in the past. This also provides for a better determination of the first human occupation along  
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5 124 with their domestic livestock in the area and subsequent impact on the flora and fauna.  
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## 8 126 **Study sites**

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10 127 Kaziranga National Park covers an area of around 430 square kilometers and is bordered on one  
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12 128 side by the Brahmaputra River (Figure 1). In 1985, KNP was declared a UNESCO World  
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14 129 Heritage Site in recognition of its significance as one of the best managed wildlife parks in the  
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16 130 world. As such, KNP is one of the best sites in India and certainly for Southeast Asia to observe  
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18 131 the long-term interrelation between plants and the indigenous wildlife, as this interrelationship  
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20 132 has not been impacted as extensively by human activities and domesticated animals as at other  
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22 133 sites in India. The park is within the Indo-Burmese biodiversity hotspot region, a critical corridor  
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24 134 for immigration of members of the Indo-Malayan fauna into the Indian subregion. It is also a  
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26 135 critical reserve for tropical species, having served as a gene reservoir for these taxa during glacial  
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28 136 periods (Tamma and Ramakrishnan, 2015).  
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## 30 138 **Climate and soil**

31 139 The climate of the region is controlled by the southwest and northeast monsoons. These  
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33 140 weather patterns result in hot, humid summers, and cold, dry winters. The temperature ranges  
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35 141 from a minimum of 4°C during winter up to 37°C in summer. The relative humidity is very high  
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37 142 and ranges between 75–86%. The annual rainfall ranges from 1800–2600 mm, and annual  
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39 143 flooding is common in KNP during the summer. The soil composition varies from site to site and  
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41 144 includes sandy loam soil in forests, sandy soil in grassland, and clayey soil in the swamp and  
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43 145 water bodies (Das et al., 2014).  
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## 45 147 **Vegetation and wildlife**

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47 148 In general, there are four main types of vegetation in the KNP; tropical evergreen forest,  
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49 149 semi-evergreen forest, deciduous forest, grassland and swamp (Champion and Seth, 1968).  
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51 150 Alluvial grassland is the most dominant vegetation type (50.6%), followed by woodland  
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53 151 (21.8%), openland areas covered by short grasses and other herbaceous associates (7.7%), and  
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55 152 eroded land caused by soil erosion and landslides during intervals of high rainfall 11.7% in the  
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57 153 national park (Das et al., 2014).  
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3 154 The evergreen forest is generally confined to the areas adjacent to the Brahmaputra River,  
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5 155 small rivers, and streamlets within the park. This vegetation remains evergreen throughout the  
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7 156 year in the core regions and is dense and composed of forest elements including *Castanopsis*  
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9 157 *indica*, *Cinnamomum bejolghota*, *Duabanga grandiflora*, *Elaeocarpus robustus*, *Toona ciliata*,  
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11 158 *Mesua ferrea*, *Symplocos paniculata*, *Terminalia myriocarpa*, *Schima wallichii*, and *Litsea*  
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13 159 *monopetala*. The common climbers are *Calamus erectus*, *Vitis latifolia*, *Paederia foetida*,  
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15 160 *Cardiospermum halicacabum*, *Trichosanthes dioica*, *Smilax ovalifolia*, *Mucuna pruriens*, *Piper*  
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17 161 *longum*, and *Thunbergia grandiflora*. Among the ferns, both terrestrial ferns and epiphytes such  
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19 162 as *Lycopodium clavatum*, *Dryopteris filix-mas*, *Gleichenia dichotoma*, *Lygodium japonicum*,  
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21 163 *Drynaria rigidula*, *Angiopteris evecta*, *Asplenium nidus*, and *Pyrrosia nummularifolia* are  
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23 164 present (Figures 2a and 2b).

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25 165 The moist deciduous forest occurs as isolated patches within grasslands and next to the  
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27 166 evergreen forest. This forest consists of primarily deciduous trees which lose their leaves during  
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29 167 the winter season. The major tree taxa are *Bombax ceiba*, *Dillenia indica*, *Albizia procera*, *A.*  
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31 168 *lebbek*, *A. odoratissima*, *Neolamarckia cadamba*, *Trewia nudiflora*, *Careya arborea*,  
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33 169 *Lagerstroemia parviflora*, and *Semicarpus anacardium*. The forest floor is covered by different  
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35 170 species of Poaceae, Cyperaceae, Convolvulaceae, and Acanthaceae. The fern allies such as  
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37 171 *Dryopteris filix-mas*, *Adiantum caudatum*, *Blechnum occidentale*, *Polypodium vulgare*, and  
38  
39 172 *Drynaria rigidula* are the common members in this forest (Figures 2c and 2d).

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41 173 The grassland areas are scattered and dominated by tall grasses mainly *Erianthus*  
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43 174 *ravennae*, *Phragmites karka*, *Arundo donax*, *Imperata cylindrica*, and *Saccharum procerum*  
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45 175 along with short grasses like *Hemarthria compressa*, *Microstegium ciliatum*, *Cynodon dactylon*,  
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47 176 and *Cenchrus ciliaris*. However, some trees and shrubs such as *Bombax ceiba*, *Careya arborea*,  
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49 177 *Dillenia indica*, *Butea monosperma*, and *Albizia lebbek* also grow scattered within the grassland  
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51 178 (Figures 3a and 3b).

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53 179 The openland areas are also scattered especially near the periphery of the swamp. Tree  
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55 180 taxa are almost absent but there are some scattered shrubs such as *Melastoma malabathricum*,  
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57 181 *Cassia tora*, and *Clerodendron viscosum*. The openland area is covered with short grasses  
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59 182 followed by Cyperaceae, Acanthaceae, Amaranthaceae, Solanaceae, and Convolvulaceae.  
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183 *Cynodon dactylon*, *Cenchrus ciliaris*, *Chrysopogon aciculatus*, *Digitaria ciliaris*, and *Paspalum*  
184 *conjugatum* are the common species in short grass communities (Figure 3c).



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3 185 The swamp habitat is restricted to generally low-lying areas and covers around 11.8% of  
4 186 the park (Das et al., 2014). It is submerged throughout the whole year but during summer (May-  
5 187 August) the swamp habitat may be expanded due to flooding of river channels resulting from  
6 188 heavy monsoonal rainfall. The major marshy and aquatic taxa include *Alpinia allughas*,  
7 189 *Clinogyne dichotoma*, *Calamus tenuis*, *Polygonum orientale*, *Cyperus rotundus*, *Sagittaria*  
8 190 *sagittifolia*, *Eichhornia crassipes*, *Potamogeton pectinatus*, *Nymphaea alba*, *Euryale ferox*,  
9 191 *Myriophyllum indicum*, *Ludwigia sedioides*, and *Nymphoides indica*. Additionally, there are  
10 192 some trees and shrub taxa including *Syzygium cumuni*, *Barringtonia acutangula*, *Dillenia indica*,  
11 193 *Bombax ceiba*, *Osbeckia stellata*, and *Costus speciosus* that commonly grow on the periphery of  
12 194 the swamp area (Figure 3d).

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15 195 With regard to wildlife, KNP is mainly famous for its *Rhinoceros unicornis* (greater one-  
16 196 horned rhinoceros), but the park is also very rich in other animals and birds. The fauna includes  
17 197 490 species of birds, 43 species of reptiles and 52 species of mammals (Choudhury, 2003).  
18 198 Besides rhinoceros, other associated large and medium sized mammalian herbivores include  
19 199 *Bubalus arnee*, *Elephas maximus*, *Bos gaurus*, *Sus scrofa*, *Cervus unicolor*, *Cervus duvauceli*,  
20 200 *Axis porcinus*, *Muntiacus muntjak*, *Presbytis entellus*, *Macaca mulatta*, *Macaca assamensis*,  
21 201 and *Hylobates hoolock*. Birds such as *Francolinus gularis*, *Anser erythropus*, *Houbaropsis*  
22 202 *bengalensis*, *Tringa guttifer*, *Sterna acuticauda*, *Ardea insignis*, and *Pelecanus philippensis* are  
23 203 commonly seen in the park.

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## 27 205 **Materials and methods**

### 28 206 *Field work*

29 207 Out of a total of 75 surface soil samples, 15 (E1-E15) were collected from the evergreen forest,  
30 208 15 (D16-D30) from deciduous forest, 15 (G31-G45) from grassland, 15 (O46-O60) from  
31 209 openland, and 15 (S61-S75) from the swamp. In each vegetation type, the samples were procured  
32 210 at about 50 meter intervals.

### 33 211 *Laboratory work*

34 212 The surface soil samples were chemically processed employing the standard acetolysis method  
35 213 (Erdtman, 1953). The soil samples were treated with 10% aqueous KOH solution to deflocculate  
36 214 the pollen and spores from the soil followed by 40% hydrofluoric acid (HF) treatment to dissolve  
37 215 silica content. This was followed acetolysis. The samples were washed 2-3 times with glacial

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3 216 acetic acid and then washed 2-3 times with distilled water and sieved through a 500µm mesh.  
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5 217 Finally, the material was kept in a 50% glycerin solution with a drop of phenol. Totals of 259-  
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7 218 335 pollen grains per slide of each sample were counted to make the pollen spectra. The pollen  
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9 219 taxa have been categorized into arboreal taxa, non-arboreal taxa, extra-regional taxa (highland  
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11 220 taxa coming from the eastern Himalaya), and ferns. Similarly, a total of 225-284 fungal spores  
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13 221 per slide were counted from the same pollen slides and were categorized into coprophilous and  
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15 222 non-coprophilous fungal spores to make fungal spore spectra. For the precise identification of  
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17 223 fossil palynomorphs in the sediments, the reference pollen slides available at Birbal Sahni  
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19 224 Institute of Palaeosciences herbarium as well as pollen and fungal spore photographs in the  
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21 225 published literature (van Geel, 2003; Basumatary et al., 2017; Basumatary and McDonald, 2017)  
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23 226 were used. Photodocumentation of palynomorphs was made using Olympus BX-61 microscope  
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25 227 with DP-25 digital camera under 40X magnification (Figure 4). The pollen and fungal spore  
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27 228 spectra were made using TILIA software (Grimm, 2011) (Figures 5 and 6.).

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*Statistical analysis: canonical correspondence analysis*

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

237 Many fungal NPPs have short dispersal distances, and can therefore be overrepresented  
238 in locations near fruitbodies but underrepresented at even a short distance from fruitbodies  
239 (Wilmshurst and McGlone, 2005; Van Asperen et al., 2021). A square-root transformation was  
240 applied to the fungal NPP percentage data to compensate for this effect (Legendre and Legendre,  
241 2012; Paliy and Shankar, 2016; Borcard et al., 2018).

242 Canonical correspondence analysis (CCA; Ter Braak 1986; Borcard et al., 2018) was  
243 carried out on the transformed NPP data and the five environmental variables to assess the  
244 influence of the five vegetation type assemblages on the distribution of NPPs. Collinearity  
245 among the vegetation type assemblages was explored by computing Variance Inflation Factors  
246 (VIFs). Based on the results of this, CCA with forward selection of explanatory variables was

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3 247 carried out. Canonical axes were tested for significance by permutation ANOVA. CCA was  
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5 248 performed in R (Version 4.0.4, R Development Core Team, 2015) using the package vegan  
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7 249 (Oksanen et al., 2017).

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## 10 251 **Results**

11  
12 252 The presence and abundance of major pollen taxa, which serve as marker taxa and their  
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14 253 ecological significance in KNP are listed in Table 2. Diagrams of the pollen and fungal spore  
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16 254 spectra are presented in Figures 5 and 6 respectively.

17 255 Evergreen forest: The surface soil samples (E1-E15) are characterized by the dominance  
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19 256 of the major evergreen taxa *Mesua*, *Schima*, *Arecaceae*, *Symplocos*, and *Litsea* with values of  
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21 257 1.6-4.9% each followed by deciduous elements at values of 1.0-3.0%. Among non-arboreal taxa,  
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23 258 *Poaceae* is recorded with values of 6.0-8.2% and other herb taxa are also consistently  
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25 259 encountered with values of 3.3-3.8% in the pollen assemblages. Extra-regional taxa are  
26  
27 260 consistently present but with low values. Ferns, both monolete and trilete, are encountered with  
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29 261 ranges of 4.5-8.0% (Figure5). The most common coprophilous fungal spores are of the taxa  
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31 262 *Sporormiella*, *Saccobolus*, and *Ascodesmis* with values of 0.8-5.6%. *Podospora*, *Sordaria*,  
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33 263 *Arnium* and *Cercophora* were also encountered at low values. Non-coprophilous fungal spores  
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35 264 are consistently represented at the ranges of 0.8-14.1% , with *Glomus*, *Meliola* and  
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37 265 *Microthyriaceae* the most common taxa.

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38 267 Deciduous forest: The samples from the deciduous forest (D16-D30) are characterized by  
39  
40 268 the dominance of deciduous taxa with the ranges of 0.3-4.7% each, compared with evergreen  
41  
42 269 taxa at values of 0.3-1.6%. Among non-arboreal taxa, *Poaceae* is dominant and varies from 6.5-  
43  
44 270 9.4% and the other associated terrestrial and aquatic herbs are also recorded with values of 0.3-  
45  
46 271 4.6%. Extra-regional taxa are represented with maximum values upto 2.1% in the pollen  
47  
48 272 assemblages. Fern spores are also consistently present with maximum ranges of 4.5% and 5.8%  
49  
273 respectively.

50 274 The coprophilous fungal spores occur with values from 0.9-4.9%. Non-coprophilous  
51  
52 275 fungal spores are dominated by *Meliola*, *Glomus*, and *Mycrothyriaceae* as in the Evergreen  
53  
54 276 forest, with ranges from 0.8-15.5%.

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3 278 Grassland: The surface soil samples (G31-G45) from the grassland habitat are  
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5 279 characterized by the dominance of Poaceae with an average value of 30.7%. Other associated  
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7 280 terrestrial and aquatic taxa occur with maximum ranges upto 9.7%. Arboreal taxa, both  
8  
9 281 evergreen and deciduous elements, namely *Mesua*, *Bombax*, and *Careya* are regularly  
10  
11 282 encountered at low values. The extra-regional taxa are also consistently recorded with maximum  
12  
13 283 values of 2.6%. The monolete and trilete ferns are represented with ranges of 1.9-5.6% in the  
14  
15 284 pollen assemblages (Figure5). Coprophilous fungal spores are dominated by *Sporormiella*.  
16  
17 285 *Saccobolus*, and *Ascodesmis* with ranges of 1.0-6.9%, with other coprophilous taxa reaching  
18  
19 286 6.2%. Among the non-coprophilous fungal spores, *Helmithosporium* is abundant with values up  
20  
21 287 to 11.5%. *Meliola* and *Glomus* are regularly recorded with values of 0.5%-11.8%.

22 288  
23 289 Openland: The samples (O46-O60) from the openland located adjacent to the swamp are  
24  
25 290 characterized by the dominance of non-arboreal taxa with an average value of 58.9% compared  
26  
27 291 to arboreal taxa at 27.3%, followed by extra-regional taxa (7.7%) and ferns (6.1%). Among  
28  
29 292 arboreal taxa, both evergreen and deciduous elements are regularly encountered at ranges of 0.3-  
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31 293 4.9%. Among non-arboreal taxa Poaceae is dominant with an average value of 19.8% and the  
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33 294 other herb taxa are consistently represented by values of 0.3-6.1% in the pollen assemblages. The  
34  
35 295 extra-regional taxa are regularly encountered at the ranges of 0.4-3.2%. The ferns, both monolete  
36  
37 296 and trilete, are recorded by ranges of 2.1-4.3% (Figure5).The coprophilous fungal spores are  
38  
39 297 much more abundant than in the evergreen and deciduous forest and the grassland. They are  
40  
41 298 dominated by *Sporormiella*, *Saccobolus*, and *Ascodesmis* which are recorded at the values of 1.0-  
42  
43 299 20.0% each. The non-coprophilous fungal spores are less abundant that in the forest and  
44  
45 300 grassland areas, with values of 0.7-8.0%.

