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# Palynological insights into an 11,700-year sequence of vegetation change in mashishing, Mpumalanga, northeastern South Africa

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# PALYNOLOGICAL INSIGHTS INTO AN 11,700-YEAR SEQUENCE OF VEGETATION CHANGE IN MASHISHING, MPUMALANGA, NORTHEASTERN SOUTH AFRICA

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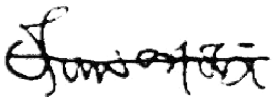
A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

2023

# DECLARATION

I, Jerry O. Olatoyan, declare that this work is my own original work. It is submitted for the degree of Doctor of Philosophy in the School of Geography, Archaeology and Environmental Studies at the University of the Witwatersrand, Johannesburg. This work has not been previously submitted for another degree or examination at any other university.



Signed by: Jerry O. Olatoyan on this the 8th day of November 2023

# ABSTRACT

In this thesis, the issue of distinguishing anthropogenic and climatic drivers of vegetation change was explored through the analysis of pollen, phytoliths and microcharcoal in core sediment records from Mashishing Fen in the Thaba Chweu Municipality, Mpumalanga province, northeastern South Africa, that date from ca. 11.2 – 11.7 ka BP to the present. In southern Africa, generally, the distinction between the contributions of anthropogenic and climatic factors to vegetation changes poses a complex challenge in palaeoenvironmental research. This difficulty often arises due to limited, well-dated palaeoenvironmental sequences suitable for correlations between archaeological and palaeoecological records. For the last 2000 years, there has been a scarcity of direct evidence for farming, such as grains and other domesticated plants, and pastoralism. A further difficulty is that some plant taxa may be indicators for intense droughts but also signify anthropogenic disturbances.

At the centre of the thesis are three papers. The first comprises a synthesis of existing literature of archaeobotanical evidence that was done to evaluate the relationship between climate, anthropogenic activities, and vegetation change during the first millennium CE in southern Africa. I focussed on this context in the paper because it is a time in which the arrival of pastoralism and farming in the region makes it the most likely period during which distinct anthropogenic vegetation change occurred. The published data demonstrates that microfossil assemblages are potential indicators of anthropogenic activities of pre-European pastoralists and farmers of the region, with patterns including a decline in tree pollen and increases in microcharcoal, spores of coprophilous fungi, open land/disturbance indicators, and ruderal species.

The second paper addresses some of the limitations of palynology as a method. A modern pollen- and phytolith-vegetation study was conducted on surface sediment samples linked to the botanical survey of five vegetation survey plots at and around Mashishing Fen to investigate the relationships between the modern pollen and phytoliths in the surface samples and the contemporary vegetation within the area. The results support the accepted view that pollen and phytoliths often do not track similar vegetation signals. The modern pollen assemblages clearly track forest and wetland vegetation, and the modern phytolith assemblages reflect grassland vegetation in the area. The study confirmed that differential phytolith and pollen production, dispersal and preservation substantially influence the proxy records and that combining phytolith and pollen data provides a more accurate basis for plant fossil interpretations in palaeoenvironmental studies. The results of this paper constrained my interpretation of the pollen data used in the third paper.

Finally, pollen, spores and microcharcoal data from the core sediment records from Mashishing Fen (formerly the Lydenburg Fen) provide palaeoenvironmental records for approximately the last 11,2 to 11,7 ka years–most of the Holocene. The data is interpreted through the patterns identified in the first paper, including potential indicators of anthropogenic activities. The data of the earlier period provide a backdrop to possible anthropogenic change in the first millennium CE; the extended data illustrate paleoenvironmental changes that took place in a region occupied by hunter-gatherers but predate any possible anthropogenic influences by pastoralists or farmers. The core data suggests that the early Holocene began with moist and warm conditions that were followed by fluctuations between wet and dry conditions during the mid-Holocene and the decline of trees with the dominance of open-land indicators during the later Holocene, thereby providing the

basis for correlating the palaeoecological records with the archaeological records in the region.

# DEDICATION

To God the Father, God the Son and God the Holy Spirit

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# CHAPTER 1: INTRODUCTION

## 1.1. GENERAL INTRODUCTION

In South Africa, the Holocene sequence, which spans ca. 11,700 BP to the present (Walker *et al.* 2012), is marked by a complex interplay of climate fluctuations, anthropogenic activities, and resultant environmental transformations. It is imperative to analyse this intricate relationship meticulously because it underpins our comprehension of the dynamic forces that have moulded and left indelible imprints on the region's vegetation landscapes. Often, these imprints are preserved in sedimentary records, offering remarkable potential for reconstructing long-term palaeoenvironmental changes at local and regional scales. This endeavour is facilitated by the application of diverse proxies, including pollen, spores, charred particles, phytoliths, and isotopes (e.g., Scott *et al.* 2012, 2022, 2023; Fitchett *et al*. 2017a; Sjöström *et al.* 2017; Esteban *et al.* 2018; Breman *et al.* 2019; Hahn *et al.* 2021; Mohale *et al.* 2022).

A meticulous examination of this intricate interplay reveals the multifaceted impact of anthropogenic activities, ranging from shifts in land use practices to industrialisation, on local and regional vegetation patterns over time (Baxter & Davies 1994; Neumann *et al.* 2011; Hahn *et al.* 2021; Olatoyan *et al.* 2022). Similarly, it reveals the region's climatic fluctuations, encompassing variations in precipitation, temperature, and sea levels, as well as its significant impact on both human communities and the broader environment (Neumann *et al.* 2010, 2011, 2014; Scott *et al.* 2012; Metwally *et al.* 2014; Brook *et al.* 2015; Sjöström *et al.* 2017).

The complex relationship between vegetation, climate, and fire activity forms a crucial nexus,

underscoring the critical role of pollen, spores, phytoliths and charcoal in reconstructing past environmental conditions. Fossil pollen, spores, and phytoliths offer insights into the past distribution of plant communities, enabling the reconstruction of past vegetation dynamics, climate fluctuations, and the extent of human influence on decadal and millennial timescales (Scott *et al.* 2012; Bamford et *al.* 2016; Ekblom *et al.* 2017; Sjöström *et al.* 2017; Breman *et al.* 2019; Morales-Molino *et al.* 2020). These proxies are invaluable when preserved in natural archives, such as lakes, wetlands, springs, swamps, marine environments, speleothems, and dung/hyrax deposits (Scott *et al.* 2004; Neumann *et al.* 2010; Festi *et al.* 2016; Breman *et al.* 2019; Hahn *et al.* 2021). Additionally, the frequencies of charred particles, when recovered from soils, peat deposits, and lake sediments, provide crucial insights into past fire occurrences and the prevailing environmental contexts (Komarek *et al.* 1973; Umbanhowar & McGrath 1998; Nichols *et al.* 2000; Rose 2004; Bamford *et al.* 2016). This integrated approach, incorporating multiple proxies and natural archives, helps to unravel the intricate tapestry of past environmental changes during the Holocene in South Africa, thereby shedding light on the interplay of natural and anthropogenic factors that have sculpted the region's vegetation landscapes during the Holocene.

This thesis focuses on the palaeoenvironmental reconstruction of the region around Mashishing, Mpumalanga, northeastern South Africa that was occupied by both hunter-gatherers and farmers. The study provides insights from pollen, spores, and microcharcoal records from the Mashishing Fen in the Gustav Klingbiel Nature Reserve on the outskirts of Mashishing. The core spans from 9900±95BP (IT-C-3107), which using OxCal v4.4 (Bronk Ramsey 2023) calibrates to a range of 11,706 – 11,205 cal BP (92.2% probability) to the very recent past -90±134BP (IT-C-3108).

The broader research project unfolds as a cohesive narrative, encompassing several pivotal phases. It commences with Olatoyan *et al*. (2022), a review of archaeobotanical evidence in southern Africa, thereby establishing a foundational context essential for assessing anthropogenic and climatic indicators. This review paper focuses on the first millennium CE, because it is a period most likely to have experienced significant anthropogenic vegetation change due to the introduction of pastoralism and farming into the region at this time (e.g., Evers 1974a, 1974b, 1975, 1977a, 1977b, 1980, 1982; Klapwijk 1974; Marker & Evers 1976; Klapwijk & Huffman 1996; Whitelaw 1996; Antonites *et al.* 2014; Lander & Russell 2018; Schoeman 2020).

The literature review is followed by a study aimed at reflecting on the limitations of palynology and phytoliths as methods. This delves into contemporary ecological dynamics, utilising the relationships between modern pollen, phytoliths, and vegetation as an approach to achieve more accurate palaeoenvironmental reconstruction. The final paper in this thesis extends its purview to encompass an exploration of the Holocene vegetation fluctuations. This paper details the vegetation change identified in the core from the Mashishing Fen. This does not predate human impact since hunter-gatherers lived in the region even before the Holocene (see e.g., Porraz & Val 2019; Backwell *et al.* 2022; Porraz *et al.* 2015 and Bader *et al.* 2020), but it does provide insights into the environmental conditions long before substantial anthropogenic change might have occurred. Subsequently, it explores the vegetation represented in the pollen record during and after the emergence of pastoralism and farming in South Africa, marking a critical juncture in the region's palaeoenvironmental history. Thus, this thesis uses a systematic structure to offer insights into the interplay of climate and anthropogenic influences on Mashishing’s vegetation landscape.

The Mashishing Fen, ca. 2500 $m^2$ in size (Sjöström *et al.* 2017), was chosen as the focal point of this research for several reasons, each underlining the significance of wetlands in palaeoenvironmental reconstruction. Wetlands, as natural archives, are sensitive to anthropogenic and environmental changes (McCarthy & Hancox 2000; Ellery *et al.* 2016). This sensitivity makes them indispensable repositories for reconstructing short and long-term historical shifts and dynamic natural processes (e.g., Scott & Nyakale 2002; Scott *et al.* 2003; Kristen *et al.* 2007; Norström *et al.* 2009; Finné *et al.* 2010; Neumann *et al.* 2014).

An essential attribute of wetlands is their preservation potential for organic remains. Over time, they accumulate sediments in a stratified manner, fostering the chronological layering of organic (e.g., micro- and macrofossils) and mineral components (McCarthy *et al.* 2010; Ellery *et al.* 2016). This stratigraphic deposition of materials within wetlands is pivotal for reconstructing past environmental conditions and the interplay of ecological elements.

Also, the fen was known to have accumulated during at least the last 1700 years (see Sjöström 2015:52; Sjöström *et al.* 2017). The archaeological sequence of this period includes occupation of the area by Later Stone Age hunter-gatherers, initial settlement by Early Farmers and the development of a terrace-based agricultural system by Bokoni Farmers. This accumulation period and the strategic proximity of the Mashishing Fen to known archaeological sites amplifies its significance. The sites are the Lydenburg Heads Site and Klingbiel (Evers 1980, 1982), and Bokoni stonewalled and terraced sites (see Delius & Schoeman 2008; Delius *et al.* 2012; Widgren *et al.* 2016 for more on Bokoni) (Fig. 1), including sites, immediately upslope from the fen.

The data from the fen enhance the capacity to contextualise palaeoecological records within

the broader framework of archaeological records. This is particularly important because although the archaeological sequence for the area has been clarified, there is a relative dearth of knowledge about concurrent shifts in vegetation composition and prevailing environmental conditions (notable exceptions in my study region include Sjöström 2013; Hattingh 2014; Sjöström *et al.* 2017; Schoeman *et al.* 2019).

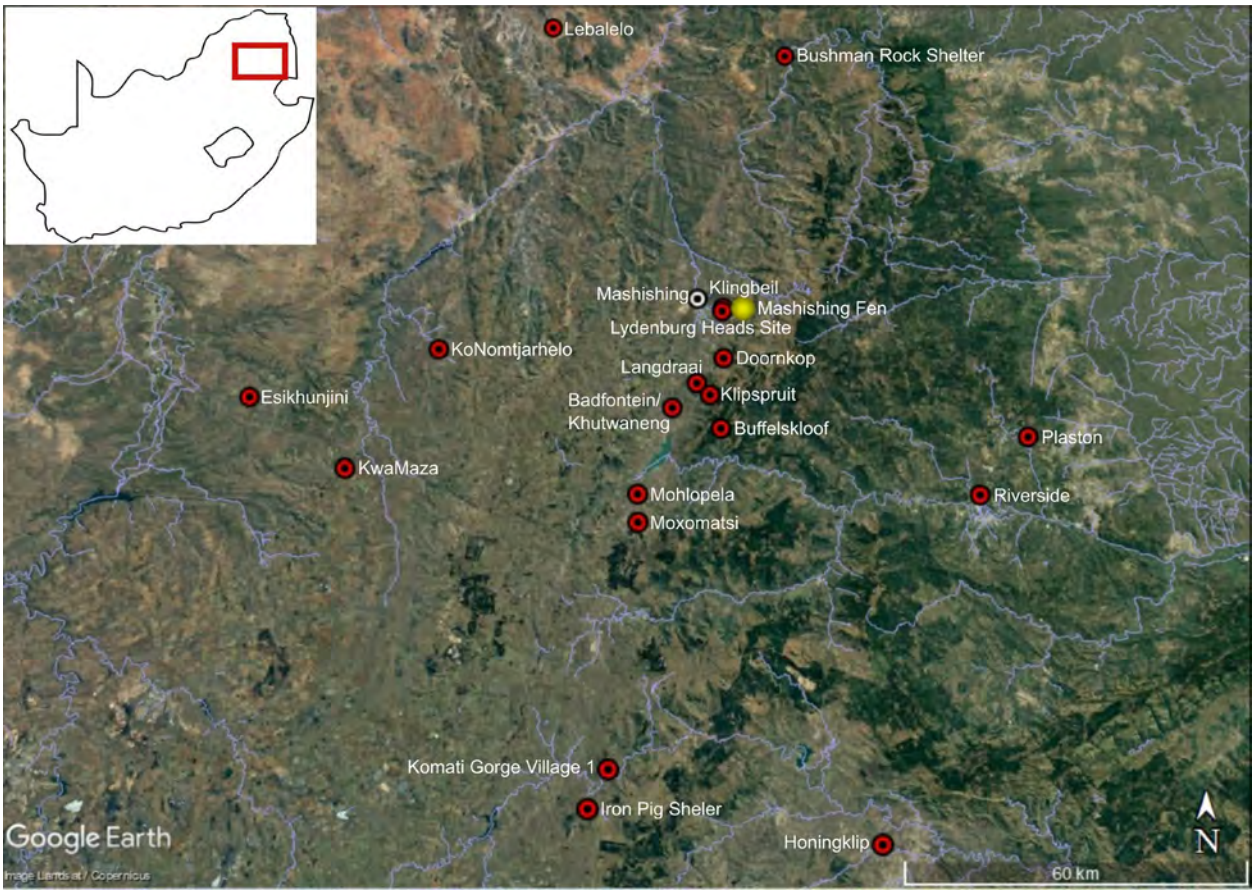


Figure 1. Mashishing Fen (yellow dot) in local archaeological context.

### *1.1.1. Palaeoenvironmental context*

Mashishing, where my study site is located, is in the summer rainfall region (SRR) of South Africa. Generally, the Holocene palaeoenvironmental record of the SRR of South Africa has

received significant attention (Breman *et al.* 2011; Scott *et al.* 2012; Fitchett *et al.* 2017b). Regional studies consistently reflect the dynamic fluctuations of past environmental conditions, with a particular focus on the late Holocene. Various records across the region (e.g., Tyson & Lindesay 1992; Holmgren *et al.* 1999; Tyson *et al.* 2000; Holmgren *et al.* 2003; Scott *et al.* 2012; Breman *et al*. 2011; 2019; Stager *et al.* 2013; Chevalier & Chase 2015) demonstrate the irregular alternation of warm and cold/cool periods with wet and dry cycles spanning the last 11,700 years.

While limited palaeoenvironmental data are available for Mpumalanga, the bordering regions have witnessed a plethora of research into past environments, with several proxy records indicating the occurrence of a widespread dry episode ca. 2000 years ago (Scott *et al.* 2012). The palaeoenvironmental records from the north, south and west of Mpumalanga (Fig. 2; Table 1), nevertheless demonstrated sufficient variability to indicate that a general climatic and environmental model would fail to recognise local variations (Holmgren *et al.* 2003; Smith *et al.* 2007; Scott *et al.* 2008; Neumann *et al.* 2008, 2010; Norström *et al.* 2009; Stager *et al.* 2013; Truc *et al.* 2013; Metwally *et al.* 2014; Woodborne *et al.* 2015, 2016). Phytolith studies at Verloren Valei, Versailles and Graskop in Mpumalanga (Fig. 2, ca. 42 km, 46 km, 40 km from the Mashishing Fen respectively) indicated cool and dry conditions during ca. 10,000-8000 BP followed by warmer and wetter conditions between ca. 8000 and 4000 BP, cooler and drier conditions between ca. 4000 and 2000 BP, and a return to general warm and wet conditions at ca. 2000 BP–present with alternating warm/wet and cool/dry episodes (Breman *et al.* 2019).

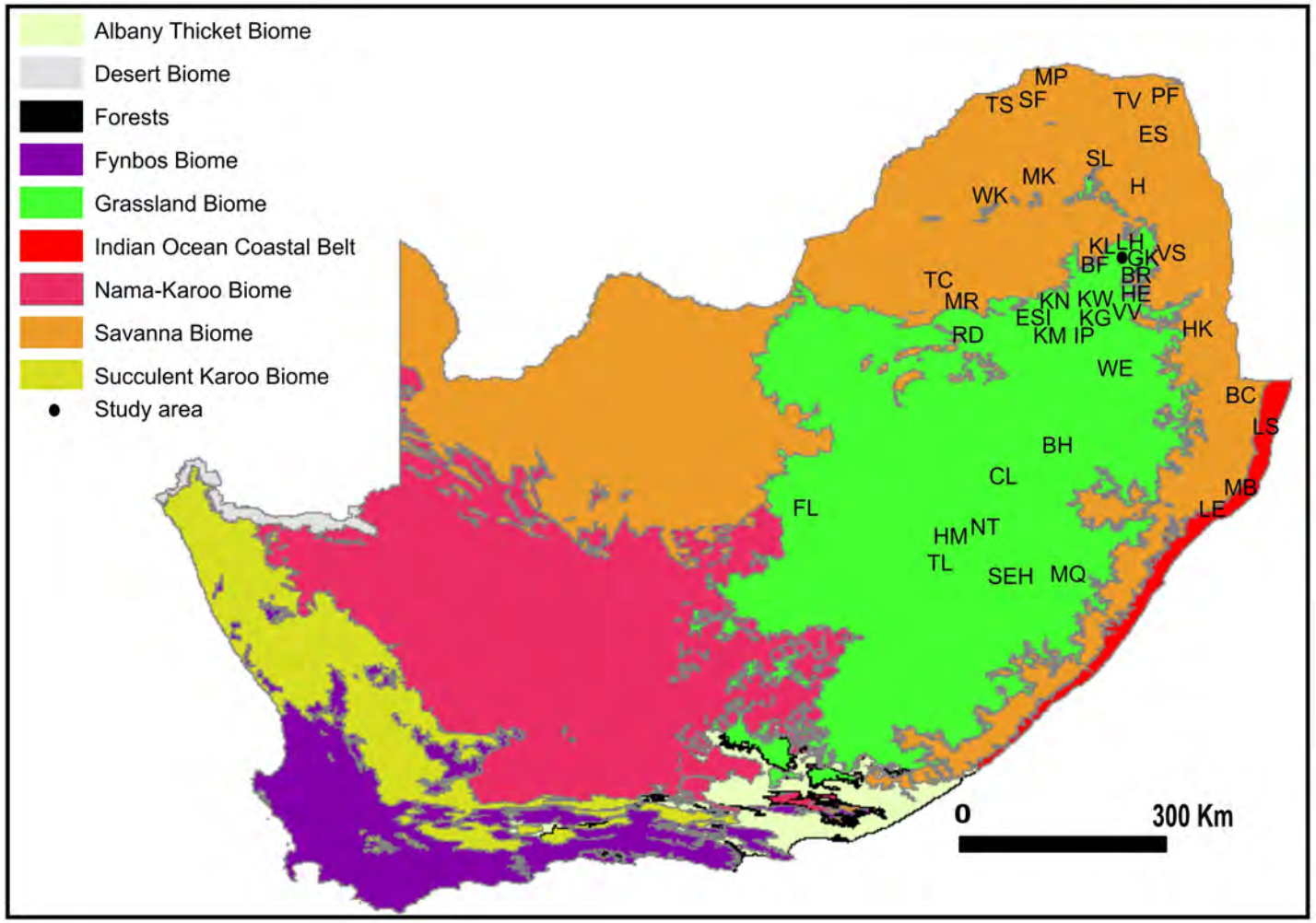


Figure 2: Map of South African Biomes (adapted after Mucina and Rutherford, 2006) showing the approximate location of the study area and sites discussed in the text, BC-Border Cave, BH- Braamhoek, BR- Bushman Rock Shelter, CL-Clarens area, ES-Eiland Salt works, ESI-Esikhunjini, FL-Florisbad, GK- Graskop, H-Harmony, HE- Heuningneskrans, HK- Honingklip, HM- Ha Makotoko, IP- Iron Pig Shelter, KG-Komati Gorge, KL-Klingbiel, KM-KwaMaza, KN- KoNomtjarhelo (Erloweni), KW-Khutwaneng (Badfontein), Lake Eteza- Lake Eteza, LS-Lake Sibaya, LH-Lydenburg Heads Site, Mfabeni peatland, MK-Makapansgat Cave, MQ- Mahwaqa mountain, MR-Moreletta Stream, NT-Ntloana Tsoana, PF-Pafuri, RD-Rietvlei Dam, SE- Sehonghong, SF- Scot's Farm, SK- SK17, SL-Silver Leaves, TC-Tswaing Crater, TL-Tloutle, TS-Tshisiku shelter, TV-Tate Vondo, VS-Versailles, VV-Verloren Valei, WE- Welgelegen; WK-Wonderkrater.

Hattingh's (2014) phytolith analysis at a Komati Gorge Homestead and Buffelskloof (Fig. 1) proposed generally cool and semi-arid climatic conditions indicative of lower rainfall than at present during Bokoni site occupation (16th–19th century). Vegetation changes were inferred, but with no clear record and chronological evidence. The lack of a clear record and the apparent absence of certain plants is not surprising because only certain taxa produce phytoliths; grasses are an exception and regularly produce phytoliths (Piperno 2006).

Grass phytolith studies at Mashishing (formerly Lydenburg) Fen (Fig. 2), ca. 98 km from Komati Gorge, indicated a different record to the inferred Komati Gorge and Buffelskloof interpretations and suggested that drier conditions around AD 1300 were followed by wetter and warm conditions that continued till present (Sjöström 2013). The early phase (ca. AD 300–AD 1350) experienced moderate to semi-arid conditions, while the latter phase (ca. AD 1350–present) witnessed increasingly mesic conditions (Sjöström *et al.* 2017). The data indicated higher moisture levels during the Bokoni occupation than at present. Schoeman *et al.* 2019 corroborated Hattingh's (2014) inferred cooler and drier climate conditions through carbon isotope analysis of tree rings from Buffelskloof. Clearly, the Lydenburg Fen and Komati Gorge data suggest the prevalence of differing and varying climatic and environmental conditions in Mpumalanga in the past.

Further south, within the Grassland Biome, recent palaeoclimatic records, including pollen, charcoal, and mineral magnetics from Braamhoek wetland (Fig. 2), shed light on the nuanced climatic dynamics in the eastern Free State. These records suggest increased moisture ca. 12,000 and 10,000-8500 BP, drier conditions ca. 7000-2000 BP, followed by a resurgence of regional wetness ca. 2000 BP-present (Norström *et al.* 2014). These data are in accord with previous phytolith and diatom studies at Braamhoek wetland, indicating a wet phase ca.

10,500-9500 BP, characterised by relatively moist conditions.

Finné *et al.* (2010) also suggested that the mid-Holocene, which they identify as ca. 8000 BP, was marked by somewhat drier conditions, with a transition to slightly more humid conditions ca. 2000 BP. The interpretation of regional dryness during the mid-Holocene is supported by Florisbad pollen data from the central Free State (Fig. 2), where warm, relatively dry conditions and high local evaporation were recorded at ca. 6500 BP. In contrast, the period from ca. 4200-2500 BP commenced with subhumid conditions but later became semi-arid after ca. 2500-1700 BP (Scott & Nyakale 2002). The pollen data from Mahwaqa Mountain in KwaZulu-Natal (Fig. 2) follow a similar climatic trend from the early to late Holocene (Neumann *et al.* 2014). However, these studies contrast with the pollen records from sites in the Clarens area, east of Florisbad (Fig. 2). Although the Holocene record at the Clarens area is incomplete, the early Holocene was dominated by grassland and fynbos vegetation, suggesting relatively warm and dry conditions during this period. In contrast, the late Holocene pollen records were dominated by grassland, indicative of subhumid conditions with summer rains (Scott 1989). These data further emphasise the variability and complexity of climatic patterns during the Holocene and their potential impacts on the local environments.

Further north of Florisbad, the Rietvlei Dam pollen record (Fig. 2) indicates contrasting Holocene climatic dynamics. This record reflects slightly drier conditions, ca. 8500 BP, and this represents the driest phase within the sequence. The mid-Holocene witnessed moist sub-humid conditions ca. 7000 BP, and after ca. 3000 BP moist conditions with a predominance of open grassland (Scott & Vogel 1983). Palynological investigations from the Moreletta Stream, near Pretoria (Fig. 2), align with the pollen data derived from Rietvlei Dam. These

investigations corroborate an early Holocene dominated by open, drier vegetation. Subsequently, the mid-Holocene record showed warm and wetter conditions and ca. 1000 BP conditions appear moist (Scott 1984). However, the absence of a well-detailed pollen sequence and radiocarbon data from the two sites between 5000 and 1000 BP limits a comprehensive comparison with other regional sites, and robust palaeoenvironmental reconstruction for the area during this period.

In the Savanna Biome, a detailed understanding of Holocene vegetation and palaeoenvironmental changes has been facilitated by recent interpretations of pollen sequences from Tswaing Crater and Wonderkrater (Scott *et al.* 2003; Kristen *et al.* 2010; Metwally *et al.* 2014; Scott 2016). The pollen and charcoal data obtained from Tswaing Crater (Fig. 2) suggest drier conditions ca. 9400-7200 BP, warm and humid conditions ca. 7200-3750 BP and warm subhumid woodland conditions during the late Holocene (ca. 3750-1800 BP) (Metwally *et al.* 2014). These data align with biomarker and stable carbon isotope analyses at Tswaing Crater, where the conditions ca. 10,000-7500 BP became predominantly arid, followed by a period of increased humidity ca. 7500-5500 BP (Kristen *et al.* 2010; Schmidt *et al.* 2014).

For the Wonderkrater sequence (Fig. 2), pollen data by Scott *et al.* (2003, 2008) show correlations with the interpreted relatively dry savanna conditions for the region during the early Holocene (Kristen *et al.* 2010; Metwally *et al.* 2014). However, this contrasts with the suggested relatively moist conditions by Chase *et al.* (2010), Truc *et al.* (2013) and Chevalier and Chase (2015) for the same period. While a relatively wetter condition was suggested during the late Holocene (4000 BP–present) (Scott & Thackeray 1987; Scott *et al.* 2008), a recent study proposed relatively dry conditions based on probability density functions (pdf)

derived from the analysis of fossil pollen data (Truc *et al.* 2013). The apparent disparities in moisture indications generated by different methodological approaches emphasise the need for additional independent records to facilitate more consistent and reliable interpretations in palaeoenvironmental reconstruction. The integration of multiple interpretive methods, enhanced by a broader and more diverse dataset, can aid accurate palaeoclimatic reconstruction and its impact on the vegetation dynamics during the Holocene.

The stalagmites data at Cold Air Cave in the Makapansgat valley (Fig. 2) accord with the Tswaing and Wonderkrater pollen records, indicating generally warm and dry conditions ca. 10,000-6000 BP, but cool and dry conditions ca. 6000-3000 BP and warm and wet conditions ca. 3000 BP-present (Tyson *et al.* 2000; Holmgren *et al.* 2003). This is also evidenced at nearby sites such as Scot's Farm and Tate Vondo (Fig. 2), showing similar conditions though with subtle temporal variations (Scott 1982a, 1987).

Further to the east, records from the coastal region of KwaZulu-Natal reflect slightly varying palaeoenvironmental conditions during the Holocene. Palynological and geochemical analyses suggested relatively cool/warm and moist conditions at Mfabeni peatland (Fig. 2) ca. 10,000-7000 BP and cool and dry conditions during ca. 7000-3000 BP and ca. 3000 BP-present (Finch & Hill 2008; Baker *et al.* 2014, 2017; Miller *et al.* 2019, Fietz *et al.* 2023). However, Baker *et al.* 2014 suggested warm conditions at Mfabeni for the late Holocene due to the continuous decrease of $\delta^{15}N$ and the positive $\delta^{13}C$, which are interpreted to indicate waterlogged conditions. These data contrast with the pollen records from Lake Eteza and Lake Sibaya (Fig. 2), where a shift from humid to drier grassy environments was recorded at Lake Eteza ca. 10,200-6800 BP. Meanwhile, both sites indicate warm and humid conditions ca. 7100-3600 BP. From ca. 3600 BP to the present, drier conditions were recorded at Lake

Eteza, while cool and moist conditions were recorded at Lake Sibaya (Neumann *et al.* 2008, 2010). The palaeoenvironmental data from these sites corroborate the extreme climatic fluctuations present during the Holocene at both local and regional scales.

Generally, Chevalier & Chase (2015) proposed a dynamic and variable climate for the late Holocene in South Africa. They suggested that the central-eastern region experienced relatively drier conditions, while the northern areas exhibited relatively moist and cool conditions during the late Holocene. For instance, carbon isotope studies at Pafuri (Fig. 2) recorded the driest period in the northeastern region during the Little Ice Age (AD 1635, AD 1695 and AD 1805) and the wettest period during the Medieval Warm Period (AD 1075) (Woodborne *et al.* 2015). A similar record at Mapungubwe (Fig. 2) accounted for the same climatic variations, though with localised effects (Woodborne *et al.* 2016). Conversely, phytolith studies at Mashishing (formerly Lydenburg), Mpumalanga, indicated a moderate to dry environment ca. AD 300–1350 and increasingly mesic conditions ca. AD 1350–present (Sjöström *et al*. 2017). Further studies in the Shashe-Limpopo River Basin using stable nitrogen isotopes identified wetter conditions until AD 1450, contradicting the drier conditions earlier suggested by Huffman (1996) based on external palaeoenvironmental data (Smith *et al.* 2007). Ekblom *et al.* (2011) indicated that expanding agricultural activities ca. AD 800–950 probably occurred because of moderate to high rainfall conditions in the Limpopo Valley. In contrast, the speleothem record from Makapansgat cave (Fig. 2) indicated cool and dry conditions ca. AD 1300 (Holmgren *et al.* 2003).

The more distant pollen record from Lake Eteza reflected vegetation changes probably due to farming ca. AD 1250 and/or generally cool and dry conditions during the late Holocene (Neumann *et al.* 2010). The pollen record from Lake Sibaya indicated more humid conditions,

ca. AD 450–650, and cool and dry conditions ca. AD 1500–1700 (Neumann *et al.* 2008). The Lake Sibaya diatom record suggested that the Medieval Warm Period had above average moisture levels, whereas the Little Ice Age was generally drier. Nevertheless, the diatom data indicated that there was no uniform wetness or dryness during the Medieval Warm Period (MWP) or Little Ice Age (LIA), respectively. For instance, several episodes of increased moisture were identified at AD 220–290, AD 790–830, AD 1470–1540 and AD 1760–1860 (Stager *et al.* 2013).

These data reflect the intricacies of precipitation and temperature distribution and underscore their irregular patterns at intra- and inter-site levels. Hence, the idea that the Medieval Warm Period or Little Ice Age was uniformly wet or dry should be treated with caution. It is, therefore, imperative to rely on more extensive and well-dated sequences of high-resolution proxies (e.g., pollen, phytoliths, isotopes, charcoal) comprising the MWP and LIA for better and accurate interpretations to refine our understanding of these climatic events (Scott *et al.* 2012). This underscores the complexity of past climatic changes and further emphasises the need for a nuanced approach in palaeoenvironmental studies.

### *1.1.2. Archaeological Context*

The Later Stone Age and Farming Communities sequences represent a significant period in the history of human occupation during the Holocene (Stynder *et al.* 2007; Stynder 2009; Villa *et al.* 2012; Lombard *et al.* 2012, 2022; Antonites & Antonites 2014; Bader *et al.* 2020; Olatoyan *et al.* 2022). In South Africa, defining and setting the Later Stone Age (LSA) time boundaries has been a somewhat problematic and challenging task, mostly due to controversial dates and variations in characteristic assemblages.

The Later Stone Age in South Africa is characterised by various lithic and other artefact assemblages that span approximately the last 40,000 years. The presence of hafted microlithic tools, bows and arrows, bored stones, fishing tools, shell beads, and engraved decorations on bones and wood marks these technocomplexes. Polished stone tools, such as awls and arrowheads, are also characteristic (Wadley 1993; Deacon & Deacon 1999; Lombard *et al.* 2012; Villa *et al.* 2012). While providing a comprehensive discussion of the classification criteria and characteristic assemblages of the LSA is beyond the scope of this thesis, Lombard *et al.* (2012) have offered a summary of the distinct LSA technocomplexes and their chronologies. These complexes include the early LSA (40-18ka), Robberg (18-12ka), Oakhurst (12-7ka), Wilton (8-4ka), final LSA (4-0.1ka), and ceramic final LSA (<2ka). Notably, this classification demonstrates that only the Oakhurst to ceramic final LSA complexes span the Holocene sequence (Lombard *et al.* 2012, 2022).

The Oakhurst complex, dated to approximately 12,000 to 7,000 years ago, is distinguished by the presence of scrapers, adzes, and polished bone tools with few or no microliths. Notable Oakhurst sites include the Bushman Rock Shelter in Mpumalanga (Fig. 2), dated to 9940±80 BP (Sampson 1974), Ha Makotoko, and Ntloana Tsoana in Lesotho (Fig. 2), dated to 9970±90 and 9690±120 respectively (Mitchell 1993; Mitchell & Arthur 2010), as well as Sehonghong in Lesotho (Fig. 2), dated to 9740±140 (Mitchell 1996). The Wilton complex, dating from approximately 8000 to 4000 years ago, is characterised by backed microliths, scrapers, ochre, beads, bone, shell, and wooden items.

Table 1: Summary of selected palaeoenvironmental studies in the summer rainfall region with inferred palaeoclimatic conditions.

| Proxy(ies) | Locations (s) | Biome | Ca. 11,700-8000 BP (early Holocene) | 8000-4000 BP (middle Holocene) | 4000 BP- present (late Holocene) | Reference(s) |
|---|---|---|---|---|---|---|
| **Phytolith** | Verloren Valei, Versailles and Graskop | Grassland | Cool and dry | Warm and wet | Cool and dry/warm and wet | Breman *et al.* 2019 |
| **Phytolith** | Mashishing Fen | Grassland | - | - | Dry/warm and wet | Sjöström *et al.* 2017 |
| **Pollen, charcoal, mineral magnetics** | Braamhoek wetland | Grassland | Wet | Dry | Wet | Norström *et al.* 2014 |
| **Phytoliths, diatom** | Braamhoek wetland | Grassland | Wet | Dry | Wet | Finné *et al.* 2010 |
| **Pollen** | Florisbad | Grassland | - | Warm and dry | Wet/dry | Scott & Nyakale 2002 |
| **Pollen** | Mahwaqa | Grassland | Wet | Dry | Wet | Neumann *et al.* 2014 |
| **Pollen** | Clarens | Grassland | Warm and dry | - | Wet | Scott 1989 |
| **Pollen** | Rietvlei Dam | Grassland | Dry | Wet | Wet | Scott & Vogel 1983 |
| **Pollen** | Moreletta Stream | Grassland | Dry | Warm and wet | Wet | Scott 1984 |
| **Pollen, charcoal** | Tswaing crater | Savanna | Dry | Warm and wet | Warm and Wet | Metwally *et al.* 2014 |
| **Biomarkers, stable carbon isotope** | Tswaing crater | Savanna | Dry | Warm and wet | - | Kristen *et al.* 2010; Schmidt *et al.* 2014 |
| **Pollen** | Wonderkrater | Savanna | Dry | Wet | Wet | Scott & Thackeray 1987; Scott *et al.* 2003, 2008 |
| **Probability density function of fossil pollen** | Wonderkrater | Savanna | Wet | Dry | Dry | Chase *et al.* 2010; Truc *et al.* 2013; Chevalier & Chase 2015 |
| **Stalagmites** | Cold Air Cave ( Makapansgat valley) | Savanna | Warm and dry | Cool and dry | Warm and wet | Tyson *et al.* 2000; Holmgren *et al.* 2003 |
| **Pollen, geochemical** | Mfabeni peatland | Indian Ocean Coastal Belt | Cool/warm and wet | Cool and dry | Cool and dry | Finch & Hill 2008; Miller *et al.* 2019; Fietz *et al.* 2023 |
| **Pollen, geochemical** | Mfabeni peatland | Indian Ocean Coastal Belt | Cool/warm and wet | Cool and dry | Warm and wet | Baker *et al.* 2014 |
| **Pollen** | Lake Eteza | Indian Ocean Coastal Belt | Dry | Warm and wet | Dry | Neumann *et al.* 2010 |
| **Pollen** | Lake Sibaya | Indian Ocean Coastal Belt | - | Warm and wet | Cool and wet | Neumann *et al.* 2008 |

Notable Wilton sites include Sehonghong in Lesotho, dated to ca. 5950±70 BP (Mitchell 1996), Tloutle (Fig. 2), dated to ca. 7230±80 BP (Mitchell 1993), and Tshisiku Shelter in Limpopo (Fig. 2), dated to ca. 5440±60 BP (van Doornum 2007). The final LSA, encompassing the period from around 4000 to 100 years ago, is marked by large flakes, scrapers, blades, bladelets, worked bones, beads, ochre, backed tools, and adzes. The final LSA at Tshisiku Shelter in the Limpopo savanna (Fig. 2) dates to 2960±60 BP (van Doornum 2007). In summary, the LSA in South Africa presents a diverse and intricate picture of cultural and technological development, comprising various technocomplexes across different chronological periods. Understanding these complexities and their environmental contexts is essential for gaining deeper insights into the dynamic societies that occupied the region.

The archaeological sequence for the last 2000 years has been clarified in previous studies suggesting that the first farmers arrived in southern Africa ca. 2000 years ago. In South Africa, the early farming sites are relatively small sites (e.g., ca. 6–8 ha) with no stone walls (Maggs & Ward 1984; Maggs & Whitelaw 1991; Smith 1992; Huffman 1996; Mitchell 1996; Mitchell & Whitelaw 2005; Lander & Russell 2018). Crops associated with the early farming communities include pearl millet (*Cenchrus americanus*, syn. *Pennisetum glaucum*), sorghum (*Sorghum bicolor*), and cowpea (*Vigna unguiculata*) were introduced into South Africa from other regions of Africa, whereas maize (*Zea mays*) is a recent introduction from the North American coast (Marshall & Hildebrand 2002; Mitchell 2002; Antonites & Antonites 2014; Crowther *et al.* 2018). Remains associated with these farmers, such as metal objects, slag, ceramics, and animal bones (cattle, sheep/goat) have been recovered from several sites in my study area (e.g., Evers 1974a, 1974b, 1977a, 1977b, 1980, 1982; Whitelaw 1996).

The earliest archaeological sites providing evidence of early farming in South Africa contain Silver Leaves/Matola pottery (fluted bowls and bevelled jar rims) belonging to the Kwale Branch of the Urewe tradition (Huffman 1989; Maggs & Whitelaw 1991; Huffman 1996; Klapwijk & Huffman 1996). The earliest records of Silver Leaves pottery identified at Silver Leaves near Tzaneen northwest of Mashishing (formerly Lydenburg) (Fig. 2) dated between AD 250 and 420 (Klapwijk & Huffman 1996). The dates from Silver Leaves are slightly later than the earliest dates from Mozambique, which are AD 140 ± 50 (R-1327) for Matola and A.D. 175 ±85 (St-9836) for the University Campus (Maggs & Whitelaw 1991). The earliest dates obtained from the Lydenburg Heads Site (Fig. 2), probably associated with Mzonjani pottery that belong to the second facies of the Urewe tradition, range between the 6th and 8th century AD (Inskeep & Maggs 1975; Evers 1982; Whitelaw 1996).

Often, the early farming sites are situated in areas with viable agricultural soils and favourable climate. Huffman (1996) proposed that the site locations provide direct evidence of past climates. He further argued that farmers chose specific habitats with favourable local climate that facilitated successful subsistence activities and settlement. These, often untested, correlations between climate change and failure or success of subsistence farming are assumed to be associated with large-scale climatic phases, namely the Medieval Warm Period (AD 900–1300) and the Little Ice Age cold period (AD 1300–1850) (Tyson & Lindesay 1992; Brook *et al.* 1997; Tyson *et al.* 2000; Holmgren *et al.* 2003; Stager *et al.* 2013; Weldeab *et al.* 2013; Zinke *et al.* 2014; Hopper *et al.* 2018). The assumptions are a result of limited-local palaeoenvironmental records largely due to scarcity of suitable archives, poor dating, low temporal resolutions and differential proxy preservation (Smith 2005; Scott *et al.* 2012; Fitchett *et al.* 2017b).

The Early and Middle Farming Communities occupations (ca. AD 900–1300) overlap in northeastern Africa, with few exclusively Middle Farming Community sites; exceptions include the Eiland Salt Works (Fig. 2) (Evers 1975) and Klingbiel (Evers & Hammond-Tooke 1986). These sites are contemporaneous with the Shashe-Limpopo Confluence Area sites.

Early Later Farming Community sites are similar in size to Early Farming Community sites. The Later Farming Community sites dating from the 15th to the mid-19th century are much larger (ca. 22–67 ha) with stonewalling components. These sites include the Ndebele capitals KwaMaza, Esikhunjini and Erloweni (Figs 1&2) (Schoeman 1997, 1998a, 1998b) and the extensive stonewalling sites of Bokoni located between Ohrigstad in the North, via Lydenburg and Machadodorp, to Carolina in the South (Collett 1979, 1982; Delius *et al.* 2012; Birin *et al.* 2021). It is likely that there was interaction between these farming communities and the hunter-gatherers already living in the region. This is evidenced by Farmer Community material culture (e.g., pottery) present in LSA contexts shelters and caves such as Heuningneskrans (Fig. 2) (Porraz & Val 2019), Border Cave (Fig. 2) (Backwell *et al.* 2022), Welgelegen (Fig. 2) (Schoonraad & Beaumont 1971), Bushman Rock Shelter (Figs 1&2) (Porraz *et al.* 2015), Honingklip (Figs 1&2) (Korsman & Plug 1994) and Iron Pig Shelter (Figs 1&2) (Bader *et al.* 2020).

## 1.2. OVERVIEW OF THESIS

In this thesis, I explore the use of microfossils (pollen, spores, microcharcoal) recovered from sediments at Mashishing Fen, Mpumalanga, northeastern South Africa (Figs 1& 2), for the palaeoenvironmental reconstruction of vegetation landscapes in the region, over the last 11,700 years. Additionally, I use a synthesis of existing archaeobotanical data to assess the pattern of

vegetation changes during the first millennium CE, and modern pollen and phytolith samples to understand the relationships between their modern assemblages in surface soils and contemporary source vegetation.

## 1.3. RATIONALE AND RESEARCH PROBLEM

Some researchers have posited a connection between widespread flake production ca. 12,000 - 7000 BP and the expansion of hunter-gatherer societies associated with the Oakhurst technocomplex ca. 11,900-10,000 BP. This linkage has been attributed to environmental influences (Wadley 1993; Chase *et al.* 2018). Furthermore, Deacon (1984) and Mitchell (2005) have proposed that the transition from the Robberg to Albany technocomplexes occurred during the early stages of the Late Glacial Climate amelioration. This transition is marked by shifts in artefact assemblages, reflecting the possible ecological challenges the LSA communities faced and their corresponding adaptations. However, it is important to note that the timing and extent of moisture conditions during this period can vary significantly across different geographical regions (Smith 2005). Additionally, it is often argued that the observed patterns in palaeoenvironmental records, such as a decline in forest areas coupled with an increase in open-land indicators, can be attributed to climate change and/or anthropogenic activities (Li *et al.* 2008; Scott *et al.* 2003; Finch & Hill 2008; Breman *et al.* 2011; Hahn *et al.* 2021). It is, therefore, imperative to undertake further research to provide additional high-resolution data with well-established chronologies to obtain independent records essential for reconstructing the long-term dynamics of human-environment relationships. Also, these independent records will provide specific insights across various spatial and temporal contexts to account for the inherent variability at different periods and regions.

Since the early 20th century, extensive research has focused on the archaeology of the Early to Later Farming Communities (AD 250-1900) in South Africa. (e.g., Evers 1974a, 1974b, 1977a, 1977b, 1980; Klapwijk 1974; Whitelaw 1991; Klapwijk & Huffman 1996; Mitchell & Whitelaw 2005; Delius *et al.* 2012; Antonites & Antonites 2014; Antonites *et al.* 2014; Jordaan 2017; Schoeman 2020). The few archaeological sites studied in northeastern South Africa have yielded key information on human settlement and architectural patterns (e.g., van Hoepen1939; Marker & Evers 1976; Maggs 1995; Coetzee 2005), the identity of the people (Schoeman 1998a; Huffman 2004; Delius & Schoeman 2008), site distribution patterns and preferred settlement locations (Maggs 2008; Delius *et al.* 2012), and trade (Evers 1974a).

In addition, previous studies from northeastern South Africa recorded the presence of farmers in the region and significant, albeit not abundant, evidence of cultivation. These studies include the recovery of potsherds with seed impressions of domesticated *Cenchrus americanus* (pearl millet) from the Silver Leaves site (Klapwijk 1974; Klapwijk & Huffman 1996), carbonised seeds of *Sorghum* sp. (sorghum) and *Vigna* sp. (cowpea) at Badfontein/Khutwaneng (Bokoni capital) (Figs 1&2) (Collett 1982), carbonised maize (*Zea mays*) stalks at Esikhunjini (Figs 1&2), (Ndebele capital) Mpumalanga (Schoeman 1998b), and domestic faunal remains (e.g., *Bos taurus* [cattle]) at Kruger National Park (Meyer 1986; Plug 1988; Maggs & Whitelaw 1991).

The archaeological sequence in the northeastern South Africa has been clarified, but relatively few are well dated, specifically palaeoenvironmental studies using pollen, spores, phytoliths and microcharcoal, are available for this region. Such studies could indicate the changes and/or shifts in vegetation composition, as well as the environmental conditions that prevailed during the periods of initial settlement by Early Farmers, and the development of a terrace-based

agricultural system by Later Farming Communities (Breman *et al.* 2011, 2019; Sjöström *et al.* 2017). Hence, untested correlations between subsistence patterns and environmental changes are assumed, citing the large-scale climatic processes/events (e.g., Medieval Warm Period, Little Ice Age) to explain the subsistence changes on a broader scale in the region (see Tyson *et al.* 2000; Scott *et al.* 2012; Fitchett *et al.* 2017b).

Also, previous research reconstructing vegetation changes, particularly during the late Holocene in southern Africa, often argues that these changes are primarily due to climate change (Scott 1999; Scott *et al.* 2003, 2012; Ekblom 2008; Chevalier & Chase 2016; compare Dubois *et al.* 2018). This argument usually precludes the possible impact of the beginning and expansion of specialist hunting/gathering, pastoralism, and farming. More often, palaeoenvironmental research tends to be biased towards reconstructing climatic fluctuations in correlation with vegetation changes while giving less attention to potential anthropogenic impact. Meanwhile, some of the pollen taxa utilised as indicators of climatic changes could also indicate anthropogenic disturbances, particularly in known archaeological contexts (see Olatoyan *et al.* 2022 for discussion).

