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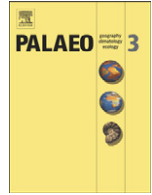
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Dung fungi as indicators of past herbivore abundance, Kruger and Limpopo National Park

A. Ekblom^{a,*}, L. Gillson^b

^a African and Comparative Archaeology, Department of Archaeology and Ancient history, SE-751 26 Uppsala, Uppsala University, Sweden

^b Plant Conservation Unit, Botany Department, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa

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ABSTRACT

Effective wildlife management needs historical data on herbivore abundance and its interactions with vegetation, climate and disturbance over longer time periods that is available through observational and archive data. Spores specific to herbivore dung provide a potential source of information on past herbivore abundances. This paper sets out to evaluate the potential of fungal spores as environmental indicators and in particular the use of coprophilous fungi in understanding past herbivore densities and their impact on the savanna landscape of Kruger and Limpopo National Parks (South Africa and Mozambique). Spore assemblages from six sedimentary cores are analysed and compared with the pollen data. Spores of coprophilous fungi, *Coniochaeta cf ligniaria*, and Sordariaceae in particular provide a valuable source of information about past herbivore densities. The spore assemblages of investigated localities show historical fluctuations in herbivore abundance. Peaks in wild/domestic herbivore densities can be seen, on a local scale from 800 to 900 AD and another at 1400 AD, however, these cannot be linked with any significant changes in vegetation. The last 200–300 years have seen an increased abundance of herbivores in the Limpopo floodplain sites, particularly domestic cattle. There is no clear correspondence between changes in herbivore abundance and local vegetation in this period or the 20th century. However, domestic cattle, together with wild herbivores, probably contributed to creating a mosaic type of landscape with heterogeneous tree cover.

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1. Introduction

A good understanding of the role of herbivory in the savanna ecosystem is important for an effective wildlife management. In Kruger National Park (KNP) a decline in tree cover has been observed since the 1950s, explained to be due to the high herbivore densities in the park. A general homogenisation of the vegetation has also been observed in the vicinity of boreholes where herbivore densities are high (Eckhardt et al., 2000). Herbivory, along with fire, is one of the important drivers of the tree versus grass ratio in the savanna. Bell (1982) proposed that vegetation structure in African savannas is controlled mainly by herbivore densities. Similarly, woody cover reduction on a regional scale has been explained to be due to the concentration of herbivores in protected areas (see review in Dublin et al., 1990).

Savannas are complex systems, consisting of a mosaic of grassland and woodland patches that are quasi-stable and frequently undergo transitions between vegetation phases. Previous equilibrium based resource competition/niche separation models have been exchanged for dynamic/non-equilibrium models where the tree–grass coexis-

tence is explained to be due to disturbance and temporal and spatial heterogeneity (Scholes and Archer, 1997; Jeltsch et al., 2000; Higgins et al., 2000; Sankaran et al., 2004; Sankaran et al., 2005). With the realisation that savannas are driven by disturbance, the role of herbivory has to be considered as interdependent with other variables. Dublin et al. (1990) have shown that herbivore densities, in this case of elephants, cannot explain the transition from woodland to open grassland. In the KNP context, Mills and Fey (2005) demonstrated that intensity of browsing after fire determined the degree of woody recruitment (see also Belsky, 1984). Meanwhile grazers have been shown to control fire frequency as high densities of grazers reduce grass biomass, the main fuel source in the savanna, resulting in a significant reduction of fire frequency and intensity (Scholes and Archer, 1997; Jeltsch et al., 2000; Van Langevelde et al., 2003). Herbivore-maintained ‘grazing lawns’ are a common feature of many semi-arid savannas (Archibald et al., 2005). There may be both positive and negative feedback processes between herbivore abundance and physiognomy. As discussed above, local factors, such as nutrient availability, water availability and fires control herbivore densities on a local scale. However, there is a range of other factors that may control densities, like local and regional scale carnivore numbers and disease. A general relationship between herbivore numbers and rainfall has for instance been shown in the case of KNP (Owen-Smith and Ogutu, 2003).

* Corresponding author. Tel.: +46 18 471 20 73; fax: +46 18 471 75 50.

E-mail addresses: anneli.ekblom@arkeologi.uu.se (A. Ekblom), Lindsey.Gillson@uct.ac.za (L. Gillson).

To effectively manage wildlife, historical data on herbivore abundance and its interactions with vegetation are needed. Climate variability and other disturbances may take place over longer time periods than are available with observational and archive data. The importance of considering the history embedded in the savanna landscape has been stressed by Higgins et al. (2000) and Gillson (2004). The changes we observe today may be historically conditioned. In the case of Serengeti–Mara, Dublin et al. (1990) suggested that savannas in the 20th century were more open than at present. The present day loss of forest cover may be a 'bounce back' from a 50 year period of bush encroachment, conditioned by the 1893–1895 rinderpest epidemic (see discussion below); another issue that has been neglected in parks is the historical role of domestic herbivory in the savanna. The exclusion of people and their domestic stock from the parks, which took place in KNP from the beginning of last century, may have resulted in a conversion of vegetation; the result of which can still be seen today.

The issue is difficult to discuss due to the general lack of data on historical herbivory densities. Archaeological data have in the KNP case contributed to a general understanding of hunting and wildlife interactions (Plug, 1987; Plug, 1989), but it is not quantifiable in the sense of overall herbivore densities. Spores of coprophilous fungi provide a potential source of information on past herbivory abundances.

This paper evaluates the potential of spores of coprophilous fungi as environmental indicators and, in particular, the use of dung fungal spores in understanding past herbivore densities and their influence on the savanna landscape. Sedimentary sequences from KNP and PNL (Limpopo National Park, Mozambique) are analysed for spore abundance. Previously presented pollen, charcoal and isotope analyses (Gillson and Ekblom, 2009a,b; Ekblom and Gillson, in press-a,b) allow a comparison with the spore data. Identification and ecological interpretation of fungal spores still need improvements, but as will be shown here, fossil spores and spores of coprophilous fungi in particular offer a unique possibility to assess herbivore abundance and its effects on the landscape over the long term.

1.1. Methodological background

Fungal spores have been shown to be a useful environmental indicator in various different contexts (see review in van Geel and Aptroot, 2006). In particular, the links between fungal spores and herbivory have been explored in different geographical regions. Davis (1987) first used the frequency of *Sporormiella* in sedimentary sequences to infer densities and extinctions of megaherbivory in North America (see also Robinson et al., 2005; Davis and Shafer, 2006). Other examples are the use of spores of coprophilous fungi such as *Sporormiella*, Sordariaceae, *Coniochaeta ligniaria* and *Podospora*-type to infer the presence of domestic stock (van Geel et al., 2003; Graf and Chmura, 2006; Marinova and Atanassova, 2006 and van Geel and Aptroot, 2006). The correlation between coprophilous spores and herbivore abundance has also been tested in a modern day situation by Raper and Bush (2009).

In Africa, fungal spores have not been widely used in palaeoecological contexts. Burney et al. (2003) used changing *Sporormiella* frequencies to discuss the decrease of grazing pressure linked with the extinction of megaherbivores, and a subsequent increase with the advent of domestic cattle in Madagascar. Carrion et al. (2000) included fungal spores in their analysis of cow dung from the Free State. Similarly Lejju et al. (2005) included the analysis of fungal spores in archaeological investigations at the earthenwork site Munsu, Uganda. A few studies on modern spore assemblages have also been carried out. Jarzen and Elsik (1986) presented an analysis of modern spore assemblages in a Zambian savanna landscape, that is used here. Wolf (1977) has also presented fungal spore assemblages from East African lakes. An important reference for the present study is the work by Ebersohn and Eicker (1992, 1997) on the fungal assemblages of modern herbivore dung in KNP.

Notwithstanding these positive examples, the use of fungal spores as an important source of environmental information has not been appreciated in the African context, particularly with regard to estimating herbivore abundance prior to the arrival of guns, colonials and intensive hunting for sport and trade in Africa; information that is pertinent to the park management of herbivore abundance today. Fungal spores, together with other palynomorphs, are important as a source of palaeo-environmental information, complementary to the pollen data or other proxies such as diatoms, isotopes etc. Fungal spore assemblages are a function of landscape type, growing both on a variety of plant species and decaying organic matter, however they have different modes of distribution and deposition than pollen and may also represent taxa that we do not find in the pollen record.

2. Area description

2.1. The physical landscape

The different landscapes in KNP and PNL are shaped by the high interannual variability in rainfall, geological substrates and main drainage systems. Rainfall in KNP and PNL is highly variable between years. The area is affected by a near decadal cyclicity of dry and wet phases, and variations in the effects of the Mozambique current and ENSO (El Niño–Southern Oscillation) with a cyclicity of 3–5 years (Tyson and Preston-Whyte, 2000). Rainfall is markedly seasonal with 95% of the yearly rainfall occurring between October and April. The mean daily temperatures are 30–34 °C in the summers, when evaporation is at its highest due to the southern hemisphere sun maxima, and 22–26 °C in the winter (FAO, 2004). The mean daily temperatures are 30–34 °C in the summers and 22–26 °C in the winter (FAO, 2004). The whole region has a rainfall gradient with 800 mm/year in the southwest part of KNP to less than 500 mm/year in the Northern most Pafuri area (Venter et al., 2003; FAO, 2004).