46 301  
47 302 Swamp: The mud samples (S61-S75) from the swamp habitat are characterized by the  
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49 303 dominance of non-arboreal taxa with an average value of 51.5% over arboreal taxa (30.7%). The  
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51 304 ferns and extra-regional taxa are also recorded with average values of 9.2% and 8.6%  
52  
53 305 respectively. Among arboreal taxa both evergreen and deciduous taxa are consistently  
54  
55 306 encountered at the values of 0.3-3.9%. Among non-arboreal taxa, Poaceae is dominant with an  
56  
57 307 average value of 15.6%. The marshy and aquatic taxa are consistently recorded with ranges of  
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59 308 0.6-4.5%. The extra-regional taxa are consistently encountered at the values of 0.3- 2.9%. The  
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3 309 fern spores, both monolete and trilete, are represented by values of 3.2-5.8% in the pollen  
4 310 assemblages (Figure5). Among fungal spores, the coprophilous fungal spores are similarly  
5 311 abundant as in the openland samples, and are dominated by *Sporormiella*, *Saccobolus*, and  
6 312 *Ascodesmis* which are represented in the range of 1.8-19.2% each. The non-coprophilous fungal  
7 313 spores are present at similarly lower ranges as in the openland samples of 0.4-7.8% .  
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### 14 315 **Statistical analysis of NPPs frequencies**

15 316 VIFs based on an initial CCA indicated significant collinearity was present among the  
16 317 environmental variables. Therefore, CCA with forward selection was carried out. Four  
17 318 environmental variables were selected for inclusion in the CCA: Deciduous forest, Grassland,  
18 319 Openland and Swamp (Figure 7). The environmental variables account for 92.4% (constrained  
19 320 inertia = 0.22728, total inertia = 0.24572) of the variance in the fungal NPP data. The first two  
20 321 CCA axes (eigenvalues: CCA1 = 0.2066, CCA2 = 0.01577) explain 90.4% of the variance. The  
21 322 permutation tests show that both the CCA as a whole ( $p = 0.001$ ) and each CCA axis (each  $p =$   
22 323  $0.001$ ) are significant and VIFs indicate collinearity among the vegetation type assemblages is  
23 324 low in this analysis. CCA1 is closely related to the openland pollen taxa (positive side) and  
24 325 deciduous pollen taxa (negative side), indicating an inverse relationship between forest pollen  
25 326 taxa and taxa typical of open environments. CCA2 is closely related to grassland pollen taxa on  
26 327 the negative side. Swamp pollen taxa have a positive relationship with both CCA1 and CCA2.  
27 328 Sites located in the different vegetation types cluster closely, with sites from deciduous and  
28 329 evergreen forest fairly well-differentiated in the upper left-hand quarter of the graph and sites in  
29 330 grassland habitats in the lower left-hand quarter of the graph, while sites from openland and  
30 331 swamp areas cluster together in the upper right-hand quarter.

31 332 NPPs cluster into four main groups (Figure 7). The coprophilous fungal spores,  
32 333 *Ascodesmis*, *Podospora*, *Sordaria*, *Sporormiella*, and *Saccobolus*, covary with the openland  
33 334 gradient. While, also present in relatively high numbers in the other vegetation types, they are  
34 335 most abundant in the openland and swamp habitats. *Helminthosporium* is the only type that  
35 336 covaries with the grassland gradient, which is unsurprising as this taxon consists mainly of molds  
36 337 that grow on grasses. Fungal NPPs that plot in the center of the graph, such as *Alternaria*,  
37 338 *Arnium*, *Helicoon*, *Tetraploa*, *Valsaria*, Type1, and Type2, are not strongly controlled by any of  
38 339 the environmental variables and occur at relatively similar proportions throughout the samples.  
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3 340 Some of these represent ubiquitous plant pathogens and decomposers (van Geel et al., 2003). All  
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5 341 other fungal NPPs (*Bipolaris*, *Cookeina*, *Dictyosporium*, *Glomus*, *Meliola*, Microthyriaceae,  
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7 342 Teleutospores) most strongly covary with the forest gradient. This group includes a number of  
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9 343 species that grow on woody debris (*Cookeina*, *Dictyosporium*), as well as plant pathogens and  
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11 344 decomposers, and the mycorrhizal fungus *Glomus*, which is well-known to form associations  
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13 345 with tree roots (van Geel et al., 2003), though it occurs in a wide variety of environments.  
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## 15 347 **Discussion**

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17 348 The modern pollen study of the different vegetation types and areas of different land-use  
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19 349 in KNP reveals a good agreement with the extant vegetation. However, some site by site  
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21 350 variation has been recorded in the fungal spores in the assemblages. A composite diagram shows  
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23 351 the relationship between, the vegetation types and wildlife in KNP based on the abundance of  
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25 352 local arboreal and non-arboreal pollen taxa and coprophilous fungal spores in the  
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27 353 palynoassemblages (Figure 8). The evergreen forest is characterized by the high abundance of  
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29 354 evergreen arboreal pollen taxa (31.3%). The high abundance of deciduous arboreal pollen taxa  
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31 355 (32.6%) in the palynoassemblages signifies the deciduous forest. The grassland is characterized  
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33 356 by the abundance of Poaceae pollen (30.6%). Similarly, the openland area is characterized by the  
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35 357 abundance of both Poaceae (20.6%) and other associated non-arboreal pollen (20.2%). The  
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37 358 swamp area is characterized by the high abundance of marshy and aquatic pollen (21.9%)  
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39 359 followed by deciduous (20.1%), evergreen (10.6%) and Poaceae (15.6%) pollen. The abundance  
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41 360 of the coprophilous fungal spores in the openland (60.7%), swamp (59.3%), and grassland  
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43 361 (23.9%) are exhibited in the palynoassemblages which indicates that these sites are highly  
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45 362 impacted by the herbivores. The evergreen and deciduous forest can be characterized as  
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47 363 moderately impacted sites as indicated by the relatively lower abundance of coprophilous fungal  
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49 364 spores with average values of 16.4% and 16.3%, respectively in the palynoassemblages.

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51 365 The samples taken from the evergreen forest reveals *Mesua-Schima-Duabanga-*  
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53 366 *Cinnamomum-Arecaceae-Litsea* assemblage, showing a good relationship between the pollen  
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55 367 and extant vegetation. The abundance of evergreen taxa, especially *Mesua*, *Duabanga*, and  
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57 368 *Syzygium* in the pollen assemblage is significant (maximum value up to 4.9%) and is indicative  
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59 369 of high rainfall activity in the region, as these taxa are high rainfall indicators (>2500 mm/y;  
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61 370 Singh et al., 1990; Barboni and Bonnefille, 2001). The evergreen forest was evident in the KNP



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3 371 by the presence of *Mesua* and *Duabanga* pollen in the rhino dung samples (Basumatary et al.,  
4 372 2017), as these aforesaid taxa are dominant in the evergreen forest of the KNP. The presence of  
5 373 marshy and aquatic taxa, such as *Cyperaceae*, *Polygonum*, *Nymphoides*, and *Nymphaea* pollen,  
6 374 which could have been transported by wild herbivores and birds, indicate natural perennial water  
7 375 bodies in and around the study area (Ekblom and Gillson, 2010; Basumatary et al., 2017; Stivrins  
8 376 et al., 2019). During the daytime after feeding in the swamp areas these animals move towards  
9 377 the surrounding forests for rest, shelter or to forage in the forest.

15 378 Among the fungal spore assemblages, the presence of non-coprophilous fungal spores,  
16 379 *Microthyriaceae*, *Glomus*, and *Meliola* was marked. These taxa are characteristic of dense forest  
17 380 vegetation under warm and humid climatic conditions in response to the high rainfall in the  
18 381 region. Specifically, the abundance of *Microthyriaceae*, *Glomus*, and *Meliola* is considered to be  
19 382 indicative of the presence of dense forest vegetation (Musotto et al., 2012, 2017; Cookson, 1947;  
20 383 Selkirk, 1975; Johnson and Sutton, 2000; Hofmann, 2010; Medeanic and Silva, 2010; Loughlin  
21 384 et al., 2017), and this is reflected in the studied samples from KNP. In the palaeoecological  
22 385 literature, *Glomus* is often seen as an indicator of erosion (Shumilovskikh et al., 2021). However,  
23 386 since this fungus is an endomycorrhiza and often associates with trees, in this case the abundance  
24 387 of its spores is due to its abundance in the forest soil (Kołaczek et al., 2013).

32 388 The presence of coprophilous fungal spores was marked in the studied samples and the  
33 389 relatively high percentages are indicative of the presence of wildlife. The coprophilous fungal  
34 390 spores may be limited to specific locations frequented by herbivores so can be considered local  
35 391 in origin since they can only actively disperse a short distance which restricts their presence to  
36 392 near to where sporulation took place (Davis et al., 1977; Parker, 1979; Wicklow, 1992;  
37 393 Richardson, 2001; Malloch and Blackwell, 1992; van Geel et al., 2003, 2008; van Geel and  
38 394 Aptroot, 2006; Ekblom and Gillson, 2010; Parker and Williams, 2011; van Asperen et al., 2021).  
39 395 The frequency of *Sporormiella*, *Ascodesmis*, and *Saccobolus* was relatively higher in openland  
40 396 and swamp areas as compared to the dense forest. In our study, the moderately high value of  
41 397 coprophilous fungal spores (5.6%) was observed in the palynoassemblage which is quite higher  
42 398 than the 2%, considered as a 'background' level (Davis, 1987; Gill et al., 2013; Baker et al.,  
43 399 2016; Raczka et al., 2016). These spores can therefore be inferred to reflect local abundance of  
44 400 the herbivore fauna. The forest area is generally dark, windless, cooler and more humid than  
45 401 outside the forest; conditions that are favorable for fungal growth (Musotto et al., 2017; Promis



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3 402 et al., 2010; Godeas and Arumbarri, 2007). Monkeys, gibbons, birds, and other arboreal animals  
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5 403 are common, and their excreta regularly falls to the forest floor. The diversity of the fungal  
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7 404 remains especially the non-coprophilous fungal spores is high in all samples.

8 405 The *Salmalia-Dillenia-Lagerstroemia-Semecarpus-Careya* pollen assemblage was in  
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10 406 agreement with the extant deciduous forest vegetation in KNP. The *Dillenia-Terminalia-Careya*  
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12 407 assemblage is significant as it is characteristic of the preferred habitat of wildlife in the  
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14 408 Balpakram valley in the Garo hills of Meghalaya (Basumatary et al., 2014) which coincided with  
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16 409 the pollen assemblages in KNP. These plants are utilized as the primary food plants preferred by  
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18 410 many herbivorous mammals including elephant and deer species (Odden et al., 2005; Steinheim  
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20 411 et al., 2005; Neupane et al., 2019; Devi et al., 2022). The consistent abundance of *Bombax* pollen  
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22 412 in the palynoassemblage which is recorded upto 4.7% was marked in comparison to the other  
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24 413 associated arboreal taxa. *Bombax* is a fire resistant plant (Troth, 1976) which is one of the  
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26 414 reasons for its abundance in the palynoassemblage. Forest fires during winter are an important  
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28 415 part of the ecology for the wildlife of KNP. Herbivory is an important driver of vegetation  
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30 416 structure in the region (Ekblom and Gillson, 2010), so the large herbivores may have played a  
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32 417 significant role in shaping the structure of plant communities in the KNP. The coprophilous  
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34 418 fungi, *Sporormiella*, *Saccobolus*, and *Ascodesmis* are represented consistently in the studied  
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36 419 samples and their abundance closely resembles that in the evergreen forest samples and is also  
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38 420 indicative of the presence of wildlife habitation in the deciduous forest. These fungi are also  
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40 421 present at relatively higher abundances than in the evergreen forest, indicative of the higher  
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42 422 impact of herbivores on the deciduous forest.

39 423 The percentages of Poaceae pollen are relatively high in the grassland samples (average 30.7%)  
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41 424 and the *Salmalia-Dillenia-Emblica-Butea-Careya-Poaceae* pollen assemblage was identified as  
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43 425 characteristic of this habitat. The presence of some arboreal taxa, especially *Mesua*, *Duabanga*,  
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45 426 and *Symplocos*, is significant as these taxa do not usually occur in this vegetation type. Given  
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47 427 that these taxa are insect-pollinated, they most likely have been secondarily deposited through  
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49 428 animal dung where the herbivores ingested the plant parts elsewhere and were subsequently  
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51 429 defecated in and around the grassland areas. The presence of arboreal pollen taxa, both evergreen  
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53 430 and deciduous, was recorded from the midden dung of rhinoceros from forested and grassland  
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55 431 regions of KNP (Hazarika and Saikia, 2010; Basumatary et al., 2018). The pollen clumping in  
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57 432 grasses and *Bombax*, is marked and indicative of their local origin. The presence of pollen grain  
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3 433 clumps is a characteristic feature of entomophilous plants whose pollen disperses shorter  
4 434 distances than wind-dispersed pollen grains (Faegri and Van Der Pijl, 1966; Martin et al., 2009).  
5 435 Since the Kaziranga National Park is enriched with swampy areas, the aquatic vegetation need to  
6 436 be included in the pollen spectra for monitoring the status of water level through pollen records  
7 437 in relation to the monsoonal activities. Moreover, the dung of the megaherbivores like one horn  
8 438 rhino also include aquatic pollen and thus, the modern aquatic pollen preservation could act as a  
9 439 baseline for the coprolite studies for tracing the megafaunal extinction during the Quaternary  
10 440 (Basumatary et al., 2017). The generated pollen data would assist in distinguishing the natural  
11 441 forest vegetation from areas impacted by human activities in the region, based on the fossil  
12 442 marker pollen taxa like Poaceae and Brassicaceae (Basumatary et al., 2018; Tripathi et al., 2021).

13 443 Among the fungal spores, coprophilous fungi such as *Sporormiella*, *Saccobolus*,  
14 444 *Podospora*, and *Ascodesmis* are dominant and represented consistently in the  
15 445 palynoassemblages. Herbivorous animals, especially rhinoceros and elephant, feed and defecate  
16 446 in the grassland, dispersing coprophilous fungal spores with their dung. However, although they  
17 447 are more common than in the forest assemblages, coprophilous fungal spores are less common in  
18 448 the grassland than in the openland and swamps. This may be due to the midden behaviour of  
19 449 some of the large mammals, especially the rhinoceros, which tends to defecate in specific areas,  
20 450 so the spores are not distributed uniformly on the landscape. The *Sporormiella-Saccobolus-*  
21 451 *Ascodesmis* assemblage was present in the midden dung of rhinoceros from grassland areas  
22 452 (Basumatary and McDonald, 2017) from the KNP. Among the non-coprophilous fungi,  
23 453 *Helminthosporium* and *Alternaria* are especially dominant. Both taxa are common pathogens of  
24 454 herbaceous plants, particularly grasses. Other fungal spores such as *Glomus*, Microthyriaceae,  
25 455 and *Tetraploa* are also present in lower values in the assemblages. However, grasses have a high  
26 456 resistivity to fungal infection due to their silica content (Park et al., 2006, 2010; Hayasaka et al.,  
27 457 2008) which is the main reason for the low fungal diversity exhibited in the grassland.

28 458 The palynological study in the openland area identified some distinguishing features of  
29 459 this habitat within the park, as it is characterized by the *Salmalia-Dillenia-Mesua-Barringtonia-*  
30 460 *Litsea-Melastoma-Poaceae-Mimosa* pollen assemblage. Grasses are dominant and recorded a  
31 461 maximum value upto 19.8%. However, the arboreal, marshy, and aquatic taxa, *Mesua*, *Bombax*,  
32 462 *Lagerstroemia*, *Syzygium*, Onagraceae, and *Nymphaea* are also consistently present in the pollen  
33 463 assemblages. This reflects the excreted dung of herbivorous animals and birds which

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3 464 incorporated these tree taxa through their ingestion in and around the openland areas. Pollen  
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5 465 clumping of Poaceae, Cyperaceae, and *Polygonum* is very common in the palynoassemblages  
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7 466 indicating they originate from local sources (Faegri and van der Pijl, 1966; Martin et al., 2009).  
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9 467 Among the fungal spores the coprophilous fungal spores *Sporormiella-Saccobolus-Ascodesmis*  
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11 468 are dominant in the assemblage and confirmed that the openland habitat can be considered to  
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13 469 function as a corridor for wildlife. The abundance of coprophilous fungal spores in the openland  
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15 470 areas suggests a direct link of abundance of wildlife and higher amount of decomposed organic  
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17 471 matter derived from dung.

17 472 The palynological study of the swamp sediments reveals that the *Salmalia-Dillenia-*  
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19 473 *Syzygium-Mesua-Duabanga-Litsea-Melastoma-Poaceae-Mimosa* pollen assemblage indicates  
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21 474 different types of forest vegetation in and around the swamp area of the national park. The  
22  
23 475 riparian forest taxa, *Lagerstroemia*, *Barringtonia*, and *Duabanga* grow luxuriantly along the  
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25 476 periphery of the wetland area. Among non-arboreal taxa, the marshy and aquatic taxa are local in  
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27 477 source. The other terrestrial non-arboreal taxa, chiefly Asteroideae, Convolvulaceae, and  
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29 478 *Mimosa*, were deposited in and around the areas by the inwash of rainwater. The presence of  
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31 479 *Rhododendron* pollen (a flood marker taxon; Basumatary et al., 2019) indicates flood activity in  
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33 480 the region.