Furthermore, differential pollen preservation, production, dispersal, and depositional environments hinder or facilitate their recovery and interpretation in palaeoenvironmental studies (Bryant & Holloway 1983; Bell & Fletcher 2016; Morales-Molino *et al.* 2020). Hence, a better understanding of the relationship between fossil pollen in soils and vegetation landscapes and their ecological implications in the region is needed. Consequently, to improve the interpretation of fossil pollen spectra and the reconstruction of past vegetation changes, there is a need to study modern pollen assemblages from surface sediments to determine how accurately they reflect the

contemporary source vegetation (see Chen *et al.* 2017; Huang *et al.* 2018; Julier *et al.* 2018; Hill & Finch 2021).

## 1.4. RESEARCH QUESTION AND AIMS

The research question is whether pollen, spores and microcharcoal can be used to reconstruct and distinguish between anthropogenic and climatic impacts on the vegetation landscapes of Mpumalanga, northeastern South Africa, during the Holocene. The aims of the thesis are to:

- Assess the relationship between climate, human activities, and vegetation in southernAfrica within the first millennium AD, using published archaeobotanical and archaeological evidence,
- Examine the correlation between modern pollen and phytoliths and the contemporary source vegetation around Mashishing Fen in the Gustav Klingbiel Nature Reserve, Mpumalanga, northeastern South Africa,
- Document the pollen microphotographs for Gustav Klingbiel Nature Reserve to extend reference collections in northeastern South Africa,
- Reconstruct the vegetation history and chronology of the Mashishing Fen region, using pollen, spores and microcharcoal records from core sediment records.

## 1.5. THESIS OUTLINE

This thesis comprises three papers, two published, one in preparation, an introduction, a chapter on materials and methods, and a chapter that synthesises and further expands on the publications. The published and in preparation papers are reproduced in their original form as chapters, and

each paper is introduced by a contents list. My PhD research and the papers incorporated a multidisciplinary approach: botanists helped with the identification of plant samples collected during the botanical survey, a phytolith analyst contributed valuable phytolith data, and my supervisors, with experience in archaeological, palynological and archaeobotanical research, supervised the project.

A summary of the thesis and the chapters is set out below:

Chapter One – Introduction

This chapter comprises an overview of the thesis, rationale, research problem, research question, and aims. Then follows the chapter summaries, including brief synopses of my papers and my respective contribution in each.

Chapter Two – Materials and Methods

This chapter describes the materials and methods used to investigate the anthropogenic and climatic impacts on the vegetation landscapes of Mpumalanga province, northeastern South Africa. References are made to the papers for the in-depth details of the processes.

Chapter Three – PAPER 1: Review of Archaeological and Archaeobotanical Research in Southern Africa.

This chapter synthesises published archaeological data and archaeobotanical evidence (e.g., pollen, spores, phytoliths, microcharcoal) from southern Africa to generate new insights into identifying anthropogenic impacts in palaeoenvironmental records. A co-authored paper summarises this:

Olatoyan, J.O., Neumann, F.H., Orijemie, E.A., Sievers, C., Evans, M., Mvelase, S., Hattingh, T. & Schoeman, M.H. 2022. Archaeobotanical evidence for the emergence of pastoralism and farming in southern Africa. *Acta Palaeobotanica* 62: 50–75.

The paper provides a background to archaeological and archaeobotanical research for the late Holocene in southern Africa. It presents the existing macro- and micro-archaeobotanical remains in the context of the archaeological evidence from the nine biomes of southern Africa. It then draws insights into possible anthropogenic indicators and patterns of vegetation changes. The archaeobotanical data is skewed towards the areas where research has been carried out, and the conclusions drawn are therefore tentative. More study in these areas and other underrepresented regions will contribute to a better understanding of the trends that led to the emergence and spread of pastoralism and farming in southern Africa.

*My contribution*: I provided the archaeological and archaeobotanical data from the review of published papers and thus, my contribution formed an essential basis for the writing of the paper. I began with reviewing and categorising the data according to biomes and chronology. All the figures and tables are my work. I participated in the writing of the paper alongside other authors.

Chapter Four – PAPER 2: Modern Pollen-Phytolith-Vegetation Relationships

This chapter explores the modern pollen-vegetation, phytolith-vegetation and pollen-phytolith relationships at Mashishing Fen to improve palaeoenvironmental reconstructions. Multivariate Correspondence Analysis (CA) was used to illustrate modern pollen-phytolith assemblages can be used to identify the sampling sites' contemporary source vegetation and track the relationship between the pollen and phytolith assemblages. The results are presented in a published co-authored paper:

Olatoyan, J.O., Neumann, F.H., Orijemie, E.A., Sievers, C., Evans, M., Hattingh, T. & Schoeman, M.H. 2023. Modern pollen- and phytolith-vegetation relationships at a wetland in northeastern South Africa. *South African Journal of Botany* 161:780-796.

The paper presents a novel approach combining modern pollen and phytolith assemblages from surface sediments at Mashishing Fen, Mpumalanga, northeastern South Africa, to explore the relationships between modern pollen assemblages and contemporary source vegetation, phytolith assemblages and the contemporary source vegetation and to investigate whether the phytolith and pollen assemblages were tracking each other.

Correspondence Analysis (CA) was used to illustrate that the pollen and phytolith proxies are not tracking the same primary vegetation signals at the Mashishing Fen. The modern pollen assemblages clearly track forests and wetland vegetation components, while modern phytolith assemblages clearly track grassland vegetation. Our sample size was small, but the study nevertheless illustrated the potential of the method. Further research is called for to support the interpretations, which indicate that the differential phytolith and pollen production, preservation, and dispersal influence sediment records more than anticipated, thus supporting that exploring multi-proxies (e.g., pollen, phytoliths) provide a more accurate vegetation reconstruction. However, to fully understand the pollen-phytolith-vegetation relationships within the nine climatically and floristically different biomes of southern Africa, additional research focused on modern pollen-phytolith-vegetation is required.

*My contribution*: I participated in the herbarium specimen collection, botanical survey, and collection of surface sediments for analyses. I prepared and analysed the pollen samples and produced the pollen diagrams and pollen microphotographs. I conducted the numerical analysis

(Correspondence Analysis) on the samples and data interpretations. I participated in the writing of the paper alongside other authors.

Chapter Five – PAPER 3: Palaeoenvironmental Reconstruction of Vegetation in Mashshing, Mpumalanga

This chapter presents a background to palaeoenvironmental and archaeological studies during the Holocene (11,700 BP to present) in South Africa. It explores the palaeoenvironmental reconstruction of Holocene vegetation in the following paper:

Olatoyan, J.O., Neumann, F.H., Orijemie, E.A., Sievers, C., Evans, M., Woodborne, S., Celliers, J.P., Knight, J. & Schoeman, M.H. in prep. Holocene palaeoenvironmental reconstruction from MashishingFen, Mpumalanga, northeastern South Africa. *Review of Palaeobotany and Palynology*.

In this paper, we document the chronology and vegetation history of the region during the last 11,700 years from core sediment samples retrieved from the Mashishing Fen. The reconstruction of the vegetation landscapes using pollen, spores and microcharcoal records from the core sequences clarifies some possible differences between anthropogenic and climatic impacts on the vegetation. The proximity of the Mashishing Fen to previously dated archaeological sites (e.g., Lydenburg Heads Site, ca. 1.7 km southwest of the Mashishing Fen and Klingbeil, ca. 600 m north of the Mashishing Fen) contributes to the understanding of the palaeoecological records within archaeological context across changing environmental conditions. The pollen, spores and microcharcoal records from the Mashishing Fen provide significant insights into understanding the region's local and regional environmental changes from the Early to Late Holocene period, including the fire history. However, there is a need for further multiproxy studies (e.g., diatoms,

isotopes, phytoliths) covering the Holocene sequence to establish a more reliable and robust palaeoenvironmental history for the region.

*My contribution*: I helped Prof. Neumann and Dr Sievers to conduct the botanical survey around the site where Prof. Schoeman and Mr Ramaoka took the core. I participated in the subsampling of the 5.5 m sediments core in the GAES soils laboratory. Proxies, e.g., pollen, spores, and microcharcoal (total of 56 samples), were then extracted from sediments and analysed. I prepared, extracted and analysed the pollen samples at the Evolutionary Studies Institute (ESI) Laboratory, University of the Witwatersrand (Wits), Johannesburg. I prepared the subsamples for AMS radiocarbon dating at the iThemba Laboratory for Accelerator-Based Sciences (iThemba LABS). I produced the pollen diagrams and age-depth model. I participated in writing the paper for publication alongside my co-authors.

Chapter Six – Synthesis

This chapter discusses the research presented in the previous chapters and looks at the overall significance of the three publications. I conclude that the thesis aims have been achieved; I have demonstrated that pollen, spores and microcharcoal records are invaluable in reconstructing anthropogenic and climatic impacts on vegetation.

Chapter Seven – Conclusions and Future Research

I summarise the key findings and achievements of the research, discuss relevant questions raised during the research and provide recommendations for future research.

# CHAPTER 2: MATERIALS AND METHODS

## 2.1. INTRODUCTION

In this research, I employed multiple approaches comprising literature review and synthesis of archaeobotanical sources, botanical survey, herbarium specimen collection, surface sediment collection, numerical analysis of pollen and phytoliths data from surface sediment samples, extraction of a core from Mashishing Fen, Mpumalanga for pollen analysis and AMS radiocarbon dating.

## 2.2. LITERATURE REVIEW AND SYNTHESIS

The review of literature and synthesis of archaeobotanical data (Olatoyan *et al.* 2022, Paper 1 of this thesis) laid the foundation for this research. It comprised the critical evaluation of palynological and archaeobotanical data from existing literature (e.g., Denbow & Wilmsen 1986; Maggs & Whitelaw 1991; Smith 1992; Mitchell 1996; Barham & Jarman 2005; Mitchell & Whitelaw 2005; Neumann *et al.* 2008, 2010; Hahn *et al.* 2021; see Olatoyan *et al.* 2022 [Paper 1 of this thesis] for discussion). This was aimed at exploring the potential evidence suggesting human impacts on the vegetation of southern Africa, particularly during the first millennium CE; these may be due to pastoralism and/or farming activities. In Paper 1, Olatoyan *et al.* 2022, the authors examined published evidence and grouped sites chronologically and according to their location within the different biomes of southern Africa after Rutherford & Westfall (1994) and Mucina & Rutherford (2006). Sites comprising marine sediments (e.g., Hahn *et al.* 2021) were considered separately rather than within specific biomes, due to the diverse sources of the pollen assemblages because of river systems and

ocean currents (Scott *et al*. 2012). The authors further synthesised the reviewed archaeobotanical proxies (e.g., charred seeds, pollen, spores, microcharcoal, phytoliths) within the context of macrobotanical and archaeological data to identify possible anthropogenic indicators and similar patterns of changes in vegetation in southern Africa during the first millennium AD (see Olatoyan *et al.* 2022/Paper 1).

## 2.3. BOTANICAL SURVEY

In January 2020, a botanical survey was conducted to document the plant taxa in survey plots within the Gustav Klingbiel Nature Reserve, Mpumalanga. We designed a method that incorporated a circular survey plot with a diameter of ten metres (10 m) to document the pollen and phytolith sources surrounding the surface sample collection area at the plot's centre. A circular survey plot method allowed us to establish five-metre transects northwards, eastwards, southwards and westwards from a central point within each survey location. To ensure accuracy, an iron dropper was hammered into the ground to remain fixed at the centre, and a second dropper was connected by a five-metre measuring string to the first dropper. We then moved the second dropper to establish the five-metre transects in the north, east, south, and west directions. To determine the directions of the transects, we used a Brunton pocket transit compass while we verified the transect distances (5 m) using a meter tape. The plant taxa along each transect were recorded. Additional plant taxa growing between the transects (and not already recorded along the transects) and plants growing close to the survey plot, which appeared very common and /or of ecological significance, were recorded and/or collected and assigned taxa numbers. The vouchers were taken to the CE Moss Herbarium, Wits, to verify identified plants.

Five survey plots were designated sampling locations within the Gustav Klingbiel Nature Reserve (Fig. 3). The same survey protocol (i.e., circular survey plot method to establish five-metre transects northwards, eastwards, southwards and westwards) was used at each plot. The survey plots were selected according to their location within areas of specific and characteristic vegetation structure, with GK 1 representing Mashishing Fen vegetation, GK 2 representing grass patches within thickets, GK 3 and GK 4 representing fen and forest margins along the northeastern and eastern extents of the fen, and GK 5 representing riparian vegetation**.** The geographical locations and altitudes of the survey plots were also documented (Olatoyan *et al.* 2023/Paper 2 for results).

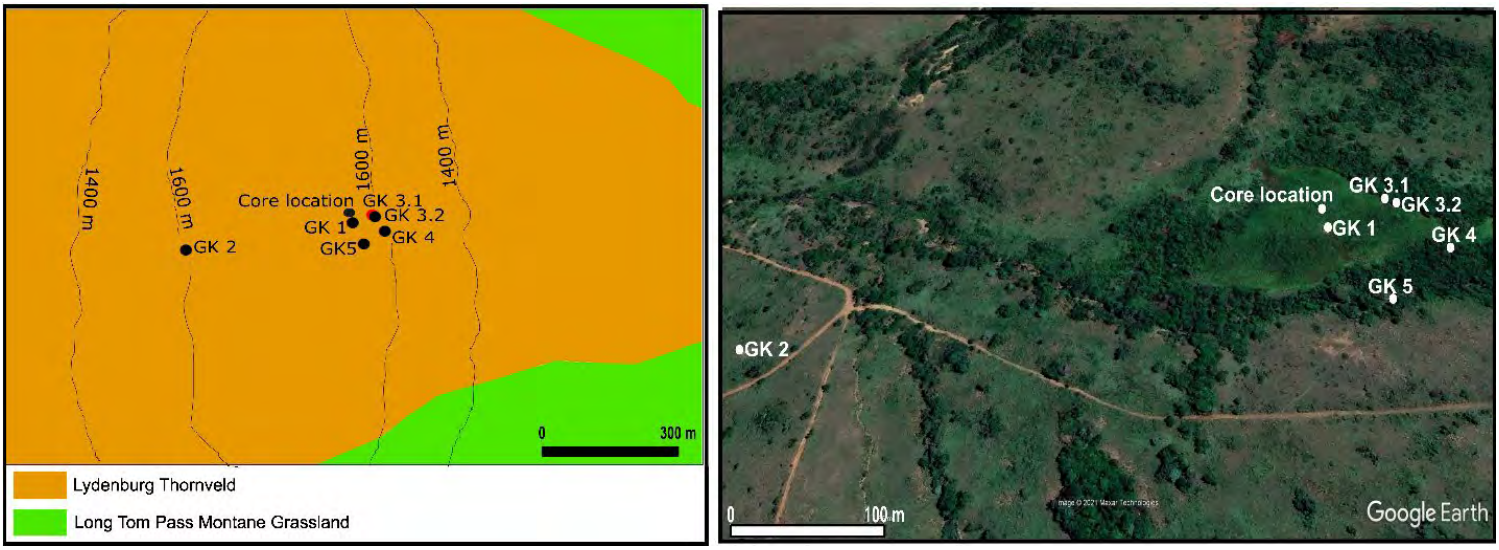


Figure 3. A Map and Google Earth satelite image of the Lydenburg Fen, showing the locations where the core and the soil samples were taken.

## 2.4. HERBARIUM SPECIMEN COLLECTION

Plant specimens were collected during the fieldwork to verify the identification of the plant taxa encountered in the survey plots at the Gustav Klingbiel Nature Reserve. The reserve authorities' authorisation was obtained before collecting the specimens of those plant taxa that

are not protected by law. The rare plant taxa protected by law were recorded but not collected. To adhere to standard botanical methodology (Fish 1999), we collected plant parts from trees, tall shrubs, low shrubs, climbers, scramblers, herbs, graminoids and horsetails that contained diagnostic features. The base, centre, and tip of fertile and sterile fern fronds were also collected. The plant taxa identified and documented in the collected vouchers were authenticated at the CE Moss Herbarium, Wits (refer to Table 1; Olatoyan *et al.* 2023/Paper 2).

## 2.5. SURFACE SEDIMENT COLLECTION

To obtain comprehensive modern pollen and phytolith spectra for each of the designated five survey plots, surface sediment samples from a 1 $m^2$ area located at the centre of each plot were collected. The surface samples comprised the top 20 mm of sediment, approximately 50 g. A 175 mm hand trowel was used to collect each sample, which was placed in a Ziploc bag (65 mm × 85 mm) and appropriately labelled. The trowel was cleaned with ethanol before each sample was collected. One surface sediment sample was collected for pollen and phytolith analyses respectively, from each plot, except for GK 3, located on the northeastern margin of the fen. Here, two surface sediment samples for pollen and two surface sediment samples for phytoliths were taken for pollen and phytolith analyses: GK 3.1, collected in the forest on the margin, and GK 3.2, collected from the fen vegetation located near a *Gunnera* plant (Fig. 3; Paper 2, Olatoyan *et al.* 2023). The geographic coordinates and elevations of the six sampling locations were recorded to accurately document their exact locations on the map (Olatoyan *et al.* 2023).

## 2.6. SEDIMENT CORING

Sediment cores were obtained from the Mashishing Fen to provide a reliable basis for reconstructing vegetation changes and a chronological sequence for the area. Exploratory coring was done at various locations to determine the deepest section of the fen (previously reported by Sjöström *et al*. 2017) before a 5.5 m long sediment core was taken using a hand-operated Watermark® Russian peat borer with a 500 mm x 50 mm chamber.

It is crucial to handle and store sediment cores carefully, to obtain accurate and reliable results from the subsequent analyses of the samples, as well as to prevent water loss, oxidation, compaction, and contamination during transport. To ensure this, each sediment sample was carefully transferred from the corner into a rigid half of a cylindrical PVC tube and wrapped with cling film (clear plastic wrap). The sediment core samples were transported to the Origins Centre at Wits and stored at a constant temperature of 16˚C. These precautions enabled the preservation of valuable information about the fen's ecological history and how it may have changed over time.

Subsampling was performed at 100 mm sampling intervals, with 10 mm slices taken for pollen and phytolith analysis, 20 mm slices for AMS radiocarbon dating, 20 mm for LOI, and 40 mm for soil analyses, resulting in a total of 56 samples. Only the pollen, charcoal and AMS data are reported in this thesis. Subsampling at regular intervals allowed the thorough examination of the sedimentary record of the cores and provided a basis for establishing chronologies using AMS radiocarbon dating. After subsampling, the samples were again stored in double Ziploc bags under refrigeration to maintain appropriate temperature and humidity conditions.

## 2.7. AMS RADIOCARBON DATING

AMS radiocarbon dating was conducted at iThemba LABS**,** Johannesburg, to establish an independent chronology for the palaeoecological data. Vials containing 1–3 g of subsampled sediments from selected depths in the core between 10–5500 mm were processed under the supervision of Dr Stephan Woodborne (iThemba LABS, Johannesburg) for the dating of bulk organic matter rather than macroplant remains (Fig. 4). This was to ensure a degree of consistency between sites with varying plant remains and to prevent the possibility of dating materials that were from a different stratum.

As a result of past (and present) fluctuations in the production of atmospheric carbon, radiocarbon dates cannot be directly equated with calendar years. This necessitates calibration, which is normally undertaken by reference to the dendrochronological sequence. To calibrate the radiocarbon dates, the OxCal 4.4 web interface and Southern Hemisphere SHCal 20 calibration curves with a 95.4% probability were used (Hogg *et al.* 2020; Bronk Ramsey 2023)**.** With the awareness that calibration can increase or decrease the likely date of an event, there was a need to exercise caution while correlating radiocarbon dates with the palaeoenvironmental sequence. Hence, the ages of each sample depth were calculated after plotting the age-depth model plotted using Bayesian modelling with the Bacon software (Olatoyan *et al*. in prep./ Paper 3; Blaauw & Christen 2011).

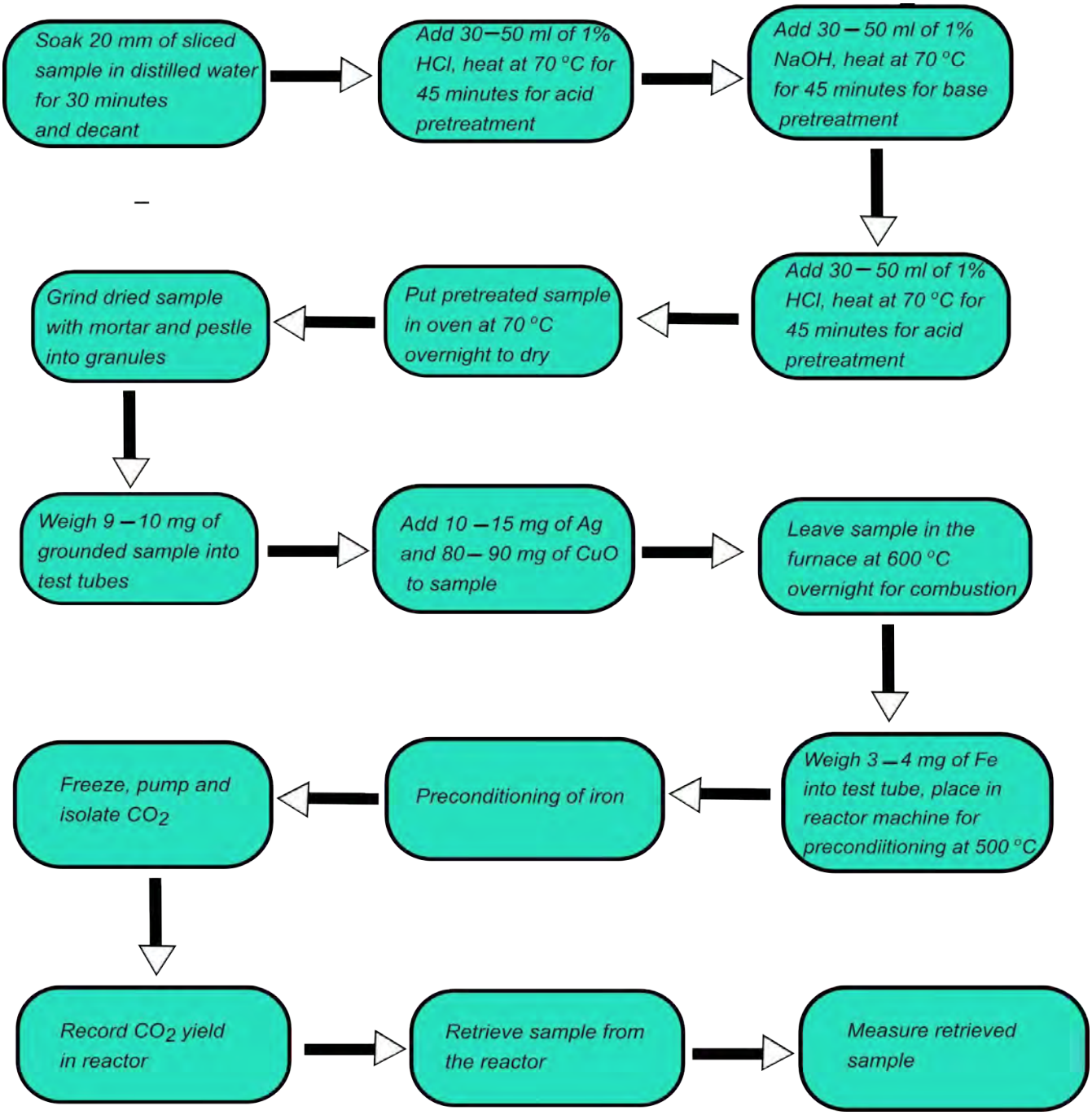


Figure 4. AMS radiocarbon dating preparation process.

## 2.8. PALYNOLOGICAL PREPARATION AND EXTRACTION

Palynological preparation and extraction were performed at the ESI Laboratory, Wits University, Johannesburg. The standard method for palynological analysis was used and adapted after Berglund & Ralska-Jasiewiczowa (1986), Faegri & Iversen (1989) and Nakagawa *et al.* (1998), which is best suited for South African sediments. About 10–30 g of the sample was treated using 10% HCl, 40% HF, 10% KOH, and then acetolyzed. This was followed by separating the residue by heavy liquid mineral separation using $ZnCl_2$/HCl with specific gravity 2.0. To remove particles greater than 250 µm and particles less than 10 µm, the 250 µm and 10 µm mesh screens were used respectively to sieve the processed samples and final residues to facilitate pollen concentration prior to mounting. Initially, pollen residues were mounted in glycerine jelly on two microscopy glass slides and, heated to dry (40-50$^{o}$C) and evenly spread on the heating plate to ensure that the standard minimum number of pollen grains from terrestrial plants (250–300) was counted even for low pollen-producing levels. However, more than two and up to ten pollen slides were prepared for some sample depths with extremely low pollen counts (Fig. 5).

After the slides were prepared, pollen taxa were identified according to their exine sculpturing and morphology (Faegri & Iversen 1989; Bradley 1999)**.** The slides were traversed horizontally and vertically using an Olympus BX51 light microscope at a magnification of 400x and 1000x in oil immersion (Fig. 5). A minimum of 150 terrestrial pollen grains were counted for each subsample. The identification of palynomorphs was based on published references (e.g., Coetzee & van Zinderen Bakker 1952; Van Geel 1978; Scott 1982b; Cugny *et al.* 2010; Gelorini *et al.* 2011; Gosling *et al.* 2013), modern pollen reference collections and photographs at the ESI and the current pollen sample we collected from the study site to extend the existing pollen

reference collections at ESI). The pollen diagrams and zonation were created using the CONISS (Constrained Incremental Sum-of-Squares) program for stratigraphically constrained cluster analysis within the TILIA softwareTILIA 2.1.1 (Grimm 2011).

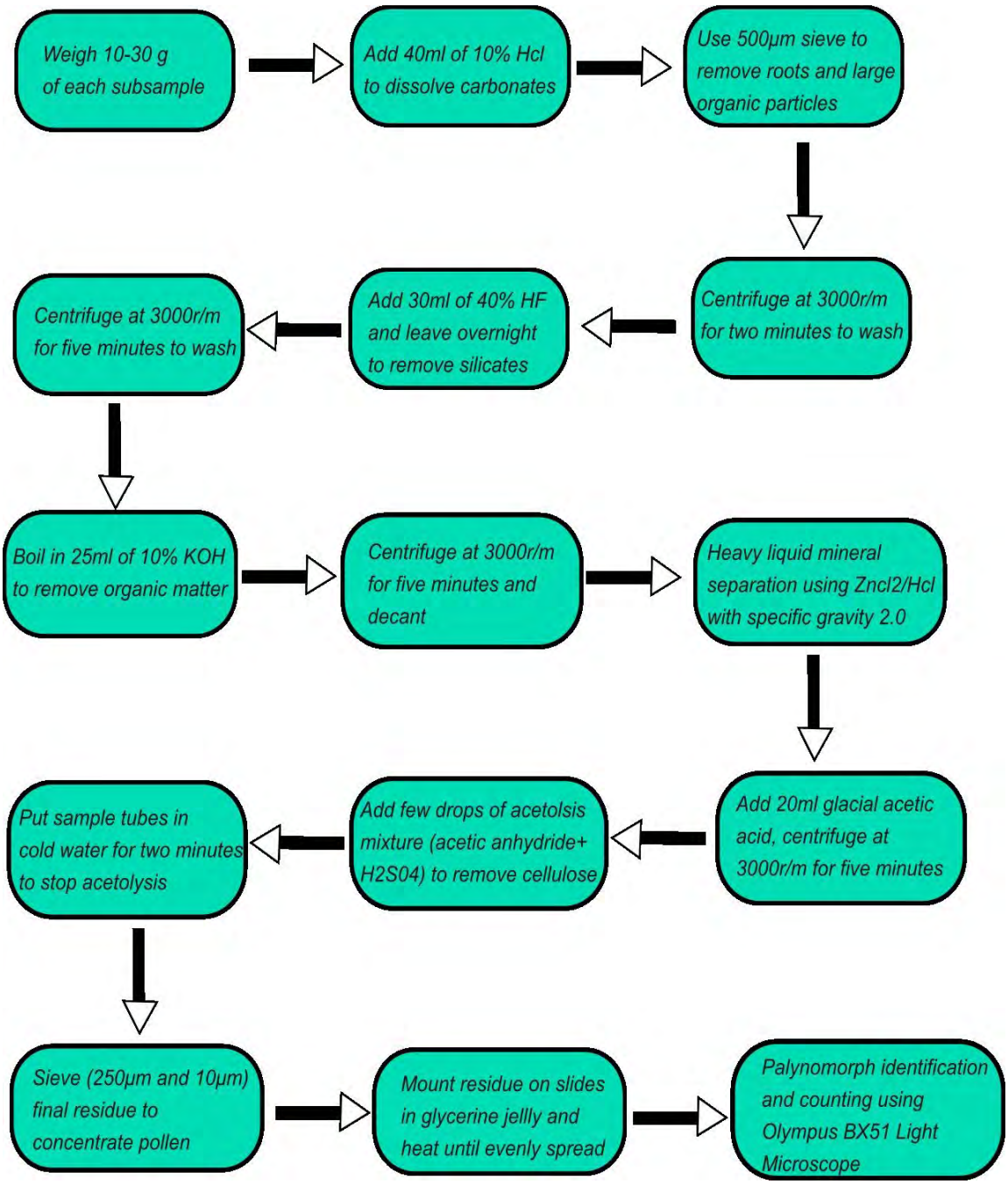

Figure 5: Palynological preparation and extraction process.

## 2.9. NUMERICAL ANALYSIS

Numerical analysis is an essential tool used in environmental research to explore the underlying patterns and relationships within collected data (Birks & Gordon 1984). It facilitates an objective analysis and interpretation of data, which then allows the investigation of the relationships between variables such as proxies, precipitation, temperature and vegetation cover. Correspondence analysis was used because it is appropriate to quantitatively evaluate and visualise the relationship between proxies (e.g., pollen grains and phytoliths), vegetation and environmental variables. Correspondence Analysis is invaluable for identifying and graphically representing key trends within modern assemblages and vegetation data through a low-dimensional representation of complex multivariate data (Court-Picon *et al.* 2005, 2006).

Correspondence Analysis (CA) was conducted on the proxy dataset using the R software to explore the general pattern between modern assemblages and the vegetation data and the interrelationships between the two proxy data sets (pollen, phytoliths). Also, the CA was used to evaluate the significance of the variations observed in both proxy datasets and to determine whether it is possible to distinguish the designated vegetation structure (survey plots) based on the modern pollen and phytolith assemblages. Lastly, the CA was useful to identify the influence of the different environmental variables on the representation of vegetation and modern assemblages.

# CHAPTER 3: PUBLISHED PAPER 1

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Thesis pages 38-65. Page numbers below refer to those in the published paper.


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# Archaeobotanical evidence for the emergence of pastoralism and farming in southern Africa

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ABSTRACT. Several models which remain equivocal and controversial cite migration and/or diffusion for the emergence and spread of pastoralism and farming in southern Africa during the first millennium AD. A synthesis of archaeobotanical proxies (e.g., palynology, phytoliths, anthracology) consistent with existing archaeobotanical and archaeological data leads to new insights into anthropogenic impacts in palaeorecords. Harnessing such archaeobotanical evidence is viable for tracing the spread of pastoralism and farming in the first millennium AD because the impact of anthropogenic practices is likely to result in distinct patterns of vegetation change.

We assess this impact through the synthesis of published archaeobotanical evidence of pastoralism and farming, as well as vegetation changes in southern Africa during the first millennium AD. It has been argued that the decline of forests during the first millennium AD in southern Africa predominantly relates to climate change. This argument often precludes anthropogenic effects on vegetation. Our reassessment of the relationship between vegetation, climate, and human activities in southern Africa reveals evidence of human impact during the same period. We also highlight gaps in the current knowledge of early pastoralism and farming and potential future research directions. We hypothesize that the pattern exhibited by the decline of forest tree pollen, coupled with the increase of open-land indicators, the occurrence of pioneer trees, as well as the spores of coprophilous fungi, and possible changes in the fire regime are reflective of, and consistent with, anthropogenic activities of pre-European pastoralists and farmers.

KEYWORDS: pastoralism, farming, southern Africa, anthropogenic impact, archaeobotany, *Tribulus* spp.

## INTRODUCTION

What impact did the introduction and spread of pastoralism and farming have on vegetation in southern Africa? Is it possible to distinguish such impact from the effect of climate change, through palynological research, complementary evidence and proxies such as archaeological, anthracological and/or phytolith data? Farming encompasses crop cultivation and the associated practices (e.g., slash-and-burn) while pastoralism comprises livestock herding/grazing.

In southern Africa, there are both contrasting and complementary models for the beginning and expansion of pastoralism (e.g., Elphick, 1977, 1985; Smith, 2008, 2017; Sadr, 2008, 2015,

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2019; Jerardino et al., 2014; Orton, 2015) and for the emergence and spread of farming (e.g., Huffman, 1982, 2007; Maggs, 1994; Phillipson, 2005; Lander and Russell, 2018). Proponents of the migration model argue that the Khoi pastoralists moved from northern Botswana/western coast of Namibia/eastern Africa into southern Africa with sheep and pottery ~2000 years ago based on archaeological (Elphick, 1985; Smith, 2008; Muigai and Hanotte, 2013; Orton et al., 2013; Pluerdeau et al., 2012), linguistic (Guldemann, 2008; Ehret, 2020) and genetic data (Henn et al., 2008; Ranciaro et al., 2014). The diffusion model proposes that pottery was independently invented by hunter-gatherers (Sadr and Sampson, 2006), and that livestock diffused among indigenous populations (Badenhorst, 2006; Prendergast, 2011; Sadr, 2014), although recent studies supporting this model suggest the interplay of a rapid cultural diffusion and population movements (Orton, 2013, 2015; Sadr, 2015, 2019).

In comparison with other parts of Africa, the relatively late emergence of farming in southern Africa during the second and third centuries AD has previously been attributed to migrations from western and eastern Africa penetrating a landscape that was previously populated by hunter-gatherers (Huffman, 1970, 1979, 1982; Phillipson, 1976; Maggs, 1980a). Recent spatial distribution studies (e.g., Sadr and Sampson, 2006; Sadr, 2008, 2015, 2019; Russell et al., 2014; Lander and Russell, 2018, 2020) have shown that pottery, cattle and sheep were present in southern Africa independent of the arrival of the so-called 'Iron Age package' and the population movements from western and eastern Africa. Furthermore, geneticists, while supporting some form of population movement (e.g., Li et al., 2014), have suggested that the demic diffusion was sex-biased (see Wood et al., 2005; Marks et al., 2015) and that the local pattern of population movement, interaction and replacement varied (Wang et al., 2020).

Direct evidence for the spread of pastoralism and farming is scarce, and proxy evidence has been used extensively. Pottery was used as a proxy for pastoralism (i.e., livestock herding) (Smith, 2008; Sadr and Sampson, 2006; Sadr, 2008), while pottery, pits, grain bins, grindstones, iron slag and iron objects were proxies for farming (i.e., crop cultivation) (Huffman, 1998). Using these proxies as evidence of pastoralism and farming remains controversial. Archaeologists such as Andah (1979, 1995), Garlake (1982) and Hall (1983, 1984) have expressed concerns about the methodological and theoretical approaches underpinning the migration model for the emergence and spread of farming in southern Africa. The linking of ceramic style to linguistic and cultural identities (Hall, 1983; Lane, 2004) and the conflation of physical attributes ('race') and culture have been of particular concern (Hall and Morris, 1983).

While the spread of people, livestock and pottery has been revisited and disentangled from the 'Iron Age package', the emergence and expansion of pastoralism and crop farming in southern Africa remain under-theorised and under-investigated. We suggest a synergy between archaeological and archaeobotanical research that integrates both types of data to provide new insights regarding pastoralism and farming practices in southern Africa.

To reassess the relationship between vegetation, climate and human activities in southern Africa, we revisit published archaeological records that give clear evidence of human occupation within the first millennium AD (e.g., Maggs, 1984; Maggs and Whitelaw, 1991; Smith, 1992; Mitchell, 1996; Mitchell and Whitelaw, 2005) and published archaeobotanical evidence (e.g., Denbow and Wilmsen, 1986; Barham and Jarman, 2005; Neumann et al., 2008, 2010; Hahn et al., 2021).

Harnessing archaeobotanical evidence is potentially viable for tracing the spread of farming and livestock herding in the first millennium AD because of the nature of first millennium AD settlements and associated practices. More often, farmers used slash-and-burn techniques to prepare fields for farming, e.g., in the coastal belt on dunes along the Indian Ocean, ~950 cal BP (~1000 AD) (Hall, 1980, 1984; MacDevette et al., 1989). Wood was also harvested and used for building, metalworking (charcoal production) (Maggs and Ward, 1984; Whitelaw, 1991) and other domestic purposes. The combination of these factors and actions is likely to have resulted in distinct patterns of vegetation change, such as forest decline and dominance of open-land indicators (e.g., Carrión et al., 2000; Breman et al., 2011; Hahn et al., 2021).

Herein, we review the archaeobotanical evidence of pastoralism and farming, as well as changes in vegetation from sites in southern Africa dating to the first millennium AD to highlight patterns, possible anthropogenic

indicators, gaps in knowledge and potential areas for further research. We hypothesize that the decline of forests (tree pollen) coupled with the increase of open-land indicators (e.g., Amaranthaceae, Asteraceae; Baxter and Davies, 1994) or pioneer trees (e.g., *Trema*; Goodale et al., 2012), within an archaeological context, can be attributed to anthropogenic activities rather than climate drivers. In addition, an increase in the spores of coprophilous fungi (e.g., *Sporormiella*, *Sordaria*; Cordova et al., 2017) during the first millennium AD could be indicative of domestic animal herds (Carrion et al., 2000).

## MATERIALS AND METHODS

### SITE SELECTION AND DATING

We consider archaeobotanical and palynological data from previously published sites (Fig. 1, Table 1) indicating the direct presence of farming and/or possible anthropogenic impacts on the vegetation in southern Africa due to pastoralism and/or farming within the first millennium AD. The second millennium AD is excluded because it is not relevant to the beginnings of pastoralism and farming in the region.

Evidence from individual sites is chronologically examined and grouped according to the classification of biomes of southern Africa (Rutherford and Westfall, 1994; Mucina and Rutherford, 2006). Although the phytogeographical map provided by Mucina and Rutherford (2006) does not include Mozambique, coastal sites from southern Mozambique (e.g., Ekblom, 2008; Ekblom et al., 2014a) are grouped under the Indian Ocean Coastal Belt Biome since the vegetation in the region is similar to the vegetation in adjacent eastern South Africa. Marine sediment cores (e.g., Shi et al., 1998; Hahn et al., 2021) are excluded from the biome classifications and grouped separately due to the possibility of mixing of pollen assemblages from diverse biome sources via the input of extensive river systems like the Limpopo or Orange River and sea currents (Agulhas current, Benguela current) (Scott et al., 2012). This grouping helps to present a refined view of the proxies and direct evidence in each biome and prevents the conflation of patterns in the data considering the great ecological diversity of the region. Radiocarbon dates for key records (see Table 1) are based on the calibrated date range using the OxCal 4.4 web interface and the SHCal 20 calibration curve with a probability of 95.4 % (Hogg et al., 2013; Bronk Ramsey, 2017).

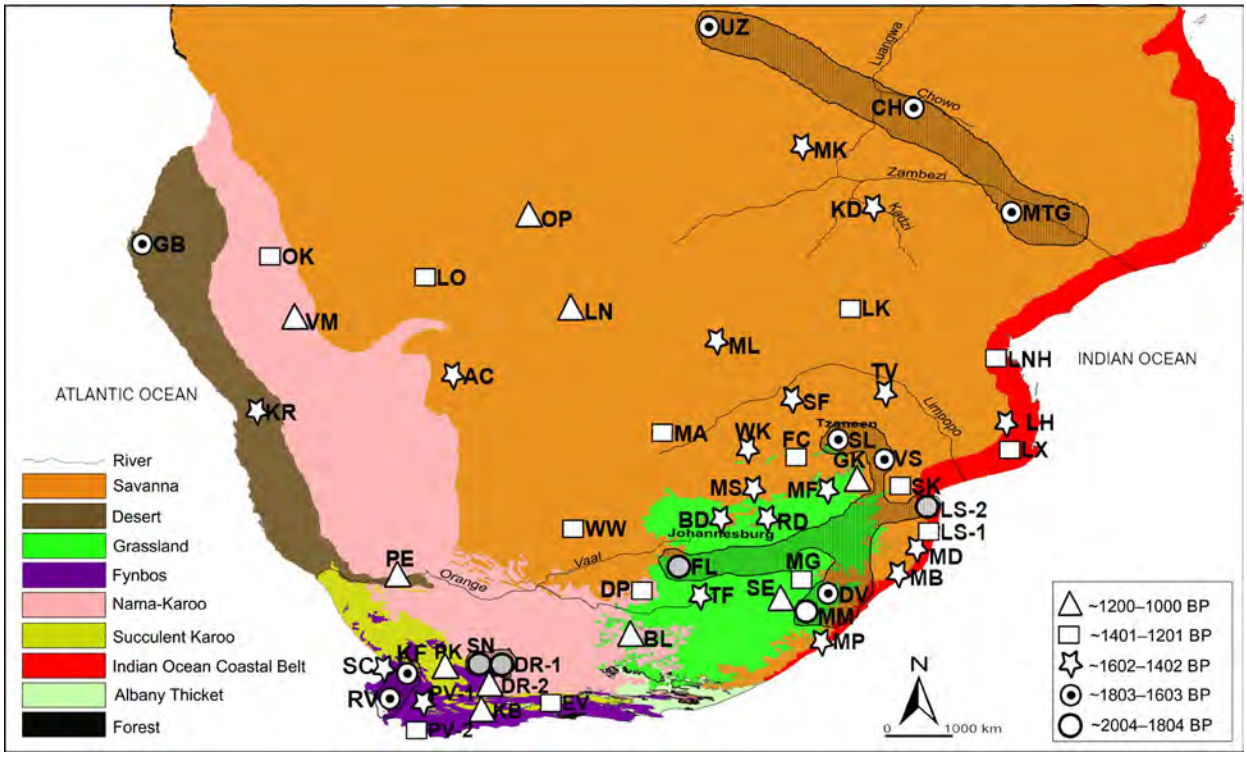


**Figure 1**. Map of southern Africa showing sites discussed in text and current biomes (adapted after Mucina and Rutherford 2006). The earliest evidence of human impact in the Western Cape and summer rainfall region north and south of Limpopo are marked with hatching lines. AC – Arnhem Cave, BD – Broederstroom, BL – Blydefontein, CH – Chowo River, DP – Deelpan, DR-1 – De Rif, DR-2 – De Rif, DV – Dartmoor Vlei, EV – Eilandvlei, FC – Ficus Cave, FL – Florisbad, GB – GeoB 1023, GK – Graskop, KB – Katbakkies, KD – Kadzi, KF – Klaarfontein, KR – Kuiseb River, LH – Lake Nhaucati, LK – Leopard's Kopje, LN – Lake Ngami, LNH – Lake Nhauhache, LO – Lake Otjikoto, LS-1 – Lake Sibaya composite core, LS-2 – Lake Sibaya, LX – Lake Xiroche, MA – Magagarape, MB – Mfabeni peatland, MD – Mdlanzi swamp, MF – Mashishing Fen (Thaba Chweu Fen), MG – Magogo, MK – Mondake, ML – Maunatlala, MM – Mahwaqa Mountain, MP – Mpondoland, MS – Morelleta Stream, MTG – Mount Gorongosa, OK – Okandjombo, OP – Okavango Panhandle, PE – Pella, PK – Pakhuis Pass, PV-1 – Princessvlei (vZB), PV-2 – Princessvlei (PV11.3), RD – Rietvlei Dam, RV – Rietvlei Still Bay, SC – Spring Cave, SE – Sekhokong, SF – Scot's Farm, SK – SK 17, SL – Silver Leaves, SN – Sneeuberg, TF – Tiffindell, TV – Tate Vondo, UZ – Upper Zambezi valley, VM – Vrede hyrax midden, VS – Versailles, WK – Wonderkrater, WW – Wonderwerk Cave

**Table 1**. Evidence of micro-botanical (A) and macro-botanical (B) remains for pastoralism and farming in southern Africa during the first millennium AD