On a regional scale, northern KNP and PNL can be divided into two main landscape types, both represented with our sampling localities. The first landscape type is the area of the larger permanent rivers, the Limpopo and Shingwedzi that cross the area in a south-east direction. In PNL the villages are concentrated in these river valleys and the same pattern is known for the KNP historically. Here, a riverine gallery forest belt can be found, supported by the high water tables associated with the proximity to the rivers, including tree/shrub species such as *Diospyros mespiliformis*, *Schotia brachypetala*, *Combretum imberbe*, *Breonadia salicina*, *Combretum erythrophyllum*, *Nuxia oppositifolia*, *Ficus sycamoros*, *Kigelia africana*, *Acacia robusta*, *Acacia xanthophloeae*, *Faidherbia albida*, *Lonchocarpus capassa*, *Trichilia emetica* and *Xanthocercis zambesiaca*. In areas that are frequently flooded *Salvadora angustifolia* may be dominant (Wild and Fernandes, 1968; Venter et al., 2003).

The other main landscape type is the savanna, where throughout the northern part of KNP as well as in PNL, the landscape is dominated by mopane (*Colophospermum mopane*). In this landscape, water is available only as semi-permanent pans and spring-fed wetlands. Within this broad landscape type, differences in vegetation depend on geological substrate. On the clayey substrates of KNP mopane is completely dominant while *Burkea africana*, *Pseudolachnostylis maprouneifolia*, *Kirkia acuminata* and *Combretum* spp occur on the shallow alluvial sands (Venter et al., 2003). In the more southerly region, south of Malahlapanga, other dominant arboreal species such *Combretum apiculatum* and *Acacia nigrescens* occur alongside mopane. Mopane usually grows as a multistemmed shrub interspersed with grasses though its growth form can vary with substrate. In large parts of PNL, mopane woodlands are common. The species may be completely dominant, with little or no undergrowth. Open grasslands occur in places surrounded by more wooded savanna. Near the semiseasonal pans, where vegetation is influenced by a higher water table other taxa can be found, such as *Terminalia sericeae*, *Sclerocarya*

sp., *Dichrostachys cinerea*, *Combretum imberbe*, *Xanthocercis zambesiaca*, *Drypetes mossambicensis*, *Cardiogyne africana* and *Grewia sulcata*.

Estimates of wildlife abundance are available from the whole of KNP. Amongst the large herbivores, zebra dominates (30 000), while populations of buffalo and wildebeest are smaller (15–11 000 respectively) (1996 data from Owen-Smith and Ogutu, 2003). According to the 2002 census elephant numbers are higher (10 459) than ever during the c. 40 years the census has been carried out (Whyte et al., 2003). Herbivore densities in PNL are relatively low. A census between the KNP border and Shingwedzi River, counted 630 elephant and a total of 2235 herbivores (Whyte and Swanepoel, 2007). The numbers of wild herbivores are most probably considerably lower east of the Shingwedzi River. Importantly PNL also has high populations of domestic stock mainly cattle (3142) and goat (527) (Whyte and Swanepoel, 2007).

2.2. Landscape history

Historically, KNP and PNL have been occupied by hunting and gathering communities for millennia (Scholes et al., 2003). Farming in the wider region is suggested to have been in place since c. 4–500 AD. The PNL and KNP areas formed part of the social-cultural node of the Limpopo Valley, where increased reliance on farming and cattle keeping, in combination with long distance trade and emergent political centres, can be seen around the end of the first millennium AD (Huffman, 1996a, 1996b, 2000; Klapwijk and Huffman, 1996; Meyer, 1984; Plug, 2000; Manyanga, 2006; Mitchell, 2003). Thus cattle keeping in this area dates back to the end of the first millennium and probably earlier. Though archaeological surveys in the region are scant, available bone assemblages suggest a rich variety of wild life (Plug, 1987, 1989). Bone assemblages from the stone walled settlement Thulamela, settled between 1400 and 1650 AD by a considerable population, shows that wildlife and fish was the most common source of food while only few cattle bones have been recovered. This is contrary to other stone walled settlements in the region, where cattle are very common (Plug, 2000, see also Manyanga, 2006). The limited evidence for cattle may possibly be explained by the fact that the region has been known to be infested with tse-tse flies (carriers of Trypanosomiasis in cattle). However, historical accounts report cattle in the region in the 19th and 20th century (Carruthers, 1995).

Reports from early travellers, such as Elton (1873) depicted a landscape abundant in wildlife. The combination of warfare, droughts and an increased local interest in the ivory trade (Manyanga, 2006) is generally thought to have decimated wildlife on a large scale (Carruthers, 1995; Mabunda et al., 2003). Historically, elephant populations are believed to have been relatively abundant but by 1896 no elephants could be found the KNP area after a century of ivory hunting reduced elephant numbers to a few relict populations in remote localities (Carruthers et al., 2008). Historically, elephant populations are believed to have been relatively low and by 1896 no elephants could be found the KNP area (see review in Whyte et al., 2003). At the end of the 19th century the whole of southern and eastern Africa was struck by the rinderpest which is believed to have killed c. 80% of both domestic and wild cattle (Young, 1977). Accordingly, wildlife populations in the beginning of the 20th century were very small in the area (Carruthers, 1995).

When KNP was proclaimed in 1926, resident rural communities were gradually expelled from KNP from the 1920s onwards (Carruthers, 1995). However, the Pafuri area, in the far North of the Park, was not included in KNP until 1969 when local communities were relocated (Carruthers, 1995). Since the proclamation there has been a varying degree of intervention with different management policies. These include suppression of fire, the extermination of predators in the early days of the park; and then later managed burns, first at fixed intervals and then at variable intervals (van Wilgen et al., 2003). In the 1930s boreholes were opened to provide water for

animals during dry periods and to disperse water dependent mammals away from permanent rivers (Mabunda et al., 2003), a practice that is now discontinued with the closing of boreholes.

PNL was formally designated in 2001 as part of the Greater Limpopo Transfrontier Park. During the Portuguese colonial period (1905–1974), the PNL area was reserved as a hunting district but with no centralised fire policy or management. During this period hunting and farming were the most important modes of subsistence complemented by cattle herding, a practice that was crucial as a social and economic resource. During the civil war (1980–1992), the PNL area was largely de-populated as the area was used as a base for the RENAMO guerrillas. After the war, people have gradually returned to the area and the villages have been reconstructed. Park management is now in the process of restocking wildlife in a corridor from KNP across the Shingwedzi River and the villages are now being relocated in resettlement schemes (see debate on this issue in Milgroom and Spierenburg, 2009).

3. Methodology

3.1. Selection of sites

All sampled pans/lakes are semi permanent, fed by underground aquifers and surface run off during wet seasons (Fig. 1 and Table 1). They have small surface drainage areas (i.e. source areas of less than c. 50–100 m in diameter), and are expected to reflect local scale changes (e.g., within 20–c. 300 m of the basin edge) (Jacobsen and Bradshaw, 1981; Sugita et al., 1999). Sedimentary sequences were obtained during the dry season using a Russian corer (Aaby and Digerfeldt, 1986) or a modified Livingstone corer for the KNP cores.

Due to the high variability in water availability, caused by regional rainfall variability and a complex local hydrology, sediment accumulation is expected to have been irregular. The amount of damaged grains is relatively high as would be expected in sediments that have been exposed to temporary droughts. Prolonged periods of drought would be reflected in peaks of eroded grains, a skewed representation of taxa and low pollen concentrations (as shown in the base of the Chixuludzi core). Overall, preservation and concentration of both spores and pollen was generally good enough to suggest that, though pan surfaces have been fluctuating, the feeding aquifers have retained a high water table during most of the time investigated.

The possible effects of disturbance of sediments by large mammals are also factors that need to be considered, particularly in a herbivore-rich environment such as the Kruger National Park. However, the results do not suggest a homogenisation of sediments that would be expected with bioturbation from large mammals. The integrity of the cores is confirmed by the stratigraphy, sequential order of radiocarbon dates, and the presence of discrete pollen and charcoal 'layers'. The sediment accumulation in these circumstances is analogous to a smoothed average; though sediment is accumulating over time, the effects of bioturbation effectively provide a 'running average' of sediment deposition and pollen rain over time. The sedimentary record probably underestimates the rapidity and/or magnitude of any observed phase changes because extreme values are smoothed out.

3.2. Spore analysis

Spores and other unidentified non-pollen palynomorphs were prepared and tallied alongside the pollen grains until a minimum of 350–500 pollen grains (excluding Cyperaceae, limnic and aquatic types) were encountered. Preparation included digestion of cellulose with NaOH, sieving through a 100 µm mesh, digestion of quartz particles through HF and concentration of pollen and spores by acetolysis (Moore et al., 1991; Bennett and Willis, 2001). A known amount of *Lycopodium* spores were added in the first stage of preparation.