32 481 Among the fungal spores the non-coprophilous fungal spores predominate but  
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34 482 coprophilous fungal spores, especially *Sporormiella*, *Podospora*, and *Saccobolus*, are still  
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36 483 comparatively abundant in comparison to the other studied sites. The preserved fungal spores  
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38 484 may have originated from surrounding areas and subsequently transported and deposited through  
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40 485 rainwater and slopewash. Furthermore, the swamp serves as a focal point for mammals and birds  
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42 486 for their food and especially drinking water. The amount of dung, especially the midden dung of  
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44 487 rhinoceros, is large. Water availability is an important factor for the germination and sporulation  
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46 488 of coprophilous fungi (Austin, 1958; Ingold and Marshall, 1962; Kuthubutheen and Webster,  
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48 489 1986a, 1986b), and dung deposited in the swamp can be expected to remain wet longer than in  
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50 490 the other vegetation types and thus enhance the potential for germination.

50 491 Among the non-coprophilous fungi *Tetraploa* was more abundant than in the other  
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52 492 vegetation types, which reflects its ecology as a saprophytic fungus of Poaceae and Cyperaceae,  
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54 493 both of which are major wetland taxa. The abundance of *Glomus* in the palynoassemblage might  
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56 494 be the result of transport directly from the surrounding forest, as *Glomus* is indicative of soil

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3 495 erosion (van Geel et al., 2003; Kiage and Liu, 2009). The diversity of the coprophilous fungal  
4 496 spores is similar to that of the openland samples with abundant spores of *Sporormiella*,  
5 497 *Saccobolus*, and *Ascodesmis*. This pattern is also seen in the rhinoceros dung midden samples  
6 498 (Basumatary et al., 2017).  
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10 499 The presence of the extra-regional taxa, *Pinus*, *Abies*, *Picea*, and *Larix* in samples from  
11 500 all vegetation types is significant and indicative of strong wind activity from the higher Himalaya  
12 501 but might also be introduced by migratory Siberian birds (Barua and Sharma, 1999), when they  
13 502 fly through pollen-laden environments. The bird diversity documented in KNP is over 521  
14 503 species of which more than 200 are residents while the rest are migrants, including local  
15 504 migrants (Rahmani et. al., 2022). Pollen may adhere to their body and feathers of migratory  
16 505 species and then subsequently be dislodged during grooming while they are in KNP, especially  
17 506 from species that may overwinter in the park.  
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24 507 Studies of modern analogues based on the pollen and fern spore assemblages have shown  
25 508 it is possible to distinguish agricultural land from the fallow and salt marsh grassland (Graf and  
26 509 Chmura, 2006). The presence of coprophilous fungal spores can aid in distinguishing grazed or  
27 510 manured land use from natural vegetation. Similarly, this study can serve as a guideline to  
28 511 differentiate and distinguish the different vegetation types and the presence and impact of  
29 512 herbivores based on the presence and absence of local arboreal pollen taxa along with  
30 513 coprophilous fungal spores especially *Sporormiella*, *Sodaria*, and *Ascodesmis* in the  
31 514 palynoassemblages. Vegetation structure is mainly controlled by herbivores density (Bell, 1982)  
32 515 in African savannah and the woody cover reduction is directly linked to the concentration of  
33 516 herbivores (Dublin et al., 1990), their presence or absence can be documented by the presence of  
34 517 coprophilus fungal spores in the palynological studies of soil sediments. In order to understand  
35 518 the actual reason of decline and extinction of megaherbivores whether by human activities or due  
36 519 to climate-induced environment change (Wroe et al., 2013) documentation of their presence,  
37 520 either directly by skeletal remains or indirectly via proxy such as coprophilous fungal spores is  
38 521 critical. Other evidence for human impact can be the ability to recognize former cropland  
39 522 whether manured or unmanured based on the representation of local arboreal pollen taxa and  
40 523 coprophilous fungal spores in the palynoassemblages preserved in sediments.  
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## 526 **Comparison of pollen spectra with canonical correspondence analysis**

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

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## 537 **Interaction between vegetation and herbivores**

538           Demonstrating the strong relationship between pollen types and vegetation in an area  
539 provides an opportunity to infer changes in wildlife habitat at both a temporal and spatial scale.  
540 Complementing the pollen record is the associated coprophilous fungal spore record which can  
541 provide an indication of the presence of herbivore populations utilizing the different vegetation  
542 types in these habitats and thus responding to their expansion or reduction over time (Ekblom  
543 and Gillson, 2010). Integrating ecological studies of all herbivores in the park and their  
544 preferred habitats is critical to integrate with the documentation of the association of pollen and  
545 vegetation types to better understand how the vegetation and fauna interact through time (Table  
546 3). Equally important is the documentation of the abundance and types of coprophilous fungal  
547 spores associated with each species' dung (Basumatary and McDonald, 2017; Basumatary et al.,  
548 2019; Basumatary et al., 2021) to provide more refined information on what species of  
549 herbivores were present and their association with specific habitats and recognize their  
550 heterogenous distribution on the landscape rather than just rough estimates of the increase or  
551 decrease in herbivore populations through time.

552

## 553 **Conclusions**

554           This study demonstrates that the depositional pattern of pollen and NPP and their relative  
555 abundance in different vegetation types in KNP parallels the vegetation present in each type of  
556 habit and the impact of herbivores that utilize them. The pollen data from the different vegetation

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3 557 types in KNP reveals a strong relationship with the extant vegetation. In contrast, the  
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5 558 depositional pattern of fungal spores varies from site to site due to different levels of wildlife  
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7 559 impact and seasonal differences in their presence and utilization of the different vegetation types  
8  
9 560 in the national park. Our study is in close agreement with the vegetation survey and existing  
10  
11 561 forest types in KNP (Champion and Seth, 1968; Das et al., 2014).

12 562 As such, the data will be helpful in providing a foundation to differentiate and distinguish  
13  
14 563 the natural forest vegetation from areas impacted by human activities in the region, based on the  
15  
16 564 fossil pollen record given the potential for misidentification of conserved landscapes such as  
17  
18 565 national parks and wildlife sanctuaries and areas that are not set aside or protected and have been  
19  
20 566 heavily impacted by human activity, such as deforestation, farming, and pastoral practices. This  
21  
22 567 may be indicated by the presence and abundance of local arboreal pollen or the relative  
23  
24 568 abundance of coprophilous fungi since unmanured soil has significantly less coprophilous fungi  
25  
26 569 than manured soil (Graf and Chmura, 2006). The openland area is also an important place for  
27  
28 570 wildlife survival as indicated by the presence of marker pollen taxa and the abundance of  
29  
30 571 coprophilous fungal spores. The overall palynological analysis of the swamp sediments could be  
31  
32 572 a reliable and complementary data for the representation of the vegetation types and abundances  
33  
34 573 of herbivores both of which can contribute to palaeoecological and palaeoherbivory analysis.

35 574

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48 583 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  
907 analysis (CCA).

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

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

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

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

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

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3 920 migratory birds, d. A view of swamp showing numbers of *Cervus duvauceli* (Swamp  
4 921 Deer) in the center.

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6 922 **Figure 4.** Palynoassemblages recovered from the surface soil samples from the Kaziranga  
7 923 National Park.

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10 924 Explanation of palynomorphs

11 925 a. *Bombax ceiba*, b. *Duabanga* in cluster, c. *Cinnamomum*, d. *Litsea*, e. *Terminalia*, f.  
12 926 *Lagerstroemia*, h. *Shorea robusta*, i. *Schima*, j. *Semecarpus*, k. *Syzygium*, l. *Arecaceae*,  
13 927 m. *Albizia*, n. *Lantana*, o. *Pinus*, p. *Rhododendron*, q. *Asteroideae*, r. *Chinoroideae*, s.  
14 928 *Impatiens*, t. *Convolvulaceae*, u. *Cyperaceae*, v. *Poaceae* in cluster, w. *Polygonum*, x.  
15 929 *Nymphaea*, y. *Typha*, z. *Monolete*, aa. *Trilete*, ab. *Sporormiella*, ac. *Sordaria*, ad.  
16 930 *Meliola*, ae. *Tetraploa*, af. *Glomus*.

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19 931 **Figure 5.** Comparative pollen spectra in relation to the different vegetation types from Kaziranga  
20 932 National Park.

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23 933 **Figure 6.** Comparative fungal spores spectra in relation to the different vegetation types and  
24 934 herbivores impact from the Kaziranga National Park.

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26 935 **Figure 7.** Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types  
27 936 and environmental variables. NPP types (red) and samples (dark green: evergreen  
28 937 forest; light green: deciduous forest; yellow: grassland; orange: openland; light blue:  
29 938 swamp) are plotted against vegetation type indicator assemblages (blue arrows).

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31 939 **Figure 8.** Composite pollen and fungal spore diagram in relation to the different vegetation types  
32 940 from Kaziranga National Park.

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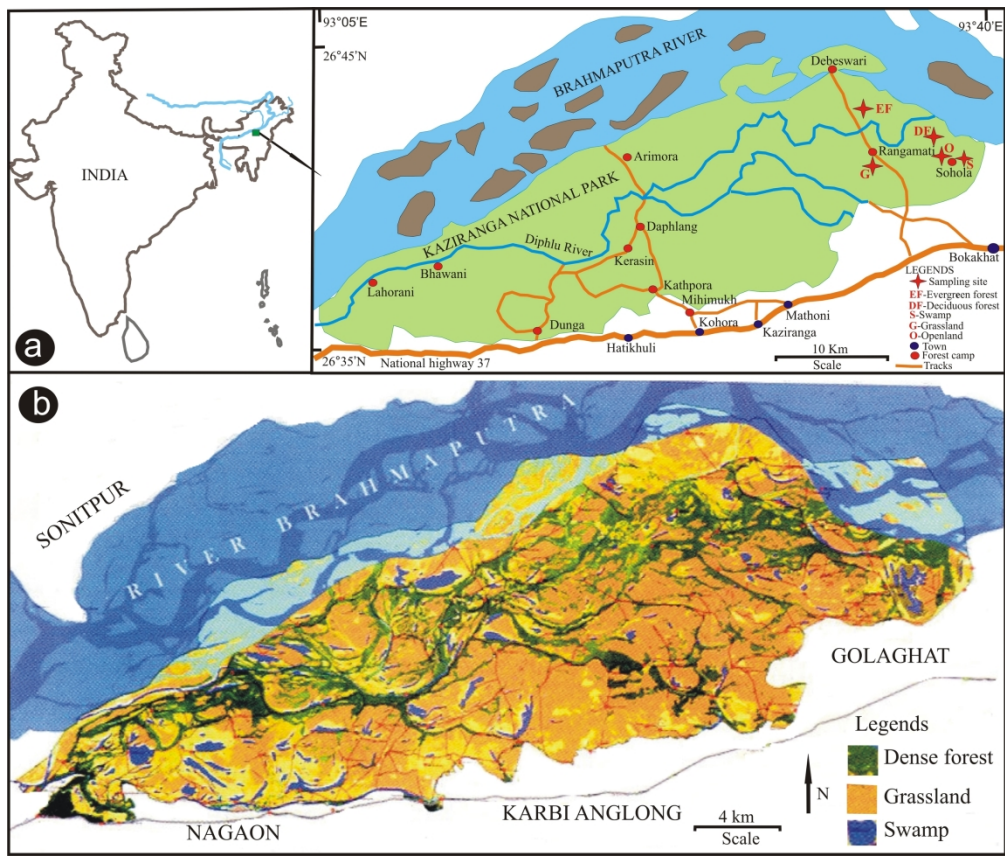


Figure 1. a. Map showing the study areas; b. Vegetation coverage map of Kaziranga National Park (modified after Das et al., 2014).

244x207mm (300 x 300 DPI)



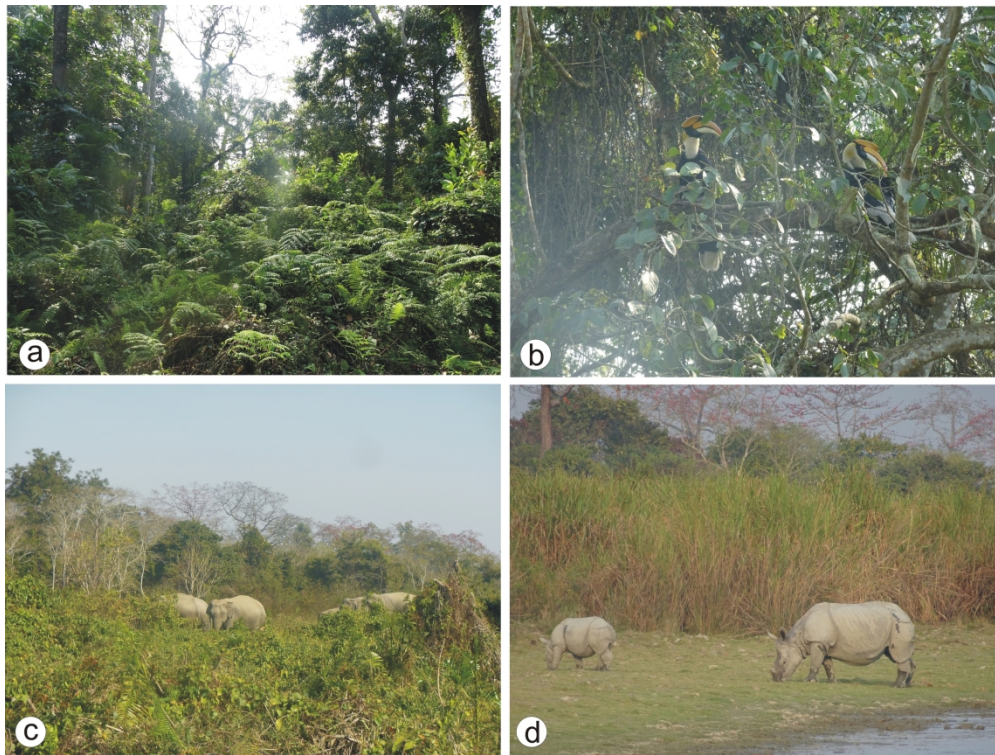


Figure 2. a. Thick evergreen forest within Kaziranga National Park, b. *Buceros bicornis* (Hornbills) sitting on the tree within the evergreen forest, c. Group of *Elephas maximus* (Asian Elephant) in deciduous forest in Kaziranga National Park, d. *Rhinoceros unicornis* grazing in the periphery near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

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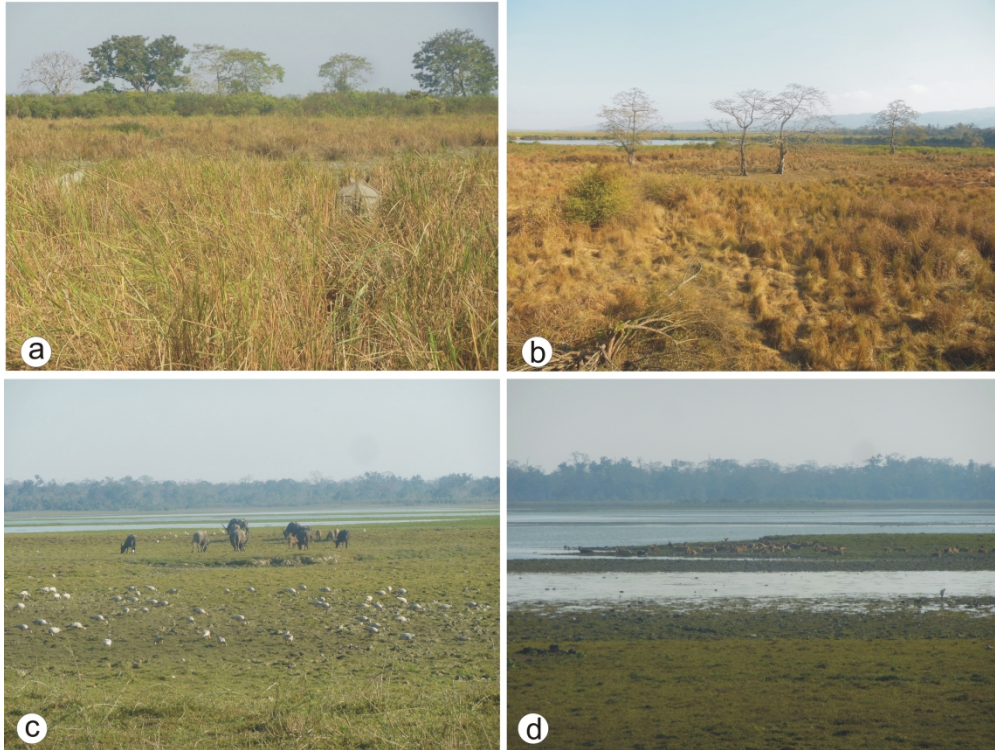


Figure 3. a. Grassland and show grazing of *Rhinoceros unicornis* b. A view of grassland during winter, c. A view of openland showing *Bubalus arnee* (Asian Buffalo) and numbers of migratory birds, d. A view of swamp showing numbers of *Cervus duvauceli* (Swamp Deer) in the center.