A. Micro-botanical remains

| | Biome | Site | Abbr. | Pollen, spores and charcoal evidence | Date (cal.) | References |
|---|---|---|---|---|---|---|
| South Africa | Savanna | Versailles | VS | Decline of *Podocarpus*, increased charred fragments | ~1800 BP | Breman et al., 2011 |
| | | Wonderkrater | WK | Decline of *Podocarpus*, increased open vegetation (e.g., Amaranthaceae), increased charred fragments, Poaceae, Cyperaceae | ~1500 BP | Scott, 1982a, 2002; Scott and Thackeray, 1987; Scott et al., 2003 |
| | | Tate Vondo | TV | Decline of *Podocarpus*, increased open vegetation (e.g., Asteraceae) | ~1500 BP | Scott, 1987 |
| | | Scot's Farm (Soutpansberg) | SF | Decline of *Podocarpus*, increased open vegetation (e.g., Amaranthaceae) | ~1500 BP | Scott, 1982c |
| | | Morelleta Stream | MS | Decline of *Podocarpus*, increased open vegetation (e.g., Amaranthaceae) | ~1500 BP | Scott, 1984 |
| | | Broederstroom | BD | Decline of trees (e.g., *Olea*), increased open-land indicators (e.g., Caryophyllaceae, and Amaranthaceae), increased coprophilous fungal spores (e.g., Sordariaceae) | ~1500 BP | Carrión et al., 2000 |
| | | Wonderwerk Cave | WW | Decline of *Podocarpus*, *Olea*, increased Asteraceae, Poaceae, Cyperaceae | ~1250 BP | Brook et al., 2010 |
| | Grassland | Mahwaqa Mountain | MM | Increased coprophilous fungal spores (e.g., Sordariaceae, *Coniochaeta lignaria*, *Gelasinospora)* and charred fragments | ~2000 BP | Neumann et al., 2014 |
| | | Florisbad | FL | Decline of trees, increased Amaranthaceae, Asteraceae and Poaceae | ~1950 BP | Nyakale, 1999; Scott and Nyakale, 2002 |
| | | Dartmoor Vlei | DV | Decline of *Podocarpus*, *Olea*, *Celtis*), dominance of Poaceae >40 µm, increased charred fragments | ~1600 BP | Geer, 2013 |
| | | Rietvlei Dam | RD | Decline of *Podocarpus*, increased open vegetation (e.g., Amaranthaceae) | ~1500 BP | Scott and Vogel, 1983 |
| | | Tiffindell | TF | Decline of trees, increased Poaceae, Asteraceae, Cyperaceae | ~1500 BP | Rosen et al., 1999 |
| | | Graskop | GK | Decline of *Podocarpus*, increased charred fragments | ~1000 BP | Breman et al., 2011 |
| | | Mashishing (Thaba Chweu) Fen | MF | Shift from the dominance of $C_4$ to $C_3$ vegetation | ~1600 BP–pres. (AD 400–pres.) | Sjöström et al., 2017 |
| | Indian Ocean Coastal Belt (IOCB) | Lake Sibaya | LS-2 | Decline of *Podocarpus*, increased charred fragments, Poaceae and Cyperaceae | ~1895 BP | Walther and Neumann, 2011 |
| | | Mdlanzi swamp | MD | Few trees, increased Asteraceae, larger Poaceae >40 µm, *Anthoceros*-type, *Typh*a and charred fragments | ~1450 BP | Turner and Plater, 2004 |
| | | Mfabeni peatland | MB | Decline of *Podocarpus*, increased *Morella serrata* and *Senegalia*/*Vachelli*a | ~1425 BP | Finch and Hill, 2008 |
| | | Lake Sibaya composite core | LS-1 | Decline of *Podocarpu*s, appearance of Cerealia-type pollen | ~1400 BP | Neumann et al., 2008 |
| | Nama Karoo | Deelpan | DP | Decline of trees, increased Amaranthaceae, Poaceae and Cyperaceae | ~1250 BP | Scott, 1988; Scott and Nyakale, 2002 |
| | | Blydefontein | BL | Decline of trees, increased Asteraceae, Poaceae | ~1200 BP | Scott et al., 2005 |
| | Marine Sites | Mpondoland | MP | Increased Asteraceae, Amaranthaceae, appearance of Poaceae >40 µm, increased coprophilous fungal spores (e.g., Sordariaceae, Gelasinospora) | ~1500 BP | Hahn et al., 2021 |
| | Fynbos | Sneeuberg (Cederberg) | SN | Decline of trees, increased disturbance indicators (Oxalidaceae, Montiniaceae, Plantaginaceae), increased Poaceae, Asteraceae and Cyperaceae | ~1800 BP | Meadows and Sugden, 1991 |
| | | Klaarfontein (KFN-B2) | KF | Decline of trees, increased charred fragments, increased Amaranthaceae, Poaceae >40 µm, and Asteraceae, sharp increase in *Juncus* | ~1600 BP | Baxter, 1996; Meadows and Baxter, 2001 |
| | | Rietvlei Still Bay | RV | Decline of trees, increased charred fragments, increased Amaranthaceae, Asteraceae and Poaceae | ~1650 BP* | Quick et al. 2015 |
| | | Spring Cave | SC | Decline of trees, increased Amaranthaceae, Poaceae >40 µm, Asteraceae, *Juncus* and *Typha* | ~1500 BP | Baxter, 1996 |
| | | Princessvlei (vZB) | PV-1 | Increased charred fragments, decline of Restionaceae and *Crassula*, increased Cyperaceae, *Carpacoce*, *Botryococcus* and *Nymphaea* | ~1450 | Neumann et al., 2011 |
| | | Princessvlei (PV11.3) | PV-2 | Increased Asteraceae, increased charred fragments, decline of Restionaceae | ~1300 BP | Cordova et al., 2019 |
| | | Eilandvlei | EV | Decline of trees (e.g., *Podocarpus*), increased charred fragments, increased Amaranthaceae, Poaceae and Cyperaceae | ~1300 BP | Du Plessis, 2015 |
| | | Pakhuis Pass | PK | Decline of trees, increased Asteraceae, Amaranthaceae, Poaceae | ~1200 BP | Scott and Woodborne, 2007 |
| | | Katbakkies | KB | Decline of trees, increased Cyperaceae | ~1100 BP | Meadows et al., 2010 |
| | | De Rif (Cederberg) | DR-1 | Decline of trees, increased charred fragments, Asteraceae, Poaceae and Cyperaceae | ~1900 BP | Valsecchi et al., 2013 |
| | | De Rif (Cederberg) | DR-2 | Decline of trees, increased Asteraceae, Poaceae and Cyperaceae | ~1000 BP | Quick, 2009; Quick et al. 2011 |

**Table 1**. Continued

| Micro-botanical Remains | | | | | | |
|---|---|---|---|---|---|---|
| | Biome | Site | Abbr. | Pollen, spores and charcoal evidence | Date (cal.) | References |
| S Afr. | Desert | Pella | PE | Decline of trees, increased *Forsskaolea*, Poaceae | ~1150 BP | Lim et al., 2016 |
| Lesotho | Grass-land | Sekhokong | SE | Decline of *Podocarpus*, increased *Crassula*, and Asteraceae | ~1100 BP | Fitchett et al., 2016 |
| Botswana | Savanna | Lake Ngami | LN | Decline of trees, increased charred fragments, increased Amaranthaceae, increased coprophilous fungal spores (e.g., *Sporormiella*) | ~1100 BP | Cordova et al., 2017 |
| | | Okavango Panhandle | OP | Increased Asteraceae and Cyperaceae | ~1000 BP | Nash et al., 2006 |
| Namibia | Savanna | Arnhem Cave | AC | Decline of trees, increased Amaranthaceae | ~1540 BP | Marais et al., 2015 |
| | | Lake Otjikoto | LO | Decline of trees, increased *Tribulus* | ~1300 BP | Scott et al., 1991 |
| | Nama Karoo | Okandjombo | OK | Decline of trees, increased *Tribulus* and Poaceae | ~1300 BP | Gil-Romera et al., 2007 |
| | | Vrede hyrax midden | VM | Increased Amaranthaceae, Asteraceae and *Tribulus* | ~1200 BP | Gil-Romera et al., 2006 |
| | Marine Site | GeoB 1023 | GB | Decline of *Podocarpus* forests and woodlands, increased *Tribulus*, fern spores and charred fragments | ~1800 BP | Shi et al., 1998 |
| | Desert | Kuiseb River | KR | Decline of trees, increased Amaranthaceae, Asteraceae and Poaceae | ~1450 BP | Scott, 1996 |
| Zambia | Savanna | Upper Zambezi valley | UZ | Decline of trees (e.g., *Podocarpus*), increased charred fragments | ~1800 BP | Burrough and Willis, 2015 |
| Mozambique | Savanna | Mount Gorongosa | MTG | Decline of Afromontane *Podocarpus* forests and Ericaceae, expansion of pioneer trees (e.g., *Macaranga*, *Trema*), and grasses, pronounced increase of charred fragments and *Pediastrum* | ~1700 BP | McWethy et al., 2016 |
| | Indian Ocean Coastal Belt (IOCB) | Lake Nhaucati | LH | Increased Asteraceae, *Trema*, *Alchornea*, and Poaceae | ~1500 BP | Ekblom, 2008 |
| | | Lake Nhauhache | LNH | Decline of trees, increased Poaceae, increased charred fragments, presence of coprophilous fungal spores (e.g., *Coniochaeta lignaria*) | ~1300 BP | Ekblom et al., 2014a |
| | | Lake Xiroche | LX | Few trees, increased Amaranthaceae, Asteraceae, *Alchornea*, *Trema*, and Poaceae | ~1300 BP | Ekblom, 2008 |

* Single radiocarbon date in the Late Holocene (upper section)

| B. Macrobotanical Remains | | | | | | |
|---|---|---|---|---|---|---|
| | Biome | Site | Abbr. | Fruits and seeds | Date (cal.) | References |
| South Africa | Savanna | Silver Leaves | SL | *Cenchrus americanus* (pearl millet) seed impressions on pottery | 1760 ± 40 BP (AD 242–415) | Klapwijk, 1974; Klapwijk and Huffman, 1996 |
| | | Ficus Cave | FC | Carbonized seeds (unidentified) | 1400 ± 40 BP (AD 605–774) | Partridge, 1966; Moore, 1981 |
| | | SK 17 | SK | Carbonized *Sorghum* seeds | 1335 ± 25 BP (AD 666–775) | Meyer, 1986; Jordaan, 2017 |
| | Grassland | Magogo | MG | *Cenchrus americanus*, *Eleusine coracana* (finger millet) and *Citrullus* (melon) seeds | 1360 ± 50 BP (AD 640–860) | Maggs and Ward, 1984; Voigt, 1984 |
| Botswana | Savanna | Maunatlala | ML | Carbonized *Cucurbita* seeds | 1570 ± 140 BP (AD 168–834) | Denbow, 1986; Denbow and Wilmsen, 1986 |
| | | Magagarape | MA | Carbonized *Sorghum* seeds | 1350 ± 80 BP (AD 594–953) | Campbell et al., 1996 |
| Zimbabwe | Savanna | Kadzi | KD | *Eleusine coracana* (finger millet) | 1475 ± 70 BP (AD 435–772) | Pwiti, 1996; Katsamudanga and Pwiti, 2017 |
| | | Leopard's Kopje | LK | *Vigna unguiculata* (cowpea) | 1280 ± 90 BP (AD 654–988) | Robinson, 1966; Huffman, 1971; Voigt, 1980 |
| Zambia/ Malawi Border | Savanna | Chowo River | CH | *Sorghum bicolor* (sorghum) seeds | 1670 ± 40 BP (AD 339–541) | Barham and Jarman, 2005 |
| Zambia | Savanna | Mondake | MK | *Sorghum*, *Vigna unguiculata* (cowpea) seeds | 1510 ± 60 BP (AD 435–668) | Robertson, 2000 |

**Table 2**. List of examined archaeobotanical sources

| Classification | Evidence | References |
|---|---|---|
| Charred seeds | *Cenchrus americanus* (pearl millet), *Sorghum bicolor* (sorghum), *Vigna unguiculata* (cowpea), *Eleusine coracana* (finger millet) and *Citrullus lanatus* (melon) | E.g., Antonites and Antonites, 2014; Lander and Russell, 2018; Crowther et al., 2018 |
| Pollen of forest trees | *Podocarpus*, *Olea*, *Celtis* | E.g., Neumann et al., 2008; Breman et al., 2011 |
| Pollen of disturbance/ open-land indicators | Asteraceae, Amaranthaceae, *Macaranga*, *Trema*, Oxalidaceae, Montiniaceae, Plantaginaceae | E.g., Meadows and Sugden, 1991; Baxter and Davies, 1994; Hahn et al., 2021 |
| Pollen of likely cultivated cereals | Larger Poaceae >40–50 µm | E.g., Turner and Plater, 2004; Hahn et al., 2021 |
| Pollen of ruderal species | *Tribulus* | E.g., Gil-Romera et al., 2007 |
| Spores of coprophilous fungi | *Sporormiella*, *Gelasinospora*, *Coniochaeta*, *Sordaria* | E.g., Carrion et al., 2000; Neumann et al., 2014 |
| Charred particles | Macro- and micro-charcoal particles | E.g., Scott, 2002; Li et al., 2008; Lebamba et al., 2016 |
| Phytoliths | Shift from $C_4$ to $C_3$ vegetation | E.g., Sjöström et al., 2017 |

## ARCHAEOBOTANICAL SOURCES

Here, we examine macro- and micro-botanical remains from southern Africa (Table 2). A significant factor explaining the relative scarcity of plant remains in comparison to temperate regions in the Northern Hemisphere is non-preservation in subtropical environments, mechanical disintegration from repeated wet and dry cycles, infrequent charring, and limited studies focused on botanical remains from botanically diverse regions (see Young and Thompson, 1999; Mitchell, 2005; Fuller and Hildebrand, 2013). Also, there is a difficulty in differentiating the pollen of African domesticates such as *Cenchrus americanus* from wild grasses, because of overlaps in sizes and an overall similar pollen morphology (Tomlinson, 1973; Andersen, 1979; Bonnefile and Riollet, 1980).

We also note that research investigating plant diversity in transformed versus untransformed areas in current grass-dominated ecosystems in southern Africa cannot be regarded as an analogue for the first millennium AD context because current transformed grassy landscapes are affected by the more recent invasion of neophytes such as *Campuloclinium macrocephalum* (Pompom Weed) and *Opuntia engelmannii* (Small Round-leaved Prickly Pear) (O'Connor and van Wilgen, 2020) and by different land-use patterns and fire management regimes (compare Muller et al., 2021). The differentiation of anthropogenic pollen indicators is complicated by the fact that taxa such as Asteraceae and Amaranthaceae, which might indicate human disturbances, are commonly interpreted also as signals for dry periods (see discussion in Hahn et al., 2021, compare Fitchett and Bamford, 2017).

In addition to the general challenge to differentiate vegetation changes resulting from climate change from fluctuations caused by anthropogenic impact, low sampling resolution and dating problems provide an obstacle to a detailed comparison between environmental records and archaeological sites (see Scott et al., 2012).

# RESULTS AND DISCUSSION

Our evaluation of the data is presented according to the biomes of southern Africa (Mucina and Rutherford, 2006) and in chronological order from earlier to more recent evidence (Table 1).

## SAVANNA

Pollen records indicate a possible anthropogenic impact since ~1800–1700 BP, representing important changes in the vegetation cover and composition of southern Africa in the savanna (Breman et al., 2011; Burrough and Willis, 2015; McWethy et al., 2016). The Versailles (Fig. 1: VS) pollen sequence suggests an open savanna extension, possibly due to intensive grazing coupled with vegetation clearance for farming and iron smelting (Mitchell, 2002; Breman et al., 2011). Also, weak representation of pollen of forest elements (e.g., *Podocarpus*) continues into the second millennium AD despite cool, moist 'Little Ice Age 'conditions around ~650–150 cal. BP, suggesting the prevalence of anthropogenic influences, e.g., wood cutting (Staver et al., 2009; Breman et al., 2011). Archaeological research in the region attests to the interpretation of a steady expansion of human occupation into a wider area with sites such as the Eiland Salt Works (Evers, 1974) and Riverside near Nelspruit in northeastern South Africa (Huffman, 1998) dated 1680 ± 30 BP (cal. AD 343–525) and 1540 ± 50 BP (cal. AD 435–645) respectively.

Around the same time, the pollen sequence from Mount Gorongosa (Fig. 1: MTG) in central

Mozambique suggests the impact of pastoralism (e.g., *Gelasinospora*) ~1700 cal. BP. In addition, the evidence of an increase of charred particles and the algae *Pediastrum*, which often signals eutrophication (which itself primarily indicates increased runoff, see Dubois et al., 2018), synchronous with the pollen records suggests possible human disturbances likely linked to the presence of early farmers in the region (McWethy et al., 2016). This vegetation change coincided with evidence of the spread of pastoralism and farming comprising ceramics and faunal remains recovered in central and southern Mozambique ~2000–1400 BP (Sinclair et al., 1987; Morais, 1988; Madiquida, 2006; Badenhorst et al., 2011; Mercader and Sillé, 2013).

Furthermore, macro-remains of domesticated *Sorghum bicolor* dated 1670 ± 40 BP (cal. AD 339–541) at Chowo River (Fig. 1: CH) on the Zambia/Malawi border (Barham and Jarman, 2005), carbonized *Cucurbita* seeds dated 1570 ± 140 BP (cal. AD 168–834) at Maunatlala (Fig. 1: ML) in eastern Botswana (Denbow, 1986; Denbow and Wilmsen, 1986) and *Pennisetum glaucum* (syn. *Cenchrus americanus*) seed impressions on pottery dated 1760 ± 40 BP (cal. AD 242–415) at Silver Leaves (Fig. 1: SL) in South Africa (Klapwijk, 1974; Klapwijk and Huffman, 1996) attest to the beginnings of farming and other human activities around this period.

The pollen analysis of dung from the cattle enclosure at Silver Leaves in northeastern South Africa and Broederstroom (Fig. 1: BD), shows treeless vegetation (Carrión et al. 2000:248) and dominance of open-land indicators (e.g., Caryophyllaceae and Amaranthaceae) respectively, indicating an opening of the landscape by pastoralists and farmers ~1500 BP (Carrión et al., 2000). Archaeological excavations at Broederstroom provide indirect evidence of livestock keeping in the form of storage pits lined with cattle dung (Mason, 1981, 1986; Huffman, 1993). Also, open vegetation taxa (e.g., Asteraceae) from a mountainous area near Tate Vondo (Fig. 1: TV) in northern South Africa coincided with the sharp decline of *Podocarpus* forests~1500 BP, probably due to wood-burning and forest clearance by farmers (Scott, 1987). This is supported by the archaeological record (e.g., ceramics, *Cenchrus americanus* seed impressions on pottery) indicating the presence of farmers as early as~1700 BP within the region (Klapwijk and Huffman, 1996; Mitchell and Whitelaw, 2005).

The surge of charcoal particles and the concurrent increase of Amaranthaceae in Wonderkrater Spring deposits (Fig. 1: WK) near Mookgophong, northeastern South Africa suggests local burning was likely driven by farmers within the area (see Scott, 1982a, 2002; Scott et al., 2003; Scott and Thackeray, 1987). More recent evidence of *Zea mays* (maize) pollen dated ~440 cal. BP further supports human habitation and possible cultivation in the area (Scott 1982a, b, 2016; Scott et al., 2003). Also, contemporaneous pollen records from sites such as Scot's Farm (Fig. 1: SF) at the foot of the Soutpansberg (Scott, 1982c) and Morelletta stream (Fig. 1: MS) near Johannesburg (Scott, 1984) conform with the Wonderkrater vegetation record ~1500 BP, except that the forest retreats did not correspond with peaks of charred fragments until ~500 cal. BP at Morelletta. A similar phenomenon has been documented in the region where there was no general correlation of increased charcoal particles with the arrival and settlement of farming communities (Scott, 2002), despite the conventional knowledge that burning was likely a common occurrence during the late Holocene in South African savannas (e.g., Turner and Plater, 2004; Govender et al., 2006).

By contrast, drier conditions were inferred from similar evidence at Arnhem Cave (Fig. 1: AC) in central Namibia ~1540 cal. BP, primarily due to the accompanying increase of Amaranthaceae and decrease of Poaceae in the pollen record (Marais et al., 2015). Poaceae are often regarded as humidity indicators, especially in comparison to more drought-adapted plants such as Amaranthaceae and Asteraceae (Fitchett and Bamford, 2017).

Meanwhile, Poaceae and Asteraceae, due to the diversity of species, are considered not useful for quantitative climatic reconstructions (Chevalier et al., 2021). However, if the increase in Amaranthaceae pollen is considered a potential indicator of anthropogenic vegetation disturbance (Baxter and Davies, 1994; Hahn et al., 2021) and is seen in conjunction with evidence of human presence indicated by the nearby archaeological sites in the area (Lander and Russell, 2018), the anthropogenic influence on the vegetation may not be completely ruled out.

Additional micro-botanical evidence of *Sorghum* sp. grains and *Vigna unguiculata* recovered at Mondake (Fig. 1: MK), in the Mulungushi drainage basin, Central Zambia dated

1510 ± 60 BP (cal. AD 435–668) (Robertson, 2000) and carbonized grains of *Eleusine coracana* from different stratified contexts at Kadzi (Fig. 1: KD) dated 1475 ± 70 BP (cal. AD 435–772) in the middle Zambezi Valley in northern Zimbabwe (Pwiti, 1996; Katsamudanga and Pwiti, 2017) further suggests the presence of humans on the landscape ~1500 BP in the savanna. By ~1300 cal. BP, minor vegetation change in the Wonderwerk Cave (Fig. 1: WW) record from northwestern South Africa might signal anthropogenic impact despite the low sample resolution for this period (Brook et al., 2010). However, the major driver(s) of the vegetation change cannot be determined without higher resolution records.

In northern Namibia, pollen records from Lake Otjikoto (Fig. 1: LO) in the Tsumeb District (Scott et al., 1991), can be used as indicators of the extension of anthropogenic activities in the region although the authors attributed the vegetation change predominantly to climate since *Tribulus* is regarded as an aridity indicator (compare Chevalier et al., 2021). However, anthropogenic impact is plausible with the increased presence of *Tribulus*, a plant typically associated with human disturbances and specifically animal husbandry (Scott and Morrison, 1996) coinciding with the decline of the forest. While further work and higher resolution records are needed at Lake Otjikoto, these changes coincide with human occupation in this region at this time, which is documented in the archaeological records from the faunal and pottery remains recovered at Jakkalsberg towards the mouth of the Orange River in northwestern South Africa (Brink and Webley, 1996).

Macro-botanical remains from various sites, for example, *Sorghum spp.*, *Vigna unguiculata*, *Citrullus vulgaris*, dating to ~1300–1400 BP (see Fig. 1: LK, MA, FC, SK) further suggest the established presence of humans in the region (Campbell et al., 1996; Partridge, 1966; Moore, 1981; Meyer, 1986; Huffman, 1971).

By ~1100 cal. BP, the pollen sequence at Lake Ngami (Fig. 1: LN) in northern Botswana reflects the emergence of pastoralism in the region with significantly increased spores of coprophilous fungi (e.g., *Sporormiella*, *Sordaria*) and charred fragments (Cordova et al., 2017). This sequence correlates with archaeological evidence comprising ceramics, iron, and faunal remains (e.g., cattle, sheep/goat) from sites such as Panga Hill, Bisoli, Chobe, Qugana, and Serondola, and further confirms the widespread presence of pastoralists and farmers in northern Botswana between 1100 and 1300 BP (see Denbow, 1986; Denbow and Wilmsen, 1986; Robbins et al., 2008; Coulson et al., 2016). Similarly, the presence of humans earlier documented by the remains of ceramics and cattle bones dated as early as ~1200–1300 BP at Divuyu and Nqoma, about 70 km west of Okavango (Denbow and Wilmsen, 1986) could have been mirrored by the significant shift from grass- to sedge (Cyperaceae)-dominated vegetation and increased Asteraceae ~1000 BP at Okavango Panhandle (Fig. 1: OP), in northwest Botswana. Other factors such as climate and hydrology are also plausible (Nash et al., 2006).

### *Tribulus*

*Tribulus terrestris* is a protein-rich fodder for livestock in parts of Zimbabwe and South Africa, especially in the Karoo (Sebata et al., 2005; Bromilow, 2018). Recent evidence from cattle dung from Shashe-Limpopo Confluence Area (SLCA), dating between AD 1000 and 1200, points to >20% *Tribulus* pollen in samples (Mvelase, 2021). A *Tribulus* mericarp (fruit) has been identified in a dung layer, although dating to a later date, at Sibudu Cave on the east coast of South Africa (Scott, 2005). Analysis of modern pollen samples from different landscape types in northcentral Namibia also indicated the dominance of pollen taxa such as *Tribulus* at grazed sites, suggesting local grazing pressure (Tabares et al., 2018). The common occurrence of *Tribulus* was recorded in distant northern China too and attributed to heavy trampling by livestock, known to increase with grazing pressure; therefore, *Tribulus* is a potential indicator of grazing pressure on local vegetation (Li et al., 2008; Wei and Zhao, 2016). Similarly, palynological analysis of coprolites in the Central Sahara points to the significant presence of *Tribulus*, suggested to spread due to selective response to animal grazing (Rotunno et al., 2020). These records suggest that *Tribulus* might reflect human disturbances since it is most abundant in overgrazed veld or along roads (Scott and Morrison, 1996; Johannsmeier, 2016)

However, *Tribulus* is spread through fruits with thorns, clinging to the hair and hooves of livestock and leaves and flowers are often not incorporated into the diet (see Kinahan, 2005; Sarwat et al., 2008). Also, *Tribulus* dates

further back in the fossil records. For example, *Tribulus* was recorded at Tswaing Crater at ~200 ky (Scott, 1999) and at least at ~50 ky in Namibia (Scott et al., 2018). *Tribulus* should be considered, however, as likely evidence for herding when significant increases in the fossil record are associated with supporting evidence such as livestock remains.

### GRASSLAND

The increase of spores of coprophilous fungi and charred fragments at the Drakensberg outlier Mahwaqa Mountain (Fig. 1: MM) after ~2000 cal. BP indicates a possible anthropogenic impact (Neumann et al., 2014) and is tentatively linked to livestock keeping by pastoralists and/or farmers who entered the region ~1500 BP (e.g., Mazel, 1989, 1992, 2022). *Glomus*, a mycorrhizal fungus often linked to an increase in erosion, which might be a consequence of human disturbance, also increased (Neumann et al., 2014). Significantly, recent investigations at Cherangani Hills in eastern Kenya correlated the increase of dung fungal spores with notable grazing activity during the late Holocene (Cheruiyot et al., 2020). Also, studies at historical sites in the western United States showed a positive correlation between *Sporormiella* and grazed areas (Davis and Shafer, 2006).

Notable vegetation changes coupled with the dominance of large Poaceae pollen grains (>40 µm) at Dartmoor Vlei (Fig. 1: DV) around Mount Gilboa situated on the headwaters of the Myamvubu River, to the east of the Drakensberg escarpment, might also indicate a possible anthropogenic impact ~1600 cal. BP (Geer, 2013). While Geer (2013) suggested the cultivation of *Zea mays* due to the large Poaceae pollen, this is unlikely because *Zea mays* only reached southern Africa through the Indian Ocean exchange in the AD 1600s (Miracle, 1965; McCann, 2001). Consequently, the large Poaceae pollen may rather be interpreted as possible early cultivated cereals such as sorghum or millet, although pollen of wild grasses cannot be excluded.

Palynological data from Tiffindell (Fig. 1: TF) in the southern Drakensberg Mountains (Rosen et al., 1999), and Rietvlei Dam (Fig. 1: RD) further north (Scott and Vogel, 1983) might also indicate anthropogenic impact in the South African Grassland Biome ~1500 BP. However, accurate palynological interpretation of Rietvlei Dam is hampered by the possible contamination of top layers by ploughing (Scott and Vogel, 1983).

Phytolith analysis at Thaba Chweu Fen (formerly Lydenburg) (Fig. 1: MF) in northeastern South Africa records a shift from the dominance of $C_4$ to $C_3$ vegetation (Sjöström et al., 2017). However, the local vegetation change reconstructed at Thaba Chweu Fen was limited to the increase in grasses only. Further to the southeast, archaeobotanical evidence recovered in the Muden area at Magogo (Fig. 1: MG), indicate the likely cultivation of *Cenchrus americanus* and *Eleusine coracana* dated 1360 ± 50 BP (AD 640–860) (Maggs and Ward, 1984).

After~1200 cal. BP, further anthropogenic impact was present in eastern Lesotho (Fig. 1: SE) (Fitchett et al., 2016). Although the pollen and diatom records from Sekhokong suggested contrasting climate and environmental conditions which are probably due to the limited samples represented by this period, the vegetation change might provide likely evidence of anthropogenic influence in eastern Lesotho.

Further north of Sekhokong, the non-recovery of *Podocarpus* pollen even during climatically favourable conditions at Graskop (Fig. 1: GK) indicates that the continuous activities of humans within the area possibly hindered the regrowth of forests, thus supporting the earlier suggestion of anthropogenic disturbances recovered at Versailles (~14 km from Graskop) (Breman et al., 2011).

### INDIAN OCEAN COASTAL BELT (IOCB)

The Lake Sibaya (Fig. 1: LS-2) pollen sequence suggests that anthropogenic disturbances after ~1900 cal. BP are more likely to be responsible for the *Podocarpus* forest decline (Walther and Neumann, 2011), thereby correlating with possible human impact along and nearby the east coast of South Africa documented by remains of houses, granaries, pits, cattle byres, and pottery mostly dated~1600–1300 BP in the archaeological records (Whitelaw, 1994; Whitelaw and Moon, 1996; Mitchell and Whitelaw, 2005).

In southern Mozambique, the Lake Nhaucati (Fig. 1: LH) pollen assemblage comprising Asteraceae, *Trema*, *Alchornea* and Poaceae (Ekblom, 2008) likely indicates anthropogenic impact~1500 cal. BP, although Ekblom (2008) attributed the vegetation shift observed in the record to climate despite the known arrival of

farmers in the region ~1600 years ago. This argument was based on the record showing that the charcoal peaks did not correlate with the forests' decline despite the archaeological evidence of the presence and continuous occupation of farming communities and possibly higher population densities since 1600 years ago (Sinclair, 1987; Ekblom, 2004, 2008). However, the dominance of pollen of *Trema* and *Alchornea*, which are usually regarded as pioneer trees, is frequently associated with human disturbances when accompanied by increased Poaceae (cf. Van Valkenburg and Ketner, 1994; Kjellmark, 1996; Dull, 2004).

In addition, Ekblom (2008) tentatively linked the non-recovery of forests despite the prevalence of favourable climatic conditions, to soil erosion. Soil erosion is often connected to human disturbances close to farming community settlements in eastern South Africa (Marker and Evers, 1976; Breman et al., 2011). Human impact cannot be ruled out for this period considering the non-recovery of forests, the possible association of soil erosion with human disturbances, and the associated regional archaeological evidence of settled human occupation during the first millennium AD (see Sinclair, 1982, 1987; Ekblom, 2004).

By~1400 cal. BP, the Mdlanzi (Fig. 1: MD) pollen sequence indicates the evidence of early anthropogenic impact along the northeastern coast of South Africa (Turner and Plater, 2004; Finch and Hill, 2008). While the change in vegetation was likely a result of tree felling and burning, the accompanying increase of large Poaceae pollen grains (>40 μm) suggests the possible cultivation of cereals (e.g., sorghum, millet) (Turner and Plater, 2004). These human disturbances mirror the archaeological records (Maggs, 1984) of farming occupations since the mid-third century AD. Further north of Mdlanzi, palynological information from the Lake Sibaya core (Fig. 1: LS-1) further supports anthropogenic disturbances in the region 1400 BP (Neumann et al., 2008). The interpretation is supported by archaeological data (e.g., cattle and sheep bones, pearl millet and sorghum grains, and ceramics) that indicate the settlement of farming communities (Maggs, 1980b; Maggs and Ward, 1984; Miller and Whitelaw, 1994). Also, the Mfabeni Peatland record (Fig. 1: MB) to the east of Lake St. Lucia supports the evidence of forest clearance and wood burning by farmers in the IOCB, showing similar forest decline and a shift to more open grassland/savanna, although due to the weak chronology, those disturbances cannot be accurately dated (see Finch and Hill, 2008).

Around 1300 BP, the pollen record in the coastal lowlands of Mozambique at Lake Nhauhache (Fig. 1: LNH) shows possible anthropogenic disturbances. While Ekblom (2008) argued that the vegetation change observed in the pollen records from the nearby sites e.g., Lake Nhaucati are not in harmony with the arrival of farmers and settlement changes, the pollen assemblages at Lake Nhauhache coupled with the presence of the coprophilous fungal spore (*Coniochaeta lignaria*) might suggest the opening of the landscape by human occupation around this time (Ekblom et al., 2014a).

Likewise, the possible human impact in the pollen record is contemporaneous with the archaeological evidence (e.g., cattle, sheep/goat remains and ceramics) of the expansion of humans within the area (Badenhorst et al., 2011; Ekblom et al., 2014b). Moreover, the pollen sequence from Lake Xiroche (Fig. 1: LX) in the Chibuene coastal plain of southern Mozambique provides evidence of sparse tree pollen accompanied by high representations of open-land indicators (e.g., Asteraceae, Amaranthaceae) and pioneer trees (e.g., *Trema*)~1300 BP (Ekblom, 2008). While Ekblom (2008) argued for the prevalence of climate change, the reassessment of the pollen record, particularly the presence of pioneer trees and open-land indicators, as discussed earlier, suggests otherwise. A similar vegetation change pattern recorded from nearby coastal pollen sites suggests possible anthropogenic impacts around this time (Ekblom et al., 2014b). Meanwhile, the slight differences in the overall pollen sequences between Lake Xiroche and Lake Nhaucati where certain variations exist in the forest decline are likely a result of localized signals. Sparse forest tree pollen was recorded at the former site, whereas the pollen record at the latter showed no significant forest decline (Ekblom, 2008). This further attests to the likely impact of the intensification of local cultivation and higher population densities already extending to other areas in the region.

### NAMA-KAROO

In northwestern Namibia, the pollen record from Okandjombo (Fig. 1: OK) in the Nama-Karoo Biome documents the retreat of forests and increased *Tribulus* ~1300 cal. BP (see

Gil-Romera et al., 2007). Also, similar pollen assemblages coupled with the increase in open-land indicators were recorded from the pollen analysis of fossil hyrax dung near Vrede (Fig. 1: VM) in the same region ~1200 cal. BP (Gil-Romera et al., 2006). The authors argued that human activities might not be the likely explanation for major vegetation change due to archaeological records showing ephemeral human presence. However, possible anthropogenic impacts cannot be excluded as the pattern of vegetation change is consistent with other records showing likely human impact. This change also correlates with the evidence of human occupation (e.g., sheep bones, ceramics, iron tools) within the different localities of northwestern Namibia around this time (see Albrecht et al., 2001; Vogelsang et al., 2002; Lenssen-Erz and Vogelsang, 2005).

After ~1300 BP, similar trends in vegetation fluctuations were recorded at different localities in the Nama-Karoo of South Africa (e.g., Scott et al., 2005). Notable vegetation changes were recorded at Deelpan (Fig. 1: DP) ~1250 BP (Scott, 1988; Scott and Nyakale, 2002) and Blydefontein Rockshelter (Fig. 1: BL) ~1200 BP (Rosen et al., 1999; Scott et al., 2005). These vegetation shifts have been attributed to climate change due to the increase in Asteraceae which might also point to anthropogenic disturbances as earlier suggested (see Baxter and Davies, 1994). While early archaeological investigations at Blydefontein suggest the presence of humans at ~1255 BP (Bousman, 1991), more recent faunal studies, albeit tentative, pushed the early presence of pastoralists in this area to 2791 ± 25 BP (cal. 967–817BC) (Bousman et al., 2016; Scott and Plug, 2016). Consequently, the pollen evidence may mirror the evidence of anthropogenic impact through herding. However, Bousman and Scott (1994) argued that similar vegetation changes noticed during the historical time in the Blydefontein area are likely due to both climate and overgrazing.

## DESERT

The Kuiseb River (Fig. 1: KR) sequence provides a possible anthropogenic impact during the first millennium AD. While Scott (1996) argued that climate was likely the major driver of these vegetation changes, the principal components taxa used for the interpretation (e.g., *Salvadora*, *Faidherbia albida*, *Tribulus*, Amaranthaceae, Asteraceae) failed to show a sound distinction for moisture and temperature conditions, which signals that the interpretation warrants a reassessment. Meanwhile, favourable conditions reported within the region supported the presence of livestock farming as early as ~1500 BP (Sandelowsky, 1977). These, coupled with the increase of archaeological sites in western Namibia during the first millennium AD (see Lander and Russell, 2018) suggest that pastoralism activities could have been responsible for the vegetation changes. Around 1500–800 cal. BP, an increase in *Forsskaolea* and Poaceae pollen at Pella, South Africa (Fig. 1: PE) associated with increased humidity in the region for this period indicating an open landscape (see Castilla-Beltrán et al., 2021) is likely due to anthropogenic influences (Lim et al., 2016).

## FYNBOS AND SUCCULENT KAROO

Intensive grazing, occasional burning, and settlement would have had a significant impact on the vegetation in the Fynbos Biome (Parkington, 1977). Notable vegetation changes from De Rif at 1900 cal. BP, (Fig. 1: DR-1) in the central Cederberg mountains might attest to anthropogenic impact (Valsecchi et al., 2013). While there is no reference to anthropogenic impact by the palynologists, the archaeological evidence of the introduction of livestock ~1800 BP into the area (Parkington, 1977) coincides with these vegetation changes and with increased charred fragments at De Rif, likely indicating the impact of human activities in the area. Also, the Sneeuberg (Fig. 1: SN) pollen sequence showing trends synchronous with increased vegetation disturbances taxa (e.g., Oxalidaceae, Plantaginaceae, Montiniaceae) which are often associated with fire suggests evidence of human disturbances after ~1800 cal. BP (Meadows and Sugden, 1991).

Sheep bones and pottery along the southern Cape coast at Byneskranskop, Die Kelders, Blombos, and Pearly Beach strongly indicate the presence of pastoralists in the southwestern parts of South Africa during the first millennium AD (Avery, 1974; Schweitzer, 1974; Schweitzer and Wilson, 1982; Henshilwood, 1996). In the southern Cape, the presence of pastoralism has been documented archaeologically with the help of ceramics and faunal remains (e.g., sheep) at Nelson Bay Cave, with the additional evidence of domesticated sheep

dung at Boomplas Cave in the interior mountains ~2000–1700 BP (Beaumont and Vogel, 1972; Deacon et al., 1978).

By ~1600 cal. BP, evidence of likely anthropogenic impact in the western part of the Cape was recorded at Klaarfontein (Fig. 1: KF; Meadows and Baxter, 2001), reflecting the impact of pastoralists, who were present on the Vredenburg Peninsula on the west coast by ~1860 BP (Smith, 1987). Additional evidence of a pronounced increase in charred fragments attests to the increase in fire possibly used to burn reedbeds and promote new growth, a practice that is still applied in the region today (see Skead, 1980). Rietvlei Still Bay (Fig. 1: RV), further south, also documents likely human presence ~1650 BP (Quick et al., 2015). While the possibility of anthropogenic impact was not considered, the pollen record follows similar trends of vegetation changes likely caused by the activities of pastoralists.

At ~1500 BP, patterns of vegetation change similar to those recorded from earlier sites in the Fynbos were documented in a pollen sequence at Spring Cave (Fig. 1: SC), collected from a dated archaeological exposure on the west coast of South Africa (Baxter, 1996). This phenomenon suggests further anthropogenic impact by pastoralists and is supported by the archaeological record indicating their presence along the west coast since ~1600 BP (Klein, 1986).

Further south, the Princessvlei (Fig. 1: PV-1) record on the Cape Flats close to Cape Town shows minor changes after 1800 BP which have been tentatively linked to the impact of early pastoralists. (Neumann et al., 2011). More pollen records from Eilandvlei (Fig. 1: EV, Du Plessis, 2015) and Princessvlei (Fig. 1: PV-2, Cordova et al., 2019) documented a similar trend of anthropogenic disturbance in the eastern and western parts of the Cape. At Princessvlei, the coincidence of vegetation changes and increased charred fragments with moist periods was likely due to greater biomass fuel loads (Cordova et al., 2019).

The likelihood of continued exploration of the landscapes by pastoralists towards the end of the first millennium AD was recorded farther north from pollen records like Pakhuis Pass (Fig. 1: PK), Katbakkies (Fig. 1: KB) and De Rif (Cederberg Mountains) (Fig. 1: DR-2) in the Western Cape (Scott and Woodborne, 2007; Meadows et al., 2010; Quick, 2009). These records agree with archaeological sites such as Diepkloof, Elands Bay Cave and Tortoise Cave along the Atlantic coast that have livestock remains and pottery dated around the mid-first millennium AD (Klein, 1986; Parkington and Poggenpoel, 1987; Sadr and Sampson, 2006).

### MARINE RECORDS

A marine pollen record (GeoB 1023) (Fig. 1: GB) obtained from a core off the southwest African coast, with main pollen source areas from the northern Namibian desert, Angolan highlands and northwestern Kalahari seems to suggest vegetation clearance for cultivation and increased burning ~1800 cal. BP, (Shi et al., 1998). The likely activities of pastoralism and farming during this period coincided with the archaeological evidence (e.g., ceramics, faunal, and iron tools) in the region between 1800 and 1500 cal. BP (Phillipson, 1977).

The possible cultivation of cereals and the practice of livestock keeping is also reflected on the east coast of southern Africa in a more recent record from offshore the Umzimvubu River (GeoB20623), Mpondoland (Fig. 1: MP), at ~1500 BP. This provided evidence of an increase in open-land indicators coupled with the dominance of large Poaceae pollen grains (>40 μm) and the increase in spores of coprophilous fungi (Hahn et al., 2021). The pollen record, evidence of increased erosion, and the presence of pastoralists and farmers in the archaeological record dated ~1400 BP (Feely and Bell-Cross, 2011), provides evidence of possible human impact in the area. However, there is a need for caution in the pollen interpretation considering the possibility of the conflation of pollen from differing source areas which are often incorporated into the marine records (see Scott et al., 2012).

## SYNTHESIS

Our review of pollen data from sites across the nine biomes of southern Africa explored the potential of using micro- and macro-botanical remains to identify the introduction and spread of pastoralism and farming in southern Africa. In general, the palynological records for southern Africa show similar patterns of vegetation change across the biomes from 2000 to 1000 years ago. Previous studies often argue that these patterns could be linked to the prevalence of generally drier conditions due

**Table 3**. Summary of possible anthropogenic indicators

| Human activity | Likely evidence | Associated taxa/remains |
|---|---|---|
| Felling of trees for wood, clearing of forest for cultivation | Decline in tree pollen | *Podocarpus*, *Olea*, *Celtis* |
| Clearing of forest for cultivation | Increase in open-land/disturbance indicators/pioneer trees | Asteraceae, Amaranthaceae, *Macaranga*, *Trema*, Oxalidaceae, Montiniaceae, Plantaginaceae |
| Crop cultivation | Increase in large Poaceae pollen (>40 µm) | Likely *Pennisetum* (syn. for *Cenchrus americanus*), *Sorghum* |
| Crop cultivation | Presence of charredgrains and seeds | *Cenchrus americanus*, *Sorghum bicolor*, *Vigna unguiculata*, *Eleusine coracana*, *Citrullus lanatus*, *Zea mays* |
| Clearance of vegetation by fire | Increase in charred fragments | Micro- and macro-charcoal |
| Livestock herding | Increase in spores of coprophilous fungi | *Sordaria*, *Sporormiella*, *Gelasinospora*, *Coniochaeta* |
| Livestock herding | Increase in ruderal species | *Tribulus* |

to climate change during the first millennium AD for this region (Scott et al., 2012; Chevalier and Chase, 2016). However, the impact of pastoralism and farming can also lead to a decline in tree pollen and consequently an increase in open-land indicators/pioneer trees, coprophilous fungal spores, and large Poaceae pollen (>40 µm) (see Li et al., 2008). To evaluate the evidence for the different scenarios we examined the patterns in the pollen data from the various sites recorded in southern Africa (see Table 1). Here we evaluate the indicators of anthropogenic impacts on vegetation (see Table 3), suggest patterns observed in the data, and identify research gaps.

## POSSIBLE ANTHROPOGENIC INDICATORS

### Tree pollen (see Table 3)

A decline in tree (forest) pollen can be driven by anthropogenic impact (e.g., Shi et al., 1998; Li et al., 2008; Neumann et al., 2008), climate (e.g., Scott et al., 2003; Chevalier and Chase, 2016), or a combination of both (Finch and Hill, 2008). A decline of *Podocarpus* (but sometimes *Olea*) was generally documented at different sites in the Savanna, Grassland, IOCB, and Fynbos of South Africa, Zambia, and Mozambique (See Table 1), suggesting possible selective exploitation of trees for wood or a combination of the impact of people and climate. It is, however, more reliable to associate the decline of trees with anthropogenic impact when accompanied by the increase of other possible anthropogenic indicators such as charred fragments, spores of coprophilous fungi, large Poaceae (Cerealia-type) pollen (>40 µm) and open-land indicators (e.g., Neumann et al., 2008; Breman et al., 2011; Hahn et al., 2021).

### Increase in open-land/disturbance indicators/pioneer trees

The high representation and diverse occurrence of open-land indicators (e.g., Amaranthaceae, Asteraceae) in the different biomes (see Table 1) are commonly interpreted as effects of anthropogenic disturbances particularly farming (Baxter and Davies, 1994; Neumann et al., 2011; Hahn et al., 2021) but often argued to be indicators of regional aridity (Scott et al., 2003; Chevalier and Chase, 2015, 2016). Following the associations of these open-land indicators with large Poaceae pollen (>40 µm), which are tentatively interpreted as cultivated cereals and known to have coincided with the arrival of farmers in southern Africa from sites such as Mdlanzi and Mpondoland (Turner and Plater, 2004; Hahn et al., 2021), they more likely indicate anthropogenic impact during the first millennium AD.

The increase of light-adapted pioneer trees such as *Trema* and *Macaranga*, which are widespread from the pollen records in Mozambique from ~1700 BP (see Table 1), often indicates anthropogenic disturbances and growth of secondary forests (Goodale et al., 2012). Their increase which coincides with high frequencies of charred fragments particularly at Mount Gorongosa in central Mozambique (McWethy et al., 2016) further points to the likely removal of canopy forests for farming which in turn favoured the expansion of trees adapted to light-demanding conditions. These changes in the vegetation have also been related to anthropogenic activities in other areas such as Europe, Asia and America (Dubois et al., 2018). Ekblom (2008) has, however, argued for climate changes suggesting that the increase of these pioneer species did not have a close relationship with anthropogenic impact owing

to the lack of increased charred fragments in the local records from southern Mozambique.

### Increase in charred fragments

Charred fragments are one of the most important indicators of anthropogenic presence and activities (e.g., Dubois et al., 2018). The clearance of vegetation by fire was commonly practised by pastoralists and farmers to prepare land for fields and settlements (e.g., Nkala et al., 2011). Burning is a common practise to stimulate grass growth (Neary and Leonard, 2020). Human-induced fires are often differentiated from natural fires when accompanied by the occurrence of other anthropogenic indicators such as weeds, large Poaceae pollen (>40 µm) and open-land indicators (Li et al., 2008), but coincidences cannot be excluded.

This phenomenon is widespread in southern Africa across the Fynbos, Savanna, Grassland, and IOCB with the co-occurrence of open-land indicators and decline of trees, and more likely indicates the impact of anthropogenic burning particularly when archaeological data provide evidence of human occupation (Scott, 1982c; Roos et al., 2016; Scott et al., 2022). Meanwhile, a few sites showing evidence of likely anthropogenic impact (e.g., Broederstroom, Mdlanzi, Mpondoland) did not show the co-occurrence of charred fragments peak with other anthropogenic indicators. The absence of evidence may not necessarily mean evidence of absence of anthropogenic impact as the lack of peaks of charred fragments might be due to effective management of fires (see Scott, 2002) or a small number of farmers moving into a landscape already managed by hunter-gatherers (Wadley, 1978, 1996).

### Large Poaceae pollen (>40 µm)

The appearance of large Poaceae pollen (>40 µm) in the Grassland Biome, marine and IOCB sites might indicate the cultivation of crops. At many sites in southern Africa, these pollen grains co-occurred with increased charred fragments and open-land indicators, as well as the decline of trees (see Table 1), indicating possible farming practices in the region. While it is possible to link the large Poaceae pollen grains with early cultivated cereals (e.g., *Pennisetum* – syn. for *Cenchrus americanus*, *Sorghum*), as has been done in other contexts (see Hahn et al., 2021), the above-mentioned size overlaps with wild grass taxa (see Bonnefille and Riollet, 1980) in the summer rainfall areas of South Africa where the early farmers settled. Also, large Poaceae pollen (>40 µm) grains may not reflect cultivated grasses in the Fynbos, as they are commonly found in pollen records before the first millennium AD when farming was known to have started in southern Africa (e.g., Baxter, 1996). So, caution must be taken in interpreting them as cultivated cereals in the Fynbos.

### Increase in spores of coprophilous fungi

Abundant fungal spores (e.g., *Sordaria*, *Sporormiella*, *Gelasinospora*) commonly associated with dung were recovered in sediment pollen archives in the Savanna, Grasslands and IOCB Biomes, possibly indicating the presence of pastoralism across South Africa, Botswana, and Mozambique beginning as early as 2000–1500 BP (Neumann et al., 2014; Ekblom et al., 2014b; Cordova et al., 2017; Hahn et al., 2021). Palaeoecological studies focused on dung fungal spores have shown that their presence is often associated with the dung of herbivores (Cugny et al., 2010; Baker et al., 2013; Cheruiyot et al., 2020; van Asperen et al., 2020), though some fungal taxa (e.g., *Gelasinospora*) grow rapidly on other substrates (Cheruiyot et al., 2020; van Asperen et al., 2020). Thus, a significant increase in dung fungal spores is a potential indicator of grazing particularly during known periods of pastoralism in the archaeological record especially if spores of coprophilous fungi co-occur with e.g., pollen of crops and weeds. It is worth noting that the absence of dung fungal spores in records from other biomes of southern Africa (e.g., Fynbos) does not preclude pastoralism, as their presence is more remarkable than their absence (see Cheruiyot et al., 2020).