Core locations and Landuse map KNP and PNL

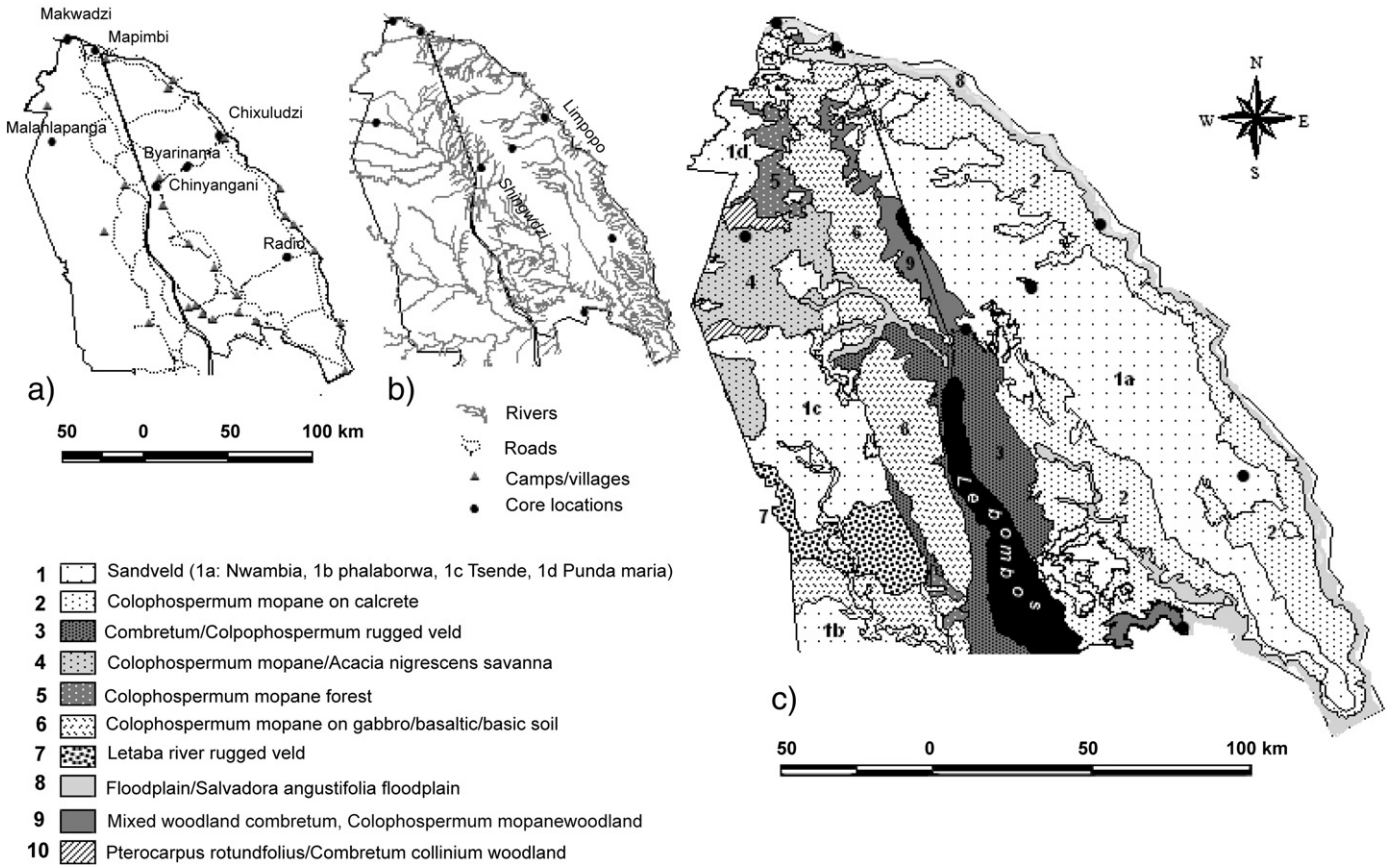


Fig. 1. Location of sampling localities and main vegetation zones (data for KNP from Gertenbach, 1983).

In the Mapimbi and Malahlapanga sequences, pollen slides were analysed for spores separately. The spore counts here are lower corresponding to a terrestrial pollen sum of >100 and 50–100 respectively. All levels were counted in the lower part of the Mapimbi core while the top 90 cm was subsampled every 4–8 cm. The Malahlapanga sequence is presented here for comparison and subsampled every 4–10 cm. Spore values are presented here in relation to the total pollen sum. The identification and interpretation of fungal spores and other palynomorphs is not straightforward as there are only few references available, particularly for the African mycoflora. References used were Jarzen and Elsik (1986); van Geel et al. (1983, 1986, 2003); van Geel and Aptroot (2006); Graf and Chmura (2006); Prager et al. (2006). Most types presented here

have only been provisionally identified or grouped together into main type groups. Types that occur infrequently or in very low numbers are displayed as ‘ungrouped’. Spores types that could not be identified to a specific taxon were grouped according to the classification suggested by Jarzen and Elsik (1986) where spore types are given a form-generic name (e.g. Dicellaesporites). As these types cannot be associated with existing taxa, the ecological significance of these types is unclear.

The spore categories include conidia, chlamydo spores, ascospores and basidiospores. Zygosporangia belonging to green Algae such as *Spirogyra* and *Zygnema* were also identified together with spores of the blue green Algae *Rivularia*. Monolete fern spores have also been identified together with trilete fern or moss spores and a general

Table 1
Sampling sites and local vegetation types with regional vegetation (in brackets), geological substrates and basin size.

Location	Coordinates	Vegetation classification	Substrate	Basin size (m/diam)
Mapimbi Lake (KNP)	S22°24'09" E31°16'48"	Riparian–Mopane shrubveld	Limpopo paleofloodplain (recent alluvial soils), responsive to the Limpopo river	75
Chixuludzi Pan (PNL)	S22°51'37.1" E31°56'33.5"	Mopane shrubveld	Limpopo paleofloodplain (recent alluvial soils), responsive to the Limpopo river	100
Byarinama Pan (PNL)	S23°01'15.3" 31°45'11.6"	Mopane shrubveld	Alluvial soils: sand and gravel	50
Radio Pan (PNL)	S23°30'40.3" E32°18'09.2"	Mopane shrubveld)	Sandy soils	50
Chinyangani Spring (PNL)	S23°16'08" E31°23'06"	Mopane shrubveld	Alluvial soils: sand and gravel	50
Malahlapanga Pan (KNP)	S22°53'20.0" E31°02'25.8"	Mopane–Combretum shrubveld	Granite and coarse sands, tributary to the Shingwedzi river	50

Bryophyta-type (moss). Other non-identified microfossil plant remains may also be included in the group. Most of the types identified are ascospores and basidiospores that are produced by Ascomycetes (sac fungi) and Basidiomycetes (club fungi).

3.3. Pollen, charcoal and isotopic analysis

The methodology and results of pollen, charcoal and isotopic analyses have been presented elsewhere (Gillson and Ekblom, 2009a, b; Ekblom and Gillson, in press-a,b). Here we present summary pollen diagrams based on the relative representation of the main ecological groupings only. Based on size classes we have separated grasses into a >40 µm as a 'possible' cereal group and a, on the basis of on morphology into a maize group. Though the indigenous African cereals overlap in size and morphology with other Poaceae (Tomlinson, 1973) the correlation between the 'possible cerealea' group and maize supports that these are indeed cereal grasses.

The ratio grass/arboreal pollen (AP) is largely representative of woody vegetation cover, meaning that an increase in AP can be interpreted as an increase in woody cover. Gillson and Duffin (2007) modelled the relationship between AP and percentage tree cover for KNP and showed a quadratic relationship. Thus a small change in AP from <2%–6.91%, as in the case of Malahlapanga, is estimated to equal a change in woody cover from less than 10% to between 13 and 27%.

We will refer to the main vegetation phases discerned in the dataset: based on the representation of pollen types in the assemblage, the ratio of AP to grasspollen, supported in some cases by other proxies such as isotopes. The boundary between phases are based on average pollen percentages and the representation of arboreal taxa

- Riparian: c. 20–60% AP and >40% contribution from riparian taxa
- Savanna–riparian: c. 10–20% AP and >30% contribution of riparian taxa,

- Savanna: c. 10–5% AP and savanna and generalist elements dominant
- Grasslands: <5% AP and savanna and generalist elements dominant.

Inferred vegetation phases are based on large scale trends, occurring on centennial to decadal scales, while smaller scale variability within a phase, i.e., a lower/higher AP than the ranges presented above, can occur within a phase.

3.4. Age depth and ¹⁴C dates

The results of each sequence analysed is presented in age depth diagrams constructed in TILIA. Sediment accumulation rates are based on AMS ¹⁴C dates on bulk sediments, calibrated in Bcal (Buck et al., 1999), complemented with Oxcal 4.1 calibrations (Bronk Ramsey, 2009), using the southern hemisphere calibration curve (McCormack et al., 2004) (Table 2). For the sites with few dates ages was modelled using a linear interpolation in Psimpoll (Bennett, 2000). For Chixuludzi and Mapimbi, other types of models were tried initially but linear interpolation gave the best age depth curve. The uppermost level of the sequences has been assumed to represent present day (2000 AD). The uppermost 40 cm of the Radio pan sequence has been dated using ²¹⁰Pb isotopes, using the Constant Flux:Constant Supply CF:CS model (Robbins and Herche, 1993). Pb²¹⁰ was unsuccessful in other cases as the amount of unsupported lead was too low.

4. Results

4.1. Mapimbi (Fig. 2)

Five main phases can be discerned in the pollen assemblage: the first riparian phase (between c. 1350 and c. 1550 AD), shows high values of trees and shrubs, dominated by typical riparian elements and with a moderate influx of microscopic charcoal (1.6 cm²/year) and low (0.7 particles/year) influx of macroscopic charcoal. The

Table 2
¹⁴C dates of presented cores.