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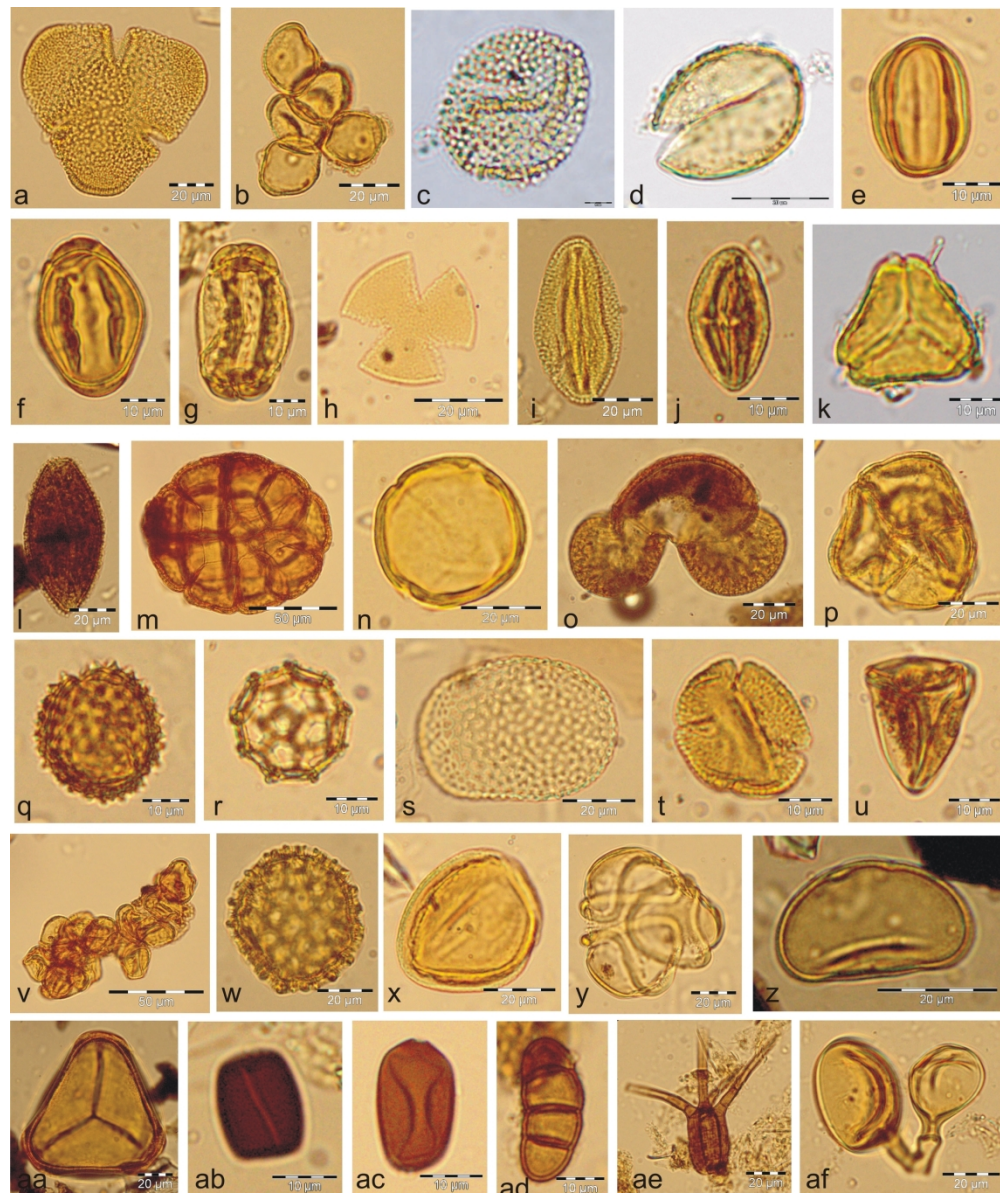


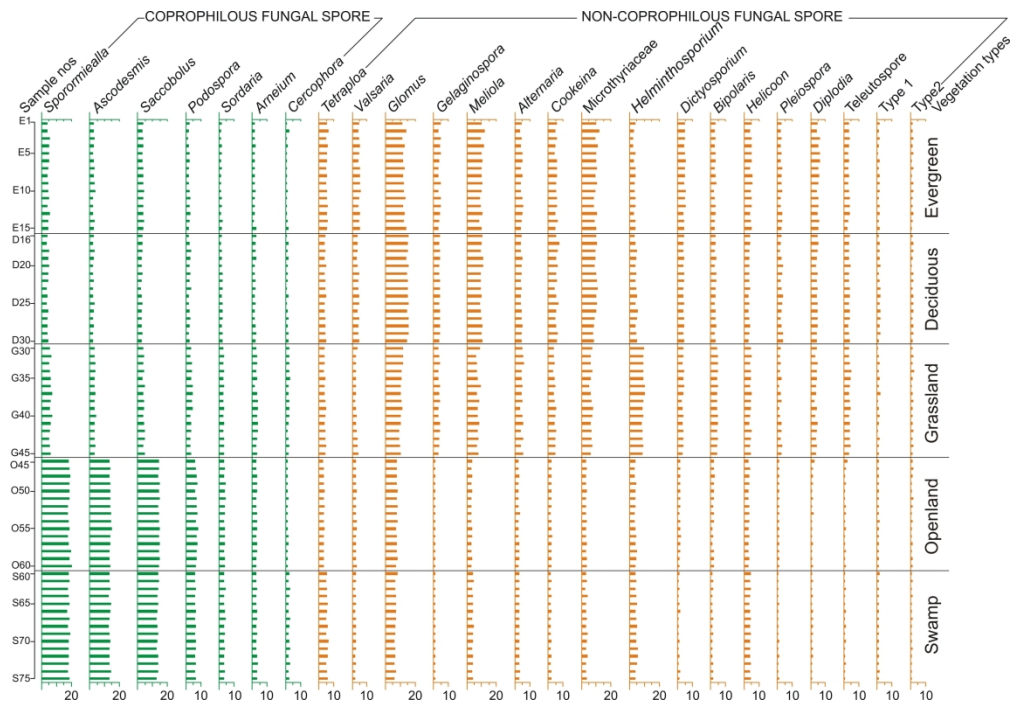
Figure 4. Palynoassemblages recovered from the surface soil samples from the Kaziranga National Park.

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*.

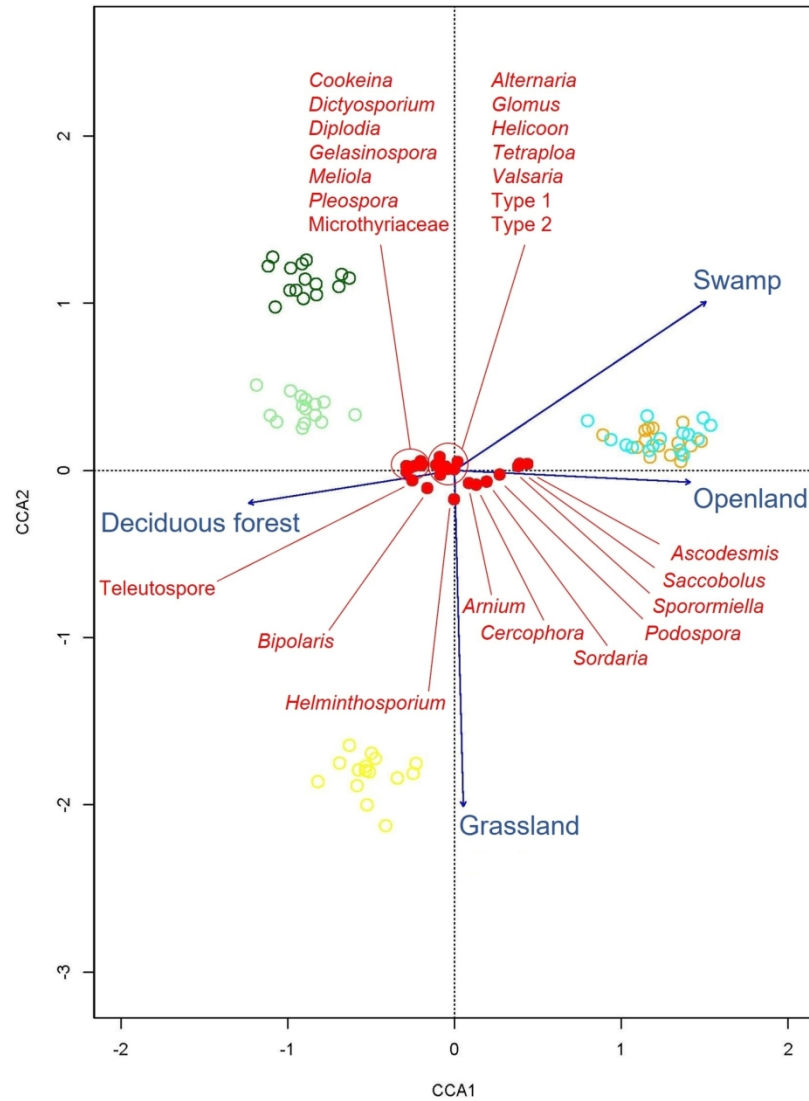
198x236mm (300 x 300 DPI)





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

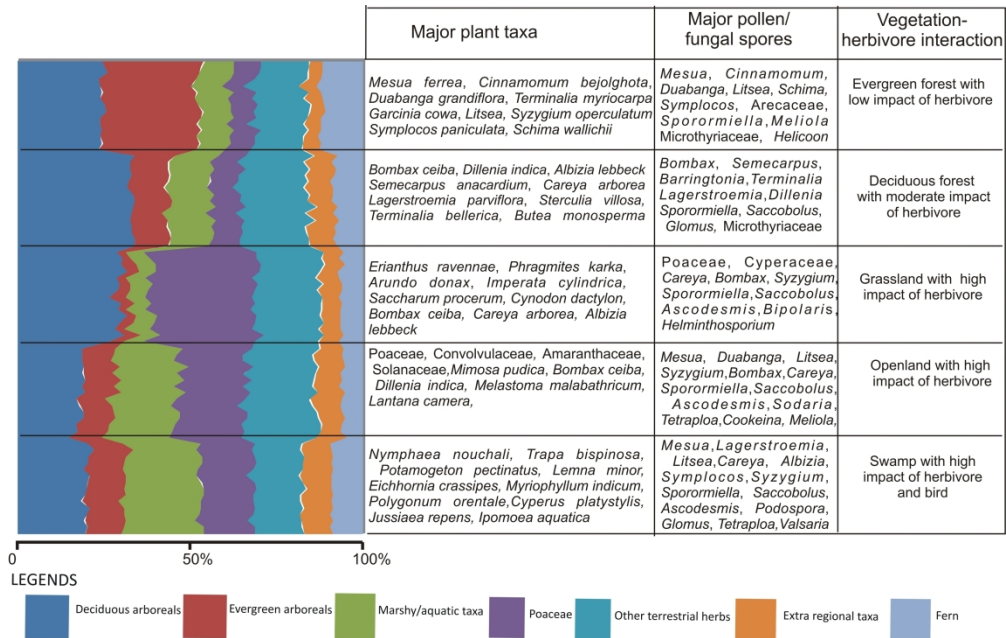
279x192mm (300 x 300 DPI)



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)	<i>Cinnamomum</i> , <i>Duabanga</i> , <i>Litsea</i> , <i>Mesua</i> , <i>Schima</i> , <i>Symplocos</i> , Arecaceae, Dipterocarpaceae, Oleaceae, <i>Impatiens</i> , Piperaceae
Deciduous (DC)	<i>Albizia</i> , <i>Careya</i> , <i>Dillenia</i> , <i>Emblica</i> , <i>Lagerstroemia</i> , <i>Lannea</i> , <i>Bombax</i> , <i>Semicarpus</i> , <i>Sterculia</i> , <i>Terminalia</i> , Convolvulaceae, Cyperaceae, Lamiaceae
Grassland (GL)	<i>Butea</i> , <i>Bauhinia</i> , <i>Dillenia</i> , <i>Bombax</i> , Asteroideae, Chinoriideae, Poaceae
Openland (OL)	<i>Barringtonia</i> , <i>Bombax</i> , <i>Clerodendron</i> , <i>Lantana</i> , <i>Melastoma</i> , <i>Bombax</i> , <i>Justicia</i> , <i>Mimosa</i> , <i>Xanthium</i> , Amaranthaceae, Convolvulaceae, Cyperaceae, Euphorbiaceae, Onagraceae, Solanaceae
Swamp (SW)	<i>Syzgium</i> , <i>Eichhornia</i> , <i>Lemna</i> , <i>Myriophyllum</i> , <i>Nymphoides</i> , <i>Polygonum</i> , <i>Potamogeton</i> , <i>Typha</i> , <i>Nymphaea</i> , 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. <i>Mesua</i>	Evergreen/High rainfall/Forestland
2. <i>Schima</i>	Evergreen/High rainfall/Forestland
3. <i>Litsea</i>	Evergreen/High rainfall/Forestland
4. <i>Cinnamomum</i>	Evergreen/High rainfall/Forestland
5. <i>Duabanga</i>	Evergreen/High rainfall/Swamp
6. Dipterocarpaceae	Deciduous/High rainfall/Forestland
7. <i>Bombax</i>	Deciduous/Forestland/Openland
8. <i>Syzygium</i>	Deciduous/High rainfall/Forestland
9. <i>Albizia</i>	Deciduous/Forestland
10. <i>Semecarpus</i>	Deciduous/forestland
11. <i>Sterculia</i>	Deciduous/Forestland
12. <i>Lagerstroemia</i>	Deciduous/Riparian/Forestland
13. <i>Barringtonia</i>	Riparian/Swamp/Forestland
14. <i>Careya</i>	Deciduous/Swamp/Forestland
15. <i>Melastoma</i>	Deciduous/Swamp/Openland
16. <i>Dendrophthae</i>	Evergreen/Deciduous/High rainfall
17. <i>Impatiens</i>	Riparian/High rainfall/Forestland
18. Poaceae	Perennial herb/Grassland/Openland
19. Cyperaceae	Marshy/Swamp
20. Onagaraceae	Marshy/Aquatic/Swamp
21. <i>Eichhornia</i>	Marshy/Aquatic/Swamp
22. <i>Polygonum</i>	Marshy/Swamp
23. <i>Xanthium</i>	Marshy/Swamp
24. <i>Nymphoides</i>	Aquatic/High rainfall/Swamp
25. <i>Nymphaea</i>	Aquatic/High rainfall/Swamp
26. <i>Potamogeton</i>	Aquatic/High rainfall/Swamp
27. <i>Typha</i>	Aquatic/High rainfall/Swamp
28. <i>Justicia</i>	Perennial herb/Openland
29. Convolvulaceae	Perennial herb/Openland
30. <i>Mimosa</i>	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
<i>Rhinoceros unicornis</i>	++	+++	+++	++	+++	Gurung and Chalise, 2015; pers. Comn. Local community
<i>Elephas maximus</i>	+++	+++	+++	+	+++	Neupane et al., 2019; pers. Comn. Local community
<i>Bubalus bubalis</i>	++	+++	+++	+++	+++	pers. Comn. Local community
<i>Bos gaurus</i>	+++	+++	+	++	+++	Imama and Kushwaha, 2013; pers. Comn. Local community
<i>Cervus unicolor</i>	++	+++	+++	+++	+++	pers. Comn. Local community
<i>Cervus duvauceli</i>	++	+++	+++	++	++	pers. Comn. Local community
<i>Axis porcinus</i>	+	+++	+++	+++	+++	Biswas 2004; Odden et al,

						2005; Peacock
						1933;
						Johnsingh et
						al. 2004
10	<i>Muntiacus</i>	++	+++	+++	+++	+++
11	<i>muntjak</i>					pers. Comn.
12						Local
13						community
15	<i>Presbytis entellus</i>	+++	+++	+	+	+
16						pers. Comn.
17						Local
18						community
20	<i>Macaca mulatta</i>	+++	+++	+	+	+
21						pers. Comn.
22						Local
23						community
25	<i>Macaca</i>	+++	+++	+	+	+
26	<i>assamensies</i>					pers. Comn.
27						Local
28						community
30	<i>Hylobates hoolock</i>	+++	+++	+	+	+
31						pers. Comn.
32						Local
33						community

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### Legends

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

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4 1 **Pollen and non-pollen palynomorph depositional patterns in Kaziranga**  
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6 2 **National Park, India: implications for palaeoecology and palaeoherbivory**  
7  
8 3 **analysis**

9 4 **Sadhan K. Basumatary<sup>1</sup>, Eline N. van Asperen<sup>2</sup>, H. Gregory McDonald<sup>3</sup>, Swati Tripathi<sup>1</sup>**  
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35 19 **Abstract**

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37 20 The main aim of this study is to produce a modern analogue for pollen and non-pollen  
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39 21 palynomorphs (NPPs) preserved in soil in relation to the different vegetation types and herbivore  
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41 22 impact in the Kaziranga National Park (KNP). The pollen data obtained reflects both the extant  
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43 23 vegetation types in each habitat as well as landuse, but some ~~site-by-site~~ variation was  
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45 24 observed with respect to the coprophilous fungal spores present in the palynoassemblage.