### Increase in ruderal species

Ruderal species (e.g., *Tribulus*) are known to spread rapidly in highly disturbed areas, which may be due to climate change and/or anthropogenic impact from pastoralism and farming (Grime, 1979; Cilliers and Bredenkamp, 1999; Verdú and Mas, 2006). The increase of *Tribulus*, which is often associated with increased grazing pressure (Li et al., 2008), coincided with the decline of trees across the Savanna, Nama-Karoo and marine sites in offshore Namibia

(Scott et al., 1991; Gil-Romera et al., 2007; Shi et al., 1998) possibly suggesting widespread anthropogenic activities, particularly pastoralism, in the region. The role of *Tribulus* as an anthropogenic indicator is underlined by the palynological results of our preliminary study on early second millennium AD cattle dung from the SLCA region (Mvelase, 2021).

## PATTERNS OF VEGETATION CHANGE

The archaeobotanical data across the biomes of southern Africa showed similar changes in vegetation during the first millennium AD (see Table 1). This was marked by the decline of forest elements (e.g., *Podocarpus*), the spread of open-land/disturbance indicators (e.g., Amaranthaceae, Asteraceae, Oxalidaceae, Plantaginaceae, Montiniaceae), as well as an extension of savanna and/or pioneer trees and coprophilous fungi (e.g., *Sordaria*, *Sporormiella*). Considering that southern African climates are diverse with a high degree of temporal and spatial variability across the region, it is unlikely that the climate in different biomes fluctuated in the same way during the first millennium AD (see Tyson and Preston-Whyte, 2000; Chevalier and Chase, 2016). More likely, anthropogenic impact is responsible for similar palynological fluctuations for this period.

Increased charred fragments were observed at several sites across all the biomes (e.g., Versailles, Mahwaqa Mountain, Mdlanzi Swamp, PrincessVlei, GeoB 1023) except in the Nama-Karoo and Desert Biomes. This is likely due to the lack of combustible mass in the two biomes (see Bond, 1997; Allen et al., 2011; Muller et al., 2016).

Also, essential resources probably played a role in site selection by pastoralists and early farmers, with fertile soils, grazing fields, an adequate supply of water and wood, and a favourable climate being likely factors. In South Africa, the early sites clustered around the northeastern region (see Fig. 1), attesting to the fact that early pastoralists and farmers likely favoured relatively lower altitudes with nutrient-rich colluvial soils and sweetveld which allowed grazing (e.g., Maggs and Ward, 1984; Parkington and Hall, 2010). This is also supported by preserved charred seed remains, which are limited to the savanna and grasslands (see Table 1). While the soils in the grasslands are especially suitable for growing cultivated grasses, pastoralists and early farmers initially avoided higher altitude regions due to highly variable rainfall, severe

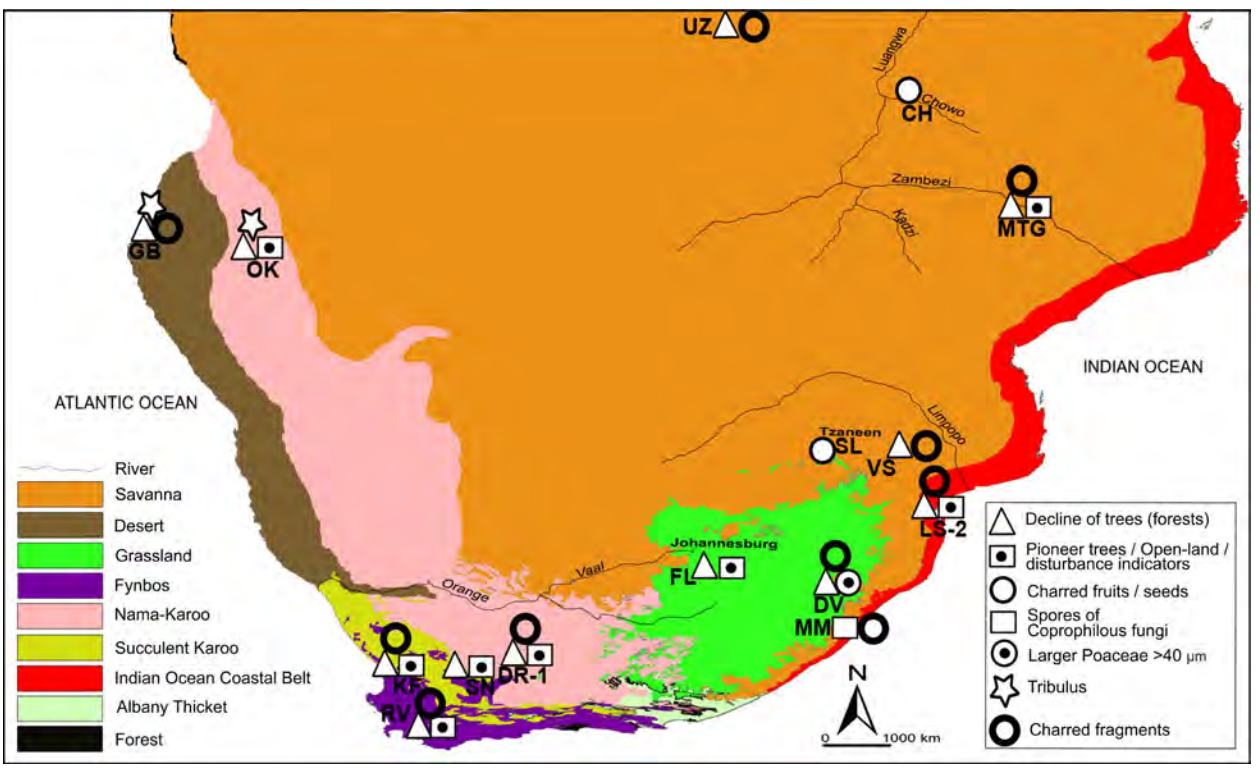


**Figure 2**. Map of southern Africa showing sites with the first occurrence of potential anthropogenic impacts in each region (adapted after Mucina and Rutherford 2006). Site abbreviations are listed in Table 1 according to biome and country

frost occurrence and low winter temperatures unfavourable for crops and livestock (see Huffman, 1996; Eeley et al., 1999; Sadr, 2020).

Furthermore, the likely anthropogenic impact observed from the archaeobotanical data suggests the continuing presence of pastoralism and farming in southern Africa beginning from ~1900–1600 BP across the Savanna, Grassland, Fynbos, and IOCB Biomes (see Figs 1 and 2). Later sites within these biomes indicated a concentration of evidence of anthropogenic impact within much of the interior, suggesting a likely spread. At ~1500 BP, a wide expansion of pastoralists/farmers into other areas of southern Africa is suggested, as revealed by a general and wide increase of archaeobotanical data showing vegetation changes likely due to anthropogenic impact (see Fig. 1). However, the records showed that the drier regions e.g., Nama-Karoo and desert were likely explored much later ~1450–1300 BP (Fig. 1). Hence, the anthropogenic disturbances might be blurred by vegetation changes due to climatic fluctuations, and vice versa.

Currently, there is a strong bias towards the understanding of climate fluctuations, rather than anthropogenic drivers, during the late Holocene in palynological studies in southern Africa (see Dubois et al., 2018). On the other hand, many indicators for intense droughts are also regarded as signals for human disturbances. We suggest that the vegetation shifts cannot be fully explained solely by climate variations particularly the gradual replacement of forest tree pollen with open-land indicators at individual sites. More often, regional pollen composition is an indicator of climate (Scott et al., 2012), while the pollen composition from local sites typically reflects the impact of anthropogenic activities and/or climate as well as other landform processes shaping the landscapes (Li et al., 2008). Thus, anthropogenic disturbances (e.g., cultivation, fire, grazing) can transform the landscapes independently of, or in conjunction with climate change, and might result in changes in the vegetation composition (Li et al., 2008; Gillson and Ekblom, 2020).

Furthermore, larger Poaceae (>40μm) pollen grains, as well as macro-charcoal, often reflect local signals due to short dispersal distances (see Edwards and McIntosh, 1988; Whittington et al. 1991), thus it is important to identify likely anthropogenic impact within a localized area. Similarly, differentiating between local and regional pollen taxa through the analysis of modern pollen-vegetation relationships fosters a more accurate interpretation of the major driver(s) of vegetation changes (see Ekblom et al., 2017; Chen et al., 2017; Geng et al., 2019). These coupled with supporting archaeological evidence of human habitation in the area facilitate the identification of likely anthropogenic disturbances as local signals.

Also, palaeoclimate studies have shown that climate in the different biomes did not fluctuate in the same way throughout the region during the late Holocene (Chevalier and Chase, 2015, 2016). For instance, although much of the observed climate variability along the eastern African margin has been attributed to changes in global conditions, the observed variations within the central and eastern South African sites, particularly during the Late Holocene, remain patchy. This lack of consistent patterning between these sites may be due to varying degrees of anthropogenic disturbances. However, the pollen data we reviewed showed similar patterns of vegetation disturbance, particularly with the decline in forests and increased open-land indicators across all the biomes for the first millennium AD.

While much of our focus in the paper has been on the decline of trees, recovery patterns are also important. For example, forest trees, which are less capable of recovery in a fire-dominated environment, mostly do not recover once they have declined, while savanna trees, which are in contrast better adapted to regenerate in such environments, prevail (Gillson and Ekblom, 2020).

## SUMMARY

A synthesis of archaeobotanical proxies within the context of existing macro-botanical and archaeological data shows the potential of exploring the beginnings and spread of pastoralism and farming in southern Africa during the first millennium AD. The pollen records indicate a distinct pattern of vegetation change evident in the decline of trees (forest), an increase of open-land indicators/pioneer trees, spores of coprophilous fungi, *Tribulus*, large Poaceae pollen (>40 μm) and charred fragments. While the data show a continuing presence of pastoralism and farming from

~2000–1000 BP in southern Africa, convincing evidence for the beginnings of likely anthropogenic impact are documented between ~1900 and 1600 BP across the Savanna, Grassland, Fynbos and IOCB Biomes, and ~1450–1300 BP in the Nama-Karoo and Desert. Also, a widespread increase of archaeobotanical data showing similar vegetation changes possibly from anthropogenic impact suggests an expansion of pastoralists and/or farmers into other areas of southern Africa at ~1500 BP.

However, our conclusions are tentative considering the bias in the archaeobotanical data towards areas where research has been focused. We hope that additional research in these countries and other under-represented areas will help to improve the overall picture and patterns of the emergence and spread of pastoralism and farming in southern Africa.

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## REFERENCES

Albrecht, M., Berke, H., Eichhorn, B., Frank, T., Kuper, R., Prill, S., Vogelsang, R., Wenzel, S., 2001. Oruwanje 95/1: a late Holocene stratigraphy in northwestern Namibia. Cimbebasia 17, 1–22.

Allen, E.B., Steers, R.J., Dickens, S.J., 2011. Impacts of fire and invasive species on desert soil ecology. Rangeland Ecology & Management 64, 450–462. https://doi.org/10.2111/REM-D-09-00159.1

Andah, B.W., 1979. Iron Age Beginnings in West Africa: Reflections and Suggestions in Perspectives on West Africa's Past. West African Journal of Archaeology 9, 135–150.

Andah, B.W., 1995. The earliest human occupation and settlement in West Africa. The Epistemology of west African Settlements. Andah. African Peoples and Their Cultural Resources Series 25, 8–33.

Andersen, S.T., 1979. Identification of wild grass and cereal pollen [fossil pollen, Annulus diameter, surface sculpturing]. Danmarks Geologiske Undersoegelse Aarbog, 69–92.

Antonites, A., Antonites, A.R., 2014. The Archaeobotany of Farming Communities in South Africa. In: Stevens, C.J., Nixon, S., Murray, M.A., Fuller, D.Q. (eds), The Archaeology of African Plant Use. Left Coast Press, Walnut Creek, pp. 225–232.

Avery, G., 1974. Open station shell midden sites and associated features from the Pearly Beach area, southwestern Cape. South African Archaeological Bulletin 29, 104–114. https://doi.org/10.2307/3888336

Badenhorst, S., 2006. Goats (*Capra hircus*), the Khoekhoen and pastoralism: current evidence from southern Africa. African Archaeological Review 23, 45–53. https://doi.org/10.1007/s10437-006-9007-0

Badenhorst, S., Sinclair, P., Ekblom, A., Plug, I., 2011. Faunal remains from Chibuene, an Iron Age coastal trading station in central Mozambique. Southern African Humanities 23, 1–15.

Baker, A.G., Bhagwat, S.A., Willis, K.J., 2013. Do dung fungal spores make a good proxy for past distribution of large herbivores?. Quaternary Science Reviews 62, 21–31. https://doi.org/10.1016/j.quascirev.2012.11.018

Barham, L., Jarman, C.L., 2005. New radiocarbon dates for the Early Iron Age in the Luangwa Valley, eastern Zambia. Azania: Journal of the British Institute in Eastern Africa 40, 114–121. https://doi.org/10.1080/00672700509480417

Baxter, A.J., 1996. Late Quaternary palaeoenvironments of the Sandveld, Western Cape Province, South Africa. PhD thesis, University of Cape Town, Cape Town.

Baxter, A.J., Davies, B.R., 1994. Palaeoecological insights for the conservation of aquatic ecosystems in dryland environments: a case study of the Verlorenvlei system, South Africa Aquatic Conservation. Marine and Freshwater Ecosystems 4, 255–271. https://doi.org/10.1002/aqc.3270040306

Beaumont, P.B., Vogel, J.C., 1972. On a new radiocarbon chronology for Africa south of the Equator: part 2. African Studies 31, 155–182. https://doi.org/10.1080/00020187208707381

Bond, W.J., 1997. Fire. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (eds), Vegetation of Southern Africa. Cambridge University Press, Cambridge.

Bonnefile, R., Riollet, G., 1980. Pollens des savanes O'Afrique Orienta1e. Editions du Centre National de la Recherche Scientifique, Paris.

Bousman, C.B., 1991. Holocene paleoecology and Later Stone Age hunter-gatherer adaptations in the South African interior plateau. PhD thesis, Southern Methodist University, Dallas.

Bousman, B., Scott, L., 1994. Climate or overgrazing?: the palynological evidence for vegetation change in the eastern Karoo. South African Journal of Science 90, 575–578.

Bousman, B.C., Mauldin, R., Zoppi, U., Higham, T., Scott, L., Brink, J., 2016. The quest for evidence of domestic stock at Blydefontein Rock Shelter. Southern African Humanities 28, 39–60.

Breman, E., Gillson, L., Willis, K., 2011. How fire and climate shaped grass-dominated vegetation and forest mosaics in northern South Africa during past millennia. The Holocene 22, 1427–1439. https://doi:10.1177/0959683611400196

Brink, J., Webley, L., 1996. Faunal evidence for pastoralist settlement at Jakkalsberg, Richtersveld, northern Cape Province. Southern African Field Archaeology 5, 70–78.

Bromilow, C., 2018. Problem Plants and Alien Weeds of Southern Africa. Briza, Pretoria, South Africa, 464 pp.

Bronk Ramsey, C., 2017. OxCal 4.3 Manual. OxCal Program 4.3. Oxford Radiocarbon Accelerator Unit, University of Oxford.

Brook, G.A., Scott, L., Railsback, L.B., Goddard, E.A., 2010. A 35 ka pollen and isotope record of environmental change along the southern margin of the Kalahari from a stalagmite and animal dung deposits in Wonderwerk Cave, South Africa. Journal of Arid Environments 74, 870–884. https://doi.org/10.1016/j.jaridenv.2009.11.006

Burrough, S.L., Willis, K.J., 2015. Ecosystem resilience to late-Holocene climate change in the Upper Zambezi Valley. The Holocene 25, 1811–1828. https://doi.org/10.1177/0959683615591355

Campbell, A.C., Van Waarden, C., Holmberg, G., 1996. Variation in the early iron age of southeastern. Botswana Botswana Notes and Records, 1–22.

Carrión, J.S., Scott, L., Huffman, T., Dreyer, C., 2000. Pollen analysis of Iron Age cow dung in southern Africa. Vegetation History and Archaeobotany 9, 239–249. https://doi.org/10.1007/BF01294638

Castilla-Beltrán, A., de Nascimento, L., Fernández-Palacios, J.M., Whittaker, R.J., Romeiras, M.M., Cundy, A.B., Edwards, M., Nogué, S., 2021. Effects of Holocene climate change, volcanism and mass migration on the ecosystem of a small, dry island (Brava, Cabo Verde). Journal of Biogeography 48, 1392–1405. https://doi.org/10.1111/jbi.14084

Chen, X., Huang, X., Wu, D., Zhang, X., Dodson, J., Zhou, A., Chen, F., 2017. Modern pollen assemblages in topsoil and surface sediments of the Xingyun Lake catchment, central Yunnan Plateau, China, and their implications for interpretation of the fossil pollen record. Review of Palaeobotany and Palynology 241, 1–12. https://doi.org/10.1016/j.revpalbo.2017.01.003

Cheruiyot, V.C., Gebregiorgis, D., Opiyo, B., Kiage, L.M., 2020. Revisiting the palaeoenvironmental and climatic history of the Cherangani Hills using fungal spores. Journal of Quaternary Science 35, 737–742. https://doi.org/10.1002/jqs.3223

Chevalier, M., Chase, B.M., 2015. Southeast African records reveal a coherent shift from high-to low-latitude forcing mechanisms along the east African margin across last glacial–interglacial transition. Quaternary Science Reviews 125, 117–130. https://doi.org/10.1016/j.quascirev.2015.07.009

Chevalier, M., Chase, B.M., 2016. Determining the drivers of long-term aridity variability: a southern African case study. Journal of Quaternary Science 31, 143–151. https://doi.org/10.1002/jqs.2850

Chevalier, M., Chase, B.M., Quick, L.J., Scott, L., 2021. An Atlas of Southern African pollen taxa and their climatic affinities. In: Runge, J., Gosling, W.D., Lézine A-M., Scott, L. (eds), Quaternary Vegetation Dynamics: The African Pollen Database. CRC Press/Balkema, The Netherlands, pp. 239–257.

Cilliers, S.S., Bredenkamp, G.J., 1999. Ruderal and degraded natural vegetation on vacant lots in the Potchefstroom Municipal Area, North West Province, South Africa. South African Journal of Botany 65(2), 163–173. https://doi.org/10.1016/S0254-6299(15)30956-X

Cordova, C.E., Scott, L., Chase, B.M., Chevalier, M., 2017. Late pleistocene-holocene vegetation and climate change in the middle kalahari, lake Ngami, Botswana. Quaternary Science Reviews 171, 199–215. https://doi.org/10.1016/j.quascirev.2017.06.036

Cordova, C.E., Kirsten, K.L., Scott, L., Meadows, M., Luecke, A., 2019. Multi-proxy evidence of late-Holocene paleoenvironmental change at Princessvlei, South Africa: The effects of fire, herbivores, and humans. Quaternary Science Reviews 221, 105896. https://doi.org/10.1016/j.quascirev.2019.105896

Coulson, S., Segadika, P., Walker, N., 2016. Ritual in the Hunter-Gatherer/Early Pastoralist Period: Evidence from Tsodilo Hills, Botswana. African Archaeological Review 33, 205–222. https://doi.org/10.1007/s10437-016-9218-y

Crowther, A., Prendergast, M.E., Fuller, D.Q., Boivin, N., 2018. Subsistence mosaics, forager-farmer interactions, and the transition to food production in eastern Africa. Quaternary International 489, 101–120. https://doi.org/10.1016/j.quaint.2017.01.014

Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. Vegetation History and Archaeobotany 19, 391–408. https://doi:10.1007/s00334-010-0242-6

Davis, O.K., Shafer, D.S., 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. Palaeogeography, Palaeoclimatology, Palaeoecology 237, 40–50. https://doi.org/10.1016/j.palaeo.2005.11.028

Deacon, H.J., Deacon, J., Brooker, M., Wilson, M.L., 1978. The evidence for herding at Boomplaas Cave in the southern Cape, South Africa. South African Archaeological Bulletin 33, 39–65. https://doi.org/10.2307/3888251

Denbow, J., 1986. A New Look at the Later Prehistory of the Kalahari. The Journal of African History 27, 3–28. https://doi:10.1017/S0021853700029170

Denbow, J.R., Wilmsen, E.N., 1986. Advent and course of pastoralism in the Kalahari. Science 234, 1509–1515. https://doi.org/10.1126/science.234.4783.1509

Dubois, N., Saulnier-Talbot, É., Mills, K., Gell, P., Battarbee, R., Bennion, H., Chawchai, S., Dong, X., Francus, P., Flower, R., 2018. First human impacts and responses of aquatic systems: A review of palaeolimnological records from around the world. The Anthropocene Review 5, 28–68. https://doi.org/10.1177/2053019617740365

Du Plessis, N., 2015. 4000 years of environmental and climate change at Eilandvlei: a palynological investigation into the late Holocene palaeoenvironment of the Wilderness Embayment. Masters thesis, University of Capetown, Capetown.

Dull, R.A., 2004. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. Quaternary Research 61, 159–167. https://doi:10.1016/j.yqres.2004.01.002

Edwards, K.J., McIntosh, C.J., 1988. Improving the detection rate of cereal-type pollen grains from Ulmus decline and earlier deposits from Scotland. Pollen et spores 30,179–188

Eeley, H.A.C., Lawes, M.J., Piper, S.E., 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. Journal of Biogeography 26, 595–617. https://doi.org/10.1046/j.1365-2699.1999.00307.x

Ehret, C., 2020. The First Spread of Food Production to Southern Africa. In: Ehret, C., Posnansky, M. (eds), The Archaeological and Linguistic Reconstruction of African History. University of California Press, California, pp. 158–181. https://doi.org/10.1525/9780520314757-010

Ekblom, A., 2004. Changing landscapes: An environmental history of Chibuene, southern Mozambique, Global Studies in Archaeology 5. Uppsala: Department of Archaeology and Ancient History.

Ekblom, A., 2008. Forest–savanna dynamics in the coastal lowland of southern Mozambique since c. AD 1400. The Holocene 18, 1247–1257. https://doi.org/10.1177/0959683608096599

Ekblom, A., Risberg, J., Holmgren, K., 2014a. Coastal forest and Miombo woodland history of the Vilankulo region, Mozambique. The Holocene 24, 284–294. https://doi.org/10.1177/0959683613518592

Ekblom, A., Eichhorn, B., Sinclair, P., Badenhorst, S., Berger, A., 2014b. Land use history and resource utilisation from AD 400 to the present, at Chibuene, southern Mozambique. Vegetation History and Archaeobotany 23(1), 15–32. https://doi.org/10.1007/s00334-013-0392-4

Ekblom, A., Gillson, L., Notelid, M., 2017. Water flow, ecological dynamics, and management in the lower Limpopo Valley: a long-term view. Wiley Interdisciplinary Reviews: Water 4, e1228. https://doi.org/10.1002/wat2.1228

Elphick, R., 1977. Kraal and Castle: Khoikhoi and the Founding of Whie South Africa. New Heaven, Connecticut. Yale University Press.

Elphick, R., 1985. Khoikhoi and the founding of white South Africa. Johannesburg. Ravan Press.

Evers, T.M., 1974. Three Iron Age industrial sites in the eastern Transvaal Lowveld. PhD thesis, University of the Witwatersrand, Johannesburg.

Feely, J.M., Bell-Cross, S.M., 2011. The distribution of early iron age settlement in the Eastern Cape: some historical and ecological implications. South African Archaeological Bulletin 66, 105–112.

Finch, J.M., Hill, T.R., 2008. A late Quaternary pollen sequence from Mfabeni Peatland, South Africa: Reconstructing forest history in Maputaland. Quaternary Research 70, 442–450. https://doi.org/10.1016/j.yqres.2008.07.003

Fitchett, J.M., Bamford, M.K., 2017. The validity of the Asteraceae: Poaceae fossil pollen ratio in discrimination of the southern African summer- and winter-rainfall zones. Quaternary Science Reviews 160, 85–95. https://doi.org/10.1016/j.quascirev.2017.02.008

Fitchett, J.M., Grab, S.W., Bamford, M.K., Mackay, A.W., 2016. A multi-proxy analysis of late Quaternary palaeoenvironments, Sekhokong Range, eastern Lesotho. Journal of Quaternary Science 31, 788–798. https://doi.org/10.1002/jqs.2902

Fuller, D.Q., Hildebrand, E., 2013. Domesticating plants in Africa. In: Mitchell, P., Lane, P. (eds),The Oxford handbook of African Archaeology. Oxford University Press, Oxford, pp. 507–525.

Garlake, P.S., 1982. Prehistory and ideology in Zimbabwe. Africa, 1–19.

Geer, A., 2013. Holocene environmental changes derived from a montane pollen sequence in the KwaZulu-Natal midlands, South Africa. Masters thesis, University of KwaZulu-Natal, Pietermaritzburg.

Geng, R., Zhao, Y., Cui, Q., Qin, F., 2019. Representation of modern pollen assemblages with respect to vegetation and climate in Northeast China. Quaternary International 532, 126–137. https://doi.org/10.1016/j.quaint.2019.11.003

Gillson, L., Ekblom, A., 2020. Using palaeoecology to explore the resilience of southern African savannas. Koedoe: African Protected Area. Conservation and Science 62, 1–12. https://doi.org/10.4102/koedoe.v62i1.1576

Gil-Romera, G., Scott, L., Marais, E., Brook, G.A., 2006. Middle-to late-Holocene moisture changes in the desert of northwest Namibia derived from fossil hyrax dung pollen. The Holocene 16, 1073–1084. https://doi.org/10.1177/0959683606069397

Gil-Romera, G., Scott, L., Marais, E., Brook, G.A., 2007. Late Holocene environmental change in the northwestern Namib Desert margin: new fossil pollen evidence from hyrax middens. Palaeogeography, Palaeoclimatology, Palaeoecology 249, 1–17. https://doi.org/10.1016/j.palaeo.2007.01.002

Goodale, U.M., Ashton, M.S., Berlyn, G.P., Gregoire, T.G., Singhakumara, B.M.P., Tennakoon, K.U., 2012. Disturbance and tropical pioneer species: Patterns of association across life history stages. Forest Ecology and Management 277, 54–66. https://doi.org/10.1016/j.foreco.2012.04.020

Govender, N., Trollope, W.S.W., Van Wilgen, B.W., 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. Journal of Applied Ecology 43, 748–758. https://doi.org/10.1111/j.1365-2664.2006.01184.x

Grime, J.P., 1979. Plant strategies and vegetation processes. New York. John Wiley and Sons.

Guldemann, T., 2008. A linguist's view: Khoe-Kwadi speakers as the earliest food-producers of southern Africa. Southern African Humanities 20, 93–132.

Hahn, A., Neumann, F.H., Miller, C., Finch, J., Frankland, T., Cawthra, H.C., Schefuß, E., Zabel, M., 2021. Mid-to Late Holocene climatic and anthropogenic influences in Mpondoland, South Africa. Quaternary Science Reviews 261, 106938. https://doi.org/10.1016/j.quascirev.2021.106938

Hall, M., 1980. Man's role in the development of threatened habitats HABCON. Working Document, vol. 5, CSIR, Pretoria.

Hall, M., 1983. Tribes, traditions and numbers: The American model in southern African Iron Age ceramic studies. South African Archaeological Bulletin 38, 51–57. https://doi.org/10.2307/3888636

Hall, M., 1984. Man's historical and traditional use of fire in southern Africa. In: Booysen, P. de V., Tainton, N.M. (eds), Ecological effects of fire in South African ecosystems. Springer- Verlag, Berlin, pp. 39–52. https://doi.org/10.1007/978-3-642-69805-7_3

Hall, M., Morris, A., 1983. Race and Iron Age human skeletal remains from southern Africa: an assessment. Social Dynamics 9, 29–36. https://doi.org/10.1080/02533958308458344

Henn, B.M., Gignoux, C., Lin, A.A., Oefner, P.J., Shen, P., Scozzari, R., Cruciani, F., Tishkoff, S.A., Mountain, J.L., Underhill, P.A., 2008. Y-chromosomal evidence of a pastoralist migration through Tanzania to southern Africa. Proceedings of the National Academy of Sciences 105, 10693–10698. https://doi.org/10.1073/pnas.0801184105

Henshilwood, C., 1996. A revised chronology for pastoralism in southernmost Africa: new evidence of sheep at c. 2000 bp from Blombos Cave, South Africa. Antiquity 70, 945–949. https://doi.org/10.1017/S0003598X00084210

Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. Radiocarbon 55, 1889–1903. https://doi.org/10.2458/azu_js_rc.55.16783

Huffman, T.N., 1970. The Early Iron Age and the spread of the Bantu. South African Archaeological Bulletin 25, 3–21. https://doi.org/10.2307/3888762

Huffman, T.N., 1971. Excavations at Leopard's Kopje Main Kraal: a preliminary report. The South African Archaeological Bulletin, 85–89.

Huffman, T.N., 1979. African origins. South African Journal of Science 75, 233–237.

Huffman, T.N., 1982. Archaeology and ethnohistory of the African Iron Age. Annual Review of Anthropology 11, 133–150. https://doi.org/10.1146/annurev.an.11.100182.001025

Huffman, T.N., 1993. Broederstroom and the central cattle pattern. South African Journal of Science 89, 220–226.

Huffman, T.N., 1996. Archaeological evidence for climatic change during the last 2000 years in southern Africa. Quaternary International 33, 55–60. https://doi.org/10.1016/1040-6182(95)00095-X

Huffman, T.N., 1998. Presidential address: the antiquity of lobola. South African Archaeological Bulletin 53, 57–62. https://doi.org/10.2307/3889180

Huffman, T.N., 2007. Handbook to the Iron Age. Pietermaritzburg. University of KwaZulu-Natal Press.

Jerardino, A., Fort, J., Isern, N., Rondelli, B., 2014. Cultural diffusion was the main driving mechanism of the Neolithic transition in southern Africa. PloS one 9, e113672. https://doi.org/10.1371/journal.pone.0113672

Johannsmeier, M.F., 2016. Bee plants of South Africa. Sources of nectar, pollen, honeydew and propolis for honeybees. South African National Biodiversity Institute.

Jordaan, G., 2017. An archaeological study of two Early Farming sites in the southern Kruger National Park, South Africa: Masters thesis. University of Pretoria, Pretoria.

Katsamudanga, S., Pwiti, G., 2017. Chronology of Early Farming Communities of northern Zimbabwe: a Reappraisal. In: Manyanga, M., Chirikure, S. (eds), Archives, Objects, Places and Landscapes: Multidisciplinary approaches to Decolonized Zimbabwean pasts. Langaa Research and Publishing CIG, Bamenda, Cameroon, pp. 119–136.

Kinahan, J., 2005. The late Holocene human ecology of the Namib Desert. M. Smith & P. Hesse (eds.) 23, 120–131.

Kjellmark, E., 1996. Late Holocene climate change and human disturbance on Andros Island, Bahamas. Journal of Paleolimnology 15, 133–145. https://doi.org/10.1007/BF00196777

Klapwijk, M., 1974. A preliminary report on pottery from the north-eastern Transvaal, South Africa. South African Archaeological Bulletin 29, 19–23. https://doi.org/10.2307/3887933

Klapwijk, M., Huffman, T., 1996. Excavations at Silver Leaves: A preliminary report. South African Archaeological Bulletin 51, 84–93.

Klein, R.G., 1986. The prehistory of Stone Age herders in the Cape Province of South Africa. South African Archaeological Bulletin Goodwin Series 5, 5–12. https://doi.org/10.2307/3858140

Lander, F., Russell, T., 2018. The Archaeological evidence for the appearance of Pastoralism and Farming in southern Africa. PloS ONE 13(6), e0198941. https://doi.org/10.1371/journal.pone.0198941

Lander, F., Russell, T., 2020. A southern African archaeological database of organic containers and materials, 800 cal BC to cal AD 1500: Possible implications for the transition from foraging to livestock-keeping. PLoS ONE 15, e0235226. https:// doi:10.1371/journal.pone.0235226

Lane, P., 2004. The 'moving frontier'and the transition to food production in Kenya. Azania: Journal of the British Institute in Eastern Africa 39, 243–264. https://doi.org/10.1080/00672700409480402

Lebamba, J., Vincens, A., Lézine, A-M., Marchant, R., Buchet, G., 2016. Forest-savannah dynamics on the Adamawa plateau (Central Cameroon) during the "African humid period" termination: A new high-resolution pollen record from Lake Tizong. Review of Palaeobotany and Palynology 235, 129–139. https://doi.org/10.1016/j.revpalbo.2016.10.001

Lenssen-Erz, T., Vogelsang, R., 2005. Populating No-Man's-Land: Rock art in northern Namibia. South African Archaeological Bulletin Goodwin Series 9, 54–62.

Li, S., Schlebusch, C., Jakobsson, M., 2014. Genetic variation reveals large-scale population expansion and migration during the expansion of Bantu-speaking peoples. Proceedings of the Royal Society B: Biological Sciences 281, 20141448. https://doi.org/10.1098/rspb.2014.1448

Li, Y., Zhou, L., Cui, H., 2008. Pollen indicators of human activity. Chinese Science Bulletin 53, 1281–1293. https:// doi:10.1007/s11434-008-0181-0

Lim, S., Chase, B.M., Chevalier, M., Reimer, P.J., 2016. 50,000 years of vegetation and climate change in the southern Namib Desert, Pella, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 451, 197–209. https://doi.org/10.1016/j.palaeo.2016.03.001

MacDevette, D.R., MacDevette, D.K., Gordon, I.G., Bartholomew, R.L.C., 1989. Floristics of the Natal indigenous forests. In: Geldenhuys, C.J. (ed.), Biogeography of the Mixed Evergreen Forests of southern Africa. Foundation of Research Development, Pretoria, pp. 124–145.

Madiquida, H., 2006. The Iron Age communities in the Zambezi river basin: excavations in Mozambique. SAFA 23–26 June, 2006, University of Calgary, Alberta, Canada.

Maggs, T., 1980a. The Iron Age Sequence South of the Vaal and Pongola Rivers: some Historical Implications. The Journal of African History 21, 1–15. https://doi:10.1017/S0021853700017825

Maggs, T., 1980b. Mzonjani and the beginning of the Iron Age in Natal. Annals of the Natal Museum 24, 71–96.

Maggs, T., 1984. The Iron Age south of the Zambezi. In: Klein, R.G. (ed.), Southern African Prehistory and Palaeoenvironments. Balkema, Rotterdam, pp. 329–361.

Maggs, T., 1994. The Early Iron Age in the extreme south: some patterns and problems. Azania: Archaeological Research in Africa 29, 168–178. https://doi.org/10.1080/00672709409511669

Maggs, T., Ward, V., 1984. Early Iron Age sites in the Muden area of Natal. Annals of the Natal Museum 26, 105–140.

Maggs, T., Whitelaw, G., 1991. A review of recent archaeological research on food-producing communities in southern Africa. The Journal of African History 32, 3–24. https://doi.org/10.1017/S0021853700025317

Marais, E., Scott, L., Gil-Romera, G., Carrión, J.S., 2015. The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia. Transactions of the Royal Society of South Africa 70, 109–115. https://doi.org/10.1080/0035919X.2014.999734

Marker, M.E., Evers, T.M., 1976. Iron Age Settlement and Soil Erosion in the Eastern Transvaal, South Africa. South African Archaeological Bulletin 31, 153–165. https://doi:10.2307/3887737

Marks, S.J., Montinaro, F., Levy, H., Brisighelli, F., Ferri, G., Bertoncini, S., Batini, C., Busby, G.B.J., Arthur, C., Mitchell, P., 2015. Static and moving frontiers: the genetic landscape of Southern African Bantu-speaking populations. Molecular Biology and Evolution 32, 29–43. https://doi.org/10.1093/molbev/msu263

Mason, R., 1981. Early Iron Age settlement at Broederstroom 24/73, Transvaal, South Africa. South African Journal of Science 77, 401–416.

Mason, R.J, 1986. Origins of Black People of Johannesburg and the Southern Western Central Transvaal, AD 350–1880 (Occasional Paper 16). University of the Witwatersrand Archaeological Research Unit, Johannesburg.

Mazel, A.D., 1989. People making history: the last ten thousand years of hunter-gatherer communities in the Thukela Basin. Southern African Humanities 1, 1–168.

Mazel, A.D., 1992. Collingham Shelter: the excavation of late Holocene deposits, Natal, South Africa. Southern African Humanities 4, 1–51.

Mazel, A.D., 2022. Mountain living: The Holocene people of the uKhahlamba-Drakensberg, South Africa. Quaternary International 611–612, 190–210. https://doi.org/10.1016/j.quaint.2021.04.039.

McCann, J., 2001. Maize and Grace: History, corn, and Africa's new landscapes, 1500–1999. Comparative Studies in Society and History 43, 246–272. https://doi.org/10.1017/S0010417501003486

McWethy, D.B., Neumann, F.H., Steinbruch, F., Ryan, C.M., Valsecchi, V., 2016. Late Quaternary vegetation development and disturbance dynamics from a peatland on Mount Gorongosa, central Mozambique. Quaternary Science Reviews 137, 221–233. https://doi.org/10.1016/j.quascirev.2016.02.004

Meadows, M.E., Baxter, A.J., 2001. Holocene vegetation history and palaeoenvironments at Klaarfontein Springs, Western Cape, South Africa. The Holocene 11, 699–706. https://doi.org/10.1191/09596830195726

Meadows, M.E., Sugden, J.M., 1991. A vegetation history of the last 14 000 years on the Cederberg, south-western Cape Province. South African Journal of Science 87, 34–43.

Meadows, M.E., Chase, B.M., Seliane, M., 2010. Holocene palaeoenvironments of the Cederberg and Swartruggens mountains, Western Cape, South Africa: pollen and stable isotope evidence from hyrax dung middens. Journal of Arid Environments 74, 786–793. https://doi.org/10.1016/j.jaridenv.2009.04.020

Mercader, J., Sillé, P., 2013. Middle and later stoneage sites from Sofala, Gorongosa (Central Mozambique). Nyame akuma 80, 1–13.

Meyer, A., 1986. 'N Kultuurhistoriese interpretasie van die ystertydperk in die Nasionale Krugerwildtuin. PhD thesis, University of Pretoria, Pretoria.

Miller, D., Whitelaw, G., 1994. Early Iron Age metal working from the site of KwaGandaganda, Natal, South Africa. South African Archaeological Bulletin 49, 79–89. https://doi.org/10.2307/3889226

Miracle, M.P., 1965. The introduction and spread of maize in Africa. Journal of African History 6(1), 39–55.

Mitchell, P., 2002. The Archaeology of southern Africa. Cambridge. Cambridge University Press.

Mitchell, P., 2005. African connections: Archaeological perspectives on Africa and the wider world. Lanham, Maryland. Rowman Altamira press.

Mitchell, P., Whitelaw, G., 2005. The Archaeology of Southernmost Africa from c. 2000 BP to the Early 1800s: A Review of Recent Research. Journal of African History 46, 209–241. https://doi.org/10.1017/S0021853705000770

Mitchell, P.J., 1996. Sehonghong: the late Holocene assemblages with pottery. South African Archaeological Bulletin 51, 17–25. https://doi.org/10.2307/3888928

Moore, M.P.J., 1981. The Iron age of the Makapan valley area, Central Transvaal. Masters Thesis, Univerisity of the Witwatesrand, Johannesburg.

Morais, J.M., 1988. The Early Farming Communities of Southern Mozambique. Studies in African Archaeology 3, Uppsala University, Uppsala.

Mucina, L., Rutherford, M., 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa.

Muigai, A.W.T., Hanotte, O., 2013. The Origin of African sheep: Archaeological and Genetic perspectives. African Archaeological Review 30, 39–50. https://doi.org/10.1007/s10437-013-9129-0

Muller, K., O'Connor, T.G., Henschel, J.R., 2016. Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa. Journal of Arid Environments 133, 112–121. https://doi.org/10.1016/j.jaridenv.2016.06.010

Muller, M., Siebert, S.J., Ntloko, B.R., Siebert, F., 2021. 'A floristic assessment of grassland diversity loss in South Africa', Bothalia-African Biodiversity and Conservation 51(1), 1–9. http://dx.doi.org/10.38201/btha.abc.v51.i1.11

Mvelase, S., 2021. Palaeoenvironments at the Shashe-Limpopo Confluence Area from 1000 to 1220 AD: Palynological Analysis of Cattle Dung Samples. BSc Honours Thesis, University of the Witwatersrand, Johannesburg.

Nash, D.J., Meadows, M.E., Gulliver, V.L., 2006. Holocene environmental change in the Okavango Panhandle, northwest Botswana. Quaternary Science Reviews 25, 1302–1322. https://doi.org/10.1016/j.quascirev.2005.11.004

Neary, D.G., Leonard, J.M., 2020. Effects of Fire on Grassland Soils and Water: A Review. In: Kindomihou, V.M. , editor. Grasses and Grassland Aspects [Internet]. London: IntechOpen;[cited 2022 Apr 28]. Available from: https://www.intechopen.com/chapters/70724 doi: 10.5772/intechopen.90747

Neumann, F.H., Botha, G.A., Scott, L., 2014. 18,000 years of grassland evolution in the summer rainfall region of South Africa: evidence from Mahwaqa Mountain, KwaZulu-Natal. Vegetation History and Archaeobotany 23, 665–681. https://doi.org/10.1007/s00334-014-0445-3

Neumann, F.H., Scott, L., Bamford, M., 2011. Climate change and human disturbance of fynbos vegetation during the late Holocene at Princess Vlei, Western Cape, South Africa. The Holocene 21, 1137–1149. https://doi.org/10.1177/0959683611400461

Neumann, F.H., Scott, L., Bousman, C., Van As, L., 2010. A Holocene sequence of vegetation change at Lake Eteza, coastal KwaZulu-Natal, South Africa. Review of Palaeobotany and Palynology 162, 39–53. https://doi.org/10.1016/j.revpalbo.2010.05.001

Neumann, F.H., Stager, J.C., Scott, L., Venter, H.J., Weyhenmeyer, C., 2008. Holocene vegetation and climate records from lake Sibaya, KwaZulu-Natal (South Africa). Review of Palaeobotany and Palynology 152, 113–128. https://doi.org/10.1016/j.revpalbo.2008.04.006

Nkala, P., Mango, N.A.R., Corbeels, M., Veldwisch, G.J.A., Huising, E.J., 2011. The conundrum of conservation agriculture and livelihoods in Southern Africa. African Journal of Agricultural Research 6(24), 5520–5528.

Nyakale, M., 1999. Palynology of Late Quaternary deposits from the central plateau, South Africa: Masters thesis. University of the Orange Free State, Bloemfontein.

O'Connor, T.G., van Wilgen, B.W., 2020. The Impact of Invasive Alien Plants on Rangelands in South Africa. In van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (eds), Biological Invasions in South Africa. Springer, Switzerland, pp. 459–487. https://doi.org/10.1007/978-3-030-32394-3_16

Orton, J.D.J., 2013. Late Holocene archaeology in Namaqualand, South Africa: hunter-gatherers and herders in a semi-arid environment. PhD thesis, University of Oxford, Oxford.

Orton J.D.J., Mitchell, P., Klein, R., Steele, T., Horsburgh, K.A., 2013. An early date for cattle from Namaqualand, South Africa: implications for the origins of herding in southern Africa. Antiquity 87, 108–120. https://doi.org/10.1017/S0003598X00048651

Orton, J.D.J., 2015. The Introduction of Pastoralism to southernmost Africa: thoughts on new contributions to an ongoing debate. Azania: Archaeological Research in Africa 50, 250–258. https://doi:10.1080/0067270X.2015.1019262

Parkington, J., 1977. Soaqua: hunter-fisher-gatherers of the Olifants river valley western Cape. South African Archaeological Bulletin 32, 150–157. https://doi.org/10.2307/3888661

Parkington, J., Hall, S., 2010. The appearance of food production in southern Africa 1,000 to 2,000 years ago. The Cambridge History of South Africa 1, 63–111. https://doi.org/10.1017/CHOL9780521517942.003

Parkington, J., Poggenpoel, C., 1987. Diepkloof Rock Shelter. In: Parkington, J., Hall, M. (eds) Papers in the Prehistory of the Western Cape, South Africa. British Archaeological Reports International Series 332(ii), pp. 269–293.

Partridge, T., 1966. Ficus Cave: an Iron Age living site in the central Transvaal. South African Archaeological Bulletin 21, 125–132. https://doi.org/10.2307/3888431

Phillipson, D.W., 1976. Archaeology and Bantu linguistics. World Archaeology 8, 65–82. https://doi.org/10.1080/00438243.1976.9979653

Phillipson, D.W., 1977. The later prehistory of eastern and southern Africa. New York. Africana Pub. Co.

Phillipson, D.W., 2005. African archaeology. Cambridge. Cambridge University Press. Pleurdeau, D., Imalwa, E., Détroit, F., Lesur, J., Veldman, A., Bahain, J-J., Marais, E., 2012. "Of sheep and men": earliest direct evidence of caprine domestication in southern Africa at Leopard Cave (Erongo, Namibia). PloS One 7: e40340. https://doi.org/10.1371/journal.pone.0040340

Pleurdeau, D., Imalwa, E., Détroit, F., Lesur, J., Veldman, A., Bahain, J-J., Marais, E., 2012. "Ofsheep and men": earliest direct evidence of caprine domestication in southern Africa at Leopard Cave (Erongo, Namibia). PLoS ONE 7: e40340.

Prendergast, M.E., 2011. Hunters and herders at the periphery: The spread of herding in eastern Africa. In: Jousse, H., Lesur, J. (eds), People and Animals in Holocene Africa: Recent Advances in Archaeozoology. Africa Magna Verlag, Frankfurt, pp. 43–58.

Pwiti, G., 1996. Settlement and subsistence of prehistoric farming communities in the mid- Zambezi valley, Northern Zimbabwe. The South African Archaeological Bulletin 51, 3–6. https://doi.org/10.2307/3888926

Quick, L., 2009. Late quaternary vegetation history and palaeoenvironments of the Cederberg Mountains, South Africa: evidence from hyrax (Procavia capensis) middens. Masters Thesis, University of Capetown, Capetown.

Quick, L.J., Carr, A.S., Meadows, M.E., Boom, A., Bateman, M.D., Roberts, D.L., Reimer, P.J., Chase, B.M., 2015. A late Pleistocene–Holocene multiproxy record of palaeoenvironmental change from Still Bay, southern Cape Coast, South Africa. Journal of Quaternary Science 30, 870–885. https://doi.org/10.1002/jqs.2825

Quick, L.J., Chase, B.M., Meadows, M.E., Scott, L., Reimer, P.J., 2011. A 19.5 kyr vegetation history from the central Cederberg Mountains, South Africa: palynological evidence from rock hyrax middens. Palaeogeography, Palaeoclimatology, Palaeoecology 309, 253–270. https://doi.org/10.1016/j.palaeo.2011.06.008

Ranciaro, A., Campbell, M.C., Hirbo, J.B., Ko, W.Y., Froment, A., Anagnostou, P., Kotze, M.J., Ibrahim, M., Nyambo, T., Omar, S.A., 2014. Genetic origins of lactase persistence and the spread of pastoralism in Africa. The American Journal of Human Genetics 94, 496–510. https://doi.org/10.1016/j.ajhg.2014.02.009

Robbins, L.H., Campbell, A.C., Murphy, M.L., Brook, G.A., Liang, F., Skaggs, S.A., Srivastava, P., Mabuse, A.A., Badenhorst, S., 2008. Recent archaeological research at Toteng, Botswana: early domesticated livestock in the Kalahari. Journal of African Archaeology 6, 131–149. https://doi.org/10.3213/1612-1651-10106

Robertson, J.H., 2000. Early Iron Age archaeology in central Zambia. Azania: Journal of the British Institute in Eastern Africa 35, 147–182. https://doi.org/10.1080/00672700009511600

Robinson, K.R., 1966. The Leopard's Kopje culture, its position in the Iron Age of Southern Rhodesia. The South African Archaeological Bulletin 21, 5–51.