Site/depth	Lab no	Age AD	Calibration Bcal (*OxCal calibration)	Est. age AD
Map 65–66	Ua-38827	103.8 ± 0.4**	1890 (31.8%) 1920, 1810 (63.6%) 1830*	1820*
Map 79–80	Ua-38828	211 ± 30	1653–1709, 1720–1809	1675
Map 92–92.5	Poz-9888	245 ± 30	1639–1684, 1731–1775, 1777–1787	1665
Map 94–95	Ua-38829	294 ± 30	1508–1583, 1619–1667	1644
Map 100–101	Ua-38830	490 ± 30	1427–1484	1447
Map 110–111	OxA-17234	501 ± 30	1413–1452	1437
Map 114–115	Ua-38831	617 ± 30	1320–1353, 1380–1423	1399
Map 116–116.5	Poz-9959	305 ± 30	1503–1592, 1615–1669	not used
Map 128–128.5	Poz-2119	705 ± 30	1284–1328, 1341–1391	1377
Chix 29–30	Ua-38832	346 ± 30	1503–1602 1608–1643	1625
Chix 38–37	Ua-38833	381 ± 30	1457–1595	1503
Chix 40–41	Ua-38834	533 ± 31	1406–1450	1432
Chix 43–44	Ua-38835	605 ± 30	1318–1352, 1384–1425	1401
Chix 48.5–49.5	Poz-25104	1065 ± 30	983–1046, 1084–1135	1020
Chix 79.5–80	Poz-22197	1270 ± 30	709–748, 764–893	862
Bya 30–32	Poz-25105	125 ± 30	1680–1730, 1803–1921	1800*
Radio 0–0.5	OxLel	2000	Pb 210, CF:CS model	2000
Radio 10–10.5	OxLel	1980	Pb 210, CF:CS model	1980
Radio 20–20.5	OxLel	1960	Pb 210, CF:CS model	1960
Radio 30–30.5	OxLel	1950	Pb 210, CF:CS model	1950
Radio 40–45.5	OxLel	1925	Pb 210, CF:CS model	not used
Rad 35–35.5	OxA-16674	109.8 ± 0.4**	709–748, 764–893	1905*
Rad 79–80	Poz-25106	690 ± 40	1287–1394	1394
Chin 42–42.5	Poz-25112	105 ± 30	1687–1727, 1806–1869, 1876–1923 1690 (13.1%) 1730, 1800 (82.3%) 1950*	1875*
Mala 72–72.5	Poz-9887	4940 ± 100	3936–3861, 3820–3500, 3432–3380 BC	3651 BC
Mala 55–55.5	OxA-15480	1280 ± 25	692–748, 765–883	795

**Modern.

Mapimbi lake

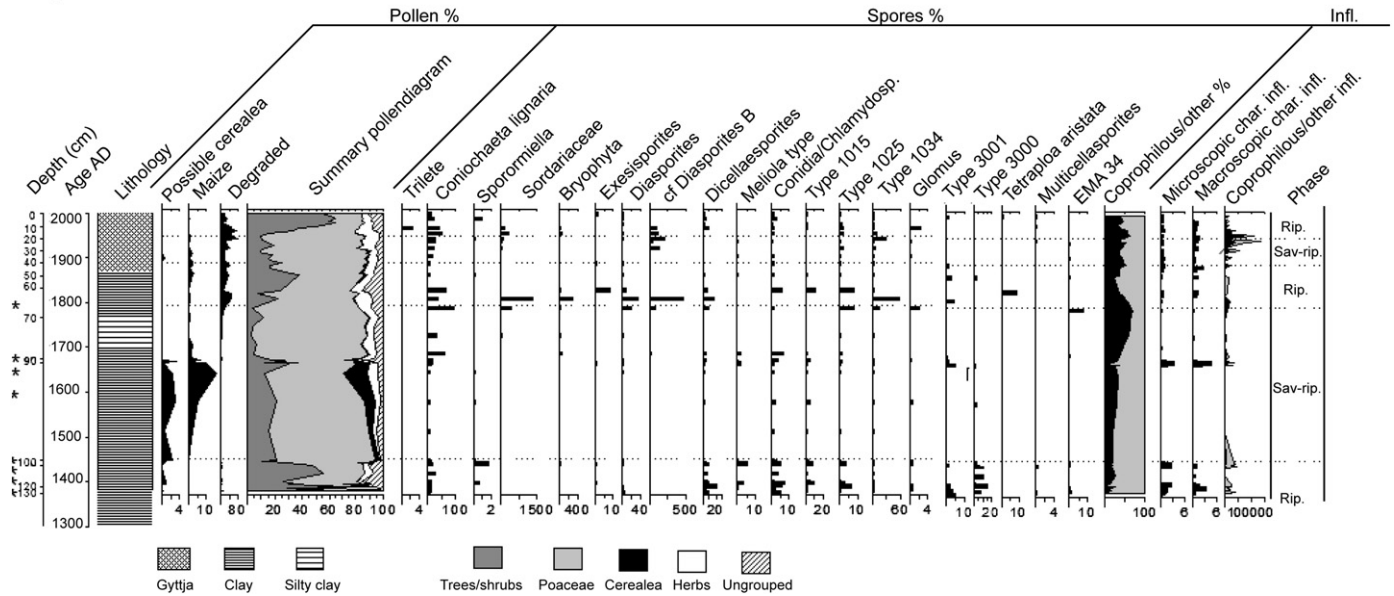


Fig. 2. Pollen summary diagram and spore percentages (based on the terrestrial pollensum) from the Mapimbi lake core. Age depth is shown on the left axis (* marks dated levels). The relative representation of coprophilous taxa over other spore taxa is shown to the right together with charcoal and spore influx (i.e. cm^2/year).

second phase (c. 1550–c. 1800 AD) shows an increase in grass pollen and a subsequent decline of riparian elements suggesting a contraction of riparian forest in the area, particularly 1700–1800 AD. There is a decrease of microscopic charcoal values ($0.92 \text{ cm}^2/\text{year}$) but an increase in macroscopic particles ($0.87 \text{ particles/year}$). Maize pollen occurs with very high numbers 1600–1700 AD and there is a peak in both micro and macroscopic charcoal influx at c. 1650 AD. From 1800 to 1900 AD, 1950 AD–present there is an increase in AP values and riparian elements. The riparian phase is interrupted by a short phase (c. 1900–c. 1950 AD) with lower AP values and decrease of riparian elements. In these phases the influx of microscopic charcoal is low ($0.44\text{--}0.76 \text{ cm}^2/\text{year}$) while macroscopic charcoal values is higher ($0.96\text{--}0.64 \text{ particles/year}$) (Ekblom and Gillson, in press-a) (Fig. 2).

The spore assemblage of Mapimbi is dominated by coprophilous ascospores such as *Coniochaeta cf. lignaria* and Sordariaceae (Van Geel et al., 1983; Van Geel and Aptroot, 2006; Jarzen and Elsik, 1986). Bryophyta (Moore et al., 1991) occurs in high numbers together with ascospores such as *Dicelleasporites* (Jarzen and Elsik, 1986), *Diasporites* (Jarzen and Elsik, 1986) together with conidia or possible chlamydiospores (Mauquoy et al., 2004; Prager et al., 2006). Other well-represented types that are not identified but probably ascospores, are types 1015, 1025, 3000 and 3001 (Plate I). Looking at the variations in the assemblage in relation to the pollen record, the abundance of spores is very low in the first riparian phase, with a higher representation only in the uppermost part of the phase. Interestingly, *Sporormiella*, which is not present in any of the other cores, sporadically occurs here. The assemblage during the first riparian phase is dominated by *Dicelleasporites*, conidia/chlamydiospores and types 1015, 1025, 3000 and 3001, i.e. spores that are not known to be produced by coprophilous fungi (see discussion). In the second savanna–riparian phase dated from 1550 AD, the relative representation of spores from coprophilous fungi becomes much higher, mainly seen in the representation of *Coniochaeta cf. lignaria*. High values are present 1700–1800 AD, just after the peak of maize pollen and charcoal. There is a general decline of spores from coprophilous fungi in the following savanna–riparian phase, dated from c. 1800 AD. Sordariaceae show high values in the beginning of this phase, however. Other spores, such as Bryophyta,

Diasporites and type 1034, occur with a high representation. From 1900 there is a relative increase in spores from coprophilous fungi again, and marked peaks in spore influx overall can be seen around c. 1950.