46 25 Canonical correspondence analysis (CCA) analysis of pollen data reveals the ~~presence of five~~  
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48 26 ~~significantly different~~ vegetation types ~~and are significantly different~~, while the non-pollen  
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50 27 palynomorphs are relatively similar in relation to the different vegetation types. ~~The~~

51 28 ~~*Sporormiella-Saccobolus-Ascodesmis* assemblage was marked and abundant in the openland and~~  
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53 29 ~~swamp habitat.~~ The ~~long-term association impact~~ of the wildlife ~~and their impact on~~ different  
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55 30 vegetation types ~~and their habitat with long-term association~~ is one of the main reasons for the  
56  
57 31 variations ~~seen in~~ of the depositional pattern in the assemblage. ~~It is observed that~~ 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 can~~ ~~ould~~ 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.

41

## 42 **Keywords**

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

45

## 46 **Introduction**

47 The study of modern pollen rain in relation to different vegetation types is a prerequisite  
48 for the interpretation of the past vegetation and climate in a region and how it has changed over  
49 time (Bent and Wright, 1963; Janssen, 1967; Wright, 1967; Overpeck et al., 1985; Prentice, 1985;  
50 Bunting et al., 2004; Wilmshurst and Mcglone, 2005; Xu et al., 2005; Deng et al., 2006; Gosling  
51 et al., 2009). ~~However, it is observed that, †The study of the modern pollen rain and extant of~~  
52 ~~vegetation in the tropical regions vegetation is more complex and critical due to high biodiversity~~  
53 ~~and heterogeneity heterogeneity of the pollen preservation ion the forest floor and nearby areas,~~  
54 ~~compared to than the subtropical and temperate vegetation, as is shown documented by the~~  
55 ~~presence and abundance of the major pollen taxa in the pollen assemblages (Mayle et al., 2000;~~  
56 ~~Gosling et al., 2018; Bush et al., 2021). It is identified that, the †Phenological factors such as the~~  
57 ~~timing of the flowering period and periods of high rainfall, along with pollen production, high~~  
58 ~~rainfall, mode of pollination, and variation in the mode of pollen dispersal variation a influence~~  
59 ~~during the pollen preservation both oin the landscape surface and eventual integration into soils~~  
60 ~~and sediments. -soil. However, based on a knowledge of the pollen spectra and how it the~~  
61 ~~represents ation of the major associated plant -taxa in relation to the different vegetation types, it~~  
62 ~~is possible to differentiate and distinguished to the different vegetation types in a region (Gaillard~~

63 [et al., 1994; Guimaraes et al., 2017](#)) and as well as [allowing the recognition of differences also](#)  
64 [between the modern and historic grassland uses \(Hjelle, 1999\).](#)

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

73 The presence of coprophilous fungi in sediments [and changes in their relative abundance](#)  
74 has been used as an indicator [not only](#) of the past presence of herbivores, ~~and changes in their~~  
75 ~~relative abundance~~ [but also](#) to document changes in population sizes and in some cases the  
76 extinction of [this part of the](#) Pleistocene megafauna (van Geel, 1972, 1976, 1978; van Geel et al.,  
77 1981, 1983; [Karanth and Sunquist, 1992; Kuhry, 1985; Feranec et al., 2011; Baker et al., 2013;](#)  
78 [Etienne et al., 2013; Lopez-VVila et al., 2014; Loughlin et al., 2018; Tunno and Mensing, 2017;](#)  
79 van Asperen et al., 2021; Pokharia et al., 2022). More recently coprophilous fungi have  
80 increasingly been used as a proxy to address questions of pastoral and other human activities  
81 (Davis, 1987; Burney et al., 2003; van Geel et al., 2003; Gill et al., 2009; Mieke et al., 2009;  
82 Cugny et al., 2010; Feeser and O'Connell, 2010; Felauer et al., 2012; Johnson et al., 2015;  
83 Kamerling et al., 2017). ~~When combined with the study of pollen grains, and fungal spores,~~  
84 ~~especially of coprophilous fungi that grow on dung of herbivorous animals, can provide useful~~  
85 ~~information for understanding the food habitats, ecology, diversity, niche partitioning and~~  
86 ~~changes in relative abundance of past herbivorous species in a region~~ ([Ebersohn and Eicker,](#)  
87 [1992; Ekblom and Gillson, 2010; Velazquez and Burry, 2012; Basumatary et al., 2017, 2018, 2019,](#)  
88 [2020, 2021; Tripathi et al., 2019; Pokharia et al., 2022](#)). ~~However, previously some work have~~  
89 ~~been carried out on the the preservation of modern pollen and non-pollen palynomorphs~~  
90 ~~preservation on the modern surface soil related to in highland grazing and past land use and other~~  
91 ~~vegetation changes has also been investigated~~ ([Ejarque et al, 2011; Henga-Botsikabobe et al.,](#)  
92 [2020; Loughlin et al., 2021](#)). ~~Since both The fungal spores and the pollen grains in the sediments~~  
93 ~~are commonly encountered in the same palynological slide (van Geel et al., 2003), the~~



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4 94 documentation of and obviously, the combination fungus spores, especially those of  
5 95 coprophilous fungus spores, along with the and pollen grains can will be useful to interpret of the  
6 96 impact of herbivores impact in relation to the different vegetation types in a region. Since As  
7 97 coprophilous fungus spores are dispersed only for a very short distance, they are and local in  
8 98 origin (Graf and Chmura, 2006; Johnson et al., 2015) so will and accumulate in sediments with  
9 99 pollen grains and are therefore indicators of the local presence of local herbivores in relation  
10 100 to the existing vegetation.

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15 101 However, some works While some research has have been conducted carried out to  
16 102 understand the past vegetation and climate history in relation to the palaeoherbivory analysis in  
17 103 the National parks in the tropical regions of the world (Burbridge et al., 2004; Ekblom and  
18 104 Gillson, 2010). Little research has been carried out on modern pollen deposition in relation to  
19 105 the different vegetation types in National Parks and Wildlife Sanctuaries in Asia (Djamali  
20 106 et al., 2009; Basumatary et al., 2014; Bera et al., 2014; Tripathi et al., 2016; Ghosh et al., 2017;  
21 107 Setyaningsih et al., 2019; Pandey and Minckley, 2019). These p These p Previous studies have  
22 108 often not recorded reordered the presence of coprophilous fungus spores so cannot be used to  
23 109 determine in relation to the presence and abundance of herbivorous animals in the region. In the  
24 110 absence of skeletal remains of these herbivores, Since coprophilous fungus spores may serve as  
25 111 an important proxy that can be used be preserved in situations when skeletal remains of the  
26 112 herbivores are not preserved absent such studies are important in order to reconstruct the  
27 113 palaeoecology of a region in relation with respect to the presence, types and abundance of  
28 114 herbivores and their impact on the local environment, including their diet, as well as how changes  
29 115 in the vegetation impacts the local wildlife (Basumatary and McDonald, 2017). However, some  
30 116 works have been carried out to understand the past vegetation and climate history in  
31 117 relation to the palaeoherbivory analysis in the National parks in the tropical region of the  
32 118 world (Burbridge et al., 2004; Ekblom and Gillson, 2010).

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48 120 The main aim of this study is to document the depositional pattern of pollen and non-  
49 121 pollen palynomorphs in different vegetation types in Kaziranga National Park (KNP) in relation  
50 122 to the types of wildlife present and their impact on the different types of habitat. Determining  
51 123 the degree of representation of the coprophilous fungus spores in the surface soil and sedimentary  
52 124 profiles serves as the primary proxy to trace the relationship between flora and fauna in the

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3 125 region through time. ~~So, †~~The combination of pollen and non-pollen palynomorphs, especially  
4 the abundance of coprophilous fungal spores, are to be taken into consideration and calibration  
5 126 during the analysis which permits an interpretation of palaeoherbivory and palaeoecology  
6 analysis. However, †~~Based on the changes increase and decrease~~in frequency of coprophilous  
7 127 fungal spores in the sedimentary profile, an analysis is could be possible to trace the presence,  
8 128 relative abundance over time and eventual declined and extinction of members of the  
9 129 herbivorous mammals in the Kaziranga National Park and to correlate the pattern with what is  
10 130 observed in other national parks located in the tropical and temperate region of the globe. So,  
11 131 †~~Based on the modern palynomorph analogues seen in different regions, it can cleared that the~~  
12 132 presence and absence of the local arboreal pollen taxa and coprophilous fungal spore in the  
13 133 pollen assemblages provides a means can possible to distinguish among the natural forest  
14 134 vegetation, from areas with heavy grazing or modified into and cropland in both tropical and  
15 135 temperate regions. in the globe The resulting information can serve as a baseline to examine the  
16 136 influence of palaeoherbivory in relation to the on vegetation palaeoecology in the National Park  
17 137 in the past. This also provides for a better determination of the first human occupation along with  
18 138 their domestic livestock in the area and subsequent impact on the flora and fauna.  
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### 143 Study sites

34 144 Kaziranga National Park covers an ~~area~~area of around 430 square kilometers and is bordered on  
35 145 one side by the Brahmaputra River (Figure 1). In 1985, KNP was declared a UNESCO World  
36 146 Heritage Site in recognition of its significance as one of the best managed wildlife parks in the  
37 147 world. As such, KNP is one of the best sites in India and certainly for southeast Asia to observe  
38 148 the long-term interrelation between plants and the indigenous wildlife, as this interrelationship  
39 149 has not been ~~as~~-impacted as extensively by human activities and domesticated animals as at other  
40 150 sites in India. The park is within the Indo-Burmese biodiversity hotspot region, a critical corridor  
41 151 for immigration of members of the Indo-Malayan fauna into the Indian subregion. -It is also a  
42 152 critical reserve for tropical species, having served as a gene reservoir for these taxa during glacial  
43 153 periods (Tamma and Ramakrishnan, 2015).  
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### 155 Climate and soil

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3 156 The climate of the region is controlled by the southwest and northeast monsoons. These  
4  
5 157 weather patterns result in ~~hot, humid~~ hot, humid summers, and cold, dry winters. The temperature  
6  
7 158 ranges from a minimum of 4°C during winter up to 37°C in summer. The relative humidity is  
8  
9 159 very high and ranges ~~between from~~ 75–86%. The annual rainfall ranges from 1800–2600 mm,  
10  
11 160 and annual flooding is common in KNP during the summer. The soil composition varies from  
12  
13 161 site to site and includes sandy loam soil in forests, sandy soil in grassland, and clayey soil in the  
14  
15 162 swamp and water bodies (Das et al., 2014).  
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## 164 **Vegetation and wildlife**

165 In general, there are four main types of vegetation in the KNP; tropical evergreen forest,  
166 semi-evergreen forest, deciduous forest, grassland and swamp (Champion and Seth, 1968;  
167 Alfred, 1989). Alluvial grassland is the most dominant ~~covering~~ vegetation type (50.6%),  
168 followed by woodland (21.8%), openland ~~areas covered by~~ ing short grasses and other  
169 herbaceous associates (7.7%), and eroded land ~~caused by due to soil erosion and land slides~~  
170 during intervals of high rainfall activities and occupies (11.7%) in the national park (Das et al.,  
171 2014).

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

183 The moist deciduous forest occurs as isolated patches within grasslands and next to the  
184 evergreen forest. This forest consists of primarily deciduous trees which lose their leaves  
185 during the winter season. The major tree taxa are *Bombax ceiba*, *Dillenia indica*, *Albizia procera*,  
186 *A. lebbek*, *A. odoratissima*, *Neolamarckia cadamba*, *Trewia nudiflora*, *Careya arborea*,

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2  
3 187 *Lagerstroemia parviflora*, and *Semicarpus anacardium*. The forest floor is covered by different  
4  
5 188 species of Poaceae, Cyperaceae, Convolvulaceae, and Acanthaceae. The fern allies such as  
6  
7 189 *Dryopteris filix-mas*, *Adiantum caudatum*, *Blechnum occidentale*, *Polypodium vulgare*, and  
8  
9 190 *Drynaria rigidula* are the common members in this forest (Figures 2c and 2d).

10 191 The grassland areas are scattered and dominated by ~~not~~ not tall grasses ~~are~~ mainly *Erianthus*  
11  
12 192 *ravennae*, *Phragmites karka*, *Arundo donax*, *Imperata cylindrica*, and *Saccharum procerum*  
13  
14 193 along with short grasses like *Hemarthria compressa*, *Microstegium ciliatum*, *Cynodon dactylon*,  
15  
16 194 and *Cenchrus ciliaris*. However, some trees and shrubs such as *Bombax ceiba*, *Careya arborea*,  
17  
18 195 *Dillenia indica*, *Butea monosperma*, and *Albizia lebbek* also grow scattered within the grassland  
19  
20 196 (Figures 3a and 3b).

21 197 The openland areas are also scattered especially near the periphery of the swamp. Tree  
22  
23 198 taxa are almost absent ~~and~~ but there are some scattered shrubs such as *Melastoma*  
24  
25 199 *malabathricum*, *Cassia tora*, and *Clerodendron viscosum*. The openland area is covered with  
26  
27 200 short grasses followed by Cyperaceae, Acanthaceae, Amaranthaceae, Solanaceae, and  
28  
29 201 Convolvulaceae. *Cynodon dactylon*, *Cenchrus ciliaris*, *Chrysopogon aciculatus*, *Digitaria*  
30  
31 202 *ciliaris*, and *Paspalum conjugatum* are the common species in short grass communities (Figure  
32  
33 203 3c).

34 204 The swamp habitat is restricted to generally ~~low lying~~ low-lying areas and covers around  
35  
36 205 11.8% of the ~~p~~ Park (Das et al., 2014). It is submerged ~~underwater~~ throughout the whole year but  
37  
38 206 during summer (May-August) the swamp habitat may be expanded due to flooding of river  
39  
40 207 channels resulting from heavy monsoonal rainfall. The major marshy and aquatic taxa include  
41  
42 208 *Alpinia allughas*, *Clinogyne dichotoma*, *Calamus tenuis*, *Polygonum orientale*, *Cyperus*  
43  
44 209 *rotundus*, *Sagittaria sagittifolia*, *Eichhornia crassipes*, *Potamogeton pectinatus*, *Nymphaea alba*,  
45  
46 210 *Euryale ferox*, *Myriophyllum indicum*, *Ludwigia sedioides*, and *Nymphoides indica*.  
47  
48 211 Additionally, there are some trees and shrubs taxa including *Syzygium cumuni*, *Barringtonia*  
49  
50 212 *acutangula*, *Dillenia indica*, *Bombax ceiba*, *Osbekia stellata*, and *Costus speciosus* that  
51  
52 213 commonly grow on the periphery of the swamp area (Figure 3d).

53 214 With regard to wildlife, KNP is mainly famous for ~~the~~ its *Rhinoceros unicornis* (greater  
54  
55 215 one-horned rhinoceros), but the park is also very rich in other animals and birds. The fauna  
56  
57 216 includes 490 species of birds, 43 species of reptiles and 52 species of mammals (Choudhury,  
58  
59 217 2003). Besides rhinoceros, other associated large and medium sized mammalian herbivores  
60

218 include *Bubalus arnee*, *Elephas maximus*, *Bos gaurus*, *Sus scrofa*, *Cervus unicolor*, *Cervus*  
219 *duvauceli*, *Axis porcinus*, *Muntiacus muntjak*, *Presbytis entellus*, *Macaca mulatta*, *Macaca*  
220 *assamensis*, and *Hylobates hoolock*. Birds such as *Francolinus gularis*, *Anser erythropus*,  
221 *Houbaropsis bengalensis*, *Tringaguttifer*, *Sterna acuticauda*, *Ardea insignis*, and *Pelecanus*  
222 *philippensis* are commonly seen in the park.