Roos, C.I., Field, J.S., Dudgeon, J.V., 2016. Anthropogenic burning, agricultural intensification, and landscape transformation in Post-Lapita Fiji. Journal of Ethnobiology 36, 535–553. https://doi.org/10.2993/0278-0771-36.3.535

Rosen, D.Z., Lewis, C.A., Illgner, P.M., 1999. Palaeoclimatic and archaeological implications of organic-rich sediments at Tifftidell Ski Resort, near Rhodes, eastern Cape province, south Africa. Transactions of the Royal Society of South Africa 54, 311–321. https://doi.org/10.1080/00359199909520630

Rotunno, R., Mercuri, A.M., Florenzano, A., Zerboni, A., di Lernia, S., 2020. The Visibility of Mobility: Coprolites, Dung and Neolithic Herders in Central Saharan Rock Shelters Environmental Archaeology, 1–16. https://doi.org/10.1080/14614103.2020.1777057

Russell, T., Silva, F., Steele, J., 2014. Modelling the spread of farming in the Bantu-speaking regions of Africa: an archaeology-based phylogeography. PLoS ONE 9(1), e87854. https://doi:10.1371/journal.pone.0087854

Rutherford, M.C., Westfall, R.H., 1994. Biomes of southern Africa: an objective categorization. Memoirs of the Botanical Survey of South Africa 63, 1–94.

Sadr, K., 2008. Invisible herders? The archaeology of Khoekhoe pastoralists. Southern African Humanities 20, 179–203.

Sadr, K., 2014. Radiocarbon dates, stone tools and the origin of herding on the West Coast of South Africa. Frankfurt. Africa Magna Verlag.

Sadr, K., 2015. Livestock first reached southern Africa in two separate events. PloS ONE 10, e0134215. https://doi.org/10.1371/journal.pone.0134215

Sadr, K., 2019. The 'Neolithic' Concept in South Africa. South African Archaeological Bulletin Goodwin Series 12, 69–71.

Sadr, K., 2020. The Archaeology of Highveld Farming Communities. In: Oxford Research Encyclopedia of African History. https://doi.org/10.1093/acrefore/9780190277734.013.731

Sadr, K., Sampson, C.G., 2006. Through thick and thin: early pottery in southern Africa. Journal of African Archaeology 4, 235–252. https://doi.org/10.3213/1612-1651-10074

Sandelowsky, B.H., 1977. Mirabib-an archaeological study in the Namib. Madoqua, 221–253.

Sarwat, M., Das, S., Srivastava, P.S., 2008. Analysis of genetic diversity through AFLP, SAMPL, ISSR and RAPD markers in Tribulus terrestris, a medicinal herb. Plant Cell Reports 27, 519–528. https://doi.org/10.1007/s00299-007-0478-5

Schweitzer, F.R., 1974. Archaeological evidence for sheep at the Cape. South African Archaeological Bulletin 29, 75–82. https://doi.org/10.2307/3888331

Schweitzer, F.R., Wilson, M.L., 1982. Byneskranskop 1: a late Quaternary living site in the southern Cape Province, South Africa. Annals of the South African Museum 88, 1–203.

Scott, C., 2005. Analysis and interpretation of botanical remains from Sibudu Cave, Kwazulu Natal. Masters Thesis, University of the Witwatersrand, Johannesburg

Scott, J.K., Morrison, S.M., 1996. Variation in populations of *Tribulus terrestris* (Zygophyllaceae). 1. Burr morphology. Australian Journal of Botany 44, 175–190. https://doi.org/10.1071/BT9960175

Scott, K., Plug, I., 2016. Osteomorphology and osteometry versus aDNA in taxonomic identification of fragmentary sheep and sheep/goat bones from archaeological deposits: Blydefontein Shelter, Karoo, South Africa. Southern African Humanities 28, 61–79

Scott, L., 1982a. A Late Quaternary pollen record from the Transvaal bushveld, South Africa. Quaternary Research 17, 339–370. https://doi.org/10.1016/0033-5894(82)90028-X

Scott, L., 1982b. Late Quaternary fossil pollen grains from the Transvaal, South Africa. Review of Palaeobotany and Palynology 36, 241–278. https://doi.org/10.1016/0034-6667(82)90022-7

Scott, L., 1982c. A 5000-year old pollen record from spring deposits in the bushveld at the north of the Soutpansberg, South Africa. Palaeoecology of Africa 14, 45–55.

Scott, L., 1984. Reconstruction of Late Quaternary palaeoenvironments in the Transvaal on the basis of palynological evidence. In: Vogel, J.C. (ed.), Late Cainozoic Palaeoclimates of the Southern Hemisphere. Balkema, Rotterdam, pp. 317–327.

Scott, L., 1987. Late Quaternary forest history in Venda, southern Africa. Review of Palaeobotany and Palynology 53, 1–10. https://doi.org/10.1016/0034-6667(87)90008-X

Scott, L., 1988. Holocene environmental change at western Orange Free State pans, South Africa, inferred from pollen analysis. Palaeoecology of Africa 19, 109–118.

Scott, L., 1996. Palynology of hyrax middens: 2000 years of palaeoenvironmental history in Namibia. Quaternary International 33, 73–79. https://doi.org/10.1016/1040-6182(95)00093-3

Scott, L., 1999. Palynological analysis of the Pretoria Saltpan (Tswaing Crater) sediments and vegetation history in the bushveld savanna biome, South Africa. In: Partridge, T.C. (ed.) Tswaing- investigations into the Origin, Age and Palaeoenvironments of the Pretoria Saltpan. Council for Geosciences, Pretoria, pp. 143–166.

Scott, L., 2002. Microscopic charcoal in sediments: Quaternary fire history of the grassland and savanna regions in South Africa. Journal of Quaternary Science 17, 77–86. https://doi.org/10.1002/jqs.641

Scott, L., 2016. Fluctuations of vegetation and climate over the last 75 000 years in the Savanna Biome, South Africa: Tswaing Crater and Wonderkrater pollen sequences reviewed. Quaternary Science Reviews 145, 117–133. https://doi.org/10.1016/j.quascirev.2016.05.035

Scott, L., Nyakale, M., 2002. Pollen indications of Holocene palaeoenvironments at Florisbad spring in the central Free State, South Africa. The Holocene 12, 497–503. https://doi.org/10.1191/0959683602hl563rr

Scott, L., Thackeray, J.F., 1987. Multivariate analysis of late Pleistocene and Holocene pollen spectra from Wonderkrater, Transvaal, South Africa. South African Journal of Science 83, 93–98.

Scott, L., Vogel, J.C., 1983. Late Quaternary pollen profile from the Transvaal highveld South Africa. South African Journal of Science 79, 266–272.

Scott, L., Woodborne, S., 2007. Vegetation history inferred from pollen in Late Quaternary faecal deposits (hyraceum) in the Cape winter-rain region and its bearing on past climates in South Africa. Quaternary Science Reviews 26, 941–953. https://doi.org/10.1016/j.quascirev.2006.12.012

Scott, L., Bousman, C.B., Nyakale, M., 2005. Holocene pollen from swamp, cave and hyrax dung deposits at Blydefontein (Kikvorsberge), Karoo, South Africa. Quaternary International 129, 49–59. https://doi.org/10.1016/j.quaint.2004.04.006

Scott, L., Cooremans, B., De Wet, J.S., Vogel, J.C., 1991. Holocene environmental changes in Namibia inferred from pollen analysis of swamp and

lake deposits. The Holocene 1, 8–13. https://doi.org/10.1177/095968369100100103

Scott, L., Holmgren, K., Talma, A.S., Woodborne, S., Vogel, J.C., 2003. Age interpretation of the Wonderkrater spring sediments and vegetation change in the Savanna Biome, Limpopo province, South Africa. South African Journal of Science 99, 484–488.

Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E., Metwally, A., 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. Quaternary Science Reviews 32, 100–118. https://doi.org/10.1016/j.quascirev.2011.11.010

Scott, L., Romera, G.G., Marais, E., Brook, G.A., 2018. Pollen in fossil hyrax dung from Marine Isotope Stages 2 and 3 reveals past environments in Namibia. Quaternary International 464, 260–272. https://doi.org/10.1016/j.quaint.2017.06.054

Scott, L., Sobol, M., Neumann, F.H., Gil Romera, G., Fernandez-Jalvo, Y., Bousman, C.B., Horwitz, L.K., van Aardt, A.C., 2022. Late Quaternary palaeoenvironments in the central semi-arid region of South Africa from pollen in cave, pan, spring, stream and dung deposits. Quaternary International 614, 84–97. https://doi.org/10.1016/j.quaint.2020.10.065

Sebata, A., Ngongoni, N.T., Mupangwa, J.F., Nyakudya, I.W., Dube, J.S., 2005. Chemical composition and degradation characteristics of puncture vine (*Tribulus terrestris*). Tropical and Subtropical Agroecosystems 5, 85–89.

Shi, N., Dupont, L.M., Beug, H-J., Schneider, R., 1998. Vegetation and climate changes during the last 21 000 years in SW Africa based on a marine pollen record. Vegetation History and Archaeobotany 7, 127–140. https://doi.org/10.1007/BF01374001

Sinclair, P.J., 1982. Chibuene – an early trading site in southern Mozambique. Paideuma 28, 159–164.

Sinclair, P.J., 1987. Space, time and social formation: a territorial approach to the archaeology and anthropology of Zimbabwe and Mozambique c 0–1700 AD. Societas Archaeologica Upsaliensis, Uppsala.

Sinclair, P.J., Nydolf, N-G., Wickman-Nydolf, G., 1987. Excavations at the University Campus, Maputo, Mozambique, 1984–85. Studies in African Archaeology 1. Maputo and Stockholm: Eduardo Mondlane University and the Central Board of National Antiquities.

Sjöström, J., Norström, E., Risberg, J., Schoeman, M.H., 2017. Late Holocene palaeoenvironmental reconstruction from Mpumalanga Province (South Africa) inferred from geochemical and biogenic proxies. Review of Palaeobotany and Palynology 246, 264–277. https://doi.org/10.1016/j.revpalbo.2017.06.011

Skead, C.J., 1980. Historical mammal incidence in the Cape Province. Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, Cape Town, pp. 11–17.

Smith, A.B., 1987. Seasonal exploitation of resources on the Vredenburg Peninsula after 2000 BP. In: Parkington, J.E., Hall, M. (eds), Papers in the Prehistory of the Western Cape, South Africa. British Archaeological Reports International Series 332, Oxford, pp. 393–402.

Smith, A.B., 1992. Pastoralism in Africa. Origins and Development Ecology. Hurst and Company, Ohio University Press/Witwatersrand University Press, London/Athens/Johannesburg.

Smith, A.B., 2008. Pastoral origins at the Cape, South Africa: influences and arguments. Southern African Humanities 20, 49–60.

Smith, A.B., 2017. Why would southern African hunters be reluctant food producers. Hunter Gatherer Research 2, 415–435. https://doi.org/10.3828/hgr.2016.28

Staver, A.C., Bond, W.J., Stock, W.D., Van Rensburg, S.J., Waldram, M.S., 2009. Browsing and fire interact to suppress tree density in an African savanna. Ecological Applications 19, 1909–1919. https://doi.org/10.1890/08-1907.1

Tabares, X., Mapani, B., Blaum, N., Herzschuh, U., 2018. Composition and diversity of vegetation and pollen spectra along gradients of grazing intensity and precipitation in southern Africa. Review of Palaeobotany and Palynology 253, 88–100. https://doi.org/10.1016/j.revpalbo.2018.04.004

Tomlinson, R.W., 1973. The Inyanga Area: An Essay in Regional Biogeography. University of Rhodesis Ocassional Paper 1, 1–67.

Turner, S., Plater, A., 2004. Palynological evidence for the origin and development of late Holocene wetland sediments: Mdlanzi Swamp, KwaZulu-Natal, South Africa. South African Journal of Science 100, 220–229.

Tyson, P.D., Preston-Whyte, R.A., 2000. Weather and climate of southern Africa. Cape Town. Oxford University Press.

Valsecchi, V., Chase, B.M., Slingsby, J.A., Carr, A.S., Quick, L.J., Meadows, M.E., Cheddadi, R., Reimer, P.J., 2013. A high resolution 15,600-year pollen and microcharcoal record from the Cederberg Mountains, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 387, 6–16. https://doi.org/10.1016/j.palaeo.2013.07.009

Van Asperen, E.N., Kirby, J.R., Shaw, H.E., 2020. Relating dung fungal spore influx rates to animal density in a temperate environment: implications for palaeoecological studies. The Holocene 30, 218–232. https://doi.org/10.1177/0959683619875804

Van Valkenburg, J.L.C.H., Ketner, P., 1994. Vegetation changes following human disturbance of mid-montane forest in the Wau area, Papua New Guinea. Journal of Tropical Ecology 10, 41–54. https://doi.org/10.1017/s0266467400007707

Verdú, A.M.C., Mas, M.T., 2006. Cohort-dependent seedling recruitment, survival and reproductive capacity of *Tribulus terrestris*. Weed Research 46, 371–378. https://doi.org/10.1111/j.1365-3180.2006.00521.x

Vogelsang, R., Eichhorn, B., Richter, J., 2002. Holocene human occupation and vegetation history in northern Namibia. Die Erde 133, 113–132.

Voigt, E.A., 1980. Reconstructing Iron Age economies of the northern Transvaal: a preliminary report. The South African Archaeological Bulletin, 39–45.

Voigt, E.A., 1984. The faunal remains from Magogo and Mhlopeni: small stock herding in the Early Iron Age of Natal. Annals of the Natal Museum 26, 141–163.

Wadley, L., 1978. Later Stone Age hunters and gatherers of the southern Transvaal: social and ecological interpretation (Vol. 25). British Archaeological Reports.

Wadley, L., 1996. Changes in the social relations of precolonial hunter–gatherers after agropastoralist contact: an example from the Magaliesberg, South Africa. Journal of Anthropological Archaeology, 15(2), 205–217. https://doi.org/10.1006/jaar.1996.0008

Walther, S.C., Neumann, F.H., 2011. Sedimentology, isotopes and palynology of late Holocene cores from Lake Sibaya and the Kosi Bay system (KwaZulu-Natal, South Africa). South African Geographical Journal 93, 133–153. https://doi.org/10.1080/03736245.2011.591982

Wang, K., Goldstein, S., Bleasdale M., Clist, B., Bostoen, K., Bakwa-Lufu, P., Buck, L.T., Crowther, A., Dème, A., McIntosh, R.J., 2020. Ancient genomes reveal complex patterns of population movement, interaction, and replacement in sub-Saharan Africa. Science Advances 6(24), eaaz0183. https://doi.org/10.1126/sciadv.aaz0183

Wei, H., Zhao, Y., 2016. Surface pollen and its relationships with modern vegetation and climate in the Tianshan Mountains, northwestern China. Vegetation History and Archaeobotany 25, 19–27. https://doi.org/10.1007/s00334-015-0530-2

Whittington, G., Edwards, K.J., Caseldine, C.J., 1991. Late-and post-glacial pollen-analytical and environmental data from a near-coastal site in north-east Fife, Scotland. Review of Palaeobotany and Palynology 68, 65–85. https://doi.org/10.1016/0034-6667(91)90058-B

Whitelaw, G., 1991. Precolonial iron production around Durban and in southern Natal. Southern African Humanities 3, 29–39.

Whitelaw, G., 1994. KwaGandaganda: settlement patterns in the Natal Early Iron Age. Southern African Humanities 6, 1–64.

Whitelaw, G., Moon, M., 1996. The distribution and ceramics of pioneer agriculturists in KwaZulu-Natal Natal Museum. Journal of Humanities 8, 53–79.

Wood, E.T., Stover, D.A., Ehret, C., Destro-Bisol, G., Spedini, G., McLeod, H., Louie, L., Bamshad, M., Strassmann, B.I., Soodyall, H., 2005. Contrasting patterns of Y chromosome and mtDNA variation in Africa: evidence for sex-biased demographic processes. European Journal of Human Genetics 13, 867–876. https://doi.org/10.1038/sj.ejhg.5201408

Young, R., Thompson, G., 1999. Missing plant foods? Where is the archaeobotanical evidence for sorghum and finger millet in East Africa? In: van der Veen, M. (ed.), The exploitation of plant resources in Ancient Africa. Plenum/Kluwer, New York, pp. 63–72. https://doi.org/10.1007/978-1-4757-6730-8_6

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# Modern pollen- and phytolith-vegetation relationships at a wetland in northeastern South Africa

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ABSTRACT

In palaeoenvironmental reconstructions, few studies have focused on comparing the presence of pollen and phytoliths in surface sediments to the local vegetation. Notwithstanding inherent differential pollen and phytolith preservation, production, and dispersal, which affect their recovery and interpretation in sediment archives, there remains a need to explore modern pollen-vegetation, phytolith-vegetation and pollen-phytolith relationships to improve palaeoenvironmental reconstructions. We carried out palynological and phytolith analysis on six surface sediment samples linked to the botanical survey of five vegetation survey plots at Gustav Klingbiel Nature Reserve, Mpumalanga province in northeastern South Africa, to understand the relationships between the modern pollen and phytolith assemblages in the surface sediments and the contemporary vegetation of the study area. Correspondence Analysis (CA) was undertaken to examine the fingerprint of the local vegetation in the modern pollen-phytolith assemblage and evaluate whether the phytolith and pollen assemblages were tracking each other. CA illustrated that pollen and phytolith proxies are not tracking the same primary vegetation signals; modern pollen assemblages best represent the components of forest and wetland vegetation. In contrast, modern phytolith assemblages best represent grassland vegetation. Our study shows that differential pollen and phytolith preservation, production and dispersal significantly affect sediment records more than anticipated, thus combining multi-proxies (e.g., phytoliths, pollen) provides a more accurate basis for the interpretation of fossil spectra in palaeoenvironmental reconstructions.
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## 1. Introduction

Palynology and phytolith analyses are standard methods used globally to reconstruct Quaternary vegetation fluctuations, climate change, and human impact on vegetation. Often, these proxies complement each other to reflect palaeoenvironments more accurately (e.g., Scott et al., 2012, 2020; Fitchett et al., 2017; Sjöström et al., 2017; Esteban et al., 2018; Breman et al., 2019; Hahn et al., 2021). Differential pollen and phytolith preservation, production, dispersal, and depositional environments, however, hinder or facilitate their recovery and interpretation (Bryant and Holloway, 1983; Piperno, 2006; Bell and Fletcher, 2016; Morales-Molino et al., 2020). A further concern is that analyses of pollen and phytolith assemblages from archaeological contexts can provide different environmental signals (Alexandre et al., 2004; Esteban et al., 2020a).

The relationship between modern pollen and phytoliths and contemporary vegetation in the northeastern region of South Africa is under-researched, and only one prior pollen study (see Duffin and Bunting, 2008) is available, with no studies that we are aware of, for phytoliths. Addressing this lacuna calls for modern pollen-phytolith-vegetation studies in the region. This is especially important for palaeoecological research seeking to understand how pastoralists and farmers who occupied the area since the first millennium AD impacted vegetation (see Mitchell and Whitelaw, 2005; Delius et al., 2012).

This paper contributes to contemporary pollen and phytolith research, especially in northern South Africa, to strengthen palaeoenvironmental reconstructions. Our aim is to gain a better understanding of fossil phytoliths and pollen assemblages in and around the Mashishing Fen, in the Gustav Klingbiel Nature Reserve in

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northeastern Mpumalanga, South Africa (Fig. 1). Modern pollen and phytolith data from surface sediment samples were compared with each other and the contemporary source vegetation (constrained in 10 m diameter survey plots) to evaluate possible correlations. A secondary aim is to present microphotographs of the regional pollen flora for an area of South Africa where no pollen atlas exists.

The study site was selected because it is surrounded by rich archaeological evidence of human occupation and subsistence, particularly during the last 2000 years BP (see Inskeep and Maggs, 1975; Evers, 1980, 1982), which provides the basis for tracing the impact of pre-European farming and the climate on the vegetation composition during this period. The choice of site was also due to its location in a nature reserve and the absence of current anthropogenic activities in its immediate vicinity.

### 1.2. Pollen and phytolith studies in southern Africa

Pollen and phytolith studies in southern Africa have been conducted on sediments of lakes, wetlands, springs, and swamps, as well as speleothems, salt pans, and dung deposits (e.g., Pearsall, 2000; Scott et al., 2004, 2012; Piperno, 2006; Neumann et al., 2010; Festi et al., 2016; Ekblom et al., 2017; Sjöström et al., 2017; Breman et al., 2019). In central southern Africa, preservation of microfossils is limited by frequent wet/dry cycles (see Chase and Meadows, 2007; Fitchett et al., 2016, 2017; Hill and Finch, 2021).

The potential of pollen to provide a broader understanding of vegetation dynamics across different vegetation types particularly in relative tree-grass abundance is well established, while phytoliths are invaluable in identifying Poaceae subfamilies because palynological identification beyond family level is challenging (Alexandré et al., 1997; Lejju et al., 2005; Parker et al., 2011; Cordova, 2013, 2023; Breman et al., 2019; Cordova et al., 2019; Esteban et al., 2020b). Consequently, combining pollen and phytoliths helps to reconstruct past environmental changes more accurately; distinguish between various vegetation types (e.g., forest, grassland, wetland), and fill specific proxy gaps in sequences. Also, the need for multiproxy studies in southern Africa has been stressed to distinguish climatic and possible anthropogenic disturbances on vegetation (e.g., Breman et al., 2019; Cordova et al., 2019).

Unfortunately, pollen and phytoliths may not always occur together in the same archives or sediment horizons (e.g., Esteban et al., 2020a). In addition, there is limited research on modern pollen-phytolith-vegetation studies in southern Africa. Where these do exist, there is a strong research bias towards regions like the Free State and

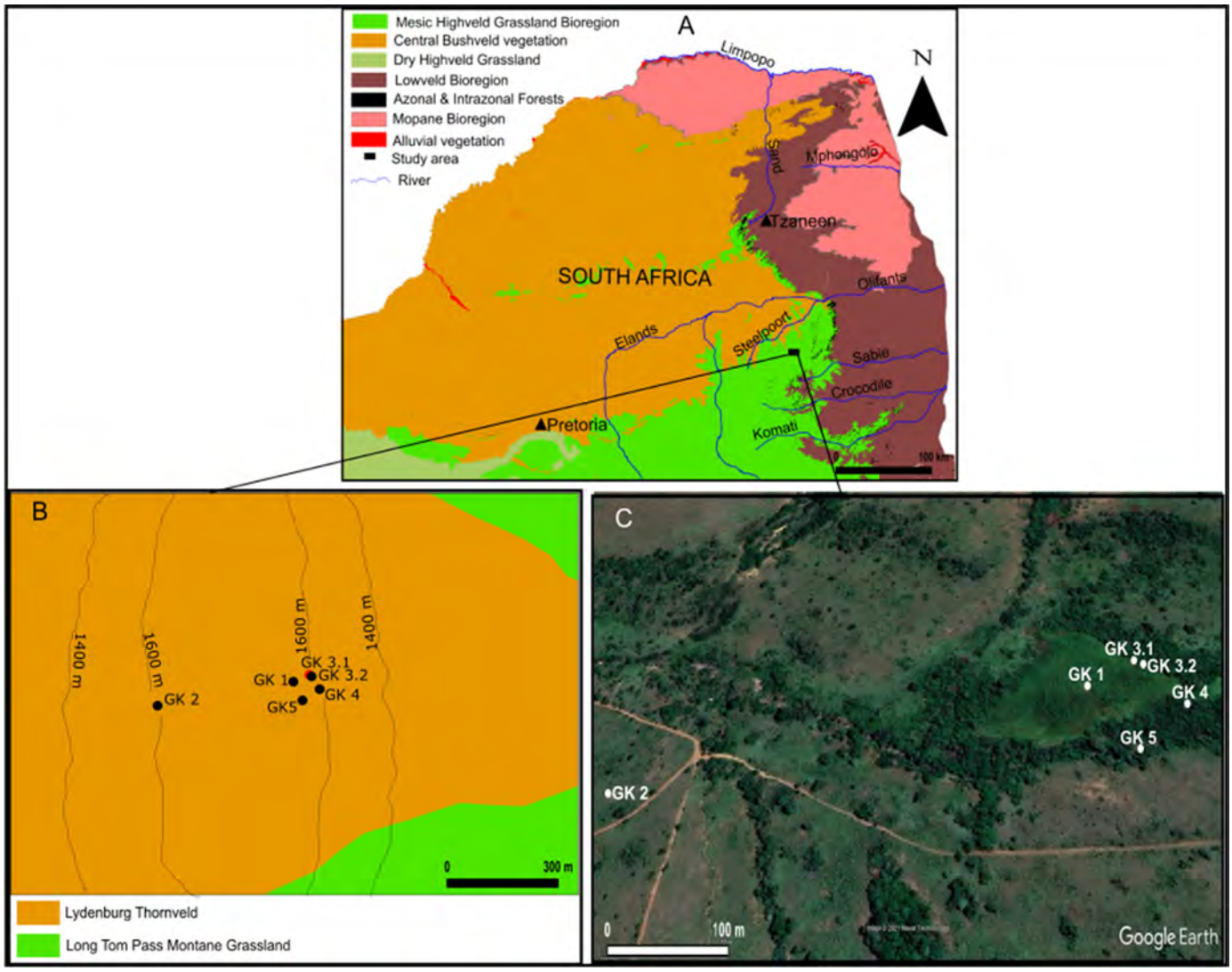


**Fig. 1.** (A) Map of South African bioregions showing study area (black rectangle) and rivers (after Mucina and Rutherford, 2006), (B) Map showing survey plots and vegetation units (after Mucina and Rutherford, 2006) at Gustav Klingbiel Nature Reserve (GK), (C) Google Earth map showing satellite image of vegetation composition and location of survey plots in the study area.

KwaZulu-Natal (see MacPherson, 2009; Sobol et al., 2019; Hill et al., 2021; Julier et al., 2021). These studies focused on the relationship between single proxies (pollen or phytoliths) and contemporary vegetation (e.g., Scott, 1982, 1984; Hill, 1995; Quick et al., 2011; Esteban et al., 2017a, 2017b; Hill and Finch, 2021). While phytolith studies on modern materials have focused on understanding the diagnostic potential of phytoliths and their use in reconstructing past environments (e.g., Cordova, 2013, 2023; Esteban et al., 2017a; Mercader et al., 2009), the pollen studies focused primarily on how representative the extant vegetation is in the modern pollen spectra, with no attempt to quantify the relationship between modern pollen and contemporary vegetation (e.g., Scott, 1984; Scott and Bousman, 1990).

Pollen and phytolith surface samples (usually the top 2 cm of sediments below vegetation litter, taken from several spots within 1 $m^2$) are frequently studied as a subset of the fossil spectrum and are often not the primary focus of the inquiry (e.g., Scott, 1984; Hill, 1995; compare Hill and Finch, 2021). Notwithstanding recent studies assessing the quantitative relationship between modern pollen and phytolith data and vegetation communities from surface samples (e.g., Barboni et al., 2007; Novello et al., 2012; Cordova, 2013; Esteban et al., 2017b; Novello et al., 2018; Mercader et al., 2019; Sobol et al., 2019; Hill et al., 2021; Hill and Finch, 2021), understanding of the relationship between phytolith production in vegetation and deposition patterns in modern soils remains a challenge (e.g., Albert et al., 2006; Mercader et al., 2019). Addressing this challenge has been complicated by research on pollen in surface samples being hampered by the lack of pollen in modern samples caused by the frequent wet/dry cycles due to the semi-arid climate over much of southern Africa (see Hill and Finch, 2021).

## 2. Materials and methods

### 2.1. Study area

The Mashishing Fen in the Gustav Klingbiel Nature Reserve (GK), Mpumalanga province, South Africa (Fig. 1), abuts the town of Mashishing (previously Lydenburg). The fen is situated at an elevation ranging from 1563 m to 1601 m above sea level in a mountainous area with deep valleys incised by the Sterkspruit and the Klipgatspruit rivers (De Swardt, 1990, 2014). Streams run north and south of the fen and merge with the Dorps and Spekboom rivers, forming part of the Olifants River catchment that drains into the Indian Ocean (Sjöström et al., 2017).

Precambrian Pretoria Group (2.3-2.1 Ga) shales and quartzites dominate the regional geology (Lenhardt et al., 2012). Bands of dolerite (diabase sills formed during the early Jurassic because of the break-up of Gondwana, [Neumann et al., 2011]) and quartzite form ridges and high ground since they are more resistant to erosion (Norman and Whitfield, 2006). The topography and rock outcrops in the area are responsible for shallow soils on the slopes and deeper soils in the valley (da Cruz, 2015). The predominant soil types are apedal, eutrophic, plinthic, and shallow soils (Mucina et al., 2006).

The study area is located within the Grassland Biome, includes Lydenburg Thornveld (a Mesic Highveld grassland type) and is bounded to the east by Long Tom Pass Montane Grassland (Lydenburg Montane Grassland) (Mucina et al., 2006) (Fig. 1B). It lies in the summer rainfall region with >66 % Mean Annual Precipitation (MAP) in the months from October to March (Mucina et al., 2006). The Drakensberg Escarpment, east of Mashishing, creates a rain shadow, and low-lying areas further west of the escarpment get substantially less rainfall than the high-lying areas (Mucina et al., 2006). Consequently, Lydenburg Thornveld, in the rain shadow, receives 707 mm MAP (580–810 mm) and, in the eastern part of the Gustav Klingbiel Nature Reserve, the Long Tom Pass Montane Grassland receives orographic precipitation and mists most of the year, with 858 mm MAP (660–1180 mm) (Mucina et al., 2006). The Mean Annual Temperature in Lydenburg Thornveld is around 16°C, and winters are cold with infrequent frost (Mucina et al., 2006: 409). Frost is more common in the high altitude of Long Tom Pass Montane Grasslands of the reserve (Mucina et al., 2006: 405)

The Lydenburg Thornveld (a transitional zone between the high-lying grasslands and the warmer and drier bushveld) (Fig. 2) comprises woodland which is dense in rocky areas but includes more grassland in the frost-ridden valleys (Mucina et al., 2006: 409). The characteristic vegetation includes grasses like *Andropogon schirensis, Themeda triandra* and *Heteropogon contortus,* and small trees, e.g., *Cussonia transvaalensis, Vachellia karroo* and *Senegalia caffra*. Low shrubs such as *Searsia gerrardii, Senecio microglossus* and *Anthospermum rigidum*, and tall shrubs such as *Diospyros lycioides* and *Vernonia crataegifolia* are present (Siebert et al., 2002; Mucina et al., 2006). Lydenburg Montane Grassland (Fig. 2) comprises Afromontane flora and small forests; thickets are common along drainage lines. It is characterised by herbaceous vegetation, including grasses *Eragrostis racemosa, Melinis repens, Panicum maximum*, and herbs such as *Aloe greatheadii, Hypoxis rigidula* and *Ipomoea* spp. The woody vegetation includes shrubs such as *Senegalia ataxacantha, Leucosidea sericea, Diospyros lycioides* and *Euclea crispa,* and trees such as *Protea caffra, Searsia pyroides, Cussonia paniculata* and *Vachellia karroo*. Common invasive species include *Ricinus communis* (Mucina et al., 2006; Ferrar and Lötter, 2007; de Swardt, 2014).

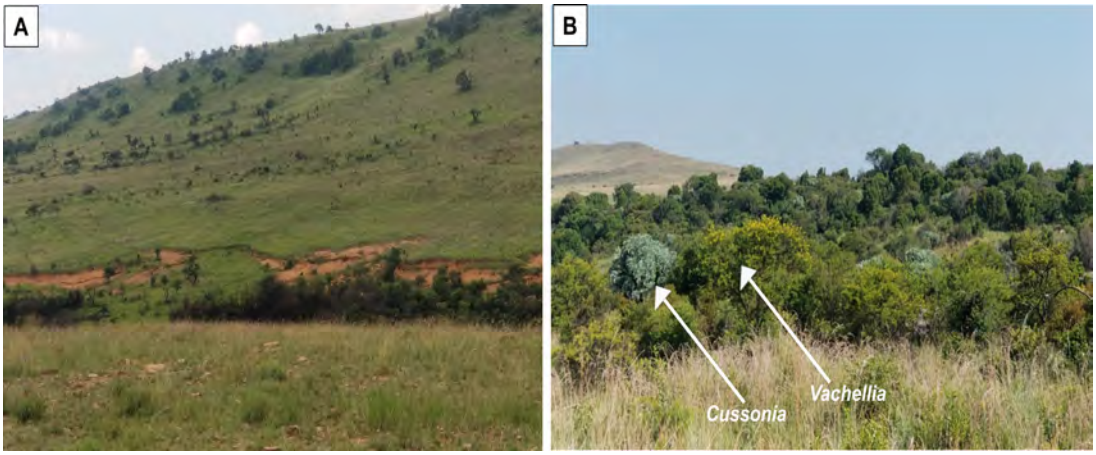


**Fig. 2.** (A) Lydenburg Montane Grassland with erosion features near the fen; (B) Lydenburg Thornveld with *Vachellia, Cussonia* and other trees and grasses, Long Tom Pass in the background (photo credit: Jerry Olatoyan, 2020).

### 2.2. Botanical survey

In January 2020, a botanical survey was conducted to document plant taxa in five survey plots. The five plots were selected according to location and/or characteristic vegetation structure. GK 1 represents Mashishing Fen vegetation (Fig. 3A); GK 2 represents grass patches within thickets (Fig. 3B); GK 3 and GK 4 represent fen and forest margins along the northeastern and eastern extents of the fen (Fig. 3C, D and E); and GK 5 represents riparian vegetation (Fig. 3F).

A circular plot with a 10 m diameter was set up to record the pollen and phytolith sources immediately surrounding the sample collection points, in the centre of the circle. An iron dropper was hammered into the ground to remain fixed at the centre. A second dropper, connected by a five-metre measuring string to the first (fixed) dropper, was installed and subsequently moved, establishing four 5 m transects northwards, eastwards, southwards, and westwards. A Brunton pocket transit compass was used to determine the transect directions and the transect distances were verified using a metre tape. Plant taxa along each transect were recorded. Taxa that were not present along the transect lines, but occurred within the sample plot were also recorded, as were dominant plant species growing beyond the sample areas. Voucher specimens were prepared and assigned taxa numbers for identification confirmation at the CE Moss Herbarium, University of the Witwatersrand (Wits). In addition, the geographical locations and elevation of the sample locations were recorded (GK- 1 25°05′54.9′′ S, 30°30′36.4" E; GK 2- 25°05′57.6′′ S, 30°30′21.2" E; GK 3.1 and 3.2 -25°05′24.1′′ S, 30°30′38.2" E; GK 4- 25°05′55.7′′ S, 30°30′39.3" E; GK 5- 25°05′57.0′′ S, 30°30′37.4" E; Fig. 1B and C).

### 2.3. Herbarium specimen collection

We obtained permission from the Gustav Klingbiel Nature Reserve authorities to collect plant specimens. Rare plants protected by law were documented, but not collected. Following standard botanical practice, we collected, as far as possible, diagnostic plant components bearing diagnostic features (Fish, 1999). The base, centre, and apex of sterile and fertile fern fronds were also collected. The voucher specimen identifications were verified at the CE Moss Herbarium, Wits (Table 1).

### 2.4. Surface sediment collection

Surface sediment samples were collected from an area of 1 $m^2$ in the centre of the five survey plots to provide representative modern pollen and phytolith spectra. After leaf litter had been removed, the top 2 cm of sediment (approx. 50 g) was collected into a Ziploc bag (65 mm × 85 mm) using a 175 mm hand trowel. One pollen and one phytolith sample were collected from each plot except for GK 3, on the northeastern margin of the fen, where two surface samples were collected. GK 3.1 was collected in the forest on the margin, whereas

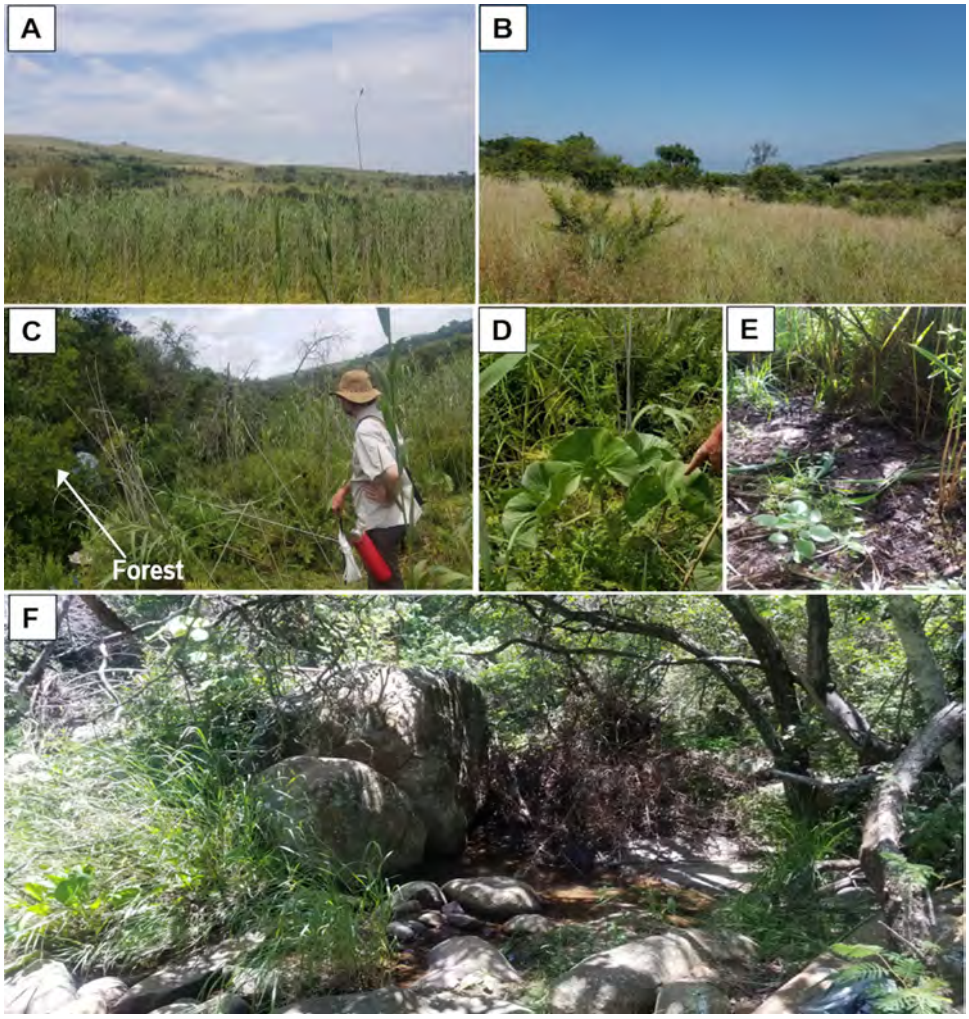


**Fig. 3.** (A) GK 1: Mashishing Fen vegetation; (B) GK 2: Grass patches within thickets; (C) and (D): GK 3 Northeast margin of Mashishing Fen and forest with *Gunnera perpensa*; (E) GK 4: East margin of Mashishing Fen and forest; (F) GK 5: Riparian vegetation.

**Table 1**
List of plant species identified as the contemporary source vegetation in the five botanical survey plots (GK 1–GK 5) at the Gustav Klingbiel Nature Reserve. Exotic taxa are indicated by *

| Family | Genus and species | GK 1 fen | GK 2 grass pockets | GK 3 fen/forest | GK 4 fen/forest | GK 5 riparian |
|---|---|---|---|---|---|---|
| **Trees and tall shrubs** | | | | | | |
| Anacardiaceae | *Searsia dentata* (Thunb.) F.A. Barkley | | | x | | |
| | *Searsia discolor* (E.Mey. ex Sond.) Moffett | | x | | | |
| | *Searsia transvaalensis* (Engl.) Moffett | x | | x | x | x |
| Ebenaceae | *Diospyros lycioides* Desf. | x | | x | x | x |
| | *Diospyros whyteana* (Hiern) F.White | | | x | x | |
| | *Euclea crispa* (Thunb.) Gurke | | | x | x | x |
| Fabaceae | *Vachellia karroo* (Hayne) Banfi & Galasso | | x | x | x | x |
| Icacinaceae | *Cassinopsis ilicifolia* (Hochst.) Kuntze | | | x | | x |
| Lamiaceae | *Syncolostemon flabellifolius* (S.Moore) A.J.Paton | | x | | | |
| Myricaeae | *Morella serrata* (Lam.) Killick | x | | | | |
| Rhamnaceae | *Ziziphus mucronata* Willd. | | | x | x | x |
| Rosaceae | *Leucosidea sericea* Eckl. & Zeyh. | x | | x | | |
| Rutaceae | *Zanthoxylum capense* (Thunb.) Harv. | | | | x | x |
| Scrophulariaceae | *Buddleja salviifolia* Lam. | | | | | x |
| Thymelaeaceae | *Dais cotinifolia* L. | | x | | | x |
| **Low shrubs** | | | | | | |
| Asparagaceae | *Asparagus virgatus* Baker | | | x | x | |
| Asteraceae | *Athrixia phylicoides* DC. | | x | | | |
| | *Senecio microglossus* DC. | | x | | | x |
| | *Senecio venosus* Harv. | | x | | | |
| | *Stoebe* sp. | | | | | x |
| Fabaceae | *Indigofera oxytropis* Benth. ex Harv. | | x | | | |
| Malvaceae | *Grewia vernicosa* Schinz | | | | x | |
| Myrsinaceae | *Myrsine africana* L. | | | x | x | |
| Verbenaceae | *Lantana rugosa* Thunb. | | x | | | |
| | *Lippia javanica* (Burm.f.) Spreng. | | x | | | |
| | **Verbena bonariensis* L. | | | | | x |
| **Climbers, scramblers** | | | | | | |
| Fabaceae | *Senegalia schweinfurthii* (Brenan & Exell) Seigler & Ebinger | | | x | | |
| Ranunculaceae | *Clematis brachiata* Thunb. | | | | x | |
| Rosaceae | *Rubus rigidus* Sm. | x | | x | x | x |
| Rubiaceae | *Rubia petiolaris* DC. | | | | x | |
| Vitaceae | *Rhoicissus tridentata* (L.f.) Wild & R.B.Drumm. | | x | | | x |
| **Herbs, including prostrate twining plants** | | | | | | |
| Acanthaceae | *Dyschoriste setigera* (Pers.) J.C.Manning & Goldblatt | | | | x | |
| Asteraceae | *Acalypha peduncularis* E.Mey. ex Meisn. | | x | | | |
| | *Haplocarpha scaposa* Harv. | | x | | | |
| Cucurbitaceae | *Cucumis zeyheri* Sond. | | x | | | |
| Fabaceae | *Rhynchosia caribaea* (Jacq.) DC. | | | x | | |
| | *Rhynchosia nervosa* Benth. ex Harv. | | x | | | |
| Gentianaceae | *Chironia palustris* Burch. | | | | x | |
| Gunneraceae | *Gunnera perpensa* L. | | | x | | |
| Hypoxidaceae | *Hypoxis hemerocallidea* Fisch., C.A.Mey. & Avé-Lall. | | x | | | |
| Iridaceae | *Freezia laxa* (Thunb.) Goldblatt & J.C.Manning | | | | x | |
| Lamiaceae | *Mentha longifolia* (L.) Huds. | x | | x | x | |
| Malvaceae | *Hermannia antonii* I.Verd. | | x | | | |
| Onagraceae | **Oenothera rosea* L'Her. ex Aiton | | | x | | |
| | **Oenothera tetraptera* Cav. | | x | | | |
| Plantaginaceae | **Plantago major* L. | | | | x | |
| Polygonaceae | *Persicaria decipiens* (R.Br.) K.L.Wilson | | | | x | |
| Ranunculaceae | *Anemone bracteata* Harv. ex J.Zahlbr. | | | x | | |
| Rosaceae | *Agrimonia procera* Wallr. | | | x | | |
| Rubiaceae | *Oldenlandia affinis (Roem. & Schult.) DC.* subsp. *fugax (Vatke) Verdc.* | | | x | | |
| **Graminoids** (including grasses, sedges and rushes) | | | | | | |
| Cyperaceae | *Carex* sp. | | | x | | |
| | *Carex spartea* Wahlenb. | | x | | | |
| | *Carex spicatopaniculata* Boeck. ex C.B.Clarke | | | | x | |
| | *Cyperus keniensis* Kuk. | | | | x | |
| | *Cyperus obtusiflorus* Vahl var. flavissimus (Schrad.) Boeck. | | x | | | |
| | *Cyperus sphaerocephalus* Vahl | | x | | | |
| | *Cyperus pseudoleptocladus* Kuk. | | | | x | |
| Juncaceae | *Juncus punctorius* L.f. | x | | | x | |
| Poaceae - Arundinoideae | *Phragmites australis* (Cav.) Steud. | x | | | x | |
| Panicoideae | *Cymbopogon nardus* (L.) Rendle | | x | | | |
| | *Melinis nerviglumis* (Franch.) Zizka | | x | | | |
| | *Melinis repens* (Willd.) Zizka | | x | | | |
| | *Panicum deustum* Thunb. | | | | x | |
| | *Setaria* sp. | | x | | | |
| | *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss | | x | | | |
| | *Eragrostis capensis* (Thunb.) Trin. | | x | | | |
| | *Eragrostis planiculmis* Nees | | x | | | |
| | *Themeda triandra* Forssk. | | x | | | |

(*continued*)

**Table 1** (*Continued*)

| Family | Genus and species | GK 1 fen | GK 2 grass pockets | GK 3 fen/forest | GK 4 fen/forest | GK 5 riparian |
|---|---|---|---|---|---|---|
| Pooideae | **Bromus catharticus* Vahl | | | x | | |
| **Ferns, horse tails, fungi and other cryptograms** | | | | | | |
| Dennstaedtiaceae | *Pteridium aquilinum* (L.) Kuhn | x | | | x | |
| Equisitaceae | *Equisetum ramosissimum* Desf. | | | | x | |
| Pteridaceae | *Adiantum capillus-veneris* L. | | | | x | |
| | *Pteris vittata* L. | | | | x | |
| Thelypteridaceae | *Thelypteris dentata* (Pers.) J.C.Manning & Goldblatt | | | | x | |

GK 3.2 was collected in the fen vegetation near a wind-pollinated wetland plant, *Gunnera perpensa* L. (Fig. 3D).

### 2.5. Pollen analysis

Surface sediment samples of approximately 10 g were sieved to remove plant materials and prepared for pollen analysis following the standard method using 10% hydrochloric acid (HCl), 40% hydrofluoric acid (HF), 10% potassium hydroxide (KOH), and acetolysis (Berglund and Ralska-Jasiewiczowa, 1986; Faegri and Iversen, 1989) with the addition of heavy liquid separation (ZnCl2/HCl with specific gravity 2.0) (Faegri and Iversen, 1989; Nakagawa et al., 1998) at the palynology laboratory at the Evolutionary Studies Institute (ESI), University of the Witwatersrand. Before mounting in glycerine jelly, the final residue was sieved through a 10 $\mu$m mesh to remove fine particles. An Olympus BX51 light microscope at 400x and 1000x magnification was used to identify pollen taxa. At least 250 terrestrial pollen grains per sample were counted and identified using published references (e.g., Scott, 1982; Cugny et al., 2010; Gelorini et al., 2011; Gosling et al., 2013) and the modern pollen reference collection housed at ESI. The pollen sum was calculated on the total sum of terrestrial pollen, and pollen diagrams were plotted using TILIA 2.1.1 (Grimm, 2011). Photomicrographs of palynomorphs were taken using a Color View Soft Imaging System, an AxioCam ICc 1 camera, and Analysis™ software.