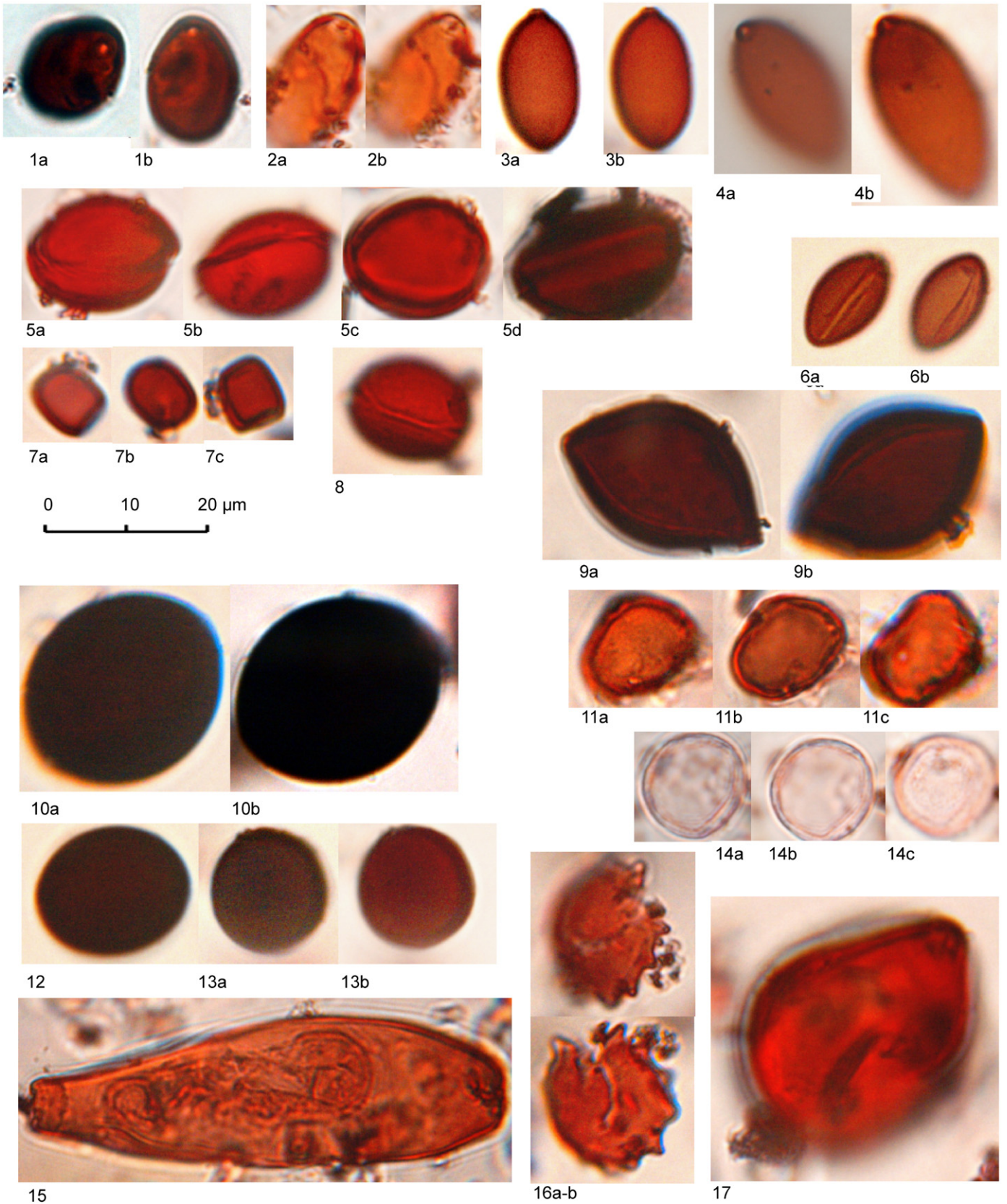
4.2. Chixuludzi pan (Fig. 3)

Two main phases can be discerned in the pollen and isotope data (Ekblom and Gillson, in press-a,b). The first savanna phase dates between c. 800 and c. 1400 AD. Generalist and savanna taxa are common while few typical riparian elements occur. The early part of this phase is marked by several hiatuses reflected by high values of degraded pollen and low pollen concentrations (not shown). This has been separated as a subphase on the basis of the isotope record and the representation of aquatics (Ekblom and Gillson, in press-b). Both micro and macroscopic charcoal influx is low overall ($0.9 \text{ cm}^2/\text{year}$). A peak in charcoal values can be seen at c. 950 AD. The second savanna–riparian phase is dated 1400–present, and marked by an increase of AP, most significant in the riparian elements. Maize pollen occurs continuously by the end of the 15th century AD, a surprisingly early date. Maize pollen occurring before this has probably been transported downward in the profile after deposition. Charcoal influx is low ($0.6 \text{ cm}^2/\text{year}$), but smaller charcoal peaks are more frequent, particularly at 1550, 1650 and 1850 AD (Fig. 3).

The spore assemblage is similar to Mapimbi but with fewer types. In the lower savanna phase, spore numbers are generally high, with Bryophyta and the unidentified EMA 34-type (cf Prager et al., 2006). Monolet fernspores occur in low numbers together with trilete fern/moss spores. *Diasporites* and *Dicelleasporites* are well represented in the phase while other types, common in the Mapimbi core, occur in low numbers only. Spores from coprophilous fungi are represented, with *Coniochaeta* sp. that occur in relatively high number around 870 AD and Sordariaceae just before that. Algal *Spirogyra* spores show an increase at the transition between the two savanna sub-phases around 950 AD, together with other algal spores and *Glomus* (van Geel et al., 1989). The more recent savanna subphase shows an increased influx of spores but the resolution of sampling here is relatively low. Spores of coprophilous fungi are not well represented. Bryophyta continues

to dominate the phase, with high numbers of the EMA 34-type and unidentified/ungrouped palynomorphs. The savanna-riparian phase, dating from 1400 AD show a continuous representation of coprophilous fungi, mainly Sordariaceae but also cf *Coniochaeta* sp.

(van Geel et al., 2003; Marinova and Atanassova, 2006; van Geel and Aptroot, 2006). Higher numbers of Sordariaceae and cf *Coniochaeta* sp. (van Geel et al., 2003; Marinova and Atanassova, 2006; van Geel and Aptroot, 2006) are displayed from c. 1700 AD



Chixuludzi pan

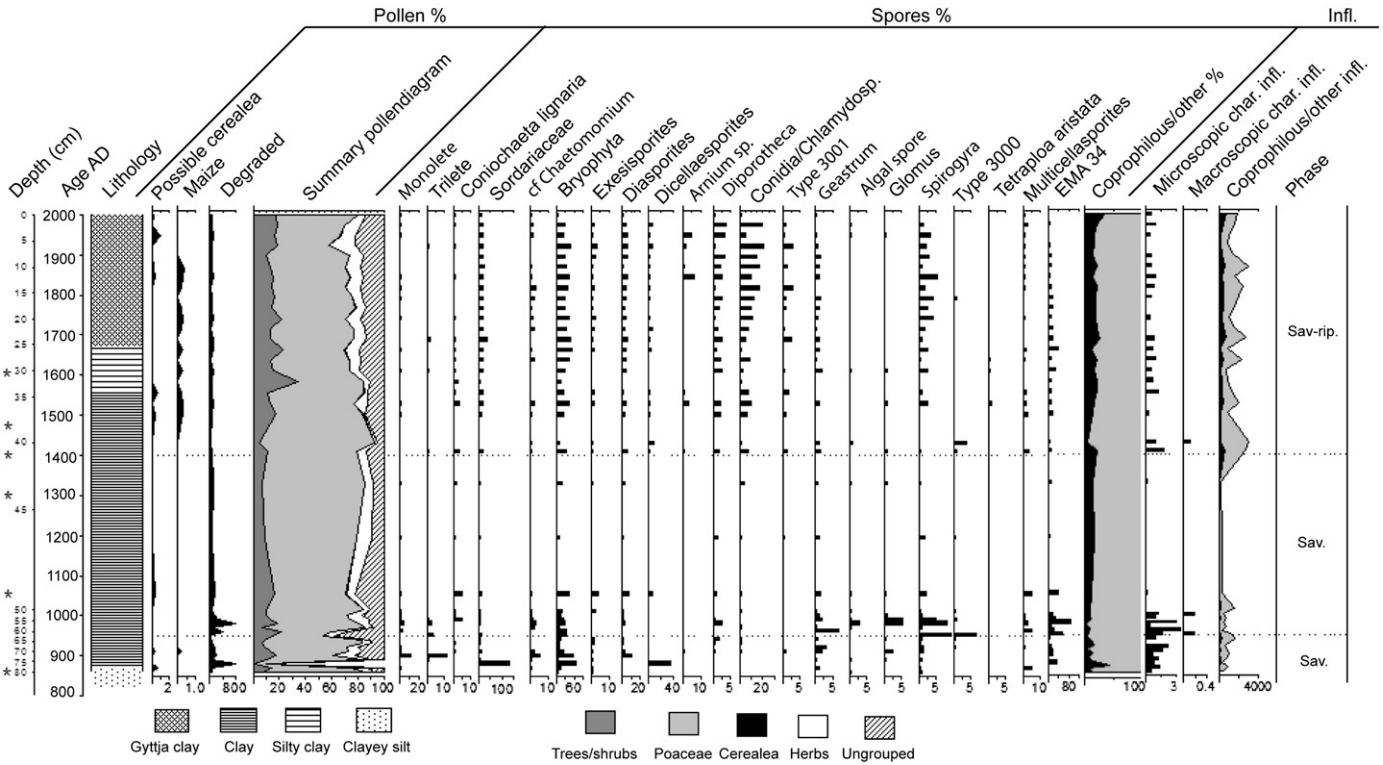


Fig. 3. Pollen summary diagram and spore percentages (based on the terrestrial pollensum) from the Chixuludzi pan core. Age depth is shown on the left axis (* marks dated levels). The relative representation of coprophilous taxa over other spore taxa is shown to the right together with charcoal and spore influx (i.e. cm²/year).

and are concurrent with the increase of charcoal and presence of maize. Other types common in this phase are unidentified conidia or possibly chlamydiospores together with Bryophyta and the EMA 34-type. *Spirogyra* is also represented in this uppermost section.

4.3. *Byarinama* pan (Fig. 4)

This short sequence reflects the last c. 200 years and represents an open savanna landscape dominated by grass with singular occurrences of trees/shrubs as today. Microscopic charcoal abundance is moderate (0.78 cm²/year) but shows a marked increase around 1950 to 2.5 cm²/year reflected also in the macroscopic charcoal (Ekblom and Gillson, in press a) (Fig. 4).