223

## 224 **Materials and methods**

### 225 *Field work*

226 ~~The collection of palynological samples from the KNP is challenging due to danger from attack~~  
227 ~~by wildlife. A total of 75 surface soil samples were procured at about 50 meter intervals for~~  
228 ~~pollen and non-pollen palynomorphs from each of the different vegetation types. Out of the total~~  
229 ~~of 75 surface soil samples, 15 (E1-E15) were collected from the evergreen forest, 15 (D16-D30)~~  
230 ~~from deciduous forest, 15 (G31-G45) from grassland, 15 (O46-O60) from openland, and 15~~  
231 ~~(S61-S75) from the swamp. In each vegetation type, the samples were procured at about 50~~  
232 ~~meter intervals.~~

### 233 *Laboratory work*

234 The surface soil samples were chemically processed employing the standard acetolysis method  
235 (Erdtman, 1953). The soil samples were treated with 10% aqueous KOH solution to deflocculate  
236 the pollen and spores from the soil followed by 40% hydrofluoric acid (HF) treatment to dissolve  
237 silica content. This was followed ~~with treatment with an acetolysis mixture (9:1 acetic anhydride~~  
238 ~~( $\text{CH}_3\text{CO}_2\text{O}$ ) and concentrated sulfuric acid ( $\text{H}_2\text{SO}_4$ )).~~ The samples were washed 2-3 times with  
239 glacial acetic acid and then washed 2-3 times with distilled water and sieved through a 500 $\mu\text{m}$   
240 mesh. Finally, the material was kept in a 50% glycerin solution with a drop of phenol. Totals of  
241 259-335 pollen ~~grains per slide of each~~ ~~per~~ sample were counted to make the pollen spectra. The  
242 pollen taxa have been categorized into arboreal taxa, non-arboreal taxa, extra-regional taxa  
243 (~~highland taxa coming from the eastern Himalaya~~), and ferns. Similarly, a total of 225-284  
244 fungal spores ~~per slide~~ were counted from the same pollen slides and ~~the fungal spores these~~ were  
245 categorized into coprophilous and non-coprophilous fungal spores to make fungal spore spectra.  
246 For the precise identification of fossil palynomorphs in the sediments, the reference pollen slides  
247 available at Birbal Sahni Institute of Palaeosciences herbarium as well as ~~the~~ pollen and fungal  
248 spore photographs in the published literature (van Geel, 2003; Basumatary et al., 2017;



249 Basumatary and McDonald, 2017) were used. Photodocumentation of palynomorphs was made  
250 using Olympus BX-61 microscope with DP-25 digital camera under 40X magnification (Figure  
251 4). The pollen and fungal spore ~~spectra diagram~~spectra were made using TILIA software  
252 (Grimm, 2011) (Figures 5 and 6). ~~The percentages 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

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

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

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

275

## 276 Results

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



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4 280 Evergreen forest: The surface soil samples (E1-E15) are characterized by the dominance  
5 281 of the major evergreen taxa namely *Mesua*, *Schima*, *Arecaceae*, *Symplocos*, and *Litsea* with  
6 282 values of 1.6%-4.9% each followed by deciduous elements at values of 1.0%-3.0%. Among non-  
7 283 arboreal taxa, *Poaceae* is recorded with values of 6.0%-8.2% and ~~other terrestrial, aquatic and~~  
8 284 ~~herb taxa~~ are also consistently encountered with values of 3.3%-3.8% in the pollen assemblages.  
9 285 Extra-regional taxa are consistently present but with ~~sporadic low~~ values. ~~The ferns~~, both  
10 286 monolet and trilete, are encountered with ranges of 4.5%-8.0% (Figure 5). The most common  
11 287 Coprophilous fungal spores include are of the taxa *Sporormiella*, *Saccobolus*, and *Ascodesmis*  
12 288 with values of 0.8%-5.6%. *Podospora*, *Sordaria*, *Arnium* and *Cercophora* were also encountered  
13 289 at low values. Non-coprophilous fungal spores, ~~including *Microthyriaceae*, *Meliola*, and~~  
14 290 ~~*Glomus*~~ are also consistently represented at the ranges of 0.8%-14.1% ~~in the~~  
15 291 ~~assemblages (Figure 6), with *Glomus*, *Meliola* and *Microthyriaceae* the most common taxa.~~  
16 292

17 293 Deciduous forest: The ~~palynological analyses samples~~ from the deciduous forest (D16-  
18 294 D30) are characterized by the dominance of deciduous taxa with the ranges of 0.3%-4.7%  
19 295 each, ~~over compared with~~ evergreen taxa at ~~the~~ values of 0.3%-1.6%. Among non-arboreal taxa,  
20 296 *Poaceae* ~~is dominant and varies from 6.5- is dominant with a maximum value of~~ 9.4% and the  
21 297 other associated terrestrial and aquatic herbs are also recorded with values of 0.3%-4.6%. Extra-  
22 298 regional taxa are ~~primarily~~ represented with maximum values upto 2.1% in the pollen  
23 299 assemblages. Fern spores, ~~both monolet and trilete~~, are also consistently present with maximum  
24 300 ranges of 4.5% and 5.8% respectively (Figure 5).  
25 301

26 302 The coprophilous fungal spores ~~include *Sporormiella*, *Saccobolus*, and *Ascodesmis* occur~~  
27 303 ~~with values from 0.9%-4.9%. Non-coprophilous fungal spores are dominated~~  
28 304 ~~by include *Tetraploa*, *Meliola*, *Glomus*, and *Helminthosporium* *Mycrothyriaceae* as in the~~  
29 305 ~~Evergreen forest, are consistently recorded~~ with ranges from 0.8%-15.5% (Figure 6).  
30 306

31 307 Grassland: The ~~palynological study of~~ surface soil samples (G31-G45) from the grassland  
32 308 habitat ~~is are~~ characterized by the dominance of *Poaceae* with an average value of 30.7% ~~over~~  
33 309 ~~Other associated terrestrial and aquatic taxa occur~~ with maximum ranges upto 9.7% ~~in the~~  
34 310 ~~pollen assemblages.~~ Arboreal taxa, both evergreen and deciduous elements, namely *Mesua*,  
35 *Bombax* and *Careya* are also regularly encountered ~~in sporadic at low~~ values. The extra-regional  
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3 311 taxa are also consistently recorded with maximum values of upto 2.6%. The monolete and trilete  
4 312 ferns are also represented with ranges of 1.9%-5.6% in the pollen assemblages (Figure5).  
5  
6 313 Coprophilous fungal spores including are dominated by *Sporormiella*, *Saccobolus*, and  
7  
8 314 *Ascodesmis* are present at the with ranges of 1.0%-6.9%, with other coprophilous taxa reaching  
9  
10 315 6.2xx%. Among the Non-coprophilous fungal spores, *Helmithosporium* is abundant with values  
11  
12 316 up to 11.5xx%. *Meliola*, *Helminthosporium*, *Alternaria*, and *Glomus* are regularly recorded with  
13  
14 317 values of 0.5%-11.8% (Figure6).  
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16 318

17 319 Openland: ~~The palynological analysis of t~~The samples (O46-O60) from the openland  
18  
19 320 located adjacent to the swamp are characterized by the dominance of non-arboreal taxa with an  
20  
21 321 average value of 58.9% compared to arboreal taxa at 27.3%, followed by extra-regional taxa  
22  
23 322 (7.7%) and ferns (6.1%). Among arboreal taxa, both evergreen and deciduous elements are  
24  
25 323 regularly encountered at the ranges of 0.3%-4.9%. Among non-arboreal taxa Poaceae is  
26  
27 324 dominant with an average value of 19.8% and the other associated herb taxa are consistently  
28  
29 325 represented by values of 0.3%-6.1% in the pollen assemblages. The extra-regional taxa are  
30  
31 326 regularly encountered at the ranges of 0.4%-3.2%. The ferns, both monolete and trilete, are  
32  
33 327 recorded by ranges of 2.1%-4.3% (Figure5). The coprophilous fungal spores are much more  
34  
35 328 abundant than in the eEvergreen and dDeciduous forest and the gGrassland. They are dominated  
36  
37 329 by include *Sporormiella*, *Saccobolus*, and *Ascodesmis* which are recorded at the values of 1.0%-  
38  
39 330 20.0% each. The non-coprophilous fungal spores, *Helminthosporium*, *Bipolaris*, *Cookeina*, and  
40  
41 331 *Glomus* are less abundant that in the fForest and gGrassland areas, consistently encountered with  
42  
43 332 values of 0.7%-8.0% (Figure6).  
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45 333

46 334 Swamp: The palynological analysis of the mud samples (S61-S75) from the swamp  
47  
48 335 habitat are characterized by the dominance of non-arboreal taxa with an average value of 51.5%  
49  
50 336 over arboreal taxa (30.7%). The ferns and extra-regional taxa are also recorded with average  
51  
52 337 values of 9.2% and 8.6% respectively. Among arboreal taxa both evergreen and deciduous taxa  
53  
54 338 are consistently encountered at the values of 0.3%-3.9%. Among non-arboreal taxa Poaceae is  
55  
56 339 dominant with an average value of 15.6%. The marshy and aquatic taxa are consistently recorded  
57  
58 340 with the ranges of 0.6%-4.5%. The extra-regional taxa are consistently encountered at the values  
59  
60 341 of 0.3%- 2.9%. The fern spores, both monolete and trilete, are represented by values of 3.2%-

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3 342 5.8% in the pollen assemblages (Figure 5). Among fungal spores, the coprophilous fungal spores  
4 are similarly abundant as in the openland samples, and are dominated by include *Sporormiella*,  
5 343 *Saccobolus*, and *Ascodesmis* which are represented in the range of 1.8%-19.2% each. The non-  
6 344 coprophilous fungal spores, *Microthyriaceae*, *Helminthosporium*, *Bipolaris*, and *Glomus* are  
7 345 present but at much similarly lower ranges as in the openland samples of 0.4%-7.8% in the  
8 346 assemblages (Figure 6).  
9 347  
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### 15 349 **Statistical analysis of NPPs frequencies**

16  
17 350 VIFs based on an initial CCA indicated significant collinearity was present among the  
18 351 environmental variables. Therefore, CCA with forward selection was carried out. Four  
19 352 environmental variables were selected for inclusion in the CCA: Deciduous forest, Grassland,  
20 353 Openland and Swamp (Figure 7). The environmental variables account for 92.4% (constrained  
21 354 inertia = 0.22728, total inertia = 0.24572) of the variance in the fungal NPP data. The first two  
22 355 CCA axes (eigenvalues: CCA1 = 0.2066, CCA2 = 0.01577) explain 90.4% of the variance. The  
23 356 permutation tests show that both the CCA as a whole ( $p = 0.001$ ) and each CCA axis (each  $p =$   
24 357 0.001) are significant and VIFs indicate collinearity among the vegetation type assemblages is  
25 358 low in this analysis. CCA1 is closely related to the openland pollen taxa (positive side) and  
26 359 deciduous pollen taxa (negative side), indicating an inverse relationship between forest pollen  
27 360 taxa and taxa typical of open environments. CCA2 is closely related to grassland pollen taxa on  
28 361 the negative side. Swamp pollen taxa have a positive relationship with both CCA1 and CCA2.  
29 362 Sites located in the different vegetation types cluster closely, with sites from deciduous and  
30 363 evergreen forest fairly well-differentiated in the upper left-hand quarter of the graph and sites in  
31 364 grassland habitats in the lower left-hand quarter of the graph, while sites from openland and  
32 365 swamp areas cluster together in the upper right-hand quarter.

33 366 NPPs cluster into four main groups (Figure 7). The coprophilous types fungal spores,  
34 367 *Ascodesmis*, *Podospora*, *Sordaria*, *Sporormiella*, and *Saccobolus*, covary with the openland  
35 368 gradient. While, they are also present in relatively high numbers in the other vegetation types,  
36 369 they are most abundant in the openland and swamp habitats. *Helminthosporium* is the only type  
37 370 that covaries with the grassland gradient, which is unsurprising as this taxon consists mainly of  
38 371 molds that grow on grasses. Fungal NPPs that plot in the center of the graph, such as *Alternaria*,  
39 372 *Arnium*, *Helicoon*, *Tetraploa*, *Valsaria*, Type 1, and Type 2, are not strongly controlled by any of

1  
2  
3 373 the environmental variables and occur at relatively similar proportions throughout the samples.  
4  
5 374 Some of these represent ubiquitous plant pathogens and decomposers (van Geel et al., 2003). All  
6  
7 375 other fungal NPPs (*Bipolaris*, *Cookeina*, *Dictyosporium*, *Glomus*, *Meliola*, Microthyriaceae,  
8  
9 376 Teleutospores) most strongly covary with the forest gradient. This group includes a number of  
10  
11 377 species that grow on woody debris (*Cookeina*, *Dictyosporium*), as well as plant pathogens and  
12  
13 378 decomposers, and the mycorrhizal fungus *Glomus*, which is well-known to form associations  
14  
15 379 with tree roots (van Geel et al., 2003), though it occurs in a wide variety of environments.  
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380

## 381 Discussion

382 The modern pollen study of the different vegetation types and areas of different land use in KNP  
383 reveals a good agreement with the extant vegetation. However, some site by site variation has  
384 been recorded in the fungal spores in the assemblages. [A composite diagram shows the](#)  
385 [relationship between, the vegetation types and wildlife in KNP based on the abundance of local](#)  
386 [arboreal and non-arboreal pollen taxa and coprophilous fungal spores in the palynoassemblages](#)  
387 [\(Figure 8\). The evergreen forest is characterized by the high abundance of evergreen arboreal](#)  
388 [pollen taxa \(31.3%\). The high abundance of deciduous arboreal pollen taxa \(32.6%\) in the](#)  
389 [palynoassemblages signifies the deciduous forest. The grassland is characterized by the](#)  
390 [abundance of Poaceae pollen \(30.6%\). Similarly, the openland area is characterized by the](#)  
391 [abundance of both Poaceae \(20.6%\) and other associated non-arboreal pollen \(20.2%\). The](#)  
392 [swamp area is characterized by the high abundance of marshy and aquatic pollen \(21.9%\)](#)  
393 [followed by deciduous \(20.1%\), evergreen \(10.6%\) and Poaceae \(15.6%\) pollen. The abundance](#)  
394 [of the coprophilous fungal spores in the openland \(60.7%\), swamp \(59.3%\), and grassland](#)  
395 [\(23.9%\) are exhibited in the palynoassemblages which indicates that these sites are highly](#)  
396 [impacted by the herbivores. The evergreen and deciduous forest can be characterized as](#)  
397 [moderately impacted sites as indicated by the relatively lower abundance of coprophilous fungal](#)  
398 [spores with average values of 16.4% and 16.3%, respectively in the palynoassemblages.](#)

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

401 The ~~palynological study in samples taken from~~ the evergreen forest reveals ~~s that~~  
402 ~~the~~ *Mesua-Schima-Duabanga-Cinnamomum-Arecaceae-Litsea* assemblage, ~~was recorded and~~  
403 showing a good relationship ~~between the pollen and with the~~ extant ~~scenario~~ [vegetation](#). The

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3  
4 404 abundance of evergreen taxa, especially *Mesua*, *Duabanga*, and *Syzygium* pollen in the pollen  
5 405 assemblage is marked significant (maximum value up to 4.9%) and is indicative of high rainfall  
6  
7 406 activity in the region, as these taxa are high rainfall indicators (>2500 mm/y; Singh et al., 1990;  
8  
9 407 Barboni and Bonnefille, 2001). The presence of evergreen forest was evident in the KNP by the  
10  
11 408 presence of *Mesua* and *Duabanga* pollen in the palynoassemblage of rhino dung samples  
12  
13 409 (Basumatary et al., 2017), as these evergreen taxa dominated that are dominant in the evergreen  
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15 410 forest of in the KNP. Our study is in close agreement with the vegetation survey and existing  
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17 411 forest types in KNP (Champion and Seth, 1968; Das et al., 2014). The presence of marshy and  
18  
19 412 aquatic taxa, such as *Cyperaceae*, *Polygonum*, *Nymphoides*, and *Nymphaea* pollen, which could  
20  
21 413 have been transported by wild herbivores and birds, indicate natural perennial water bodies in  
22  
23 414 and around the study area (Ekblöm and Gillson, 2010; Basumatary et al., 2017; Stivrins et al.,  
24  
25 415 2019). During the daytime after feeding in the swamp areas these animals move towards the  
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27 416 surrounding forests for rest, shelter or to forage search for dietary plants in the forest.