### 2.6. Phytolith analysis

After the surface sediment samples were ashed at 500°C in a muffle furnace for 5-6 hours to remove organic materials, phytoliths were extracted using the standard laboratory techniques described by Albert et al. (1999) at ESI, University of the Witwatersrand. Nitric acid ($HNO_3$), hydrochloric acid (HCl), hydrogen peroxide ($H_2O_2$), and sodium polytungstate solution [$Na_6(H_2W_{12}O_{40}).H_2O$ of 2·4 g/ml density] were used to isolate phytoliths from soil particles and minerals. Glycerin jelly was used to mount 1 mg of processed sample onto microscope slides.

Slides were examined with an Olympus BX51 microscope at 400x and 1000x magnification under polarised light. Photographs were taken using ColorView Soft Imaging System, an AxioCam ICc 1 camera, and Analysis™ software. Phytoliths were identified using literature, for example, Twiss (1992), Twiss et al. (1969), Rossouw (2009), Neumann et al. (2019), Murungi and Bamford (2020), and Piperno and McMichael (2020). For phytolith analysis, 200 phytoliths were counted.

After analysis of the slides, the climatic index (Ic), aridity index (Iph), and the tree cover density/broadleafed index (D/P° ratio) were calculated. These are proxies used to establish past temperatures, moisture levels and tree coverage (see Twiss, 1992). The following calculations were used (cf. Bremond et al., 2008, Esteban et al., 2020b):

$$Ic\ \% = \frac{Pooideae}{(Pooideae + Chloroidoideae + Panicoideae)} x100$$

$$Iph\ \% = \frac{saddles}{(saddles + bilobates + crosses + polylobates)} x100$$

$$D/P^{\circ} = \frac{(psilate + regulate\ spheroids)}{(bilobates + crosses + saddles + rondels + trapezoids + crenates)}$$

An Ic value of above 60% is indicative of a cool climate, in which Pooideae are dominant, whereas an Ic value of below 40% suggests a warm or arid climate, in which plant growth is dominated by Panicoideae and Chloridoideae (Barboni et al., 2007; Bremond et al., 2008). Ic values between 40 and 60% imply a transition zone between $C_3$ and $C_4$ grasses (Sjöström, 2013:37). An Iph value above 60% indicates xeric grasslands, while values lower than 45% are indicative of a mesic habitat. Fredlund and Tieszen (1997) consider Iph values between 45 and 60% indicative of a transition from mesic to xeric climatic conditions. A D/P° ratio larger than 1 is often indicative of a forest environment, whereas a ratio below 1 suggests a grassland or savanna environment (Barboni et al., 1999: 96; Strömberg, 2004: 241).

### 2.7. Numerical analysis

Correspondence Analysis (CA) was conducted using R software to examine the general pattern in the modern pollen and phytolith assemblages and vegetation data, as well as the significance of the variations in both datasets, i.e., whether vegetation is distinguished by the modern pollen and phytolith assemblages (Court-Picon et al., 2005, 2006). Unconstrained ordination analysis, e.g., correspondence analysis, is considered appropriate for quantitative evaluation of the relationship between pollen and phytolith, vegetation and environmental variables (see Court-Picon et al., 2005). CA is often used to detect the major patterns within modern assemblages and vegetation data by providing a low-dimensional representation of complex multivariate data.

## 3. Results

### 3.1. Botanical survey and herbarium specimen collection

In total, 77 plant taxa belonging to 36 families and 57 genera were identified (Table 1). The most abundant tree taxa and tall shrubs include *Vachellia karroo, Euclea crispa, Diospyros lycioides,* (characteristic Lydenberg Thornveld taxa [Mucina et al., 2006]) *Searsia transvaalensis* and *Ziziphus mucronata. Dais cotinifolia, Leucosidea sericea, Diospyros whyteana, Myrsine africana* and *Zanthoxylem capense* were common. A scrambling shrub, *Rubus rigidus*, was present at four of the five survey plots. The dominant herbaceous taxa include *Senecio microglossus* and *Mentha longifolia* (both are important Lydenberg Thornveld taxa, Mucina et al., 2006), *Asparagus virgatus* and *Senecio venosus.* The dominant graminoids are the common reed *Phragmites australis*, sedges *Cyperus* spp., and *Carex* spp. and Poaceae (grasses), dominated by Panicoideae. Bracken, *Pteridium aquilinum*, is the most common fern.

### 3.2. Palynomorphs

#### 3.2.1. Pollen assemblages of GK 1 (Mashishing Fen vegetation)

The modern pollen assemblage from the Fen vegetation (Fig. 3A) was characterised by *Phragmites* sp. (12.0%), Cyperaceae (4.0%), and Sparganiaceae (3.3%) pollen. Other aquatic elements and grasses were represented by *Typha* sp. (1.4%), and Poaceae (>25 $\mu$m pollen diameter, wild grass-type; 7.0%). Pollen of the exotic Northern Hemisphere tree *Pinus* sp. (28.0%) and the shrublet *Anthospermum* sp. (4.0%) were recovered (Plate 1). Other elements like Asteraceae (Tubuliflorae) (6.3%) and *Crassula* sp. (1.0%) were moderately present. Ferns included those producing monolete spores such as *Thelypteris* sp.; lycopod spores (*Lycopodium* sp.) were also detected. Fungal spores such as *Glomus* sp. and *Neurospora* sp. were abundant (Fig. 4). Plate 1, 1-76 shows the characteristic pollen and spores from the plots.

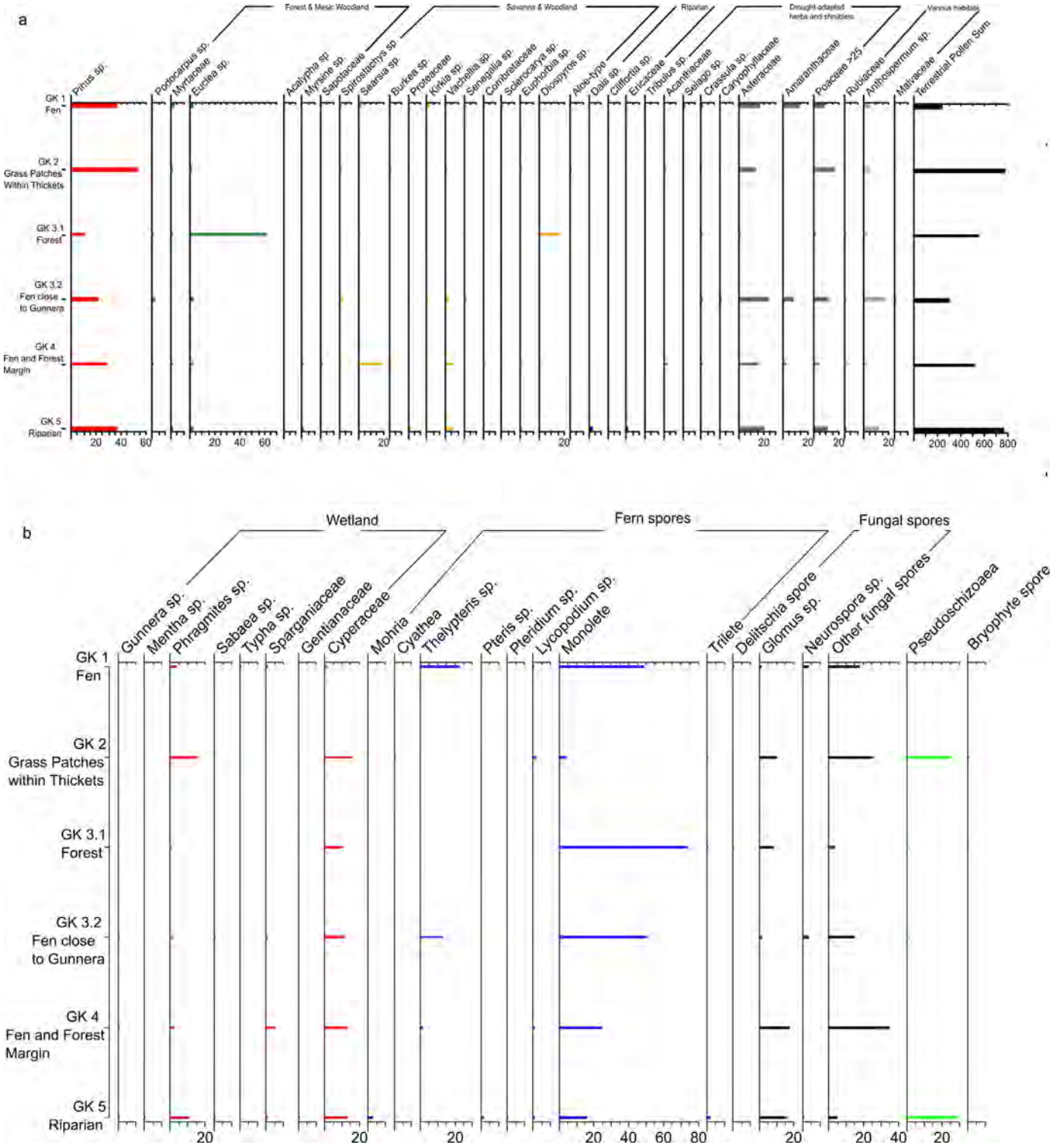


**Fig. 4.** a. Pollen spectra showing terrestrial pollen taxa recovered in percentages from the Gustav Klingbiel Nature Reserve. Fig. 4b. Pollen spectra showing aquatic and spores recovered in percentages from the Gustav Klingbiel Nature Reserve.

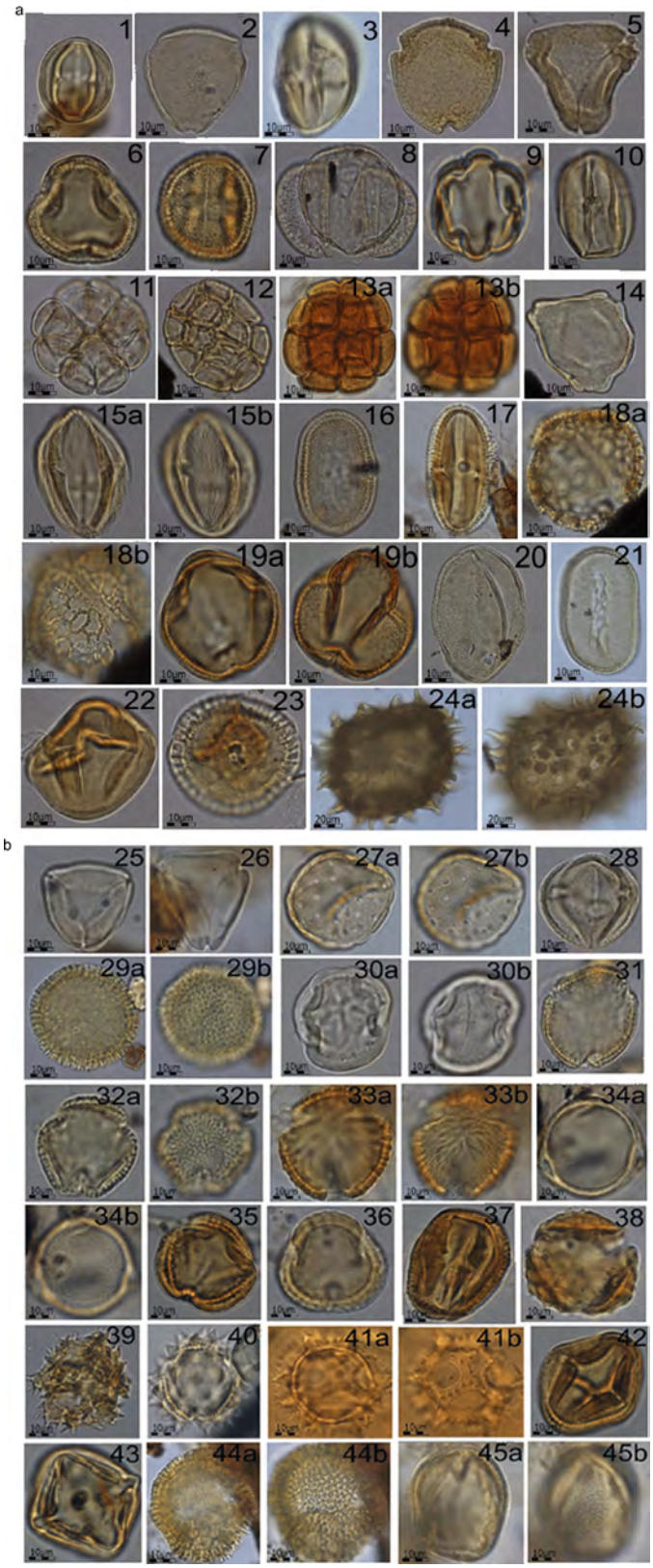


**Plate 1.** a. Modern palynomorphs recovered from surface sediment samples at the Gustav Klingbiel Nature Reserve (Arranged by taxa from terrestrial to aquatics to spores). 1. *Euclea* sp., 2. Proteaceae, 3. *Crassula* sp., 4. *Canthium* sp., 5. *Eucalyptus* sp., 6,7. *Anthospermum* sp., 8. *Pinus* sp., 9. Combretaceae, 10. *Diospyros* sp., 11,12. *Vachellia*-type, 13. *Senegalia*-type, 14. *Myrica* sp., 15. *Searsia* sp., 16. Acanthaceae, 17. *Dicliptera*-type, 18. *Kirkia* sp., 19. *Spirostachys* sp., 20,21. *Aloe*-type, 22. *Alchornea*-type, 23. *Isoglossa* sp., 24. Malvaceae. Plate 1b. Modern palynomorphs recovered from surface sediment samples at the Gustav Klingbiel Nature Reserve. 25,26. Myrtaceae, 27. Amaranthaceae, 28. *Dodonea* sp., 29. *Dais* sp., 30. *Myrsine* sp., 31. Rubiaceae, 32. *Olea* sp., 33. *Sclerocarya* sp., 34. *Acalypha* sp., 35. *Artemisia* sp., 36. *Stoebe* sp., 37,38. *Dicoma*-type, 39. *Berkheya*-type, 40. *Pentzia*-type, 41. *Vernonia*-type, 42. Araliaceae, 43. Solanaceae, 44. *Croton* sp., 45. *Teclea* sp. Plate 1c. Modern palynomorphs recovered from surface sediment samples at the Gustav Klingbiel Nature Reserve. 46. Caryophyllaceae, 47. Moraceae, 48. *Manilkara* sp. (Sapotaceae), 49. Apiaceae, 50. *Heteromorpha*-type, 51,52. Gentianaceae, 53. Zanthoxylum sp., 54. *Burkea* sp., 55. *Sebaea* sp., 56. *Grewia* sp., 57. *Podocarpus* sp., 58,59. *Gunnera* sp., 60. *Mentha* sp., 61. Sparganiaceae, 62,63. Poaceae, 64. *Selago* sp., 65,66. Cyperaceae. Plate 1d. Modern palynomorphs recovered from surface sediment samples at the Gustav Klingbiel Nature Reserve. 67. *Glomus* sp., 68,69. Non-identified fungal spores, 70. *Cyathea* sp., 71. *Pteris* sp., 72. *Mohria* sp., 73. *Lycopodium* sp., 74. *Thelypteris* sp., 75. Monolete spore, 76. *Pseudoschizoaea* sp.




**Plate 1.** Continued.

*3.2.2. Pollen assemblages of GK 2 (Grass patches within thickets)*

Modern pollen from the grass patches within thickets (Fig. 3B) was characterised by the abundance of Poaceae (>25 $\mu$m diameter) pollen with a relatively high presence of 16.6%. Trees and shrubs consisting of *Pinus* sp. (47.9%), Asteraceae (5.4%), *Anthospermum* sp. (4.0%), Acanthaceae (1.6%) and *Vachellia karroo* (0.6%) were recorded. Aquatic taxa comprising *Phragmites* sp. (4.0%) and Cyperaceae (4.0%) were identified (Plate 1). Fungal spores like *Glomus* sp. were moderately present alongside the high occurrence of *Pseudoschizoaea* sp. (algal cysts). Cryptogam spores such as monolete and trilete spores (e.g., *Lycopodium* sp., *Cyathea* sp., *Pteris* sp.) were rare (Fig. 4).

*3.2.3. Pollen assemblages of GK 3.1 (Forest vegetation on the northeast margin of the fen)*

The modern pollen assemblage from the forest area on the northeast margin of the fen (Fig. 3C) was characterised by dominant *Euclea* sp. (61.0%) and *Diospyros* sp. (16.0%). Other tree taxa such as *Searsia* sp. (1.0%), *Vachellia karroo* (0.4%), Myrtaceae (0.3%), Proteaceae (0.3%) and *Spirostachys* sp. (0.2%) made up slightly more than 2.0% of the assemblage. Elements such as Asteraceae (1.8%) and *Anthospermum* sp. (2.0%) were also sparsely represented. Grasses and sedges comprising Poaceae (>25 $\mu$m diameter; 2.0%) and Cyperaceae (7.0%) were present. Ferns such as monolete spores were abundant. Fungal spores such as *Glomus* sp. were rare (Fig. 4).

*3.2.4. Pollen assemblages of GK 3.2 (Fen vegetation on the northeast margin of the fen)*

Modern pollen from the fen vegetation close to a *Gunnera* plant (Fig. 3D) was characterised by Cyperaceae (19.0%), *Phragmites* sp. (3.0%), and Sparganiaceae (2%) pollen. Pollen of other taxa like Asteraceae (23.2%), *Anthospermum* sp. (16.1%), Poaceae (>25 $\mu$m; 11.7%), and Amaranthaceae (9.1%) was also recorded (Plate 1). Fern spores comprising monolete (e.g., *Thelypteris* sp.) and trilete forms were abundant. Fungal spores, including *Glomus* sp. and *Neurospora* sp., were moderately represented. However, *Typha* sp. and *Gunnera* sp. were rare, representing 1.0% of the assemblage (Fig. 4).

*3.2.5. Pollen assemblages of GK 4 (Fen and forest margin at the east of the fen)*

Modern pollen from the fen and forest margin at the east of the fen (Fig. 3E) was characterised by the dominance of *Searsia* sp. (18.6%), *Vachellia* sp. (7.2%), and *Euclea* sp. (2.9%) trees. Asteraceae (9.0%), Combretaceae (2.0%), Poaceae (>25 $\mu$m diameter, wild grass-type) (3.5%) and *Diospyros* sp. (2%) were also represented. Characteristic aquatic elements included Cyperaceae (6.5%), Spargianaceae (2.6%), and *Phragmites* sp. (1.0%). Fungal spores like *Glomus* sp. were moderately present alongside the occurrence of cryptogam spores such as monolete (e.g., *Thelypteris* sp.) and trilete spores (e.g., *Lycopodium* sp.) (Fig. 4).

*3.2.6. Pollen assemblages of GK 5 (Riparian vegetation)*

Modern pollen from the riparian vegetation (Fig. 3E) was characterised by Poaceae (>25 $\mu$m diameter) (10.5%), *Vachellia* sp., (6.0%), Cyperaceae (3.0%), *Phragmites* sp. (2.6%), and *Dais* sp. (2.5%). Other elements like *Anthospermum* (11.0%), Asteraceae (8.7%) and *Euclea* sp. (2.3%) were represented. Fungal spores like *Glomus* sp. were moderately present and a high occurrence of *Pseudoschizoaea* sp. was recorded. Cryptogam spores such as monolete and trilete spores (e.g., *Lycopodium* sp., *Pteris* sp.) were rare (Fig. 4).

*3.3. Phytoliths*

*3.3.1. Phytolith assemblages of GK 1 (Mashishing Fen vegetation)*

The GK 1 sample comprised phytoliths belonging to Poaceae, Cyperaceae, Cucurbitaceae, and other eudicotyledonous (eudicot) taxa (Fig. 5). Undiagnostic phytoliths were most frequent (42.5% of the sample). Phytoliths of Poaceae, namely grass short cells (25.5%), bulliforms and long cells (10.5%), and eudicot phytoliths, such as ornate, psilate and rugose spheroids (19.0%) were common in the GK1 sample too (Plate 2). Phytoliths linked to Cyperaceae (1.0%) and Cucurbitaceae (1.5%) were rare.

Most of the Poaceae phytoliths were produced by Pooid grasses (13.0% of the overall phytolith sample). Phytoliths linked to Panicoideae (6.0%) and Chloridoideae (6.5%) were common.

*3.3.2. Phytolith assemblages of GK 2 (Grass patches within thickets)*

Short cell phytoliths (47.5%) dominated the GK 2 sample, and other phytoliths associated with Poaceae (10.5%) were also common. Cyperaceae (2.0%), Cucurbitaceae (1.0%) and other eudicot (9.0%) phytoliths were present in low numbers (Fig. 5). A significant portion of the phytoliths (21.0%) was undiagnostic.

Panicoideae phytoliths were the most common phytoliths observed in GK 2 samples, comprising 27.0% of the overall phytolith assemblage. Chloridoid phytoliths (16.0%) were also frequently encountered, while Pooideae phytoliths were rare (4.5%). Plate 2, 1-10 shows the characteristic phytoliths from the plots.

*3.3.3. Phytolith assemblages of GK 3.1 (Forest vegetation on the northeast margin of the fen)*

The majority of the phytoliths observed were undiagnostic (44.0%). Phytoliths associated with Cyperaceae (2.0%) and Cucurbitaceae phytoliths (4.0%) were less abundant while other eudicots (37.5%) were common. Phytoliths belonging to Poaceae were rare. Three percent (3.0%) of GK 3.1's phytoliths were short cell phytoliths and other phytoliths also linked to Poaceae, for example, epidermal long cells and bulliforms, comprising 9.5% (Fig. 5).

Only Pooideae and Chloridoideae phytoliths were observed. Of the overall sample, 2.5% comprised phytoliths associated with Pooid grasses, and 0.5% of the phytoliths belonged to Chloridoideae (Fig. 5). No index values were calculated for this sample due to the absence of Panicoideae phytoliths.

*3.3.4. Phytolith assemblages of GK 3.2 (Fen vegetation on the northeast margin of the fen)*

The most frequently observed phytoliths in the GK 3.2 sample were undiagnostic (44.0%). Phytoliths associated with Poaceae were abundant. Of the phytoliths observed, 29.0% were short cells, and 19.0% were other undiagnostic Poaceae phytoliths. Phytoliths linked to eudicots (5.0%), Cyperaceae (2.0%) and Cucurbitaceae (1.0%) were rare (Fig. 5).

Pooideae phytoliths were most abundant and comprised 12.0% of the GK 3.2 sample. Panicoideae and Chloridoideae phytoliths were common (8.5% each) (Fig. 5).

*3.3.5. Phytolith assemblages of GK 4 (Fen and forest margin)*

Poaceae phytoliths dominated this sample. Of sample GK4, 62.5% were short cell phytoliths, and 4.5% were undiagnostic Poaceae phytoliths. Undiagnostic phytoliths (28.5%) were common, while Cyperaceae (1.5%), Cucurbitaceae (0.5%) and other eudicot (2.5%) phytoliths were rare (Fig. 5).

Panicoideae (26.0%) and Chloridoideae (26.0%) phytoliths were similarly abundant. Pooideae phytoliths were less common (10.5%) (Fig. 5).

*3.3.6. Phytolith assemblages of GK 5 (Riparian vegetation)*

Most phytoliths observed were associated with eudicot taxa (69.0%). Undiagnostic phytoliths (25.0%) were also common, while all other phytoliths, including those linked to Poaceae (1.0% for short cells and 4% for other Poaceae phytoliths), Cyperaceae (0.5%) and Cucurbitaceae (0.5%) were rare (Fig. 5).

Only phytoliths of the Poaceae sub-family Panicoideae were observed and therefore, no index values could be calculated.

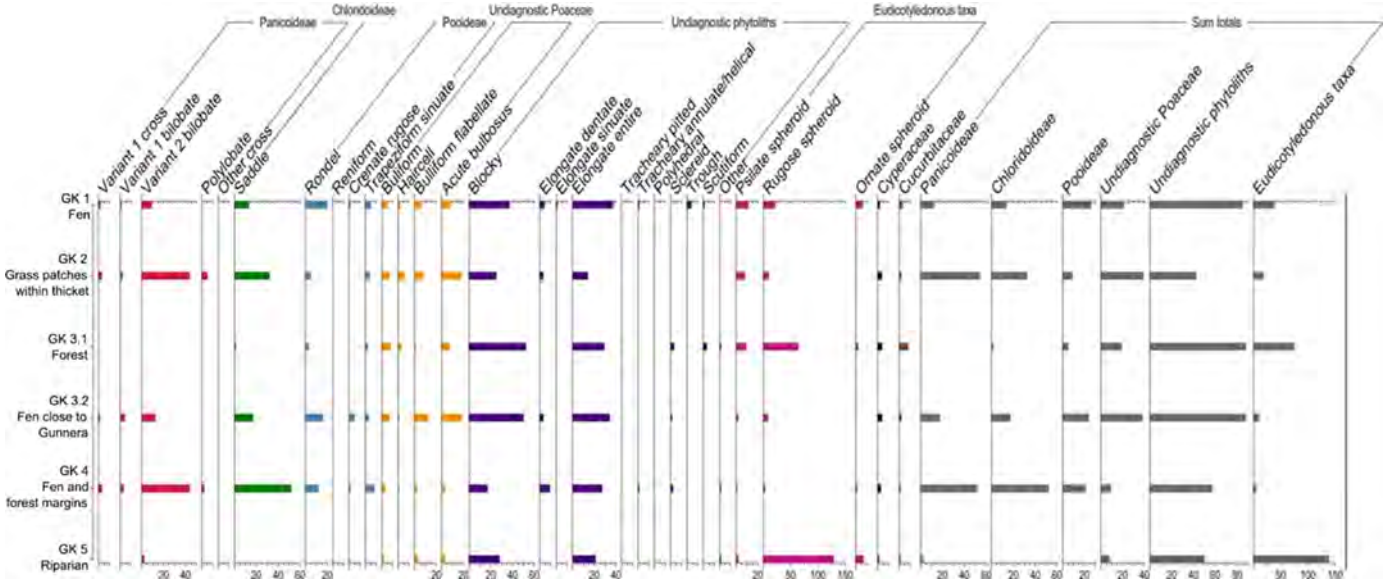


**Fig. 5.** Phytolith data counts from the Gustav Klingbiel Nature Reserve surface sediment samples (N=200 phytoliths per sample).

### 3.4. Numerical Analysis (CA.)

The first two axes together explain 77.31% of the total variance in pollen data sets (Fig. 6) and 91.09% in the phytolith data set (Fig. 7). Three major groups may be visually distinct in the overall CA dispersion diagram of the pollen samples (Fig. 6).

GK 2, GK 4 and GK 5 are similar to each other along axis 1 (44.05% of inertia), while GK 3.2 and GK 1 compositions are quite similar along axis 2 (33.26% of inertia) (Fig. 6). The CA pollen diagram shows the relationship between pollen and spore taxa and the vegetation. GK 3.1 (Forest) is associated with forest taxa, e.g., *Diospyros* sp., *Euclea* sp. and *Podocarpus* sp. showing positive axis 2 scores. *Neurospora* sp., *Thelypteris* sp., *Typha* sp., *Phragmites australis*, monolete fern spores, *Kirkia* sp., Amaranthaceae, *Crassula* sp., Sparganiaceae and fungal spores are largely associated with GK1 (Fen vegetation). *Gunnera* sp., Gentianaceae, *Spirostachys* sp. and Cyperaceae are best related to GK

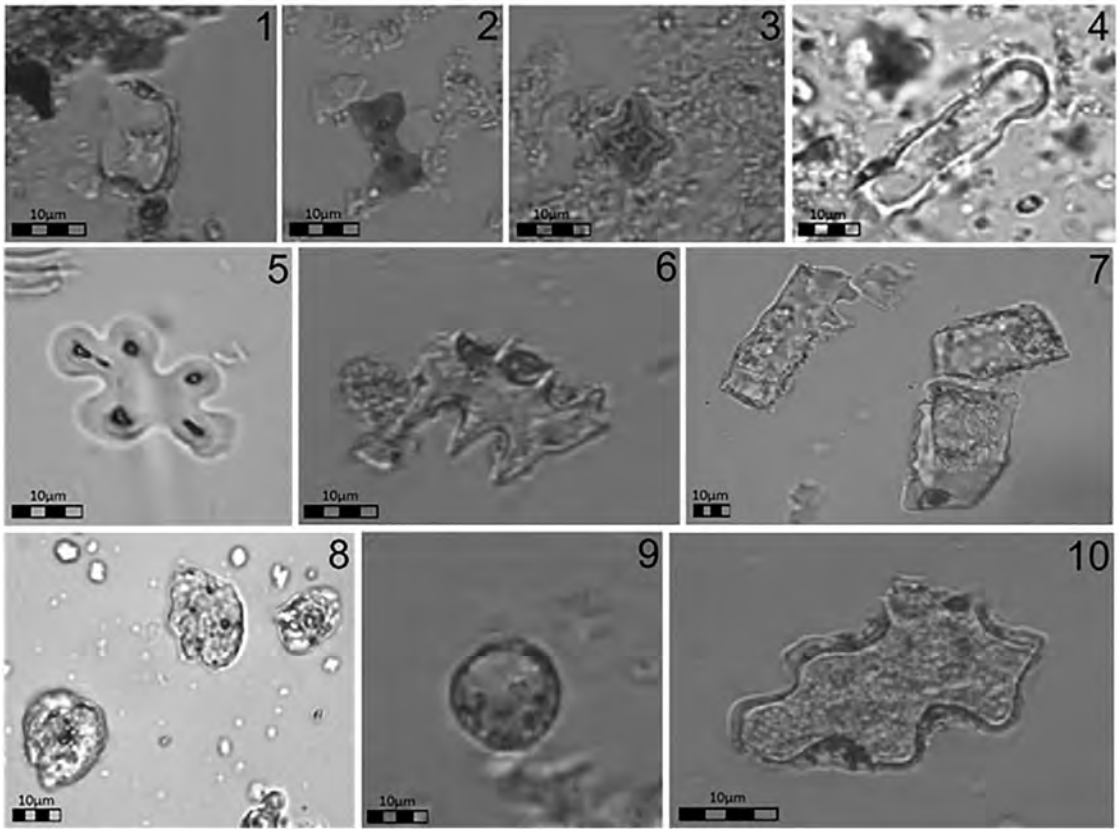


**Plate 2.** 1-5. Grass short cell phytoliths, 6. Epidermal long cell phytolith from Poaceae, 7. Blocky phytoliths, 8-9. Spheroid phytoliths from eudicot taxa, 10. Epidermal jigsaw phytoliths.

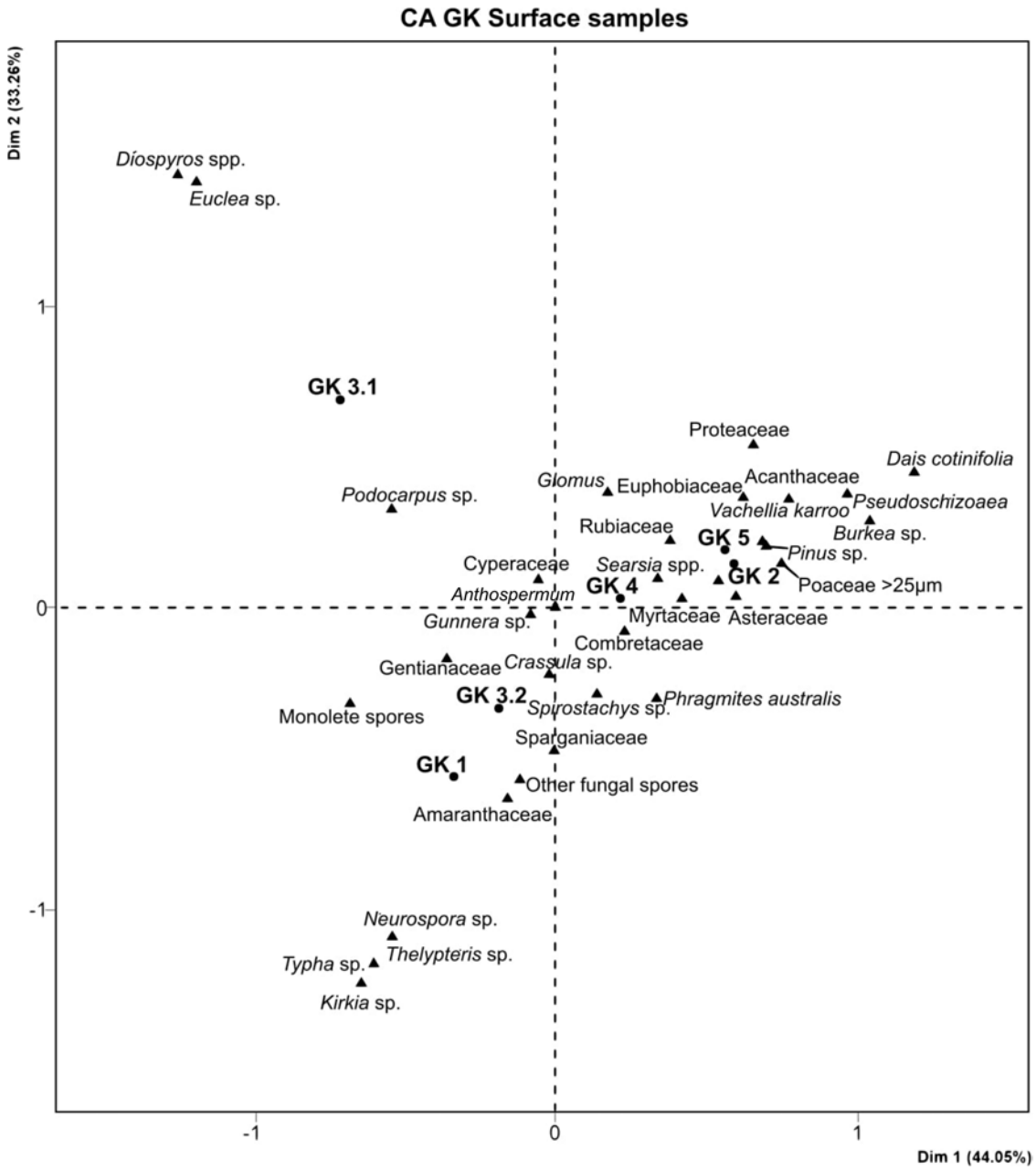


**Fig. 6.** The Correspondence analysis (CA) of the modern pollen samples in relation to different vegetation (survey plots) in Gustav Klingbiel Nature Reserve, Mpumalanga. GK 1- Fen vegetation, GK 2- Grass patches within thickets, GK 3.1- Forest vegetation on the northeastern margin of the fen, GK 3.2- Fen vegetation on the northeastern margin of the fen, GK 4- Fen and forest margin on the east side of the fen, GK 5- Riparian vegetation.

3.2 (Fen vegetation close to the *Gunnera*). *Vachellia karroo, Dais cotinifolia,* and Proteaceae are linked to GK 5 (Riparian vegetation). *Searsia* sp., Combretaceae, Myrtaceae, and Euphorbiaceae occur at GK 4 (Fen and forest margins). *Pinus* sp., Poaceae (>25 $\mu$m diameter), Asteraceae and *Burkea* sp. are best associated with GK 2 (Grass patches within thickets). Several taxa situated close to the origin in the CA plot indicate that their abundances do not vary considerably between assemblages. For instance, looking at the taxa scores along the first two CA axes, it appears that Rubiaceae and *Glomus* sp. are recorded both at GK 4 and 5, *Spirostachys* sp. is recorded both at GK 2 and GK 3.2 while Myrtaceae is recorded at GK 2, 4 and 5. The position of Acanthaceae and *Pseudoschizoaea* sp. is influenced by their high values in GK 2 and GK 5. Additionally, *Anthospermum* sp. is found at the origin, reflecting its common occurrence or importance in all the studied sites.

The CA of phytolith data shows distinct composition between GK 5, GK 2 and GK 4 along axis 1 (72.73% of inertia), and distinct composition between GK 3.2 and GK 1 along axis 2 (18.36% of inertia). The relationship between phytoliths taxa and the vegetation types is also depicted in the CA phytolith diagram (Fig. 7). Eudicot taxa are best associated with GK 5 (Riparian vegetation). Cucurbitaceae are largely associated with GK 3.1 (Forest vegetation on the fen margin). Undiagnostic phytoliths, for example, blocky phytoliths, are linked to GK 1 (Fen vegetation). Cyperaceae, Pooideae and undiagnostic Poaceae, for example, bulliform and epidermal long-cell phytoliths, occur at GK 3.2 (Fen vegetation close to *Gunnera*). Panicoideae and Chloridoideae are common at GK 2 (Grass patches within thickets), and at GK 4 (margins between fen and forest).

Generally, the CA of phytolith data shows that riparian vegetation (GK5) composition is distinct from the vegetation composition found

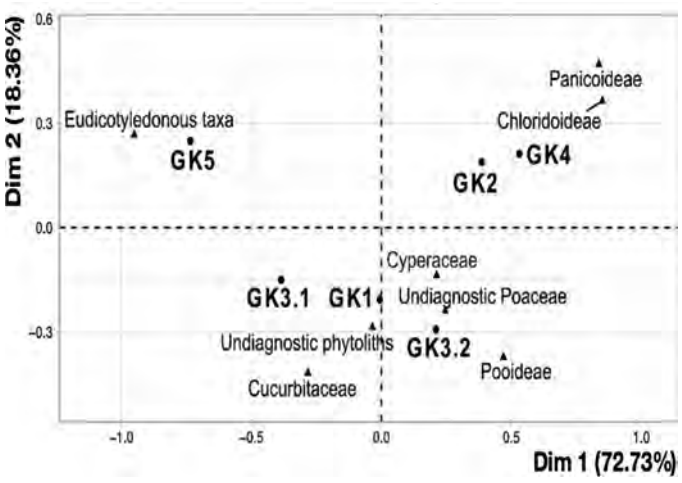


**Fig. 7.** Correspondence analysis (CA) of the phytolith assemblages observed in the GK surface samples in relation to different vegetation (survey plots).

at grass patches within thicket (GK 2), as well as from fen and forest margins on the eastern margin of the fen (GK 4) (along axis 1: 72.7% of inertia), but the CA pollen data shows the opposite, where GK 5, GK 2 and GK 4 are similar to each other along axis 1 (44% of inertia) (Figs. 6 and 7). Also, the ranking along axis 1 for the pollen CA is unrelated to the ranking of samples along axis 1 for phytolith CA (Spearman's rho: = 0.31, $p$ = 0.56). The CA of pollen and phytolith, however, show that only GK 2 and GK 4 compositions are similar along axis 1.

## 4. Discussion

### 4.1. Modern pollen-phytolith-vegetation relationships at Gustav Klingbiel Nature Reserve

Previous studies comprising modern pollen and phytolith assemblages have shown that these proxies allow the differentiation of vegetation types, providing essential reference for palaeoenvironmental reconstructions (Delhon et al., 2003; Watling et al., 2016; Huang et al., 2018; Zhang et al., 2018; Guo et al., 2020; de Wolf et al., 2022). The results from this study, showing distinct assemblages for the fen, forest, grassland and riparian vegetation encountered in and around Mashishing Fen, support these observations (Figs. 6 and 7).

The high abundances of the pollen assemblages of *Phragmites* sp. and *Typha* sp. at GK 1 show that pollen better characterised the wetland (Fen) vegetation than phytoliths. These taxa often form a significant component of wetlands globally and are widely distributed in South African wetlands (Burgoyne et al., 2000; Myburgh and Bredenkamp, 2004; Mabhungu et al., 2019). This is consistent with previous studies showing that pollen spectra reflect the composition of local wetland communities (see Court-Picon et al., 2005; Amami et al., 2010). Fern spores (see Fig. 4b) are probably of local origin and reflect the relatively high rainfall recorded in the highveld area (Burgoyne et al., 2000). In contrast, phytoliths are not commonly produced by ferns (Piperno, 2006). Consequently, the fen's phytolith assemblage shows no indications of the abundance of this plant group, illustrating the limited use of phytoliths as a proxy in this case.

The abundance of the pollen of shrublets and herbs (e.g., *Crassula* sp. and Amaranthaceae) at GK 1 suggest they are not solely indicators of drier conditions as commonly suggested by previous studies (Scott et al., 2003; Chevalier and Chase, 2015, 2016; Fitchett and Bamford, 2017). Sometimes, they might be indicators of wet environments or like many Amaranthaceae, they might signal local disturbances (Sieben et al., 2017; Van Ginkel and Cilliers, 2020). Thus, they have variable applicability as palaeoenvironmental indicators, which might be related to the impact of anthropogenic activities (see Baxter and Davies, 1994; Neumann et al., 2011; Hahn et al., 2021; Olatoyan et al., 2022), regional aridity, high salinity, and evaporative conditions (see O'Connor and Bredenkamp, 1997; Scott et al., 2003; Boon, 2010; Neumann et al., 2010; Scott et al., 2012; Chevalier and Chase, 2015, 2016).

The associated species (e.g., Poaceae and Asteraceae) with sample GK 2 (Figs. 6 and 7), which are characteristic of the contemporary source vegetation (Table 1), likely indicate a more open grass-dominated landscape (see Hahn et al., 2021). Also, the significant occurrence of open savanna/woodland elements (e.g., *Burkea* sp. and *Spirostachys* sp.), known as regional vegetation components (Lötter et al., 2014; O'Donoghue et al., 2020), indicating long-distance dispersal by the wind, reinforces a regional vegetation signal in pollen assemblages from open landscapes. This is complemented by the presence of Cucurbitaceae phytoliths occurring in low numbers and showing a strongly negative axis 2 score as well as the common occurrence of Panicoideae and Chloridoideae phytoliths and the rarity of phytoliths associated with Pooideae. This result agrees with previous studies suggesting that land openness affects local pollen richness (see Gosling et al., 2009; Meltsov et al., 2013; Tabares et al., 2018). Also, it confirms the potential of phytoliths contributing to a more local signal and pollen to a more regional signal in open landscapes (Carrión, 2002; Court-Picon et al., 2005; Lézine et al., 2009; Guimarães et al., 2017; Hyland et al., 2019; Crifò and Strömberg, 2020, 2021). This, however, should be treated with caution as phytoliths can be sometimes transported over long distances once they are released from organic remains, thereby providing both local and regional signals (Parker et al., 2011; Esteban et al., 2020b). Similarly, pollen assemblages can also reflect local as well as regional signals (see Scott and Neumann, 2018; Tabares et al., 2018). Scientific studies on phytolith and pollen transport pathways in South Africa are limited, and more research is needed to determine the influence that wind and other transportation methods have on modern assemblages. It is therefore imperative to combine pollen and phytoliths for a more precise vegetation reconstruction for open landscapes.

The overrepresentation of the exotic element *Pinus* sp. (pine tree) pollen in all the plots except forest, supports the significant influence of wind in open landscapes. Previous studies attributed this to the taxon's high pollen productivity and dispersal efficiency by wind over long-distance transport between 30-1000 km (see Scott, 1984; Williams, 2008; Klemm et al., 2016; Quamar, 2019; Chevalier et al., 2020) and possible facilitation by the upward transport of pine pollen to higher elevations (Markgraf, 1980). Major pine plantations exist ca. 15 km from the study site, suggesting that the pollen might have been transported by the prevailing wind from the east (see Burgess and Wingfield, 2001; van Wilgen and Richardson, 2012; Bennett and Kruger, 2015). Thus, pollen representation in open landscapes, particularly in higher elevations, could be misleading, thereby posing challenges to accurate interpretations of fossil pollen assemblages for such vegetation types (see Birks et al., 2016; Senn et al., 2021).

The marked differences in the CA phytolith and pollen composition and the ranking of samples along axis 1 (Figs. 6 and 7) suggest that the two proxies are not tracking the same primary vegetation and environmental signals. This could be due to various factors, including differential preservation, production, depositional environments and dispersal (e.g., the different proxies sample the environment at different scales and provide signals covering a lesser or greater extent of the landscape; see Prentice, 1985; Piperno, 1988; Crifò and Strömberg, 2020).

The forest vegetation and the margins between fen and forest are distinguishable through modern pollen and phytolith assemblages. GK 3.1 is differentiated by characteristic forest pollen assemblages (e.g., *Euclea* sp., *Diospyros* sp. and *Podocarpus* sp.) (Fig. 6). These taxa indicate an area dominated by trees and woody shrubs and correlate with the botanical survey data as *Euclea* sp. and *Diospyros* sp. were often found together as shrubs at the forest margins (Table 1). The significant presence of *Podocarpus* sp. in the CA plot, though the

taxon was not recorded during the botanical survey, is likely due to the high pollen productivity and effective wind dispersal and deposition of conifer pollen (Scott, 1982). This conforms with previous studies suggesting that pollen provides a reliable distinction of forest vegetation and shows local signal in dense canopy (see Scott, 1982; 1984; Hill, 1995; Gosling et al., 2018; Tabares et al., 2018; Hill and Finch, 2021). It remains unclear, however, why other tree taxa (e.g., *Myrica* sp., *Myrsine* sp., *Olea* sp.) were less commonly recorded in the pollen assemblage. The high number of undiagnostic phytoliths (Fig. 5), confirms the accepted knowledge that phytoliths are less taxonomically significant for identifying trees/shrubs (see Piperno, 2006, 2009).

GK 3.2 is differentiated by pollen and phytoliths showing the presence of a mosaic of wetland (e.g., *Gunnera* sp., Gentianaceae, and Cyperaceae) and savanna trees (e.g., *Spirostachys* sp.) (Figs. 6 and 7). This suggests that the most reliable taxa for reconstructing similar vegetation structure within the studied site are the wetland and savanna taxa (see Neumann et al., 2011; Romanowski, 2011; Mabhungu et al., 2019). Poaceae were well represented by phytoliths, despite *Bromus catharticus* being the only Poaceae taxon identified in the sampling plot. Phytoliths associated with Pooideae, grasses that prefer cooler and wetter climates, were common, and it is possible that *B. catharticus* was their source. The remainder of the phytoliths, i.e., those linked to Panicoideae and Chloridoideae, are likely the result of wind or water transportation. It is unclear why there is such a large discrepancy between the Poaceae phytoliths from sampling areas GK 3.1. and GK 3.2., which are near one another. Further investigations could clarify this phenomenon.

The pollen and phytolith assemblages associated with GK 4 are consistent with the contemporary vegetation (Table 1). The abundances of tree pollen and phytoliths belonging to Panicoideae and Chloridoideae characterise GK 4 (Figs. 6 and 7). Panicoid grasses and *Phragmites australis* were commonly found during the botanical survey and are the most likely sources of the observed phytoliths. Similarly, the CA shows GK 5 to be closely associated with typical riparian trees dominated by pollen of *Dais* sp., *Vachellia karroo,* Proteaceae, Rubiaceae, and Myrtaceae (compare Myburgh and Bredenkamp, 2004) which are in good agreement with the vegetation composition during the botanical survey (Table 1). The pollen data agree with quantitative studies in the region where riparian vegetation comprises similar plant taxa (Myburgh and Bredenkamp, 2004; Schachtschneider and Reinecke, 2014). The CA shows close association of phytoliths linked to eudicots (Fig. 7) comprising morphotypes such as psilate spheroid, ornate spheroid, which are likely produced by the trees and herbs in the contemporary vegetation. Phytoliths associated with Poaceae were extremely rare in this phytolith sample. This reflects the source vegetation for the area well, as no grasses were noted during the survey. No indices could be calculated due to the rarity of short cell phytoliths.