The sequence is dominated by *Glomus* and algal spores (*Spirogyra*). Bryophyta shows high values together with the coprophilous *Coniochaeta* sp. The percentage data do not indicate any correlation between the spores from coprophilous fungi and possible cereal grains or charcoal but the influx data suggest an increase in all these categories together during the 20th century.

4.4. *Radio* pan (Fig. 5)

A stable open savanna dominated by grasses has been present here over the last 600 years. The pollen assemblage shows a low variation in woody cover and herb vegetation. AP percentages range from 3 to 11% with an average of 6%. Charcoal abundance is moderate, on average 0.2 cm²/year, during most of the 650 years represented. During the last c. 50 years there was an increase of charcoal to 6 cm²/year, which is high compared to the other cores presented (Ekblom and Gillson, in press-a,b) (Fig. 5).

Radio pan has a smaller range of spore and palynomorphs represented than other cores. Spore abundance and representation generally corresponds to suggested hydrological changes at c. 1400 AD (Ekblom and Gillson, in press-b). During the dry pan phase, spores are abundant with high values of *Dicellaesporites*, *Exesisporites* and *Lycoperdon*-type (Jarzen and Elsik, 1986) that is not very common in other cores. Bryophyta and conidia/chlamydiospores occur in high number together with the unidentified EMA 34-type. *Spirogyra* and *Gelasinospora* are common in this part of the core

Plate I. Spores of coprophilous fungi and unidentified types.

- Plate 1–4. Sordariaceae 4,
- 8. *Coniochaeta* cf *ligniaria*, 6,
- 9. *Coniochaeta* spp,
- 7. *Sporormiella* spp,
- 10. Type 1025,
- 11. Type 3000,
- 12–13. *Bryophyta*,
- 14. Type 3001,
- 15. Type 1015,
- 16. Type 3003,
- 17. Type 1034.

Byarinama pan

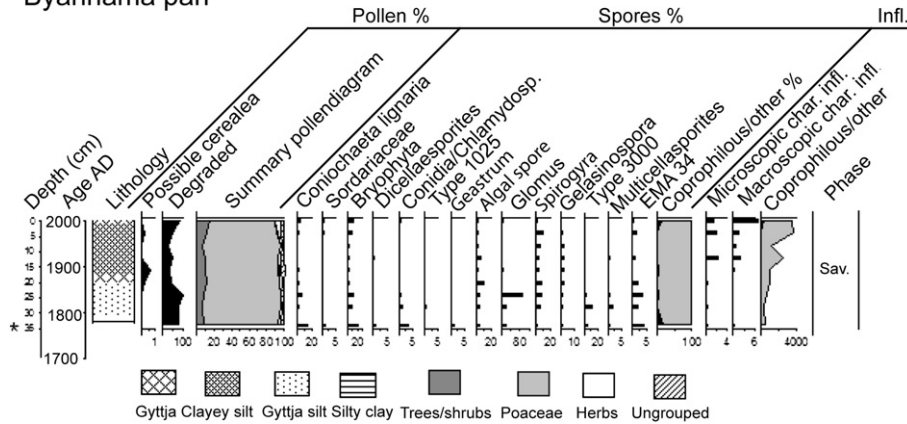


Fig. 4. Pollen summary diagram and spore percentages (based on the terrestrial pollensum) from the Byarinama pan core. Age depth is shown on the left axis (* marks dated levels). The relative representation of coprophilous taxa over other spore taxa is shown to the right together with charcoal and spore influx (i.e. cm²/year).

together with other algal zygosporites. The relative amount of spores from coprophilous fungi is low here compared to the other sequences. From c. 1600 AD there is a general decrease in spore abundance, visible in particular amongst the algal spores and Dicellaesporites and Exesisporites that now occur in low numbers. Instead there is a relative increase in Bryophyta and EMA 34-type. The relative amount of spores from coprophilous fungi remains low after 1600 AD. *Coniochaeta cf lignaria* and Sordariaceae increase in the last c. 50 years at the same time as there the increase of micro and macroscopic charcoal.

4.5. Chinyangani spring (Fig. 6)

The sequence is estimated to represent the last 200 years and the pollen assemblage suggests a vegetation type similar to the present day wooded savanna dominated by riparian elements. AP is well represented in this core (16–57%), and therefore it referred to here as a riparian site. The proximity to a settlement is reflected in the abundance of maize pollen, particularly from the middle part and upwards in the core (c. 1940s–present day). Generally charcoal abundance is very high, ranging from 2.7 to 22.8 cm²/year, with

highest influx in the 19th century. Surprisingly the amount of macroscopic charcoal fragments is low, suggesting that the Chinyangani charcoal record is mostly representing extra-local fires (Ekblom and Gillson, in press-a) (Fig. 6).

The spore assemblage of Chinyangani has the widest range of types and generally a very high spore abundance. Spores from coprophilous fungi, particularly *Coniochaeta cf lignaria* (100–400%) and *Chaetomium* (Jarzen and Elsik, 1986; van Geel et al., 2003) occurs in higher numbers. Bryophyta similarly occurs in very high numbers (c. 200–400%) together with Dicellaesporites and the unidentified type 1025. *Arniium* (van Geel and Aptroot, 2006) and the unidentified type 3003, which were not common in any of the other cores, are well represented here. Algal spores are also common as well as *Glomus*. The changing distribution of spores with a decrease of spores in the upper part, corresponds to a decrease in microscopic charcoal influx, an increase in maize and high percentages of AP. The common types listed above all show high values before c. 1900 but a decrease after this. The exception are types 3001 and 3003 (Plate 1) that displays higher values after c. 1900. *Coniochaeta cf lignaria* continues to be well represented but the relative amount of spores from coprophilous fungi is lower in this part of the core than previously.

Radio pan

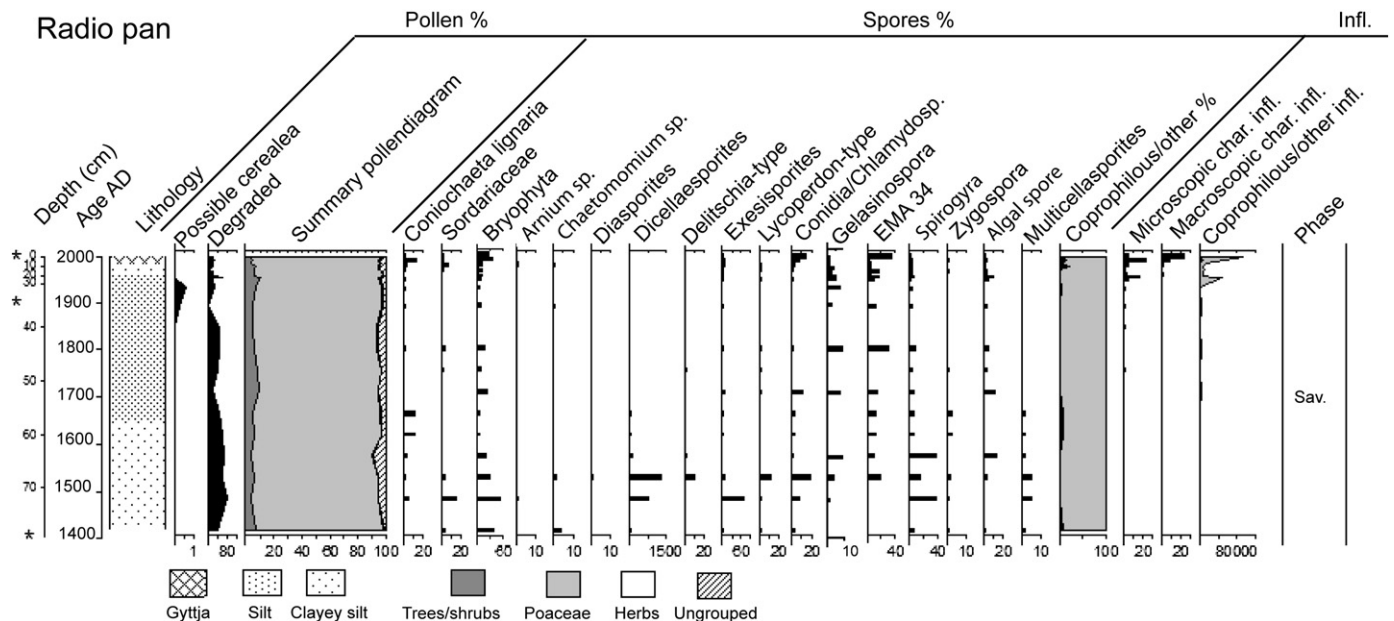


Fig. 5. Pollen summary diagram and spore percentages (based on the terrestrial pollensum) from the Radio pan core. Age depth is shown on the left axis (* marks dated levels). The relative representation of coprophilous taxa over other spore taxa is shown to the right together with charcoal and spore influx (i.e. cm²/year).