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29 417 Among the fungal spore assemblages, the presence of the non-coprophilous fungal  
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31 418 spores, Microthyriaceae, *Glomus*, and *Meliola*, and *Dictyosporium* was marked. These taxa are is  
32  
33 419 is characteristic of dense forest vegetation under warm and humid conditions in response to the  
34  
35 420 high rainfall in the region. Specifically, the abundance of Microthyriaceae, *Glomus*, and *Meliola*  
36  
37 421 is considered to be indicative of the presence of dense forest vegetation (Musotto et al., 2012,  
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39 422 2017; Cookson, 1947; Selkirk, 1975; Johnson and Sutton, 2000; Hofmann, 2010; Medeanic and  
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41 423 Silva, 2010; Loughlin et al., 2017), and this is reflected in the studied samples from KNP. In the  
42  
43 424 palaeoecological literature, *Glomus* is often seen as an indicator of erosion (Shumilovskikh et al.,  
44  
45 425 2021). However, since this fungus is an endomycorrhiza and often associates with trees, in this  
46  
47 426 case the abundance of its spores is due to its abundance in the forest soil (Kołaczek et al., 2013).

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49 427 The presence of coprophilous fungal spores, *Sporormiella-Saccobolus-*  
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51 428 *Aseodesmis* assemblage was marked in the studied samples and the relatively high percentages are  
52  
53 429 indicative of the presence of wildlife. The coprophilous fungal spores may be limited to specific  
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55 430 locations frequented by herbivores so can be considered local in origin since they can only  
56  
57 431 actively disperse over a short distance which restricts their presence to near to where sporulation  
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59 432 took place (Davis et al., 1977; Parker, 1979; Wicklow, 1992; Richardson, 2001; Malloch and  
60  
433 Blackwell, 1992; van Geel et al., 2003, 2008; van Geel and Aptroot, 2006; Ekblom and Gillson,  
434 2010; Parker and Williams, 2011; van Asperen et al., 2021). The frequency of *Sporormiella*,



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3 435 *Ascodesmis*, and *Saccobolus* was relatively higher in openland and swamp areas as compared to the dense forest. In our study, *Ascodesmis* and *Saccobolus* are considered  
4 436 openland and swamp areas as compared to the dense forest. In our study, and is considered  
5 437 significant with a maximum value upto the moderately high value of coprophilous fungal spores  
6 438 (5.6%) was observed in the palynoassemblage. 5.6% in the assemblages, which is quite higher  
7 439 than the 2% considered as a 'background' level (Davis, 1987; Gill et al., 2013; Baker et al.,  
8 440 2016; Raczka et al., 2016). These spores can therefore be inferred to reflect local abundance of  
9 441 the herbivore fauna. The forest area is generally dark, windless, cooler and more humid than  
10 442 outside the forest; conditions that are favorable for fungal growth (Musotto et al., 2017; Promis  
11 443 et al., 2010; Godeas and Arumbarri, 2007). Monkeys, gibbons, birds, and other arboreal animals  
12 444 are common, and their excreta regularly falls down to the forest floor. The diversity of the fungal  
13 445 remains especially the non-coprophilous fungal spores is high in all samples.

14 446 The *Salmalia-Dillenia-Lagerstroemia-Semecarpus-Careya* pollen assemblage was in  
15 447 agreement with the extant deciduous forest vegetation in this national park KNP. The  
16 448 subassemblage of *Dillenia-Terminalia-Careya* assemblage is significant as it is characteristic of  
17 449 the preferred habitat of wildlife in the Balpakram valley in the Garo hills of Meghalaya  
18 450 (Basumatary et al., 2014) which coincided with the pollen assemblages in KNP. These plants are  
19 451 utilized as the primary food plants preferred by many herbivorous mammals including elephant  
20 452 and deer species (Odden et al., 2005; Steinheim et al., 2005; Neupane et al., 2019; Devi et al.,  
21 453 2022). The consistent abundance of *Bombax* pollen in the palynoassemblage which is recorded  
22 454 upto 4.7% was marked in comparison to the other associated arboreal taxa. *Bombax* is a fire  
23 455 resistant plant (Troth, 1976) which is one of the reasons for its abundance in the  
24 456 palynoassemblage. Forest fires during winter are an important part of the ecology for the wildlife  
25 457 of KNP. Herbivory is an important driver of vegetation structure in the region (Ekblom and  
26 458 Gillson, 2010), so the large herbivores may have played a significant role in shaping the structure  
27 459 of plant communities in the KNP. The coprophilous fungi, *Sporormiella*, *Saccobolus*, and  
28 460 *Ascodesmis* are represented consistently in the studied samples and their abundance closely  
29 461 resembles that in the evergreen forest samples and are also indicative of the presence of  
30 462 wildlife habitation in the deciduous forest. These fungi are also present at relatively higher  
31 463 abundances than in the evergreen forest, indicative of the higher impact of herbivores on the  
32 464 deciduous forest.



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3 465 The percentages of Poaceae pollen are relatively high in the grassland samples (average 30.7%)  
4 466 and the *Salmalia-Dillenia-Emblica-Butea-Careya-Poaceae* pollen assemblage was identified as  
5 467 characteristic of this habitat. The presence of some arboreal taxa, especially *Mesua*, *Duabanga*,  
6 468 and *Symplocos*, is significant as these taxa do not usually occur in this vegetation type. Given  
7 469 that these taxa are insect-pollinated, they most likely have been secondarily deposited through  
8 470 animal dung where the herbivores ingested the plant parts elsewhere and were subsequently  
9 471 defecated in and around the grassland areas. The presence of arboreal pollen taxa, both evergreen  
10 472 and deciduous, was recorded from the midden dung of rhinoceros from forested and grassland  
11 473 regions of KNP (Hazarika and Saikia, 2010; Basumatary et al., 2018). The pollen clumping in  
12 474 grasses and *Bombax*, is marked and indicative of their local origin. The presence of pollen grain  
13 475 clumps is a characteristic feature of entomophilous plants whose pollen disperses shorter  
14 476 distances than wind-dispersed pollen grains (Faegri and Van Der Pijl, 1966; Martin et al., 2009).  
15 477 [Since the Kaziranga National Park is enriched with swampy areas, the aquatic vegetation need to](#)  
16 478 [be included in the pollen spectra for monitoring the status of water level through pollen records](#)  
17 479 [in relation to the monsoonal activities. Moreover, the dung of the megaherbivores like one horn](#)  
18 480 [rhino also include aquatic pollen and thus, the modern aquatic pollen preservation could act as a](#)  
19 481 [baseline for the coprolite studies for tracing the megafaunal extinction during the Quaternary](#)  
20 482 [\(Basumatary et al. 2017\). The generated pollen data would assist in distinguishing the natural](#)  
21 483 [forest vegetation from areas impacted by human activities in the region, based on the fossil](#)  
22 484 [marker pollen taxa like Poaceae and Brassicaceae \(Basumatary et al., 2018; Tripathi et al., 2021\).](#)

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38 485 Among the fungal spores, coprophilous fungi such as *Sporormiella*, *Saccobolus*,  
39 486 *Podospora*, and *Ascodesmis* are dominant and represented consistently in the  
40 487 palynoassemblages. Herbivorous animals, especially rhinoceros and elephant, feed and defecate  
41 488 in the grassland, dispersing coprophilous fungal spores with their dung. However, although they  
42 489 are more common than in the forest assemblages, coprophilous fungal spores are less common in  
43 490 the grassland than in the openland and swamps. This may be due to the midden behaviour of  
44 491 some of the large mammals, especially the rhinoceros, which tends to defecate in specific areas,  
45 492 so the spores are not distributed uniformly on the landscape. The *Sporormiella-Saccobolus-*  
46 493 *Ascodesmis* assemblage was present in the midden dung of rhinoceros from grassland areas  
47 494 (Basumatary and McDonald, 2017) from the KNP. Among the non-coprophilous fungi,  
48 495 especially *Helminthosporium* and *Alternaria*, are especially dominant. Both taxa are common

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3 496 pathogens of herbaceous plants, particularly grasses. Other fungal spores such as *Glomus*,  
4 497 Microthyriaceae, and *Tetraploa* are also present in ~~sporadic~~ lower values in the assemblages.  
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6 498 However, grasses have a high resistivity to fungal infection due to their silica contents (Park et  
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8 499 al., 2006, 2010; Hayasaka et al., 2008) which is the main reason for the low fungal diversity  
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10 500 exhibited in the grassland.

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12 501 The palynological study in the openland area identified some distinguishing features of  
13  
14 502 this habitat within the pPark, ~~as it which is characterized by T~~the *Salmalia-Dillenia-Mesua-*  
15  
16 503 *Barringtonia-Litsea-Melastoma-Poaceae-Mimosa* pollen assemblage. ~~was marked and~~  
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18 504 ~~significant.~~ The gGrasses are dominant and recorded a maximum value upto 19.8%. However,  
19  
20 505 the arboreal, marshy, and aquatic taxa, *Mesua*, *Bombax*, *Lagerstroemia*, *Syzygium*, Onagraceae,  
21  
22 506 and *Nymphaea* are also consistently present in the pollen assemblages. This reflects the excreted  
23  
24 507 dung of herbivorous animals and birds which incorporated these tree taxa through their ingestion  
25  
26 508 in and around the openland areas. Pollen clumping of Poaceae, Cyperaceae and *Polygonum*  
27  
28 509 very common in the palynoassemblages indicating they originate from local sources (Faegri and  
29  
30 510 van der Pijl, 1966; Martin et al., 2009). Among the fungal spores the coprophilous fungal spores  
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32 511 *Sporormiella-Saccobolus-Ascodesmis* are dominant in the assemblage and confirmed that the  
33  
34 512 openland habitat can be considered to function as a corridor for wildlife. The abundance of  
35  
36 513 coprophilous fungal spores in the openland areas suggests a direct link of abundance of wildlife  
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38 514 and higher amount of decomposed organic matter derived from dung.

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40 515 The palynological study of the swamp sediments reveals that the *Salmalia-Dillenia-*  
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42 516 *Syzygium-Mesua-Duabanga-Litsea-Melastoma-Poaceae-Mimosa* pollen assemblage indicates a  
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44 517 composition of different types of forest vegetation in and around the swamp area of the  
45  
46 518 nNational pPark. The riparian forest taxa, *Lagerstroemia*, *Barringtonia*, and *Duabanga* are grow  
47  
48 519 luxuriantly growing along the periphery of the wetland area. Among non-arboreal taxa, the  
49  
50 520 marshy and aquatic taxa are local in source. The other terrestrial non-arboreal taxa, chiefly  
51  
52 521 *Asteroidae*, *Convolvulaceae*, and *Mimosa*, were deposited in and around the areas by the inwash  
53  
54 522 of rainwater. The presence of *Rhododendron* pollen (a flood marker taxona; Basumatary et al.,  
55  
56 523 2019) indicates flood activity in the region.

57  
58 524 Among the fungal spores the non-coprophilous fungal spores predominate but  
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60 525 coprophilous fungal spores, especially *Sporormiella*, *Podospora*, and *Saccobolus*, are still  
61  
62 526 comparatively abundant in comparison to the other studied sites. The preserved fungal spores

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3 527 may have originated from surrounding areas and ~~were~~ subsequently transported and deposited  
4  
5 528 through rainwater and slopewash. Furthermore, the swamp ~~is serve as the~~ focal point for  
6  
7 529 mammals and birds for their food and especially drinking water. The amount of dung, especially  
8  
9 530 the midden dung of rhinoceros, is large. Water availability is an important factor for the  
10  
11 531 germination and sporulation of coprophilous fungi (Austin, 1958; Ingold and Marshall, 1962;  
12  
13 532 Kuthubutheen and Webster, 1986a, 1986b), and dung deposited in the swamp can be expected to  
14  
15 533 remain wet longer than in the other vegetation types and thus enhance the potential for  
16  
17 534 germination.

17 535 Among the non-coprophilous fungi ~~the presence of~~ *Tetraploa* was ~~marked~~ more abundant  
18  
19 536 than in the other vegetation types, which ~~might~~ reflects its ecology as a saprophytic fungus of  
20  
21 537 Poaceae and Cyperaceae, both of which are major wetland taxa. The abundance of *Glomus* in the  
22  
23 538 palynoassemblage might be the result of transport directly from the surrounding forest, as  
24  
25 539 *Glomus* is indicative of soil erosion (van Geel et al., 2003; Kiage and Liu, 2009). ~~The fungal~~  
26  
27 540 ~~diversity observed in the samples may be due to herbivores feeding habits and food choice~~  
28  
29 541 ~~(Ebersohn and Eicker, 1992; Feranee et al., 2011).~~ The diversity of the coprophilous fungal  
30  
31 542 spores is similar in all the studied surface soil samples to that of the openland samples with  
32  
33 543 abundant spores of *Sporormiella*, *Saccobolus*, and *Ascodesmis*. This pattern is also seen in the  
34  
35 544 rhinoceros dung midden samples (Basumatary et al., 2017).

34 545 The presence of the extra-regional taxa, *Pinus*, *Abies*, *Picea*, and *Larix* in samples from  
36  
37 546 all vegetation types is significant and indicative of strong wind activity from the higher Himalaya  
38  
39 547 ~~and but~~ might also be introduced by migratory Siberian birds (Barua and Sharma, 1999), when  
40  
41 548 they fly through pollen-laden environments. The bird diversity documented in KNP is over 521  
42  
43 549 species of which more than 200 are residents while the rest are migrants, including local  
44  
45 550 migrants (Rahmani et. al., 2022). ~~and the p~~ Pollen may adheres to their body and feathers of  
46  
47 551 migratory species and then subsequently be dislodged ~~which may be lost~~ during grooming while  
48  
49 552 they are in KNP., especially from species that may overwinter in the park.

48 553 Studies of It is recorded that, the modern analogues based on the pollen and fern spore  
49  
50 554 assemblages have shown it is possible to ,it could be distinguished the agricultural land from the  
51  
52 555 fallow and salt marsh grassland (Graf and Chmura, 2006). ~~but t~~ The presence of coprophilous  
53  
54 556 fungal spores can aid in distinguishing grazed or manured land use from natural vegetation and  
55  
56 557 other. Similarly, this study can serve as ,it will be a guideline and applicable to differentiate and

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3 558 distinguish the different vegetation types and the presence and impact of herbivores based on  
4 the presence and absence of local arboreal pollen taxa along with coprophilous fungal spores  
5 especially *Sporormiella*, *Sodaria*, and *Ascodesmis* in the palynoassemblages. The VAsegetation  
6 structure is mainly controlled by herbivores density (Bell, 1982) in African savannah and the  
7 woody cover reduction is directly linked to the concentration of herbivores (Dublin et al., 1990).  
8 their presence or absence can be documented by the presence of coprophilus fungal spores in the  
9 palynological studies of soil sediments. In order to understand the actual reason of decline  
10 and extinction of megaherbivores is very difficult and controversial and the two view always  
11 come into account, whether by the human activities both on continent and large Island (Johnson  
12 et al. 2015) and other view or due to climate-induced environment change (Wroe et al. 2013)  
13 documentation of their presence, either directly by skeletal remains or indirectly via proxy such  
14 as coprophilous fungal spores is critical. Other evidence for human impact can be the ability to  
15 recognize former cropland whether using the dung manured or unmanured based on the representation of local arboreal pollen taxa  
16 and coprophilous fungal spores in the palynoassemblages preserved in sediments.  
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### 576 **Comparison of pollen spectra with canonical correspondence analysis**

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36 577 The CCA confirms that the five vegetation types present in KNP are significantly  
37 578 different in their taxonomic composition and this is reflected in both the vegetation and pollen  
38 579 assemblages. While the fungal NPP assemblages are relatively similar in overall composition  
39 580 between the different vegetation types, there are some differences in abundance of the taxa  
40 581 recovered reflecting the populations levels of herbivores. Coprophilous fungal spores are present  
41 582 in significant numbers in all vegetation types, but the concentration is greater in the openland and  
42 583 swamp areas, where herbivores are more abundant than in the forested areas. The other  
43 584 vegetation types are dominated by mycorrhizal fungi, pathogens and decomposers of the plant  
44 585 species common in these vegetation types.  
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### 587 **Interaction between vegetation and herbivores**

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3 588 Demonstrating the strong relationship between pollen types and vegetation in an area  
4 provides an opportunity to infer document changes in wildlife habitat at both a temporal and  
5 589 spatial scale. Complementing the pollen record is the associated coprophilous fungal spores  
6 590 record which can provide estimates of the sizean indications of the presence of herbivore  
7 591 populations utilizing the different vegetation types in these habitats and thus responding to their  
8 592 expansion or reduction over time (EkblomandGillson, 2010). Integrating ecological studies of  
9 593 all herbivores in the park and their preferred habitats is critical to integrate with the  
10 594 documentation of the association of pollen and vegetation types to better understand how the  
11 595 vegetation and fauna interact through time (Table 3). Equally important is the documentation of  
12 596 the value-abundance and types of coprophilous fungal spores associated with each species' dung  
13 597 (Basumatary and McDonald, 2017; Basumatary et al., 2019; Basumatary et al., 2021) is needed to  
14 598 provide more refined information on what species of herbivores were present and their  
15 599 associationed with specific habitats and recognize their heterogenous distribution on the  
16 600 landscape rather than just rough estimates of the increase or decrease in herbivore populations  
17 601 through time.  
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## 604 Conclusions

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

617 As such, the data will be helpful in providing a foundation to differentiate and distinguish  
618 the natural forest vegetation from areas and the impacted by of human activities in the region.