However, not all taxa in the botanical survey were represented in the pollen and phytolith assemblages and vice versa. For instance, *Juncus* sp. and *Leucosidea* sp. were not recorded in the modern pollen assemblage at GK 1 as well as *Cucumis zeyheri* [Cucurbitaceae], *Indigofera oxytropis, Lippia javanica* and *Hypoxis hemerocallidea* at GK 2, despite being represented in the botanical survey (Table 1). This is likely due to the rare preservation of *Juncus* sp. pollen due to the low amount of sporopollenin in the exine (Traverse, 1988, Marsh and Cohen, 2016) and low pollen dispersal efficiency particularly of Cucurbitaceae which produce heavy, large and ornamented pollen grains which are transferred by insects (Aswathi, 1961). While phytoliths associated with Cucurbitaceae were present (e.g., at GK 3.1), they have a strongly negative axis 2 score and occurred in low numbers (Figs. 5 and 7). Cucurbitaceae are prolific producers of phytoliths and the low numbers of phytoliths associated with these taxa could be due to a number of factors. Since phytoliths are preserved well in the sediments, it can be assumed that phytolith dissolution is not the cause. The diagnostic phytoliths produced by Cucurbitaceae are mainly produced in the fruit rinds. Low production of fruit or removal of fruit by animals or humans may be the cause of the low numbers of Cucurbitaceae phytoliths in the surface samples. Alternatively, the species of Cucurbitaceae present in the area may be one of the rare exceptions in the plant family that does not produce diagnostic phytoliths (see Piperno et al., 2000). Further research into the phytoliths produced by African Cucurbitaceae could shed more light on this. The absence of pollen of insect pollinated *Leucosidea* sp. and *Hypoxis* sp. may be due to their usual minor representation in surface spectra, which might signal weak pollen dispersal and/or degradation (see Carrión et al., 1999; Nyakale, 1999; Johnson and Anderson, 2002; Jeske-Pieruschka et al., 2010; Ren et al., 2019).

On the other hand, the savanna element *Kirkia* sp. has a strongly negative axis 2 score and is present at low frequency though not recorded in the botanical survey at GK 1. *Kirkia* sp. pollen recovered from fossil samples from the savanna dates to the Holocene and correlates with warm climate (Scott, 1982). These highlight the need to consider the importance of identifying silent taxa for more accurate fossil interpretations in the region. Also, taxa belonging to Combretaceae, Myrtaceae, and Euphorbiaceae families were not recorded during the botanical survey. This lack of correlation between pollen and vegetation may be partly because some of the pollen taxa are identifiable only to family level. Some of these pollen grains could represent plant species that may be present in a wide range of vegetation types. Many tree pollens are wind-transported, widely dispersed and abundant and are often present even if they are not presently growing locally. There is a need for caution in making too precise interpretations regarding forested regions solely based on the Arboreal Pollen/Non-Arboreal pollen ratio. The presence of common *Glomus* sp. spores, which also have high dispersal efficiency, might suggest increased erosion maybe due to anthropogenic disturbances (Anderson et al., 1984; Neumann et al., 2014).

The location of *Anthospermum* sp. pollen at the origin in the CA pollen diagram (Fig. 6) indicates similar abundance across the different plots. *Anthospermum* sp. characterises various environmental conditions and varying land-use types (see Court-Picon et al., 2006) and its high occurrence is likely because the pollen is widely dispersed across different grassland types, thus significantly representing part of the regional vegetation (Scott, 1982; Mucina et al., 2006). Aerobiological studies on *Anthospermum* sp. pollen in South Africa, however, are not currently available to ascertain the likely transport mechanism.

Based on the phytolith indexes calculated, GK 4 has the same moisture levels as GK 1 and GK 3.2, which is to be expected. The Ic values differ between GK 4 and those of GK 1 and GK 3.2. GK 4's Ic value is comparable to that of GK 2, which indicates a warm climate. Unlike the indications from the pollen assemblage, the broadleaf index indicated an open area with few trees (Table 2).

**Table 2**
Ic%, Iph%, and broadleaf (D/P°) indices calculated for the Gustav Klingbiel Nature Reserve surface sediment phytolith samples.

| Sample number | Ic% | Iph% | D/P° |
|---|---|---|---|
| GK1 | 50.98 | 52 | 0.647 |
| GK2 | 9.47 | 37.2 | 0.2 |
| GK3.1 | N/A | N/A | N/A |
| GK3.2 | 41.379 | 50 | 0.17 |
| GK4 | 16.8 | 50 | 0.03 |
| GK5 | N/A | N/A | N/A |

## 5. Conclusion and outlook

This study is novel for South Africa because, to our knowledge, it is the first to compare the taxa identified in modern pollen and phytolith surface assemblages from fen, fen margin, grassland, forest and riparian areas to each other, and individually and as combined proxies, to the contemporary source vegetation recorded in five sampling areas/botanical survey plots.

The pollen and phytolith proxies did not track similar vegetation and environmental signals and they also documented the environment at different spatial scales; typically, the scale was more local for phytoliths and more regional for pollen, possibly due to differential preservation, production, depositional environments and dispersal. The interpretations from combined proxies also reflected the vegetation in the sampling areas. The ordination analyses showed that major patterns of variation in the pollen assemblages, the phytolith assemblages and the vegetation were related to soil moisture levels, elevation, open landscape (grassy) versus forested areas, and wetlands versus drier areas, complementing previous numerical analyses showing these are dominant factors in modern assemblage studies. The fen, forest, and riparian vegetation was best reflected in the pollen assemblages, while the phytolith assemblages best identified the grassland composition.

This study serves as a baseline for identifying components of vegetation, which can help interpret fossil pollen and phytolith assemblages for palaeoenvironmental reconstructions. Extensive studies are needed, however, to further investigate pollen-phytolith-vegetation relationships within southern Africa and across its nine climatically and floristically diverse biomes. Published data on the floral biology (e.g., pollen and phytolith production) of taxa indigenous to Africa is often lacking, which can influence the interpretations of assemblages. The effects of temperature, moisture, and pH on phytoliths and pollen are well known (see e.g., Pearsall, 2000). However, it is unclear how these elements affect the assemblages, which can skew results and their interpretation. Due to the limited research done on pollen and phytoliths in southern Africa, there are many research areas that need attention to provide better interpretations based on these proxies. These include research on the transport distances of phytoliths and into the quantity and dispersal patterns of pollen.

## Declaration of Competing Interest

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

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.sajb.2023.08.025.

## References

Albert, R.M., Bamford, M.K., Cabanes, D., 2006. Taphonomy of phytoliths and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio-Pleistocene palaeoanthropological samples. Quat. Int. 148, 78–94.
Albert, R.M., Lavi, O., Estroff, L., Weiner, S., Tsatskin, A., Ronen, A., Lev-Yadun, S., 1999. Mode of occupation of Tabun Cave, Mt Carmel, Israel during the Mousterian period: a study of the sediments and phytoliths. J. Archaeolog. Sci. 26, 1249–1260.
Alexandré, A., Meunier, J.D., Lézine, A.M., Vincens, A., Schwartz, D., 1997. Phytoliths: Indicators of grassland dynamics during the late Holocene in intertropical Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 136, 213–229.
Amami, B., Muller, S.D., Rhazi, L., Grillas, P., Rhazi, M., Bouahim, S., 2010. Modern pollen–vegetation relationships within a small Mediterranean temporary pool (western Morocco). Rev. Palaeobot. Palynol. 162, 213–225.
Anderson, R.S., Homola, R.L., Davis, R.B., Jacobson, Jr, G.L., 1984. Fossil remains of the mycorrhizal fungal *Glomus fasciculatum* complex in postglacial lake sediments from Maine. Can. J. Bot. 62, 2325–2328.
Awasthi, P., 1961. Palynological investigations of Cucurbitaceae Part II. Proc. Natl. Inst. Sci. India-B 28, 485–496.
Barboni, D., Bonnefille, R., Alexandre, A., Meunier, J.D., 1999. Phytoliths as palaeoenvironmental indicators, west side Middle Awash Valley, Ethiopia. Palaeogeogr, Palaeoclimatol. Palaeoecol. 152, 87–100.
Barboni, D., Bremond, L., Bonnefille, R., 2007. Comparative study of modern phytolith assemblages from inter-tropical Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 246, 454–470.
Baxter, A.J., Davies, B.R., 1994. Palaeoecological insights for the conservation of aquatic ecosystems in dryland environments: a case study of the Verlorenvlei system, South Africa. Aquat. Conserv. Mar. Freshw. Ecosyst. 4, 255–271.
Bennett, B., Kruger, F., 2015. Forestry and Water Conservation in South Africa: History, Science and Policy. ANU Press, Canberra.
Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. Pollen analysis and pollen diagrams. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons, Chichester, pp. 455–484.
Bell, B.A., Fletcher, W.J., 2016. Modern surface pollen assemblages from the Middle and High Atlas, Morocco: Insights into pollen representation and transport. Grana 55, 286–301.
Birks, H.J.B., Felde, V.A., Bjune, A.E., Grytnes, J-A., Seppä, H., Giesecke, T., 2016. Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. Rev. Palaeobot. Palynol. 228, 1–25.
Boon, R., 2010. Pooley's trees of eastern South Africa: Flora and Fauna Publications Trust.
Breman, E., Ekblom, A., Gillson, L., Norström, E., 2019. Phytolith-based environmental reconstruction from an altitudinal gradient in Mpumalanga, South Africa, 10,600 BP–present. Rev. Palaeobot. Palynol. 263, 104–116.
Bremond, L., Alexandre, A., Wooller, M.J., Hely, C., Williamson, D., Schafer, P.A., Majule, A., Guiot, J., 2008. Phytolith indices as proxies of grass subfamilies on East African tropical Mountains. Global Planet. Change 61, 209–224.
Bryant, Jr, V.M., Holloway, R.G., 1983. The role of palynology in archaeology. Adv. Archaeol. Method Theory 6, 191–224.
Burgess, T., Wingfield, M.J., 2001. Exotic pine forestry in the Southern Hemisphere: a brief history of establishment and quarantine practices. Southern Afr. For. J. 192, 79–84.
Burgoyne, B.M., Bredenkamp, G.J., Van Rooyen, N., 2000. Wetland vegetation in the north-eastern Sandy Highveld, Mpumalanga, South Africa. Bothalia 30, 187–200.
Carrión, J.S., 2002. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. Rev. Palaeobot. Palynol. 120, 217–232.
Carrión, J.S., Scott, L., Vogel, J.C., 1999. Twentieth century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens. J. Quat. Sci. 14, 1–16.
Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter rainfall zone. Earth Sci. Rev. 84, 103–138.
Chevalier, M., Chase, B.M., 2015. Southeast African records reveal a coherent shift from high to low-latitude forcing mechanisms along the east African margin across last glacial–interglacial transition. Quat. Sci. Rev. 125, 117–130.
Chevalier, M., Chase, B.M., 2016. Determining the drivers of long-term aridity variability: a southern African case study. J. Quat. Sci. 31, 143–151.
Chevalier, M., Davis, B.A.S., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., 2020. Pollen-based climate reconstruction techniques for late Quaternary studies. Earth Sci. Rev. 210, 103–384.
Cordova, C.E., 2013. $C_3$ Poaceae and Restionaceae phytoliths as potential proxies for reconstructing winter rainfall in South Africa. Quat. Int. 287, 121–140.
Cordova, C.E., Kirsten, K.L., Scott, L., Meadows, M., Luecke, A., 2019. Multi-proxy evidence of late-Holocene paleoenvironmental change at Princessvlei, South Africa: The effects of fire, herbivores, and humans. Quat. Sci. Rev. 221, 105896.
Court-Picon, M., Buttler, A., de Beaulieu, J.-L., 2005. Modern pollen–vegetation relationships in the Champsaur valley (French Alps) and their potential in the interpretation of fossil pollen records of past cultural landscapes. Rev. Palaeobot. Palynol. 135, 13–39.
Court-Picon, M., Buttler, A., de Beaulieu, J.-L., 2006. Modern pollen/vegetation/land-use relationships in mountain environments: An example from the Champsaur valley (French Alps). c 15, 151–168.
Crifò, C., Strömberg, C.A.E., 2020. Small-scale spatial resolution of the soil phytolith record in a rainforest and a dry forest in Costa Rica: Applications to the deep-time fossil phytolith record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 537, 109107.

Crifò, C., Strömberg, C.A.E., 2021. Spatial patterns of soil phytoliths in a wet vs. dry neotropical forest: Implications for paleoecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 562, 110100.
Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): The use of coprophilous fungi to reconstruct pastoral activity. Veg. Hist. Archaeobot. 19, 391–408.
da Cruz, P. 2015. Lydenburg – Merensky 132kV power lines project –surface water impact assessment study – revision 3. Royal Haskoning DHV.
Delhon, C., Alexandre, A., Berger, J.-F., Thiébault, S., Brochier, J.-L., Meunier, J.-D., 2003. Phytolith assemblages as a promising tool for reconstructing Mediterranean Holocene vegetation. Quat. Res. 59, 48–60.
Delius, P., Maggs, T., Schoeman, M., 2012. Bokoni: Old structures, new paradigms? Rethinking pre-colonial society from the perspective of the stone-walled sites in Mpumalanga. J. Southern Afr. Stud. 38, 399–414.
De Swardt, D., 1990. Birds of the Gustav Klingbiel Nature Reserve & Sterkspruit Area. Witwatersrand Bird Club, Lydenburg.
De Swardt, D.H., 2014. Bird distribution changes in the Lydenburg area, Mpumalanga (2530AB Lydenburg and 2530BA Long Tom Pass) using SABAP data to compare with historical data: a period since the 1980s. Biodivers. Observ. 5, 431–449.
de Wolf, I.K., McMichael, C.N.H., Philip, A.L., Gosling, W.D., 2022. Characterising Dutch forests, wetlands and cultivated lands on the basis of phytolith assemblages. Neth. J. Geosci. 101, e17.
Duffin, K.I., Bunting, M.J., 2008. Relative pollen productivity and fall speed estimates for southern African savanna taxa. Veg. Hist. Archaeobot. 17, 507–525.
Ekblom, A., Gillson, L., Notelid, M., 2017. Water flow, ecological dynamics, and management in the lower Limpopo Valley: a long-term view. Wiley Interdiscip. Rev. Water 4, e1228.
Esteban, I., Bamford, M.K., House, A., Miller, C.S., Neumann, F.H., Schefuß, E., Pargeter, J., Cawthra, H.C., Fisher, E.C., 2020. Coastal palaeoenvironments and hunter-gatherer plant-use at Waterfall Bluff rock shelter in Mpondoland (South Africa) from MIS 3 to the Early Holocene. Quat. Sci. Rev. 250, 106664.
Esteban, I., De Vynck, J.C., Singels, E., Vlok, J., Marean, C.W., Cowling, R.M., Fischer, E.C., Cabanes, D., Albert, R.M., 2017. Modern soil phytolith assemblages used as proxies for Paleoscape reconstructions on the south coast of South Africa. Quat. Int. 434, 160–179.
Esteban, I., Marean, C.W., Cowling, R.M., Fisher, E.C., Cabanes, D., Albert, R.M., 2020. Palaeoenvironments and plant availability during MIS 6 and MIS 3 on the edge of the Palaeo-Agulhas plain (south coast, South Africa) as indicated by phytolith analysis at Pinnacle Point. Quat. Sci. Rev. 235, 105–667.
Esteban, I., Marean, C.W., Fischer, E.C., Karkanas, P., Cabanes, D., Albert, R.M., 2018. Phytoliths as an indicator of early modern humans plant gathering strategies, fire fuel and site occupation intensity during the Middle Stone Age at Pinnacle Point 5-6 (south coast, South Africa). PLoS One; 13 (6), e0198558.
Esteban, I., Vlok, J., Kotina, E., Bamford, M.K., Cowling, R.M., Cabanes, D., Albert, R.M., 2017. Phytoliths in plants from the south coast of the Greater Cape Floristic Region (South Africa). Rev. Palaeobot. Palynol. 245, 69–84.
Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. John Wiley & Sons, Chichester.
Ferrar, A.A., Lötter, M.C., 2007. Mpumalanga Biodiversity Conservation Plan Handbook. Mpumalanga Tourism & Parks Agency, Nelspruit.
Festi, D., Hoffmann, D.L., Luetscher, M., 2016. Pollen from accurately dated speleothems supports alpine glacier low-stands during the early Holocene. Quat. Res. 86, 45–53.
Fish, L., 1999. Preparing herbarium specimens. Strelitzia **7**. National Botanical Institute, Pretoria.
Fitchett, J.M., Grab, S.W., Bamford, M.K., Mackay, A.W., 2017. Late Quaternary rese`arch in southern Africa: progress, challenges and future trajectories. Trans. R. Soc. South Afr. 72, 280–293.
Fitchett, J., Knight, J., Grab, S., 2016. Minerogenic microfossil records of Quaternary environmental change in southern Africa. In: Knight, J., Grab, S. (Eds.), Quaternary Environmental Change in Southern Africa: Physical Human Dimensions. Cambridge University Press, Cambridge, pp. 324–348.
Fredlund, G.G., Tieszen, L.T., 1997. Calibrating grass phytolith assemblages in climatic terms: application to late Pleistocene assemblages from Kansas and Nebraska. Palaeogeogr. Palaeoclimatol. Palaeoecol. 136, 199–211.
Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C., Verschuren, D., 2011. Modern non-pollen palynomorphs from East African lake sediments. Rev. Palaeobot. Palynol. 164, 143–173.
Gosling, W.D., Julier, A.C.M., Adu-Bredu, S., Djagbletey, G.D., Fraser, W.T., Jardine, P.E., Lomax, B.H., Malhi, Y., Manu, E.A., Mayle, F.E., Moore, S., 2018. Pollen-vegetation richness and diversity relationships in the tropics. Veg. Hist. Archaeobot. 27, 411–418.
Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. Rev. Palaeobot. Palynol. 153, 70–85.
Gosling, W.D., Miller, C.S., Livingstone, D.A., 2013. Atlas of the tropical West African pollen flora. Rev. Palaeobot. Palynol. 199, 1–135.
Grimm, E.C., 2011. Tilia 2.1.1 Software. Illinois State Museum, Springfield.
Guimarães, J.T.F., Rodrigues, T.M., Reis, L.S., de Figueiredo, M.M.J.C., da Silva, D.F., Alves, R., Giannini, T.C., Carreira, L.M.M., Dias, A.C.R., da Silva, E.F., 2017. Modern pollen rain as a background for palaeoenvironmental studies in the Serra dos Carajás, southeastern Amazonia. Holocene 27, 1055–1066.
Guo, C., Ma, Y., Li, D., Pei, Q., 2020. Modern pollen and its relationship with vegetation and climate in the Mu Us Desert and surrounding area, northern China: Implications of palaeoclimatic and palaeocological reconstruction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 547, 109699.
Hahn, A., Neumann, F.H., Miller, C., Finch, J., Frankland, T., Cawthra, H.C., Schefuß, E., Zabel, M., 2021. Mid-to Late Holocene climatic and anthropogenic influences in Mpondoland, South Africa. Quat. Sci. Rev. 261, 106938.
Hill, TR, 1995. Analysis of contemporary pollen rain in South Africa - a review. Trans. R. Soc. South Afr. 50, 27–39.
Hill, T.R., Duthie, T.J., Bunting, J., 2021. Pollen productivity estimates from KwaZulu-Natal Drakensberg, South Africa. Palaeoecol. Afr. 35, 259–274.
Hill, T.R., Finch, J.M., 2021. Modern pollen-vegetation relationships in the Drakensberg Mountains, South Africa. Palaeoecol. Afr. 35, 275–292.
Huang, X., Chen, X., Du, X., 2018. Modern pollen assemblages from human-influenced vegetation in northwestern China and their relationship with vegetation and climate. Veg. Hist. Archaeobot. 27, 767–780.
Hyland, E.G., Sheldon, N.D., Smith, S.Y., Strömberg, C.A.E., 2019. Late Miocene rise and fall of C4 grasses in the western United States linked to aridification and uplift. Bulletin 131, 224–234.
Jeske-Pieruschka, V., Fidelis, A., Bergamin, R.S., Vélez, E., Behling, H., 2010. Araucaria forest dynamics in relation to fire frequency in southern Brazil based on fossil and modern pollen data. Rev. Palaeobot. Palynol. 160 (1-2), 53–65.
Johnson, S.D., Andersson, S., 2002. A simple field method for manipulating ultraviolet reflectance of flowers. Can. J. Bot. 80, 1325–1328.
Julier, A.C.M., Manzano, S., Razanatsoa, E., Razafimanantsoa, A.H.I., Githumbi, E., Hawthorne, D., Oden, G., Schüler, L., Tossou, M., Bunting, M.J., 2021. Modern pollen studies from tropical Africa and their use in palaeoecology. Palaeoecol. Afr. 35, 317–347.
Klemm, J., Herzschuh, U., Pestryakova, L.A., 2016. Vegetation, climate and lake changes over the last 7000 years at the boreal treeline in north-central Siberia. Quat. Sci. Rev. 147, 422–434.
Lejju, B.J., Taylorl, D., Robertshaw, P., 2005. Late-Holocene environmental variability at Munsa archaeological site, Uganda: A multicore, multiproxy approach. Holocene 15, 1044–1061.
Lenhardt, N., Eriksson, P.G., Catuneanu, O., Bumby, A.J., 2012. Nature of and controls on volcanism in the ca. 2.32–2.06 Ga Pretoria Group, Transvaal Supergroup, Kaapvaal craton, South Africa. Precambrian Res. 214, 106–123.
Lézine, A.-M., Watrin, J., Vincens, A., Hély, C., 2009. Are modern pollen data representative of west African vegetation? Rev. Palaeobot. Palynol. 156, 265–276.
Lötter, M.C., Mucina, L., Witkowski, E.T.F., 2014. Classification of the indigenous forests of Mpumalanga Province, South Africa. South Afr. J. Bot. 90, 37–51.
Mabhungu, L., Adam, E., Newete, S.W., 2019. Monitoring of phytoremediating wetland macrophytes using remote sensing: The case of common reed (*Phragmites australis* (cav.) Trin. Ex steud.) and the giant reed (*Arundo donax* L.). Rev. Appl. Ecol. Environ. Res. 17, 7957–7972.
MacPherson, J., 2009. Applying palaeoecology to conservation: A long-term perspective for informed management of a fynbos nature reserve. Plymouth Stud. Sci. 2, 218–269.
Markgraf, V., 1980. Pollen dispersal in a mountain area. Grana 19, 127–146.
Marsh, P.E., Cohen, A.D., 2016. *Atrotorquata lineata* as a proxy for *Juncus roemerianus*, Part I: *Atrotorquata lineata* as a proxy for *Juncus roemerianus* in surface sediments from high-level salt marshes in the southeastern United States. Acta Palaeobot. 56, 523–535.
Meltsov, V., Poska, A., Reitalu, T., Sammul, M., Kull, T., 2013. The role of landscape structure in determining palynological and floristic richness. Veg. Hist. Archaeobot. 22, 39–49.
Mercader, J., Bennett, T., Esselmont, C., Simpson, S., Walde, D., 2009. Phytoliths in woody plants from the miombo woodlands of Mozambique. Ann. Bot. 104, 91–113.
Mercader, J., Clarke, S., Bundala, M., Favreau, J., Inwood, J., Itambu, M., Larter, F., Lee, P., Lewiski-McQuaid, G., Mollel, N., Mwambwiga, A., Patalano, R., Soto, M., Tucker, L., Walde, D., 2019. Soil and plant phytoliths from Acacia-Commiphora mosaics at Oldupai Gorge (Tanzania). PeerJ 7, e8211.
Mitchell, P., Whitelaw, G., 2005. The archaeology of southernmost Africa from c. 2000 BP to the early 1800s: A review of recent research. J. Afr. Hist. 46 (2), 209–241.
Morales-Molino, C., Devaux, L., Georget, M., Hanquiez, V., Goñi, M.F.S., 2020. Modern pollen representation of the vegetation of the Tagus Basin (central Iberian Peninsula). Rev. Palaeobot. Palynol. 276, 104193.
Mucina, L., Hoare, D.B., Lötter, M.C., du Preez, P.J., Rutherford, M.C., Scott-Shaw, C.R., Bredenkamp, G.J., Powrie, L.W., Scott, L., Camp, K.G.T., Cilliers, S.S., Bezuidenhout, H., Mostert, T.H., Siebert, S.J., Winter, P.J.D., Burrows, J.E., Dobson, L., Ward, R.A., Stalmans, M., Oliver, E.G.H., Siebert, F., Schmidt, E., Kobisi, K., Kose, L., 2006. Grassland Biome. In: Mucina, L., Rutherford, M.C. (Eds.), The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, pp. 349–437.
Mucina, L., Rutherford, M.C, 2006. The vegetation of South Africa. Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.
Murungi, M.L., Bamford, M.K., 2020. Revised taxonomic interpretations of Cyperaceae phytoliths for (paleo) botanical studies with some notes on terminology. Rev. Palaeobot. Palynol. 275, 104189.
Myburgh, W.J., Bredenkamp, G.J., 2004. Macro-channel riparian vegetation of the Olifants River System in the Grassland Biome. Mpumalanga. Koedoe 47, 41–54.
Nakagawa, T., Brugiapaglia, E., Digerfeldt, G., Reille, M., Beaulieu, J.L.D.E., Yasuda, Y., 1998. Dense-media separation as a more efficient pollen extraction method for use with organic sediment/deposit samples: Comparison with the conventional method. Boreas 27, 15–24.
Neumann, E.-R., Svensen, H., Galerne, C.Y., Planke, S., 2011. Multistage evolution of dolerites in the Karoo Large Igneous Province, Central South Africa. J. Petrol. 52 (5), 959–984.

Neumann, F.H., Botha, G.A., Scott, L., 2014. 18,000 years of grassland evolution in the summer rainfall region of South Africa: Evidence from Mahwaqa Mountain, KwaZulu-Natal. Veg. Hist. Archaeobot. 23, 665–681.
Neumann, F., Scott, L., Bamford, M., 2011. Climate change and human disturbance of fynbos vegetation during the late Holocene at Princess Vlei, Western Cape, South Africa. Holocene 21, 1137–1149.
Neumann, F.H., Scott, L., Bousman, C., Van As, L., 2010. A Holocene sequence of vegetation change at Lake Eteza, coastal KwaZulu-Natal, South Africa. Rev. Palaeobot. Palynol. 162, 39–53.
Neumann, K., Strömberg, C.A.E., Ball, T., Albert, R.M., Vrydaghs, L., Cummings, L.S., 2019. International code for phytolith nomenclature (ICPN) 2.0. Ann. Bot. 124, 189–199.
Norman, N., Whitfield, G., 2006. A Traveller's Guide to South Africa's Rocks and Landforms: Geological Journeys. Struik Nature, Cape Town.
Novello, A., Bamford, M.K., van Wijk, Y., Wurz, S., 2018. Phytoliths in modern plants and soils from Klasies River, Cape Region (South Africa). Quat. Int. 464, 440–459.
Novello, A., Barboni, D., Berti-Equille, L., Mazur, J., Poilecot, P., Vignaud, P., 2012. Phytolith signal of aquatic plants and soils in Chad, Central Africa. Rev. Palaeobot. Palynol. 178, 43–58.
Nyakale, M., 1999. Palynology of Late Quaternary Deposits From the Central Plateau, South Africa. University of the Free State, Bloemfontein. Unpublished M.Sc. dissertation.
O'Connor, T.G., Bredenkamp, G.J., 1997. Grassland. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp. 215–257.
O'Donoghue, T.L., Slater, K., Brown, L.R., 2020. Seasonal habitat utilisation and morphological characteristics of *Chamaeleo dilepis* on Telperion Nature Reserve, Mpumalanga, South Africa. Afr. J. Herpetol. 69, 182–199.
Olatoyan, J.O., Neumann, F.H., Orijemie, E.A., Sievers, C., Evans, M., Mvelase, S., Hattingh, T., Schoeman, M.H., 2022. Archaeobotanical evidence for the emergence of pastoralism and farming in southern Africa. Acta Palaeobot. 62, 50–75.
Parker, A.G., Lee-Thorp, J., Mitchell, P.J., 2011. Late Holocene Neoglacial conditions from the Lesotho highlands, southern Africa: Phytolith and stable carbon isotope evidence from the archaeological site of Likoaeng. Proc. Geol. Assoc. 122, 201–211.
Pearsall, D.M., 2000. Paleoethnobotany: A Handbook of Procedures, second ed Academic Press, London.
Piperno, D.R., 1988. Phytolyth Analysis: An Archaeological and Geological Perspective. Elsevier.
Piperno, D.R., Andres, T.C., Stothert, K.E., 2000. Phytoliths in Cucurbita and other neotropical Cucurbitaceae and their occurrence in early archaeological sites from the lowland American tropics. J. Archaeolog. Sci. 27, 193–208.
Piperno, D.R., 2006. Phytoliths. A Comprehensive Guide For Archaeologists and Palaeoecologists. Altamira Press, Lantham-New York-Toronto-Oxford.
Piperno, D.R., 2009. Identifying crop plants with phytoliths (and starch grains) in Central and South America: a review and an update of the evidence. Quat. Int. 193, 146–159.
Piperno, D.R., McMichael, C., 2020. Phytoliths in modern plants from Amazonia and the Neotropics at large: Implications for vegetation history reconstruction. Quat. Int. 565, 54–74.
Prentice, I.C., 1985. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. Quat. Res. 23, 76–86.
Quamar, M.F., 2019. Palynological study of surface soil samples from the Kartala Forest Range of the Korba District, Chhattisgarh, central India: Modern pollen-rain/vegetation relationship. Geophytology 49 (1&2), 37–48.
Ren, Z.X., Bernhardt, P., Edens-Meier, R., Zweck, J., Arduser, M., Li, H.D., Wang, H., 2019. Comparative pollen–pistil interactions and insect pollination in two Hypoxis species (Hypoxidaceae) in China and North America. Plant Syst. Evol. 305, 115–126.
Romanowski, N., 2011. Wetland Weeds: Causes, Cures and Compromises. CSIRO Publishing, Collingwood VIC, Australia.
Rossouw, L., 2009. The application of fossil grass-phytolith analysis in the reconstruction of Cainozoic environments in the South African interior. Unpublished PhD thesis, University of the Free State, Free State.
Schachtschneider, K., Reinecke, K., 2014. Riparian trees as common denominators across the river flow spectrum: Are ecophysiological methods useful tools in environmental flow assessments? Water SA 40, 287–296.
Scott, L., 1982. A late quaternary pollen record from the Transvaal bushveld, South Africa. Quat. Res. 17, 339–370.
Scott, L., 1984. Palynological evidence for Quaternary palaeoenvironments in southern Africa, in Klein, R.G. (Ed.), Southern African Prehistory and Palaeoenvironments. Balkema, Rotterdam, pp. 65-80.
Scott, L., Bousman, C.B., 1990. Palynological analysis of hyrax middens from Southern Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 76, 367–379.
Scott, L., Holmgren, K., Talma, A.S., Woodborne, S., Vogel, J.C., 2003. Age interpretation of the Wonderkrater spring sediments and vegetation change in the Savanna Biome, Limpopo province, South Africa. S. Afr. J. Sci. 99, 484–488.
Scott, L., Marais, E., Brook, G.A., 2004. Fossil hyrax dung and evidence of Late Pleistocene and Holocene vegetation types in the Namib Desert. J. Quat. Sci. 19 (8), 829–832.
Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E., Metwally, A., 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. Quat. Sci. Rev. 32, 100–118.
Scott, L., Neumann, F.H., 2018. Pollen-interpreted palaeoenvironments associated with the Middle and Late Pleistocene peopling of Southern Africa. Quat. Int. 495, 169–184.
Scott, L., Sobol, M., Neumann, F.H., Romera, G.G., Fernández-Jalvo, Y., Bousman, C.B., Horwitz, L.K., van Aardt, A.C., 2020. Late Quaternary palaeoenvironments in the central semi-arid region of South Africa from pollen in cave, pan, spring, stream and dung deposits. Quat. Int. 614, 84–97.
Senn, C., Tinner, W., Felde, V.A., Gobet, E., van Leeuwen, J.F.N., Morales-Molino, C., 2021. Modern pollen–vegetation–plant diversity relationships across large environmental gradients in northern Greece. Holocene 32 (3), 159–173.
Siebert, S.J., Van Wyk, A.E., Bredenkamp, G.J., 2002. The physical environment and major vegetation types of Sekhukhuneland, South Africa. S. Afr. J. Bot. 68, 127–142.
Sobol, M.K., Scott, L., Finkelstein, S.A., 2019. Reconstructing past biomes states using machine learning and modern pollen assemblages: A case study from Southern Africa. Quat. Sci. Rev. 212, 1–17.
Sieben, E.J.J., Glen, R.P., Muasya, A.M., 2017. The wetland flora of South Africa: Occurrence patterns, frequency and dominance across a diverse landscape. Aquatic Botany 142, 112–118.
Sjöström, J., 2013. Late Holocene palaeoenvironmental reconstruction on a peat sequence from northeastern South Africa, using grass phytoliths as main proxy. Unpublished MSc dissertation, Stockholm University.
Sjöström, J., Norström, E., Risberg, J., Schoeman, M.H., 2017. Late Holocene palaeoecological reconstruction from Mpumalanga, South Africa. Rev. Palaeobot. Palynol. 246, 264–277.
Strömberg, A.E., 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 239–275.
Tabares, X., Mapani, B., Blaum, N., Herzschuh, U., 2018. Composition and diversity of vegetation and pollen spectra along gradients of grazing intensity and precipitation in southern Africa. Rev. Palaeobot. Palynol. 253, 88–100.
Traverse, A., 1988. Paleopalynology. Unwin Hyman, Boston.
Twiss, P.C., Suess, E., Smith, R.M., 1969. Morphological classification of grass phytoliths. Soil Sci. Soc. Am. J. 33, 109–115.
Twiss, P.C., 1992. Predicted world distribution of C 3 and C 4 grass phytoliths. In: Rapp, G., Mulholland, S.C. (Eds.), Phytolith Systematics: Emerging Issues. Plenum Press, New York, pp. 113–128.
Van Ginkel, C.E., Cilliers, C.J., 2020. Aquatic and Wetland Plants of Southern Africa. Briza Publications, Pretoria.
van Wilgen, B.W., Richardson, D.M., 2012. Three centuries of managing introduced conifers in South Africa: Benefits, impacts, changing perceptions and conflict resolution. J. Environ. Manag. 106, 56–68.
Watling, J., Iriarte, J., Whitney, B.S., Consuelo, E., Mayle, F., Castro, W., Schaan, D., Feldpausch, T.R., 2016. Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions II: Southwestern Amazonian forests. Rev. Palaeobot. Palynol. 226, 30–43.
Williams, C.G., 2008. Aerobiology of *Pinus taeda* pollen clouds. Can. J. For. Res. 38, 2177–2188.
Zhang, Y.-J., Duo, L., Pang, Y.-Z., Felde, V.A., Birks, H.H., Birks, H.J.B., 2018. Modern pollen assemblages and their relationships to vegetation and climate in the Lhasa Valley, Tibetan Plateau, China. Quat. Int. 467, 210–221.

# CHAPTER 5: IN PREP. PAPER 3

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# HOLOCENE PALAEOENVIRONMENTAL RECONSTRUCTION FROM MASHISHING FEN, MPUMALANGA, NORTHEASTERN SOUTH AFRICA

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# 1. INTRODUCTION

Holocene wetlands serve globally as an archive for both natural climate and vegetation fluctuations and human impact and are researched by combining methods like palynology, phytolith analysis and isotope analysis (Norström et al., 2009; Finné et al., 2010; Sjöström et al., 2017; Breman et al., 2019; Hahn et al., 2021). In South Africa, palynology as a tool to reconstruct Holocene landscapes started in the 1940s when a Dutch palynologist, van Zinderen Bakker introduced this study field to the subcontinent (see Neumann and Scott, 2018). In recent decades, palaeoecological research has focused on climate change, exploring the variability and biogeography of this highly diverse region (e.g., Truc et al., 2013; Huntley et al., 2014; Chase et al., 2015; Chevalier and Chase, 2015, Fitchett and Bamford, 2017). Several researchers also studied anthropogenic disturbances before the arrival of the European settlers (e.g., Neumann et al., 2014, Hahn et al., 2021). Olatoyan et al. (2022) comprise a review of these previously published palaeoecological records, suggesting that the patterns in the regional dataset could suggest human disturbances resulting from the arrival of pastoralism and farming.

The changes noted in this review dated to the first millennia CE after the development of the South African Neolithic (Sadr, 2002, 2019) when the hunter-gatherers were joined by pastoralists and farmers approximately 2000 years ago (Maggs and Whitelaw, 1991; Mitchell and Whitelaw, 2005; Huffman, 2007; Sadr, 2008, 2014, 2015; Lander and Russell, 2018, 2020; Schoeman, 2020; Olatoyan et al., 2022). It did not include the early and mid-Holocene, when South Africa was occupied by hunter-gatherers whose technocomplexes changed from the Oakhurst to the Wilton and then the final Later Stone Age (Sampson, 1974; Wadley, 1993; Deacon and Deacon, 1999; Lombard et al., 2012, 2022).

The archaeological evidence for the Holocene shows significant shifts in technology and human occupation. Some researchers, for example, have linked the widespread flake production ca. 12,000–7000 BP and the expansion of hunter-gatherers with Oakhurst technocomplex ca. 11,900 and 10,000 BP to environmental forcing (Wadley, 1993; Chase et al., 2018). Also, Deacon (1984) and Mitchell (2005) argued that the transition from the Robberg to Albany technocomplex occurred after the beginning of the Late Glacial Climate amelioration, where the changes in artefact assemblages demonstrate the ecological difficulties faced by the people and the accompanying adaptations. Similarly, the spread of pastoralism in South Africa has been linked to deteriorating environmental conditions in the northern Kalahari (Smith, 2016). Change in farming occupations has also been linked to environmental events. Ekblom et al. (2011) suggested that the expansion of agricultural activities ca. 800–950 CE probably occurred due to moderate to high rainfall conditions in the Limpopo Valley and the development of complexity in the Shashe-Limpopo Confluence Area and the end of the Mapungubwe occupation has been linked to climate change, including the Medieval Warm Epoch (MWP) (AD 900 to 1300) and the Little Ice Age (LIA) (AD 1300 to 1850) (Huffman, 1996, 2000, 2008, 2009; Meyer, 1998; Tyson, et al., 2002; see Smith, 2005 and Smith, et al., 2012 for a critique).

While there may indeed be links between environmental and societal change in some areas, the timing and degree of moisture conditions in other areas vary significantly (Smith, 2005). It is also often argued that the patterns observed (e.g., decline in forest trees, increased open-land indicators) in palaeoenvironmental records relate to the effects of climate change and/or anthropogenic impact (Li et al., 2008; Scott et al., 2003; Finch and Hill, 2008; Breman et al., 2011; Hahn et al., 2021). There, however, are relatively few well-dated palaeoenvironmental sequences to contextualise these shifts, partly due to sparse continuous terrestrial records and

spatial variations among records due to regional climatic differences (Klein, 1984:113; Prior and Williams, 1985:471; Korsman and Plug, 1994: 26; Porraz et al., 2015:166; Bousman and Brink, 2018:132).

Without a large body of well-dated palaeoenvironmental data, correlations between technology, subsistence strategy, and environmental changes have been assumed. Large-scale climatic processes/events e.g., Holocene Thermal Maximum, African Humid Period, Younger Dryas, Medieval Warm Period (MWP), Little Ice Age (LIA) have been used to assess technological and subsistence changes (Deacon, 1984; Huffman, 1996; Mitchell et al., 1998; Vogel and Fuls, 1999; Badenhorst, 2018) without acknowledging regional or local climate manifestations.

Our research helps to address the need for additional high-resolution and well-dated independent records and studies to reconstruct the long-term changes in human-environment relationships and their variability across different spatial and temporal contexts. We do this by developing the chronology and vegetation history of the Mashishing during the last 11,700 years based on pollen, spores, and charcoal records derived from core sediment sequences. Our interpretation is informed by the differences between anthropogenic and climate drivers of vegetation changes and their resulting impact on local and regional vegetation identified by Olatoyan et al. (2022). The proximity of the Mashishing Fen to archaeological sites with secured chronologies allows an assessment of human responses to varying local environments. To contextualise this data, we briefly summarise the published paleoenvironmental record and occupation sequence for the surrounding region in the next section.

## 2. ENVIRONMENTAL AND ARCHAEOLOGICAL CONTEXT

Palaeoclimatic variability across the Summer Rainfall Region (SRR) show that large-scale

climatic models fail to recognise local variations (Holmgren et al., 2003; Smith et al., 2007; Neumann et al., 2008, 2010; Scott et al., 2008, 2012; Norström et al., 2009; Stager et al., 2013; Truc et al., 2013; Chevalier et al., 2014, 2015; Metwally et al., 2014; Woodborne et al., 2015, 2016; Hahn et al., 2016; Chase and Quick, 2018, Granger et al., 2018; Hahn et al., 2021). Evidence for variability is found in the pollen sequences at Wonderkrater and Tswaing Crater in the central interior (Fig. 1). These, as well as geochemical data, suggest an arid early Holocene ca.11.7–8 ka BP (Scott et al., 2003; Kristen et al., 2010; Neumann et al., 2010; Metwally et al., 2014) in contrast to records, such as the Braamhoek wetland (Fig. 1) that show alternating dry/wet moisture changes (Norström et al., 2009) and the moderately humid conditions at Rietvlei Dam and Tate Vondo (Scott, 1983, 1989; Fig. 1). Phytolith studies at Verloren Valei, Versailles and Graskop (Fig. 1) show cool and dry conditions during the early Holocene (Breman et al., 2019), which contrasts with the suggested relatively moist conditions during this period for the SRR (Chase et al., 2010, Truc et al., 2013; Chevalier and Chase, 2015).

During the Middle Holocene, ca. 7–4 ka BP, the Wonderkrater, Tswaing Crater, Eteza, Tate Vondo and Florisbad records (Scott, 1989; Scott and Nyakale, 2002; Scott et al., 2003; Neumann et al., 2010; Metwally et al., 2014; Fig. 1) show wetter and considerably variable conditions over an area stretching from central to northern South Africa. The lower $\delta^{13}C$ and the higher $\delta^{18}O$ in the stalagmites at Makapansgat (Fig. 1) also suggest wetter and warmer conditions for this period (Holmgren et al., 1999; Lee-Thorp et al., 2001).

The late Holocene, ca. <4 ka BP records from Scot's Farm (Scott, 1982b) and Wonderkrater (Scott et al., 2003, 2008, 2012) (Fig. 1) indicate drier conditions, particularly around 2000 BP, while other studies (e.g., Neumann et al., 2011; Scott et al., 2012) suggest widespread drought probably coincident with the southward spread of pastoralists in the Cape region (Neumann et

al., 2011; Scott et al., 2012). While a relatively wetter condition was suggested during the late Holocene (Scott and Thackeray, 1987; Scott et al., 2008), a recent study proposed relatively dry conditions using the probability density functions (pdf) derived from the fossil pollen data (Truc et al., 2013). Further terrestrial records from the Tswaing impact crater (Fig. 1, southwest of Wonderkrater) indicated relatively warm and subhumid conditions during the late Holocene (Kristen et al., 2010; Metwally et al., 2014).

Palaeoenvironmental studies in northern and northeastern South Africa provide varying evidence of environmental shifts during the last 2000 years. A period that included notable climatic events like the LIA and the MWP. In the Savanna Biome in northern South Africa, carbon isotope studies at Pafuri (Fig. 1) recorded the driest period in the northeastern region during the LIA (ca. 1635 CE, 1695 CE and 1805 CE) and the wettest period during the MWP (ca. 1075 CE) (Woodborne et al., 2015). A similar record at Mapungubwe (Fig. 1), west of Pafuri, accounted for the same climatic variations with localised effects (Woodborne et al., 2016). The high rainfall in the mediaeval warm period aligns with Smith et al.'s (2007). Further studies in the Shashe-Limpopo River Basin using stable Nitrogen isotopes identified wetter conditions until 1450 CE (Smith et al., 2007). In contrast, the speleothem record from Makapansgat Cave (Fig. 1), south of Mapungubwe, indicated cool and dry conditions ca. 1300 CE (Holmgren et al., 2003). Conversely, phytolith studies at the Mashishing Fen (formerly Lydenburg), Mpumalanga (Fig. 1), indicated a moderate to dry environment ca. 300–1350 CE and increasingly mesic conditions ca. 1350 CE–present (Sjöström et al., 2017).

This brief review highlights the irregularity of the distribution of precipitation and temperature both at intra- and inter-site levels**.** Consequently, the idea that any period, such as the MWP or LIA, was uniformly wet or dry should be treated with caution, and more well-dated sequences of

high-resolution data (pollen and other proxies) are required for better interpretation of these climatic events (Scott et al., 2012). Interpreting the temperature and moisture oscillations during the last 2000 years is further complicated by the possible impact the increasing numbers of pastoralists and farmers had on the landscape (Scott et al., 2012; Lander and Russell, 2018, 2020; Schoeman, 2020; Olatoyan et al., 2022).

The pastoralists and farmers were joining the Late Stone Age hunter-gatherers that became widespread in the region after ca. 13,000 BP (Wadley, 1993). Final Pleistocene and Holocene LSA remains, which may include the end of the Robberg (11,195–17,973 BCE), the Oakhurst (6755–10,839 BCE), Wilton (2686–5834 BCE), final LSA (632 CE–1948 BCE) and ceramic final LSA ( 1493–97 CE) techno-complexes (Lombard et al., 2022), are present at Bushman Rock Shelter (12,500–8500 BP [Porraz et al., 2015; Fig. 1]), Heuningneskrans (ca. 16,000–8000 BP [Porraz and Val, 2019; Fig. 1]), Iron Pig (ca. 16,000–9000 BP [Bader et al., 2020; Fig. 1]), Honingklip (ca. 5000 BP– 200 CE [Korsman and Plug, 1994; Fig. 1], and Welgelegen (unknown date in the Wilton to the historic past [Schoonraad and Beaumont, 1971; Fig. 1]).

In the last 2000 years, these hunter-gatherer shelter deposits started to include material culture, e.g., thick-walled pottery (see Sadr and Sampson, 2006 and Sadr, 2008 for a detailed discussion of the differences between farmers and hunter-gatherer pottery) from the open-air semi-permanent and sedentary farmer settlements. Such pottery has also been found in shelters and caves such as Border Cave (Backwell et al., 2022), Bushman Rock Shelter (Porraz et al., 2015), Heuningneskrans (Porraz and Val, 2019), Honingklip (Korsman and Plug, 1994), Iron Pig Shelter (Bader et al., 2020), and Welgelegen (Schoonraad and Beaumont, 1971). Most of these are associated with farming communities that grow crops and keep livestock (Lander and Russell, 2018; 2020; Schoeman, 2020; Olatoyan et al., 2022).

Early Farming Community occupations, which date to the first millennium CE, have been the subject of significant interest as this brought about a notable change to the region's history and culture and also marked a transition to a more sedentary lifestyle (e.g., Evers, 1974, 1975, 1977, 1980, 1982; Klapwijk, 1974; Marker and Evers, 1976; Meyer, 1984, 1986; Klapwijk and Huffman, 1996; Antonites, 2013, 2016; Antonites et al., 2014; Jordaan, 2017). These sites tend to be small (ca. 6–8 ha) and include sites such as Silver Leaves (Klapwijk, 1974; Klapwijk and Huffman, 1996; Fig. 1), Lydenburg Heads (von Bezing and Inskeep, 1966; Evers and Vogel, 1980; Evers, 1982; Whitelaw, 1996; Fig. 1), Plaston (Evers, 1977, Fig. 1), Harmony (Evers, 1974; Fig. 1) and Klingbiel (Evers, 1980; Fig. 1). The material culture of occupations by Early and Middle Farming Communities (ca. 900–1300 CE) overlap in northeastern South Africa, and very few exclusively Middle Farming Community sites have been excavated. One of the few is Eiland Salt Works (Evers, 1975; Fig. 1).