Chinyangani pan

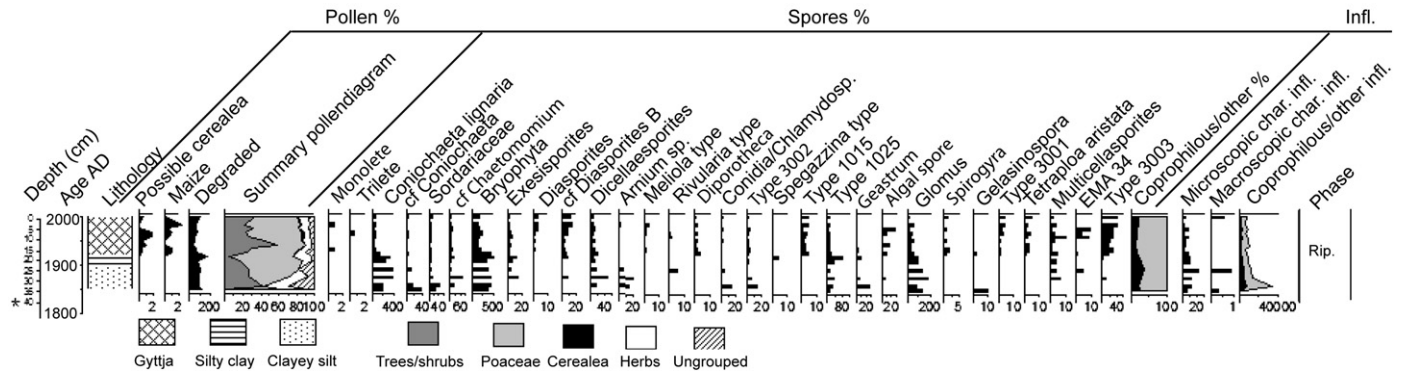


Fig. 6. Pollen summary diagram and spore percentages (based on the terrestrial pollensum) from the Chinyangani pan core. Age depth is shown on the left axis (* marks dated levels). The relative representation of coprophilous taxa over other spore taxa is shown to the right together with charcoal and spore influx (i.e. cm^2/year).

4.6. Malahlapanga (Fig. 7)

Two main phases are present in the Malahlapanga profile that is the oldest profile covering the last 6000 years. Most probably the lower part of the sequence contains a number of hiatuses which is reflected in a low rate of accumulation. The sequence is completely dominated by grass pollen, with <2% AP until c. 800 AD. Microscopic charcoal values in this phase are extremely low ($0.003 \text{ cm}^2/\text{year}$) and similarly the rate of accumulation in this phase is very low ($0.0042 \text{ cm}^2/\text{year}$). After 800 AD there is a shift from the grassland phase to a savanna phase with a higher representation of trees and shrubs than before (c. 7%). Charcoal abundance increases significantly, to $0.4 \text{ cm}^2/\text{year}$, which is moderate compared to other sites investigated (Gillson and Ekblom, 2009b; Ekblom and Gillson, in press-a) (Fig. 7).

The spore assemblage of the Malahlapanga sequence has only been analysed in a few selected levels. The assemblage show less variety than the other cores, and spore counts are also lower here. The most significant difference in the Malahlapanga sequence is the high number of fern spores throughout this sequence but in particular in the uppermost savanna phase. The amount of *Spirogyra* spores is also higher here than in the Mapimbi core as is also the abundance of *Glomus* spp. The grassland phase is marked by a very low influx of both spores and pollen. The representation of spores in this phase is very low, dominated by the *Spirogyra* spores and *Glomus*. The savanna phase shows a marked increase in spore abundance together with an increase in pollen. In general the spores from coprophilous fungi *Coniochaeta* cf *lignaria* and *Sordariaceae* are represented in moderate numbers, with an increase in the upper part of the core. Bryophyta, *Dicellaesporites*, conidia/chlamydiospores and type 1015 are also well represented.

5. Discussion

5.1. The spore assemblage and environmental interpretation

The interpretation of the spore assemblage has to be largely deductive as many of the types are not identified to any specific species. Some palynomorphs identified as 'types' may also belong to a wide range of other members of the floral kingdom than fungi or algae. Similarly, the knowledge of the ecology of spores that have been positively identified is not well known. Thus, basic research on fungal ecology as well as spore morphology would greatly enhance the palaeo-environmental interpretation.

The spore assemblage of the cores presented here is quite similar to the Zambian savanna assemblages presented by Jarzen and Elsik (1986). Recurring types are Bryophyta, *Dicellaesporites*, *Diasporites* and unidentified conidia/chlamydiospores. *Exesporites* are also common in some cores. The affinities of Bryophyta, a spherical

medium sized ($20 \mu\text{m}$) spore with no visible apertures, are not certain and its inclusion into the family Bryophyta (i.e. mosses) may come to be revised.

The riparian sites Mapimbi and Chinyangani have the highest representation of fungal taxa and total spore abundances. Unidentified fungal spore types as 1015 and 1025 occur in all cores in relatively high numbers. EMA-34, which may be an algal spore or undetermined plant material, is also present in all the cores. The presence of *Glomus* is important as related spores are formed underground in soil and not usually dispersed by air (van Geel et al., 1989; Marinova and Atanassova, 2006). *Glomus* is very common in the Byarinama and Chinyangani cores where sediments are dominated by silt and we suggest *Glomus* peaks to indicate dry conditions. Spores of *Spirogyra* and other unidentified algae are common, particularly in the early dry phase of Radio pan and throughout the Byarinama core. *Spirogyra* usually grows as macroalgal mats in shallow standing waters (Simons, 1994). The concurrence of *Glomus* and *Spirogyra* in the Malahlapanga and Chixuludzi cores suggests that *Spirogyra* is favoured during overall drier phases, when the waterbody fluctuates between completely dry periods and periods with relatively shallow standing water. This also explains the high values of *Spirogyra* in the lower part of the Radio pan core.

5.2. Spores of coprophilous fungi and possible links with herbivory

Many of the fungal spores grouped as coprophilous here were identified by Ebersohn and Eicker (1992) growing on dung substrates in KNP. *Sordariaceae*, which was common in most of the cores, were found by Ebersohn and Eicker (1992) growing on both elephant and giraffe dung. *Sordariaceae*, is often reported as coprophilous, common at archaeological sites with domestic cattle (Graf and Chmura, 2006; van Geel and Aptroot, 2006). Similarly *Podospora*, present in low numbers in many cores, has been found growing on elephant, wildebeest and zebra dung in KNP (Ebersohn and Eicker, 1992). This genus is broadly regarded as coprophilous, associated both with domesticated animals (Graf and Chmura, 2006) as well as with wild animals (van Geel and Aptroot, 2006). Other fungi represented in the KNP dung samples (Ebersohn and Eicker, 1992) included *Chaetomium* which is present in high numbers in the Chinyangani sequence. Representatives of this genus may grow on wood and plant fibre and are also common on archaeological sites (van Geel and Aptroot, 2006). Fossil *Sporormiella* has been widely used for assessing herbivore abundance (Davis, 1987; Burney et al., 2003; Robinson et al., 2005; Davis and Shafer, 2006) and has been identified on dung in KNP (Ebersohn and Eicker, 1992). *Sporormiella* was only found in the Mapimbi core and in low numbers. *Coniochaeta* cf *lignaria* was identified in large numbers in all the cores. The species grows on decaying wood and plant material but is also associated with dung