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3 619 based on the fossil pollen record given, as there is the potential for misidentification of between  
4 620 conserved landscapes such as (national parks and wildlife ~~sanctuaries~~sanctuaries) and areas that  
5 621 are not set aside ~~unconserved~~ or protected and have been and heavily impacted by human  
6 622 activity, such as deforestation, farming, and pastoral practices, ~~timber harvest or simply due to~~  
7 623 ~~the building of infrastructure such as roads or housing and other buildings.~~ The presence and  
8 624 abundance of local arboreal pollen taxa in the recovered pollen assemblages may play an  
9 625 important role for the differentiation and identification between natural vegetation coverage and  
10 626 areas of high human activity. This may also be indicated by the presence and abundance of local  
11 627 arboreal pollen or the relative abundance of coprophilous fungi since unmanured soil has  
12 628 significantly less coprophilous fungi than manured soil (Graf and Chmura, 2006). The openland  
13 629 area is also an important place for ~~the~~wildlife ~~for their~~ survival as indicated by the presence of  
14 630 marker pollen taxa and the abundance of coprophilous fungal spores. ~~Lastly, the~~ overall  
15 631 palynological analysis of the swamp sediments could be a reliable and complementary data for  
16 632 the representation of the vegetation types and abundances of herbivores both of which can  
17 633 contribute to ~~both~~palaeoecological and palaeoherbivory analysis.  
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31 635  
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### 642 Declaration of conflicting interests

43 642  
44 643 The authors declared that they have no conflict of interest.  
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50 646  
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52 648 ~~assemblage of large herbivores in a seasonal tropical forest. *Journal of Tropical*~~  
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## 1062 LEGENDS

1063 **Table 1:** Taxa included in each environmental variable for the Canonical correspondence  
1064 analysis (CCA).

1065 **Table 2:** Characterization of marker pollen taxa recovered from the surface soil samples in  
1066 relation to the different vegetation and land use from the Kaziranga National Park.

1067 **Table 3:** Association between major mammalian herbivores and vegetation types in Kaziranga  
1068 National Park.

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3 1069 **Figure 1.**a. Map showing the study areas; b. Vegetation coverage map of Kaziranga National  
4 Park (modified after Das et al., 2014).  
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6 1071 **Figure 2.**a. Thick evergreen forest within Kaziranga National Park, b. *Buceros bicornis*  
7 (Hornbills) sitting on the tree within the evergreen forest, c. Group of *Elephas maximus*  
8 (Asian Elephant) in deciduous forest in Kaziranga National Park, d. *Rhinoceros*  
9 *unicornis* grazing in the periphery near swamp.  
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13 1075 **Figure 3.**a. Grassland and ~~show~~ grazing ~~by of~~ *Rhinoceros unicornis* b. A view of grassland  
14 during winter, c. A view of openland showing *Bubalus arnee* (Asian Buffalo) and  
15 numbers of migratory birds, d. A view of swamp showing numbers of *Cervus duvauceli*  
16 (Swamp Deer) in the center.  
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20 1079 **Figure 4.** Palynoassemblages recovered from the surface soil samples from the Kaziranga  
21 National Park.  
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24 1081 Explanation of palynomorphs

25 a. *Bombax ceiba*, b. *Duabanga* in cluster, c. *Cinnamomum*, d. *Litsea*, e. *Terminalia*, f.  
26 1082 *Lagerstroemia*, h. *Shorea robusta*, i. *Schima*, j. *Semecarpus*, k. *Syzygium*, l. *Arecaceae*,  
27 1083 m. *Albizia*, n. *Lantana*, o. *Pinus*, p. *Rhododendron*, q. *Asteroideae*, r. *Chinoroideae*, s.  
28 1084 *Impatiens*, t. *Convolvulaceae*, u. *Cyperaceae*, v. *Poaceae* in cluster, w. *Polygonum*, x.  
29 1085 *Nymphaea*, y. *Typha*, z. *Monoete*, aa. *Trilete*, ab. *Sporormiella*, ac. *Sordaria*, ad.  
30 1086 *Meliola*, ae. *Tetraploa*, af. *Glomus*.  
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36 1088 **Figure 5.** Comparative pollen spectra in relation to the different vegetation types from  
37 the Kaziranga National Park.  
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39 1090 **Figure 6.** Comparative fungal spores spectra in relation to the different vegetation types and  
40 herbivores impact from the Kaziranga National Park.  
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42 1092 **Figure 7.** Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types  
43 and environmental variables. NPP types (red) and samples (dark green: evergreen  
44 forest; light green: deciduous forest; yellow: grassland; orange: openland; light blue:  
45 swamp) are plotted against vegetation type indicator assemblages (blue arrows).  
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49 1096 Canonical correspondence analysis (CCA) of non-pollen palynomorph (NPP) types and  
50 environmental variables. NPP types (red) and samples (green) are plotted against  
51 vegetation type indicator assemblages (blue arrows).  
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1099 **Figure 8.** Composite pollen and fungal spore diagram in relation to the different vegetation types  
1100 from the Kaziranga National Park.

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For Peer Review

### 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 'discussion 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.

**Response to the reviewer Comments made on the pdf file of the manuscript**

**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)

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3 **Reply 3:** Yes, I agree with your point, we have revised this sentence in the text of the manuscript  
4 (Line nos. 228-232). During the field work, in each of the vegetation types, the samples were  
5 collected at about 50 m intervals within the Kaziranga National Park.  
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8 **Comment 4:** Line no-180-185 (can you explain why 259-335 pollen grains? Is there any  
9 particular reason for that? What do you mean by extra-regional taxa?)  
10

11 **Reply 4:** We have counted these pollen grains covering the whole pollen slide covered by cover  
12 glass (22 X 40 mm). So, based on the availability of the pollen grains in each studied slide, the  
13 total number of pollen grains were counted which varies from 259-335 (pls. see Fig. 5). We  
14 maintained a minimum of 150 pollen grains for the total pollen count, for a satisfactory  
15 representation of the vegetation composition and to make pollen spectra.  
16  
17

18 We considered highland taxa such as *Pinus*, *Betula*, *Alnus*, *Rhododendron* which are not growing  
19 in and around the Kaziranga National Park as the “extra-regional taxa” that grows in the higher  
20 Himalaya (Line nos. 242-243).  
21

22 **Comment 5:** Line no-193-194 (what is the reason for including the aquatic taxa in the total  
23 sum?)  
24  
25

26 **Reply 5:** Sir, we have now included the discussion on the importance of incorporating aquatic  
27 pollen in the total pollen sum (Line nos. 477-482). We have added the reference pertinent to this.  
28 Since the Kaziranga National Park is enriched with swampy areas, the aquatic vegetation need to  
29 be included in the pollen spectra (Fig. 5) for monitoring the status of water level through pollen  
30 records in relation to the monsoonal activities. Moreover, the dung of the megaherbivores like  
31 one horn rhino also include aquatic pollen and thus, the modern aquatic pollen preservation  
32 could act as a baseline for the coprolite studies for tracing the megafaunal extinction during the  
33 Quaternary.  
34  
35

36  
37  
38 **Comment 6:** Line no-220-221 (It would be nice if you include the names of each taxon you are  
39 referring to here?).  
40

41 **Reply 6:** As per your suggestion, I have included the major evergreen taxa (*Mesua*, *Schima*,  
42 *Arecaceae*, *Symplocos*, and *Litsea*). Please see the same in the text of the manuscript (Line no.  
43 281).  
44

45 **Comment 7:** Line no-221 (values of 1.6%-4.9%; When I look at the figure, I cannot see this  
46 values. You should work on the scale of the figure).  
47  
48

49 **Reply 7:** As per your suggestion the scale has been revised. Kindly see Fig. 5.  
50  
51

52 **Comment 8:** Line no-223 (What “other terrestrial” means ?).  
53  
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3 **Reply 8:** Sir, We have revised the term “other terrestrial” which is used for the herbs growing in  
4 the land in association with the grasses (Line nos. 283-284).  
5

6 **Comment 9:** Line no-226-227 (How about the other coprophilous types?).  
7

8  
9 **Reply 9:** Yes, we have revised the sentence (Line nos. 286-287). The coprophilous fungal spore  
10 is the standard term used in the previous published records. Kindly refer the marked copy of  
11 manuscript.  
12

13 **Comment 10:** Line no-231-232, (This part is confusing?).  
14

15  
16 **Reply 10:** Yes Sir and I have revised the same in the text (Line nos. 293-295). Please see the  
17 same.  
18

19 **Comment 11:** Line no-233 (maximum value of 9.4%); You should follow the same pattern as in  
20 the previous section and cite the range, not only the maximum value)  
21

22 **Reply 11:** The same has been done (Line nos. 293-295). Kindly see the same in the manuscript.  
23

24 **Comment 12:** Line no-237-238 (see the comment in the previous section for this group?).  
25

26 **Reply 12:** Yes Sir, the same has been done. Kindly see the same.  
27

28  
29 **Comment 13:** Line no-238-239 (Also check the comment about this group in the previous  
30 section?).  
31

32 **Reply 13:** The same has been done. Please see the result section in the marked copy.  
33

34 **Comment 14:** Line no-244-245 (sporadic values is too vague, You should describe the arboreal  
35 elements with more detail ?).  
36

37  
38 **Reply 14:** Yes Sir, we have revised the same including the name of some taxa (Line nos. 309-  
39 310). Kindly see the same in the marked copy of the manuscript.  
40

41  
42 **Comment 15:** Line no- 247-250 (*Helminthosporium*, this spore has very different values from  
43 the previous zone. You should be more detailed in describing this vegetation types).  
44

45 **Reply 15:** As per your suggestion, we have revised the same (Line nos. 315-317). Kindly see the  
46 same in the marked copy.  
47

48  
49 **Comment 16:** Line no-252-255 (Not sure if this part is informative because you are describing  
50 each category below).  
51

52 **Reply 16:** I have deleted the repeated text and revised the sentence as per your suggestion (Line  
53 no. 319). Kindly see in the marked manuscript.  
54  
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3 **Comment 17:** Line no-260-263 (Check previous comments about these groups).  
4

5 **Reply 17:** Sir, as per your suggestion, we have revised the same. Kindly see the same in the  
6 marked manuscript.  
7

8  
9 **Comment 18:** Line no-301-312 (Check previous comments and apply where necessary in this  
10 section).  
11

12 **Reply 18:** As per your suggestion, we have revised the same accordingly. Please see the same.  
13

14 **Comment 19:** Line no-281 (Figure-7, It would be good to work on the labels of this figure. The  
15 way it is now is impossible to read the name of the fungal types. You could re do the names in  
16 graphic software or something similar).  
17

18  
19 **Reply 19:** Honestly, I agreed your point, and as per your suggestion, the figure 7 has been  
20 revised. Kindly see the same in the figure no 7.  
21

22 **Comment 20:** Line no-294-297 (Which ones? Direct what you want to say to the figure the  
23 reader should look. Is it figure 8? ; I think it would be good if you give an explanation on why  
24 this is the case).  
25

26  
27 **Reply 20:** No sir, this is not figure 8, this is figure 7 and I have included Fig. 7 under the heading  
28 ‘**Statistical analysis of NPPs frequencies**’ (Line no. 366). Accordingly, we have already  
29 explained this matter in the Discussion part of the manuscript (Openland and Swamp samples  
30 discussion part). Please see the same in the text of the manuscript.  
31

32  
33 **Comment 21:** Line no-339 (I think a reference is needed here).  
34

35 **Reply 21:** The same has been given in the text (Line no. 374). Please see in the manuscript.  
36  
37

38  
39 **Comment 22:** Line no-320-322 (This is confusing may be rewrite this part or give some more  
40 explanation on this?).  
41

42 **Reply 22:** Sir, as per your suggestions, I have revised the sentence (Line nos. 407-411). Kindly  
43 see the same.  
44

45  
46  
47 **Comment 23:** Line no-324-328 (Any references to support this?).  
48

49 **Reply 23:** Yes Sir, I have given references in relation to this point (Line nos. 414-415). Besides,  
50 as per my field observation and forest people after grazing in swamp and surrounding areas, the  
51 herbivores and other animals then move towards the core forests for their rest and other needs  
52 which are supported by our pollen data.  
53

54  
55 **Comment 24:** Line no-329-330 (Are you still referring to the evergreen ?).  
56  
57  
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3 **Reply 24:** Yes, it refers to the evergreen forest.  
4

5 **Comment 25:** Line no-343-346 (why 5.6% is considered significant? What are the implications  
6 of finding higher values of coprophilous fungal spores in the dense forest than in the cropland  
7 and swamp areas? What does this indicates?).  
8  
9

10 **Reply 25:** Sir, as per your comments, I have reframed and revised these sentences (Line nos.  
11 434-440). Given their limited dispersal ability as discussed in the text, the presence of  
12 coprophilous fungal spores in the palyassemblage are indicative of the immediate presence of the  
13 herbivorous animals. However, the values of coprophilous fungal spores in the  
14 palyoassemblages of forest samples are lower than openland and swamp samples, which is now  
15 well expressed in the reframed sentences.  
16  
17

18 **Comment 26:** Line no-353-354 (Is this assemblage in Figure 8? May be it is the case to rethink  
19 how to graphically display this information Figure 8 is very confusing and does not match with  
20 the text?).  
21  
22

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

27 **Comment 27:** Line no-356-358 (Reference is needed here).  
28

29 **Reply 27:** The same has been done. Kindly see the same (Line nos. 452-453).  
30  
31

32 **Comment 28:** Line no-458 (How can you estimate the size of the population with abundance of  
33 spores?)  
34

35 **Reply 28:** Sir, as per your comment, I have revised this line (Line nos. 590-592). Please see in  
36 the text of the manuscript.  
37  
38

39 **Comment 29:** Line no-475-478 (This conclusion does not bring a new finding. I think has been  
40 establish by multiple studies.  
41

42 **Reply 29:** Sir, as per your comments, we have revised the conclusion section (Line nos. 605-  
43 627). Kindly see.  
44

45 **Comment 30:** Line no-479-483 (I think the important/impact of human activity is missing in the  
46 discussion).  
47  
48

49 **Reply 30:** Yes Sir, It has now been added in the discussion section (Line nos. 482-484).  
50

51 **Comment 31:** Line no-484-486 (This is indeed very important but it was not explored  
52 previously?).  
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3 **Reply 31:** Sir, as per our recorded data, based on the presence and abundance of the local  
4 arboreal pollen taxa it could be possible to distinguish and characterize among the natural forest,  
5 cropland and other land-use form in the regional and global level. So, this data will be useful as a  
6 baseline for the identification and differentiation between natural vegetation and human activities  
7 areas (Cropland, farmland, etc.). The same has been added in the discussion section. Kindly see  
8 (Line nos. 482-484); Line nos. 553-572).  
9

10  
11 **Comment 32:** Figure 5 and Figure 6 (Align the vegetation types label?).  
12

13 **Reply 32:** The same has been corrected. Please see Figure 5 and Figure 6.  
14  
15

16 **All the corrections in the manuscript have been made under the guidance of reviewer's and**  
17 **Editor's suggestions. Revisions like inclusion and deletion of references, deletion and reframing of**  
18 **sentences, etc., have been done in the text of the manuscript and related line numbers have been**  
19 **provided with each response (pls. refer marked copy). The figures have been revised as per**  
20 **suggestion for more clearance. We are extremely thankful to editor and anonymous reviewer's for**  
21 **such a valuable suggestions which helped a lot in the improvement of the manuscript.**  
22  
23  
24

25 **Dr. Sadhan K. Basumatary**  
26 **Corresponding author**  
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