Malahlapanga pan

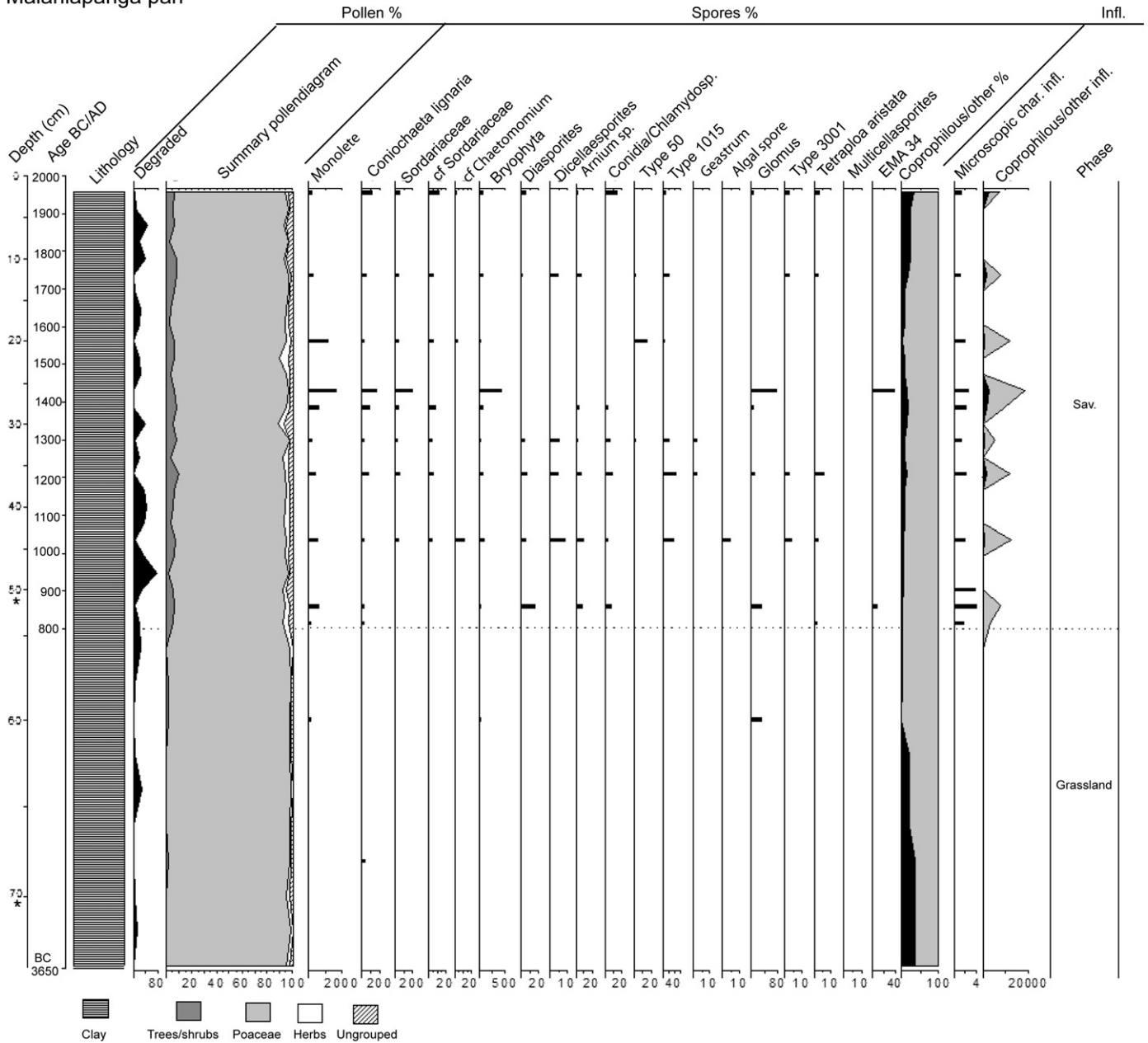


Fig. 7. Pollen summary diagram and spore percentages (based on the terrestrial pollensum) from the Malahlapanga pan core. Note that the age depth axis has been compressed for the time period 3650 BC–800 AD. Age depth is shown on the left axis (* marks dated levels). The relative representation of coprophilous taxa over other spore taxa is shown to the right together with charcoal and spore influx (i.e. cm²/year).

(van Geel et al., 2003; Marinova and Atanassova, 2006; van Geel and Aptroot, 2006). Though *Coniochaeta* was not identified in the KNP dung samples (Ebersohn and Eicker, 1992), the distribution of *Coniochaeta* spores is similar to that of Sordariaceae and therefore the grouping of *Coniochaeta* as coprophilous is supported.

The coprophilous types represent a relatively large proportion of the spore assemblage. The highest numbers of coprophilous types can be found in the Chinyangani spring, Mapimbi and Chixuludzi pan sequences. These are all localities situated near the rivers (Shingwedzi and Limpopo) where water is available all year round, giving us reason to believe that there have been permanent settlements close to these locations over time. In these cores, high herbivore densities are suggested by the amount of *Coniochaeta cf lignaria* and Sordariaceae during the last 200 years. The occurrence of these spores together with cereal pollen (i.e. maize and other possible cereal pollen) and a high influx of charcoal suggest that they are

associated with domestic stock, and cattle in particular. Spores from coprophilous fungi are very common in Mapimbi 1700–1800 AD but low during the period when maize is most abundant. Interestingly, the coprophilous taxa decline in the uppermost section of the Mapimbi core, which can be perhaps correlated with the 1969 inclusion of the Pafuri area in KNP resulting in the relocation of settlements and cattle herds.

The link is more difficult to make for periods where we have high numbers of spores from coprophilous types but no direct evidence of cultivation or other indications of settlement. Until archaeological surveys have been carried out in the region, the discussion therefore has to be tentative. Peaks in coprophilous taxa can be seen in the Chixuludzi sequence 800–900 AD, together with possible cereal grass pollen and a high charcoal influx. Cattle herding is known to have become important in Limpopo valley region by the end of the first millennium (Huffman, 2000; Mitchell, 2003). Thus, this early peak in spores from coprophilous

fungi is suggestive of local herding and farming that needs to be confirmed with archaeological surveys.

The other cores analysed (Radio pan, Byarinama pan and Malahlapanga pan) are all from areas where surface water is scarce. Therefore it is unlikely that domestic stock was herded in these areas. The exception is the top 15 cm of Radio pan, corresponding to the last c. 30 years, where increased values of coprophilous types and charcoal abundance may be linked with clearances of vegetation by people and possibly grazing of domestic cattle in the close vicinity. Notwithstanding these recent events, changes in the abundance of spores from coprophilous types in these dry cores are probably associated with local changes in wild herbivore densities. In Radio pan, Sordariaceae was common in the period 1400–1500 AD with high numbers also of *Coniochaeta cf ligniaria* until 1600 AD. Evidence for higher densities of herbivores is also present in the Malahlapanga sequence in the same period. The peaks in suggested wild herbivore abundance might be due to an overall increase in wild herbivore numbers or a local aggregation of herbivores due to dry conditions.

Malahlapanga represents the longest sequence, spanning over the last 6000 years (though probably with temporal gaps within this period). It has elsewhere been suggested that the early grassland phase represents a stable 'grazing lawn' phase maintained by grazers, as charcoal influx in this period is low (Gillson and Ekblom, 2009b). We would therefore have expected higher numbers of spores from coprophilous fungi in relation to other spores in the grassland phase. The low abundance of coprophilous types may be unrepresentative as total spore abundance in this part of the core anyhow is very low.

5.3. Links between herbivory and vegetation dynamics

Though herbivore populations around the investigated localities are suggested to have been high in periods, no direct causal link could be observed between herbivore densities and vegetation composition. In the Mapimbi sequence, AP decline when the coprophilous fungi related spores increase. Here the decline in AP can most probably be linked with clearing of vegetation for cultivation and grazing. A regeneration of forest/shrub, which may actually reflect a process of bush encroachment, can be seen after c. 1950 when local farmers and their herds were forced to relocate. This pattern is less clear when looking at the upper part of the Chixuludzi sequence where there is also evidence of farming and clearing of vegetation. Here AP increases together with what, on the basis of an increase in coprophilous fungi, is interpreted as higher populations of domestic stock. Thus domestic stock, though possibly responsible for smaller shifts in the vegetation composition, did not transform vegetation on a significant scale. It is important to point out that cattle in this region, contrary to what may be the case in other areas, are browsers as well as grazers, as leaves from *Colophospermum mopane* makes up a large part of the diet.

In the sequences from Radio, Malahlapanga and Byarinama pans, where the spores of coprophilous fungi are associated with wild herbivores, there is no clear correlation between spore abundance and vegetation. Importantly, though herbivore densities in KNP today are high, there is no corresponding change in the local vegetation around the two KNP cores analysed (Malahlapanga and Mapimbi). The pattern would perhaps be different if more cores were analysed as we would then have a landscape scale overview. Meanwhile PNL, though no formal census has been carried out, has probably had a low population density of wild herbivores during the 20th century and has seen an increase in wild populations only in recent years. As discussed above, variations in abundances of wild herbivory is recorded at 1400 AD, and cannot be directly linked with changes in woody cover (as suggested by AP abundance).

Our data do not suggest a significant correlation between herbivory and vegetation. This has to be explained as we do believe herbivory is an important driver of vegetation structure. Some possible explanations are that as vegetation structure changes, the herbivore assemblage

responds in terms of browsers and grazers, but the overall herbivore abundance remains the same. Another possible explanation may be that it is primarily megaherbivores that are important in shaping tree abundance, but in terms of the fungal signature, changes in megaherbivore abundance may be masked by changes in the rest of the herbivore assemblage. Another factor relates to the representativity of our sampling sites, as all sites investigated are wetland sites where aggregation of animals is dependent on available water resources in the surrounding landscape. Even though animals may graze close to the sampling site, they move over large distances and the vegetation signature of the actual pan may not be representative for the surrounding landscape.

As shown here, coprophilous spores do show a potential for assessing herbivory abundance over time, however additional research is needed as to the ecology and mode of dispersal of the spores before we can get a convincing picture of changing patterns on herbivore abundance on a landscape scale.

6. Conclusion

It has been demonstrated that fossil fungal spores are an important source of environmental information. The abundance of spores from coprophilous fungi, *Coniochaeta cf ligniaria*, and Sordariaceae in particular provide a valuable source of information of past herbivore densities that is not available from other types of data. The spore assemblages of investigated localities show historical fluctuations in both wild and domestic herbivore abundance. Peaks in spores from coprophilous fungi, interpreted as changes in wild herbivore densities on a local scale can be seen at c. 1400 AD (Radio pan, PNL and Malahlapanga pan, KNP). At this point it is not possible to conclude if these peaks are due to local aggregations of herbivores brought on by droughts amongst other things, or to higher herbivore population densities occurring on a landscape scale. In Chixuludzi pan (PNL) high values of spores from coprophilous fungi 800–900 AD is tentatively interpreted as suggestive of herding and farming and in the Mapimbi sequence coprophilous taxa in general, is associated with herding.

During the last 200–300 years an increased abundance of herbivores, in this case domestic cattle, is suggested by the abundance of spores from coprophilous fungi in combination with cultigens and charcoal for the Limpopo floodplain sites (Mapimbi lake, KNP and Chixuludzi pan, PNL). In the Mapimbi case this is linked with a marked decrease in woody vegetation that is not reflected in Chixuludzi. There is no indication that domestic herbivory transformed vegetation composition at a landscape scale, but rather together with wild herbivores and fire contributed to the creation of a mosaic type landscape.

Importantly, though herbivore densities in KNP are probably higher today than ever in history, this it is not reflected in the local vegetation around the two KNP cores (Malahlapanga and Mapimbi). The pattern would perhaps change if more cores were analysed as we do not at this moment have a proper landscape scale overview.

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