Later, Farmer Community sites are much larger in general and tend to have some stonewalling components. Sites include the Ndebele capitals KwaMaza, Esikhunjini and KoNomtjarhelo (capital Erloweni) (Schoeman, 1997, 1998a, b; Fig. 1) and Bokoni sites Komati Gorge, Moxomatsi and Khutwaneng (Badfontein) (Collett, 1979, 1982; Delius et al., 2012; Widgren et al., 2016; Masolo, 2020; Birin et al., 2021; Maggs and Widgren, 2023; Fig. 1).

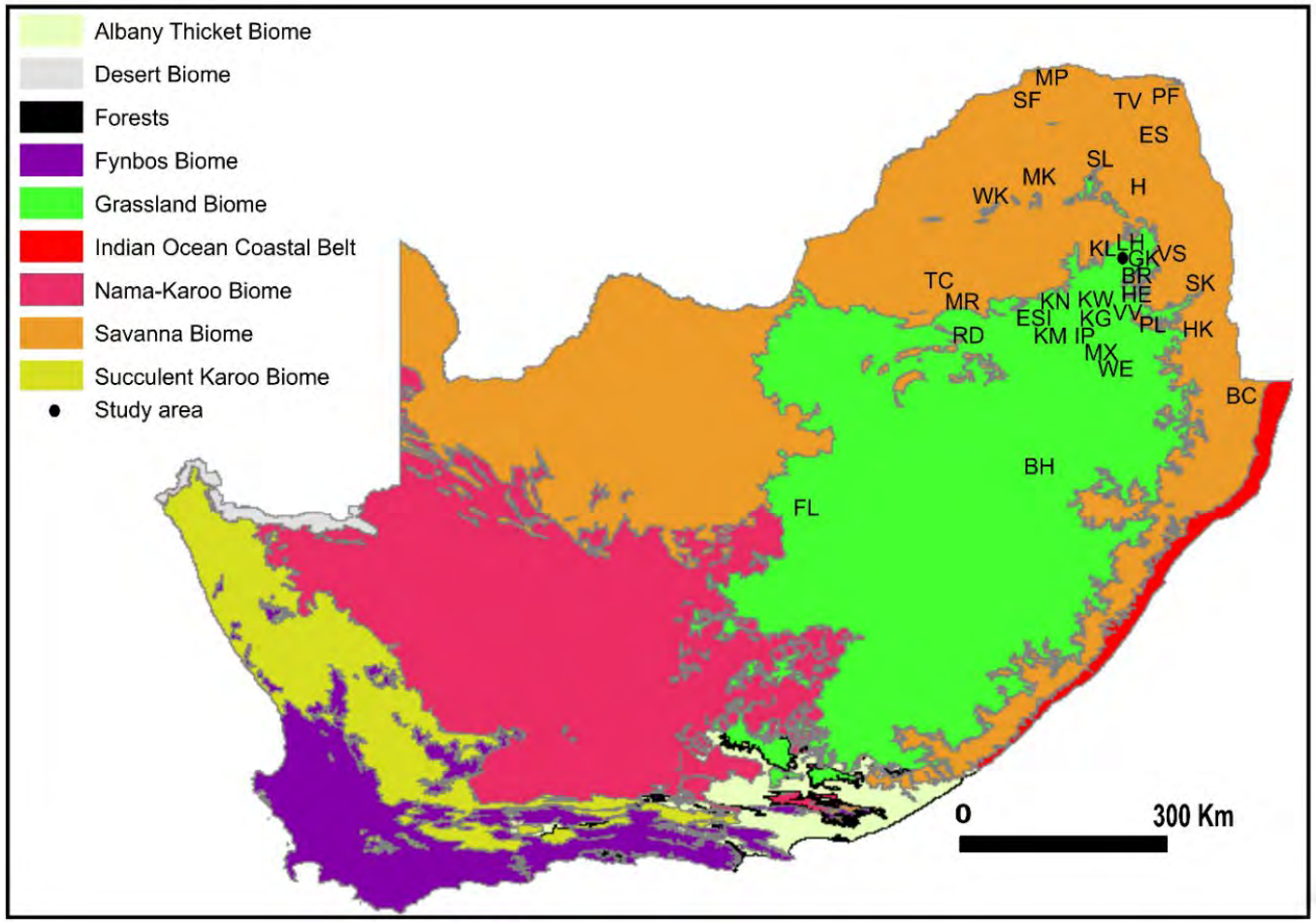


Figure 1. Map of South African Biomes (adapted after Mucina and Rutherford, 2006) showing the approximate location of the study area and sites discussed in the text, BC-Border Cave, BH- Braamhoek wetland, BR- Bushman Rock Shelter, ES-Eiland Salt works, ESI- Esikhunjini, FL-Florisbad, GK- Graskop, H-Harmony, HE- Heuningneskrans, HK-Honingklip, IP- Iron Pig Shelter, KG-Komati Gorge, KL-Klingbiel, KM-KwaMaza, KN- KoNomtjarhelo (Erloweni), KW-Khutwaneng (Badfontein), LH-Lydenburg Heads Site, MK-Makapansgat Cave, MR-Moreletta Stream, MX-Moxomatsi, PF-Pafuri, PL-Plaston, RD-Rietvlei Dam, SF- Scot's Farm, SK- SK17, SL-Silver Leaves, TC-Tswaing Crater, TV-Tate Vondo, VS-Versailles, VV-Verloren Valei, WE- Welgelegen; WK-Wonderkrater.

## 2. MATERIALS AND METHODS

### *2.1. Study area*

The Mashishing Fen (25° 05′54.4″S, 30° 30′36.0″E) is in Mpumalanga Province, South Africa, at an altitude of 1580 m above sea level. The regional geology predominantly comprises strata of shales, bands of dolerite (diabase sills) and quartzites of the Neoarchaean to Palaeoproterozoic Pretoria Group (Transvaal Supergroup, Vaalian) (Eriksson and Altermann, 1998; Norman and Whitfield, 2006; Lenhardt et al., 2012). The incised valleys reflect erosional processes on the landscape, where the softer shales have undergone faster erosion to form valleys, and the resistant quartzites form ridges (da Cruz, 2015). The topography and rock outcrops in the region often lead to the dominance of shallow soils on hillsides and deeper soils in valleys (da Cruz, 2015). The red clay soils form primarily from shale rock formations of the Pretoria Group (da Cruz, 2015). Typical soil types in the area include apedal, plinthic, eutrophic, and shallow soils (Mucina and Rutherford, 2006).

The Sterkspruit and the Klipgatspruit watercourses, which currently run through the outskirts of Mashishing, have caused erosion in the mountainous regions and formed deep valleys with cliffs (De Swardt, 1990). The general fluvial drainage pattern in the area is dendritic, and the steep, mountainous terrain often leads to narrow drainage lines for surface water, which tend to be of higher energy fluvial features (da Cruz, 2015; Sjöström et al., 2017). The Mashishing Fen itself is surrounded by perennial streams that flow into the Dorps River and Spekboom River, which form part of the Olifants River, which ultimately drains into the Indian Ocean (Sjöström et al., 2017).

It is situated in Lydenburg Thornveld within the Grassland Biome and is bordered to the east by the Long Tom Pass Montane Grassland (Mucina and Rutherford, 2006). Lydenburg Thornveld bioregion is a transitional zone within the Savanna Biome between the high-lying grasslands and the warmer and drier bushveld (Mucina et al., 2010).

Rainfall is highly seasonal, with more than 66% of mean annual precipitation falling between October and March (Mucina and Rutherford, 2010).The general climate of the region is primarily influenced by the seasonal shifts of high-pressure belts and easterly air flows associated with the Intertropical Convergence Zone (ITCZ) and the El Niño Southern Oscillation (ENSO), with the southwest Indian Ocean as a significant source of atmospheric moisture (Tyson and Preston-Whyte, 2000; Holmgren et al., 2003; Chase and Meadows, 2007; Woodborne et al., 2016). The predominant occurrence of summer rainfall relates to the ITCZ's southward movement from the equatorial regions, providing moisture to the southern African interior plateau (Mucina and Rutherford, 2006; da Cruz, 2015).

The Drakensberg Escarpment east of Mashishing creates a rain shadow effect, resulting in low-lying regions to the west of the escarpment receiving significantly less rainfall than the high-altitude regions (Mucina and Rutherford, 2006).

Thus, proximity to the Drakensberg Escarpment accounts for the rainfall received in the area. For instance, the Lydenburg Thornveld present in the rainfall shadow of the escarpment receives mean annual precipitation of 707 mm (580–810 mm), while the Long Tom Pass Montane Grassland in the eastern part of the Gustav Klingbiel Nature Reserve receives orographic precipitation and mists throughout most of the year with mean annual precipitation of 858 mm (660–1180 mm). The mean annual temperature in the Lydenburg Thornveld is 16ºC; relatively

infrequent frost occurs mainly in the higher elevation montane grasslands (Mucina and Rutherford, 2010).

The contemporary vegetation of the Lydenburg Thornveld comprises grasses like *Themeda triandra,Setaria nigrirostris*, *Andropogon schirensis, Heteropogon contortus*, and trees such as *Dombeya rotundifolia, Cussonia transvaalensis, Senegalia caffra* (syn. *Acacia caffra*), *Vachellia karroo* (syn. *Acacia karroo*), and *Combretum erythrophyllum.* Low shrubs like *Senecio microglossus, Anthospermum rigidium, Searsia gerrardii*, and tall shrubs, e.g., *Vernonia crataegifolia, Diospyros lycioides* are also present (Siebert et al., 2002; Mucina and Rutherford, 2010). Lydenburg Montane Grassland is dominated by herbaceous vegetation comprising grasses such as *Panicum maximum, Eragrostis racemosa, Melinis repens* and herbs such as *Hypoxis rigidula,Ipomoea* spp. and *Aloe greatheadii*. The woody vegetation comprises shrubs such as *Leucosidea sericea, Senegalia ataxacantha* (syn. *Acacia ataxacantha*), *Euclea crispa, Senecio microglossus, Diospyros lycioides*, and trees such as *Faurea galpinii, Cussonia paniculata, C. transvaalensis, Celtis africana, Dichrostachys cinerea, Protea caffra, Searsia pyroides, Vachellia karroo* and *Senegalia caffra*. Common invasive species include *Ipomoea alba, Ricinus communis* and *Eucalyptus grandis* (Ferrar and Lötter, 2007; Mucina and Rutherford, 2010; de Swardt, 2014).

### *2.2. Coring*

A Russian corer with a 50 x 5 cm chamber was used to retrieve a 5.5 m long core at the centre of the fen (25°05'54.9"S, 30°30'36.4"E) in January 2020. Each sediment sample was transferred from the corner into a rigid half-cylindrical PVC tube and wrapped with cling film to prevent contamination, compaction, water loss, and oxidation. The core samples were transported to

Bokoni Laboratory, University of the Witwatersrand, and stored at 16˚C. It was subsampled at 10 cm sampling intervals (total of 56 samples) in 1 cm slices for pollen and phytolith analysis, 2 cm slices for AMS radiocarbon dating and Loss on Ignition (LOI) analysis, and 4 cm for soil analysis. Only the pollen, charcoal and AMS data are recorded in this study. The phytolith, LOI and soil analyses are aspects for further studies. Each sample was stored in double Ziploc bags under refrigeration at 4°C (39.2°F) to maintain viability and prevent degradation.

### *2.3. Radiocarbon dating*

Eighteen AMS radiocarbon dates were obtained from the core (Table1) at the iThemba Laboratory for Accelerator-Based Sciences (iThemba LABS), Johannesburg. Dates were calibrated using the OxCal 4.4 web interface and the Southern Hemisphere SHCal 20 calibration curves with a 95.4 % probability (Hogg et al., 2020; Bronk Ramsey, 2023). The age-depth model (Fig. 2) was developed using Bayesian modelling using Bacon software (Blaauw and Christen, 2011).

### *2.4. Palynological preparation and extraction*

Samples of 10–30 g were treated for palynological analysis following the standard method using 10% HCl, 40% HF and 10% KOH, and acetolyzed (Berglund and Ralska-Jasiewiczowa, 1986; Faegri and Iversen, 1989) at the Evolutionary Studies Institute (ESI) Laboratory, University of the Witwatersrand, Johannesburg. The samples were concentrated by heavy liquid mineral separation using $ZnCl_2$/HCl with a specific gravity of 2.0 (Faegri and Iversen, 1989; Nakagawa et al., 1998). Pollen concentration (e.g., by adding *Lycopodium*spore tablets [Stockmarr, 1971]) was not calculated. Processed samples and final residues were sieved using 250 µm and 10 µm mesh screens to concentrate pollen.

Pollen residues were mounted in glycerine jelly, and pollen taxa were identified using an Olympus BX51 light microscope at a magnification of 400x and 1000x. The aim was to count a minimum of 300 terrestrial pollen grains, but in some cases, only 150 grains were obtained after traversing up to 10 pollen slides for those samples. Modern pollen reference collection and photographs at the ESI Laboratory, University of the Witwatersrand, Johannesburg, as well as published references were used for the identification of the palynomorphs (Coetzee and van Zinderen Bakker, 1952; Van Geel, 1978; Scott, 1982c; Coetzee and Praglowski, 1984; Cugny et al., 2010; Gelorini et al., 2011; Gosling et al., 2013). Modern pollen samples collected from the study site were extracted and prepared to extend ESI's existing pollen reference collections. Aquatics, ferns, and fungal spores were excluded from the pollen sum. TILIA 2.1.1 was used for the pollen diagram and zonation using the CONISS (Constrained Incremental Sum-of-Squares) program for stratigraphically constrained cluster analysis within the TILIA software (Grimm, 2011).

### *2.5. Charred plant particles*

Charred plant particles (black, angular, opaque) including both charred wood and charred grass cuticles were counted and grouped into three categories based on the length of the longest axis; >10 µm, >50 µm (microcharcoal) and >100 µm (macrocharcoal) which helped to differ between locally dispersed charred particles and regionally transported charcoal fragments (>100 µm) (Rhodes, 1998; Mooney and Radford, 2001; Mooney and Tinner, 2011). Often, charred particles become fragmented because the processing of samples for palynological analysis involves centrifuging which might lead to fragmentation of charred fragments; consequently, tiny fragments <10 µm were ignored (Mooney and Tinner, 2011).

## 3. RESULTS

### *3.1. Chronology*

Nine (9) samples provided AMS radiocarbon dates, indicating a Holocene age for the sequence. Nine additional radiocarbon dates were obtained to produce 18 dates (Table 1). The samples were calibrated using the southern hemisphere curve (OXCal SHCal20) OxCal v4.4.4 (Bronk Ramsey 2023). The age-depth model was plotted using Bayesian modelling and Bacon software (Fig. 2) (Blaauw and Christen, 2011). However, three radiocarbon dates at depths of 243 cm, 253 cm, and 263 cm showed inversion of the dates (Table 1).

Table 2: Radiocarbon dates of the profile sequence of Mashishing Fen (*represents inversion of the dates)

| Core | Lab ID | Depth (cm) | $\delta^{13}C$ (‰) | Age yr BP | error | Unmodelled (cal. BP) | | Unmodelled BCE/CE | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | From (95.4) | To (95.4) | From (95.4) | To (95.4) |
| B1 | R_Date IT-C-3108 | 3 | -27.4 | -90 | 134 | 280 | … | 1670CE | … |
| B2 | R_Date IT-C-3343 | 33 | -25.0 | 130 | 68 | 280 | ... | 1671CE | … |
| B3 | R_Date IT-C-3109 | 103 | -25.8 | 810 | 51 | 788 | 569 | 1162CE | 1382 CE |
| B4 | R_Date IT-C-3111 | 153 | -22.1 | 980 | 60 | 957 | 732 | 994 | 1218 CE |
| B5 | R_Date IT-C-3554 | 173 | -25.0 | 1390 | 51 | 1354 | 1118 | 597 | 833 CE |
| B5 | R_Date IT-C-3580 | 193 | -25.0 | 2230 | 145 | 2700 | 1834 | 751 BCE | 116 CE |
| B6 | R_Date IT-C-3552 | 223 | -25.0 | 3680 | 79 | 4232 | 3720 | 2283 | 1771 BCE |
| B6 | R_Date IT-C-3599 | 233 | -25.0 | 4680 | 69 | 5582 | 5055 | 3633 | 3106 BCE |
| B6 | R_Date IT-C-3582 | 243 | -25.0 | 6940 | 82 | 7929 | 7589 | 5980* | 5640 BCE* |
| B6 | R_Date IT-C-3115 | 253 | -24.7 | 5190 | 79 | 6181 | 5663 | 4232* | 3714 BCE* |
| B6 | R_Date IT-C-3544 | 263 | -25.0 | 4470 | 66 | 5289 | 4866 | 3340* | 2917 BCE* |
| B7 | R_Date IT-C-3537 | 273 | -22.3 | 6050 | 81 | 7157 | 6663 | 5208 | 4714 BCE |
| B7 | R_Date IT-C-3533 | 283 | -25.0 | 7690 | 95 | 8639 | 8205 | 6690 | 6256 BCE |
| B8 | R_Date IT-C-3112 | 353 | -25.9 | 8960 | 77 | 10235 | 9747 | 8286 | 7798 BCE |
| B9 | R_Date IT-C-3114 | 403 | -25.0 | 9290 | 91 | 10663 | 10236 | 8714 | 8287 BCE |
| B10 | R_Date IT-C-3110 | 453 | -24.5 | 9470 | 98 | 11107 | 10386 | 9158 | 8437 BCE |
| B11 | R_Date IT-C-3113 | 503 | -23.0 | 9840 | 75 | 11615 | 10811 | 9666 | 8862 BCE |
| B12 | R_Date IT-C-3107 | 553 | -24.2 | 9990 | 95 | 11760 | 11205 | 9811 | 9256 BCE |

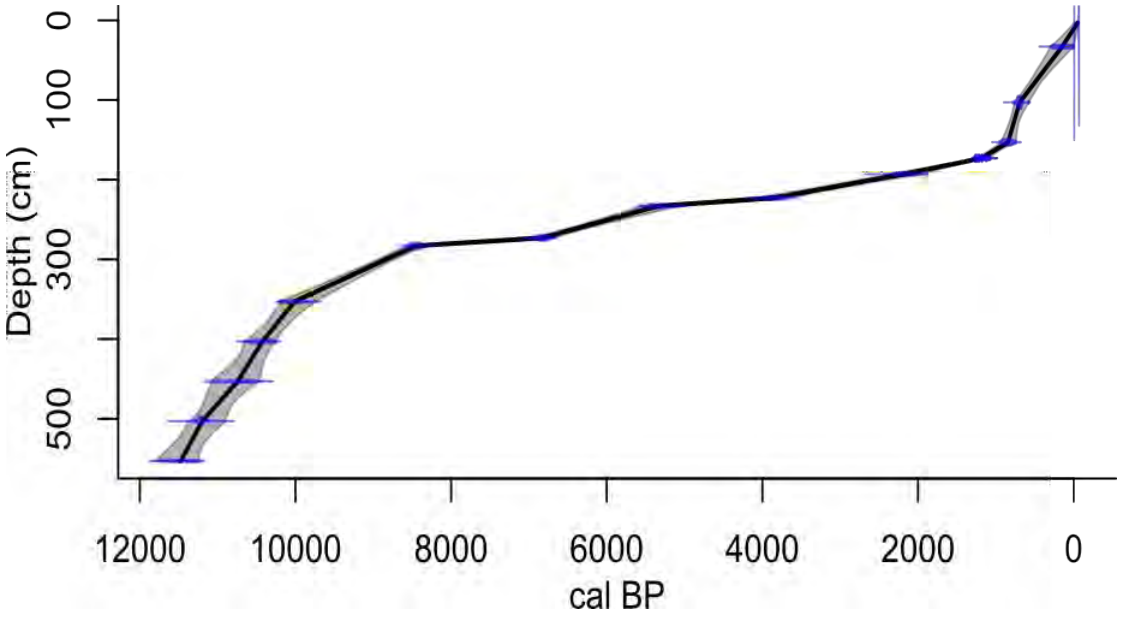

Figure 2: Age depth model of AMS radiocarbon dates of Mashishing sequence, Dates were plotted using Bayesian modelling and Bacon software (Blaauw and Christen, 2011).

*3.2. Palynology*

The pollen sequence from the Mashishing Fen core, starting about 11,700-11,200 years ago at the beginning of the Holocene, is subdivided into six pollen zones, PZ 1-6 (Figs. 3 and 4), based on CONISS results (cluster analysis). The pollen zones are summarised in Table 2. Palynomorphs are grouped according to their preferred habitats and characteristics (neophytes, forest/mesic woodland, savanna/woodland, drought-adapted herbsand shrublets). The Poaceae group is divided into three size classes. Poaceae <25µm includes wetland taxon *Phragmites*. Poaceae >25µm but <40µm are grouped within the general Poaceae group (wild grass-type), and Poaceae grains >40µm include possible domesticated cereal grasses, although they overlap in sizes and overall morphology with wild grasses (Tomlinson, 1973; Andersen, 1979; Bonnefile and Riollet, 1980). Cryptogam spores, wetland taxa and other non-pollen palynomorphs (e.g.,

*Pseudoschizoaea*) are classified and counted as wetland/aquatic plants and spores (Fig. 4). Pollen frequencies of trees, shrubs, herbs, Poaceae > 25µm and Poaceae >40µm are presented as a percentage of the terrestrial pollen sum, representing a total count of 160–560 terrestrial pollen grains (Fig. 3). Aquatic and wetland taxa such as *Typha*, *Gunnera*, *Phragmites* (Poaceae <25µm), and sedges (Cyperaceae), being local taxa are excluded from the pollen sum due to overrepresentation. Poaceae >25µm are included in the pollen sum as they are dominant in the region and indicate open grassland vegetation. Exotic pollen (e.g., *Pinus*, *Platanus*) encountered in the uppermost part of the sequence are included in the pollen sum.

Table 2. Pollen Zonation of the Mashishing Fen Core (AP: Arboreal pollen, NAP: Nonarboreal pollen, NPP: Non-pollen palynomorphs)

| **Zone** | **Depth (cm)** | **Age (cal. yr BP)** | **Main palynomorph taxa** |
|---|---|---|---|
| PZ 1 | 82-0 | ca. 500-0 | AP: Presence of pollen of exotic *Pinus* (ca. 17%) and *Platanus* (ca. 7%), decreased forest tree pollen percentages between ca. 0-2% (e.g., *Podocarpus, Olea, Celtis, Canthium*). |
| | | | NAP: Peak of Amaranthaceae pollen (ca. 91%), increased Caryophyllaceae (ca. 11%) Poaceae >40µm (ca. 8%), Asteraceae (ca. 47%), Poaceae pollen (ca. 16% and Cyperaceae (ca. 37%) pollen, decrease of *Phragmites* pollen (ca. 10%).<br>NPP: increased Hyphae (ca. 12%), *Glomus* (ca. 12%), other fungal spores (74%), and Monolete spores (ca. 25%).<br><br>Lower boundary: sharp increase of Amaranthaceae (ca. 79%), decrease of Poaceae (ca. 4%), Asteraceae (ca. 1%), Cyperaceae (ca. 24%) and *Phragmites* (ca. 18%) pollen increased microcharcoal (10 and 50µm). |
| PZ 2 | 224-82 | ca. 4000-500 | AP: Prominent tree pollen such as *Podocarpus* (ca. 1%), *Searsia* (ca. 1%), *Celtis* (ca. 1%), *Olea* (ca. 2%) generally decreased.<br>NAP: Pollen of Poaceae (ca. 34%), Asteraceae (ca. 47%) and Amaranthaceae (ca. 79%) increased, increased *Artemisia* (ca. 5%), *Anthospermum* (ca. 8%) and Poaceae >40 µm (ca. 16%) pollen, increase of pollen of wetland taxa, e.g., Cyperaceae (ca.77%), *Phragmites* (ca. 36%), *Persicaria* (ca. 12%), and *Gunnera* (ca. 10%), increased microcharcoal (size categories 10 and 50µm).<br>NPP: Increased monolete spores (ca. 10%), *Glomus* (ca. 17%) and other fungal spores (ca. 37%).<br><br>Lower boundary: Sharp increase of pollen of Amaranthaceae (ca. 77%), near disappearance of major tree pollen e.g., *Podocarpus* (ca. 1%), *Searsia* (ca. 0%), *Celtis* (ca. 0%), *Olea* (ca. 0%), Myrtaceae (ca. 0%), decrease of Poaceae (ca. 5%) and Asteraceae (ca. 5%) pollen, increased pollen of wetland elements e.g., Cyperaceae (ca. 69%), *Persicaria* (ca. 12%). |
| PZ 3 | 350-224 | ca. 10,000-4000 | AP: Prominent tree pollen such as *Podocarpus* (ca. 5%), *Canthium* (ca. 5%), *Searsia* (ca. 10%), *Olea* (ca. 7%) *and* Combretaceae pollen (ca. 10%) increased.<br>NAP: Increased pollen of *Anthospermum* (ca. 13%), *Artemisia* (ca. 10%), and Poaceae (ca. 32%), increased pollen of wetland indicators, e.g., *Phragmites* (ca.30%), *Gunnera* (ca. 18%), and Cyperaceae (ca. 79%).<br>NPP: Increased monolete (ca. 34%) and fungal spores (ca. 37%) peak of *Pseudoschizoaea* (ca 9%), increase in percentages of microcharcoal (size categories: >10, |

| | | | |
|---|---|---|---|
| | | | >50 and >100µm).<br><br>Lower boundary: Increased pollen of Asteraceae (ca. 56%), *Anthospermum* (ca. 13%), *Gunnera* (ca. 17%), decreased pollen of *Poaceae* (ca. 9%), *Olea* (ca. 1%), *Searsia* (ca. 0%), Cyperaceae (ca. 13%), monolete spores (ca. 21%). |
| PZ 4 | 394-350 | ca. 10,400-10,000 | AP: Increased pollen of *Canthium* (ca. 8%), *Olea* (ca. 6%), Proteaceae (ca. 10%).<br>NAP: Decreased pollen of *Artemisia* (ca. 5%) and *Stoebe* (ca. 1%), increased Poaceae (ca. 30%) and Asteraceae (ca. 56%) pollen.<br>NPP: Decreased monolete spores (ca. 8%) and fungal spores (32%).<br><br>Lower boundary: Increased wetland pollen e.g., Cyperaceae (ca. 65%) and *Typha* (ca. 10%), decreased pollen of *Olea* (ca. 4%), *Searsia* (ca. 2%), *Canthium* (3%), Proteaceae (ca. 4%), decreased pollen of Poaceae (ca. 24%), Asteraceae (ca. 24%), *Artemisia* (ca. 5%), *Stoebe* (ca.0%). |
| PZ 5 | 487-394 | ca. 11,000-10,400 | AP: Increase in pollen of *Canthium* (ca. 7%) and Proteaceae (ca. 10%), peak of *Olea* pollen (ca. 12%), decrease of *Searsia* pollen (4%)<br>NAP: Peak of pollen of *Stoebe* (ca. 20%), decrease of Poaceae (ca. 13.8%) and Asteraceae (ca. 13.4%), increase of *Anthospermum* (ca. 10%), increased Cyperaceae (ca. 76%)<br>NPP: Peak of fern spores e.g., monolete (ca. 76%), and fungal spores e.g., fungal Hyphae (ca. 62%)<br><br>Lower boundary: Decrease of tree pollen e.g., *Olea* (0%), *Searsia* (ca.2%), *Canthium* (ca. 2%), Proteaceae (ca. 3%), decrease in pollen of Poaceae (ca. 31%), Asteraceae (ca. 22%) |
| PZ 6 | 550-487 | ca. 11,700-11,000 | AP: Prominent occurrence of tree pollen where Myrtaceae (ca. 6%), *Searsia* (ca. 6%), *Olea* (ca. 8%), Proteaceae (ca. 5%), *Canthium* (ca. 4%) reached a maximum.<br>NAP: High percentages of pollen of *Artemisia* (ca. 19%), Poaceae (ca. 34%) and Asteraceae (ca. 45%) reaching a maximum in this zone, high occurrence of pollen of aquatics e.g., Cyperaceae (ca. 78%), *Gunnera* (20%)<br>NPP: High occurrence of fungal hyphae (ca. 16%).<br><br>Lower boundary: Bottom of core. |

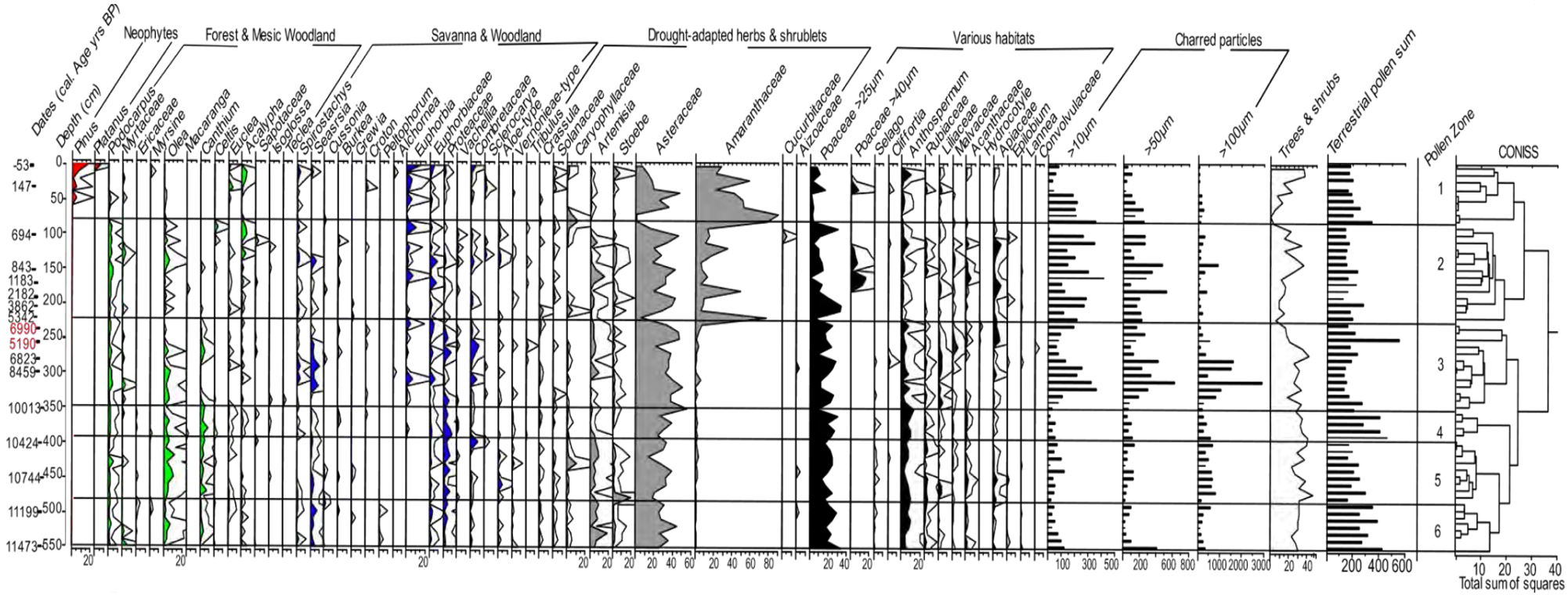


Figure 3: Pollen spectra showing terrestrial pollen taxa with exaggeration of x5 (hollow curves) together with percentage of trees and shrub pollen, charred particles and pollen zones (PZ1-6) according to CONISS. Inverted dates marked in red.

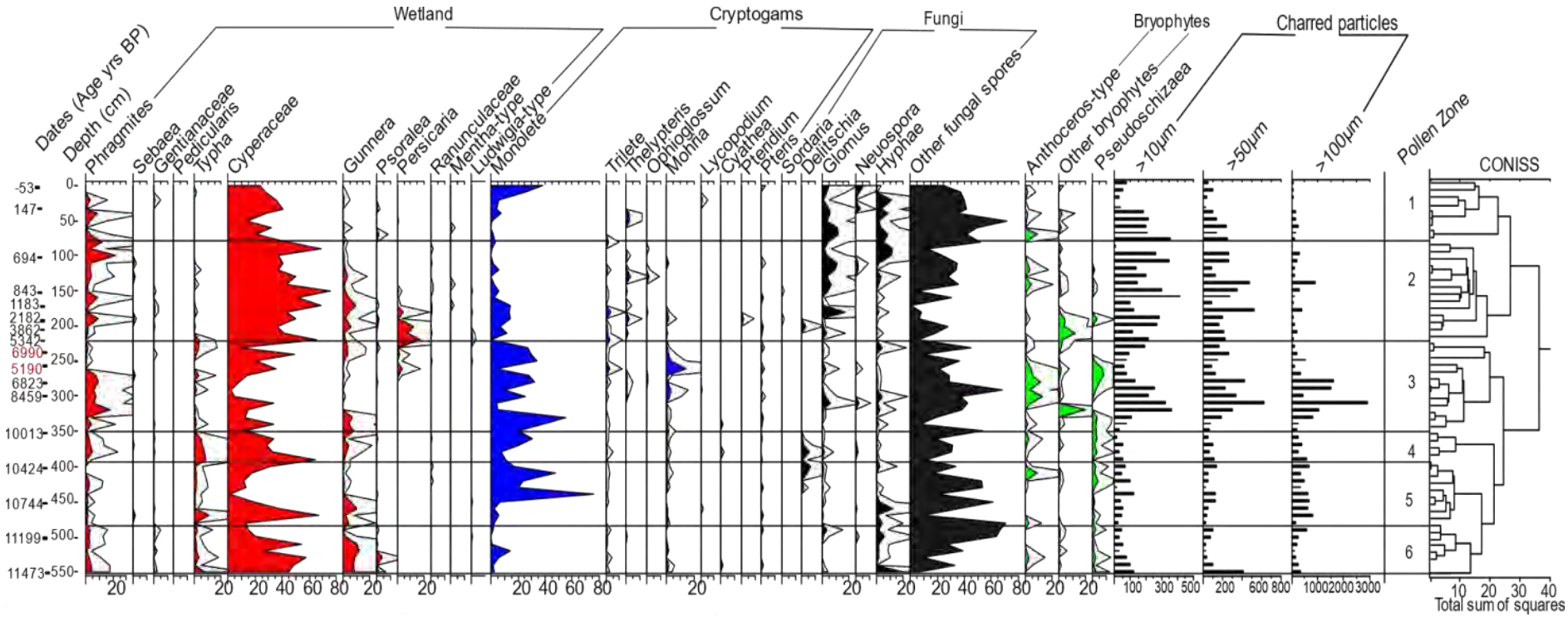


Figure 4: Fig. 4 Pollen spectra showing the aquatics and spores with exaggeration of ×5 (hollow curves) together with microcharcoal and pollen zones (PZ1–6) according to CONISS. Inverted dates marked in red.

## 4. DISCUSSION

The Mashishing Fen pollen record provides insights into the changing environmental conditions in the area over the last 11,700 years BP. Each pollen zone is defined by identifiable changes in the abundance and distribution of pollen and spore assemblages within the Holocene core sequence. The changes in pollen, spore and charcoal proxies across the pollen zones are related to climate changes, local environmental conditions, and anthropogenic impact. We compare and synthesise data from nearby sites to reconstruct a broader understanding of the environmental changes within the region for the Holocene. The pollen of *Podocarpus*, Proteaceae, and Myrtaceae are noticeable at the beginning of the sequence (11,700-11,000 cal. yr BP), indicating moisture availability. The high percentages of Poaceae and Asteraceae pollen ca. 11,000-10,400 cal. yr BP suggest the dominance of open grassland for this period. The peak of Amaranthaceae and Asteraceae pollen coupled with increased charred fragments ca. 1500 BP suggests anthropogenic impact possibly due to deforestation and increased fire activity. The uppermost sequence showing evidence of *Platanus* and *Pinus* pollen suggests occupation of European settlers after ca. 500 BP.

### *4.1. Zone 6 (ca. 11,700-11,000 cal. yr BP (550–487 cm)*

Tree pollen, including *Podocarpus*, Proteaceae and Myrtaceae, are present in low percentages, indicating sparse woody vegetation of the montane forests in the region ca. 11,700 cal. yr BP (Fig. 3). The pollen of these trees typically signals moist conditions (Scott, 1982a; Mustart and Cowling, 1993; Geldenhuys and von dem Bussche, 1997; Matthys et al., 2022). The accompanying high representation of aquatics and swamp elements, e.g., Cyperaceae and *Gunnera* (Fig. 4), suggests local moist conditions for this period (Pooley, 2003; Collins, 2011). Cyperaceae often grows in wetlands, though some species have also been observed in savannas

and grasslands. The increase in Cyperaceae may be linked to wetter conditions that provide a more extensive habitat for its growth (Partridge, 1993; Gillson, 2006; Breman et al., 2011). The occurrence of Asteraceae alongside the strong fluctuations of Poaceae, though on a smaller scale, indicates open grassland.

The amount of charred particles is low, suggesting that fire was a minor factor during this period. This reflects the spreading of forest since the impact of fire is excluded from the area (see Bond et al., 2003a). This is evident by the pollen from trees that grow along forest margins and streams, such as *Olea* and *Searsia*, peaking at ca. 11,200 cal. yr BP together with *Canthium* (Fig. 3). This suggests warm and subhumid conditions for this period, which were preceded by a slightly drier phase at ca. 11,300 cal. yr BP when *Artemisia* and Asteraceae were prominent (Dyer, 1975; Scott, 1982c). The relatively high frequencies of *Canthium* pollen indicate a localised presence of the species as its pollen grains are often heavy and not well dispersed (Scott, 1982c; Tilney and van Wyk, 1997; Dessein et al., 2005). Relatively lower numbers of *Podocarpus* suggest regional sparseness of *Podocarpus* during this period. These data correlate with Mfabeni data related to moderately warm and moist conditions (Finch and Hill, 2008).

These results are similar to the pollen records from Wonderkrater, where relatively moist conditions were recorded between 11.5–10.5 ka, though it was generally dry during the early Holocene (Scott and Thackeray, 1987; Scott et al., 2003; Scott et al., 2012). Regional records from speleothem, isotopes and geochemical analyses from Cold Air Cave, Tswaing Crater in South Africa and Okavango Panhandle, northwest Botswana, also suggest a wetter phase for the beginning of early Holocene (Holmgren et al., 2003; Nash et al., 2006; Kristen et al., 2007) although, based on previous records suggesting variable conditions for the same period (see Scott et al., 2012 for discussion), the region may not be homogenously wet. A relatively moist

environment was, however suggested for the entire early Holocene sequence (Chase et al., 2010; Truc et al., 2013; Chevalier and Chase, 2015). The beginning of the early Holocene was probably subhumid and locally wet to have supported the occurrence of aquatics, swamp, and Afromontane forest elements within the area.

*4.2. Zone 5 ca. 11,000–10,400 cal. yr BP (487–394 cm)*

Poaceae (21%) and Asteraceae (28%) pollen continued at high percentages until ca. 10,900 cal. yr BP, indicating that open grasslands prevailed. This was accompanied by the significant decline of tree pollen (e.g., *Olea*, *Canthium*, Myrtaceae), Cyperaceae, and other aquatics, likely suggesting subhumid/semi-arid conditions around this period. This low representation of tree pollen suggests that the forest was restricted, probably due to the cool and dry climate in the area and/or the direct physiological impact of reduced atmospheric $CO_2$ (Cowling, 1999; Levis et al., 1999; Monnin et al., 2001) as recorded at other sites (e.g., Metwally et al., 2014; Neumann et al., 2014; Nyakale and Scott, 2002). Dryness is also indicated by the sparseness of *Phragmites*, which might signal higher water tables in palaeorecords (Hahn et al., 2021), suggesting that the wetland probably decreased in size during this period (Burgoyne et al., 2000; Mabhungu et al., 2019). The pollen of *Stoebe* reached a peak (4%), likely suggesting relatively cooler environmental conditions at the beginning of this zone (Coetzee, 1967; Morrison, 1968; Scott, 1984b).

The semi-arid conditions recorded for this period are consistent with data from pollen sequences at Wonderkrater, Tate Vondo, Rietvlei Dam and Tswaing Crater (Fig. 1), showing indications of drier conditions with increased temperatures (Scott and Vogel, 1983; Scott, 1984a; Scott et al., 2003; Scott et al., 2012). This also concurs with the dry conditions inferred from the biomarker and isotope analyses of sediments from Lake Tswaing Crater (Kristen et al., 2010) and

stalagmites data at Cold Air Cave in the Makapansgat Valley (Holmgren et al., 2003). The sparse occurrence of floral remains (seeds) belonging to forests and forest margins (e.g., *Podocarpus falcatus, Celtis africana¸Ziziphus mucronata*) from the archaeological records at Bushman Rock Shelter also suggests prevalent dry conditions (Plug, 1981: 21). The values of charred particles show higher frequencies than the previous zone, indicating an increase of fire activity possibly due to fuel availability which was likely as a result of moisture availability (Daniau et al., 2019). As indicated earlier it has been argued that the widespread development of arid conditions (though fluctuating) over vast parts of South Africa coincided with the expansion of hunter-gatherers with Oakhurst technocomplexes (Chase et al., 2018). The larger tools were linked to declining subsistence resources associated with harsh and arid climatic conditions (Wadley, 1993; Chase et al., 2018). These conditions may have presented ecological challenges to the LSA hunter-gatherers, which in turn may be responsible for the low proportion of LSA sites often reported in archaeological studies during this period and the changes in resource exploitation and stone tool production (Deacon, 1984; Mitchell, 2005; Lombard et al., 2012, 2022). But, correlating major subsistence and cultural changes to environmental or climate changes is often complex. Thus, the relationships probably are not as simplistic and these changes might also be due to a combination of multiple factors, including climate, societal, or cultural differences.

The near absence of pollen of disturbance indicator pollen (e.g., Chenopodiaceae, Caryophyllaceae) accompanied by the lowest record of charred particles throughout the sequence indicates undisturbed conditions due to climate change and/or fire. The relatively high percentages of *Canthium, Podocarpus,* and Proteaceae and the peak of *Olea* suggest a return to warmer and moister conditions after ca.10,900 cal yr BP. This likely reflects the recovery of the forest due to warm and moist conditions during this period (Scott, 1982a; Mustart and Cowling,

1993; Geldenhuys and von dem Bussche, 1997; Matthys et al., 2022). *Anthospermum*, characteristic of forest margins or grasslands (Pooley, 1998), regularly occurred during the zone. A strong peak of Cyperaceae coupled with high percentages of fern spores (Fig. 4) indicates moist conditions. Poaceae and Asteraceae pollen show oscillations in the pollen sequence at Mashishing Fen (Fig. 3), likely indicating stronger seasonality due to responses to summer rainfall variability considering the absence of anthropogenic impact for this period (Coetzee, 1967; Fitchett and Bamford, 2017). Asteraceae and Poaceae grow in a wide range of climatic and ecological conditions (Scott, 1982a,b; Cooremans, 1989; Carbutt and Edwards, 2004; Chevalier et al., 2021) and pollen from these families are prevalent. Poaceae is widely distributed almost throughout South Africa and is typically found in grasslands with high rainfall during the summer season, whereas Asteraceae, which is also commonly found in the region, often indicates regions with comparatively lower rainfall and/or dry summers (Coetzee, 1967; Cooremans, 1989, O'Connor and Bredenkamp, 1997).

### *4.3. Zone 4 ca. 10,400–10,000 cal. yr BP (394–350 cm)*

The percentage of forest trees *Canthium, Olea,* Combreteaceae and Proteaceae pollen increased at Mashishing Fen. Forest remained prominent throughout the zone, suggesting warm subhumid conditions. The increase of Cyperaceae, *Typha,* and fern spores suggests moist conditions for this period. The decrease of Asteraceae pollen, particularly *Artemisia and Stoebe,* further suggests that humid conditions prevailed during this period. Low charred particles of all size classes (>10 µm, >50 µm and >100 µm) suggest minimal burning likely due to moist conditions. Climate is often argued to be the main driver of fire regimes at local and regional scales until recent incidences of anthropogenic fires (Marlon et al., 2013; Daniau et al., 2019). More often, increased fire activity is related to drier conditions (Power et al., 2008; van Leeuwen et al., 2014;

Hantson et al., 2017), while decreased fire is related to wetter conditions (Rius et al., 2011; Vannière et al. 2011; Daniau et al., 2019) although significant and extensive fires in open grassland-savanna have also occurred during periods of elevated moisture levels in sub-tropical Africa (Daniau et al., 2019; Haliuc et al., 2023). This contrasts with conditions recorded in nearby sites like Wonderkrater and Tswaing Crater, where dryness was even argued to become well-established at Wonderkrater ca. 10,500 BP (Scott et al., 2012). The suggested humid conditions at Mashishing Fen during this period reflect local variations and reinforce the apparent non-uniformity of moisture changes due to varying influences of the Benguela and Agulhas currents in the region (Walker, 1990; Tyson and Preston-Whyte, 2000; Holmgren et al., 2003; Reason et al., 2006).

### *4.4. Zone 3 ca. 10,000–4000 cal. yr BP (350–224 cm)*

The transition to Pollen Zone 3 records an abrupt change in the relative composition of forest and typical open vegetation. While major forest trees declined (except *Olea*), Asteraceae reached a maximum (almost 60%). The peak of Asteraceae pollen ca. 9900-8500 cal. yr BP might indicate more pronounced seasonality with less annual rain (Cooremans, 1989; O'Connor and Bredenkamp, 1997). The abundance of Asteraceae in pollen spectra from the grasslands has been argued to indicate a strong seasonal moisture or cooler growth periods amid relatively dry conditions (Scott and Nyakale, 2002). This aligns with the present distribution of Asteraceae pollen and its parents' plants, especially in regions with lower overall rainfall (Cooremans, 1989). The increase in the pollen of Asteraceae at the beginning of this zone is likely due to prevailing less moist conditions, especially with the accompanying decline of tree pollen and aquatics, with no known evidence of human occupation within the area for this period. It is also likely that the synchronous decrease of Cyperaceae and *Phragmites* pollen typically associated

with South African wetlands indicates the shrinking of the wetland, further supporting the prevalence of dry local conditions during this period.

The accompanying increase in the pollen percentage of the grassland element *Anthospermum*, indicative of relatively cooler environmental conditions, likely suggests that forest diminished and open land vegetation increased (Pooley, 1998). The low representation of tree pollen (except *Olea*) might indicate that the forest is limited, possibly due to prevailing cool and dry conditions or to anthropogenic impact with frequent natural or human fires (Bond et al., 2003a). The increase in charcoal predominantly in the >100 µm fraction (likely large charcoal of local origin) suggests disturbances by natural veld fires for this period close to the site, which in turn may have resulted in a decline of forest trees, e.g., fire-sensitive *Podocarpus* (Giddey et al., 2022). This is supported by the fact that naturally occurring veld fires are frequent in the Grassland Biome (Bond et al., 2003a, b). It is plausible that the previous s prevailing moist conditions, which were conducive to forest growth, contributed to an accumulation of forest biomass, serving as potential fuel for fires. Subsequently, the drier conditions suggested in the current zone may have facilitated more frequent burning, as dry periods tend to experience higher fire frequencies than wetter periods (Umbanhowar and McGrath, 1998; van Wilgen, 2009; Vannière et al., 2011; Archibald et al., 2012; Crawford and Belcher, 2014; Daniau et al., 2019; Cardoso et al., 2022).

Around 8600 cal. yr BP, Poaceae became dominant while Cyperaceae and fern spores began a steady decline, suggesting open grassy vegetation. This decline of Cyperaceae and fern spores probably reflects the shrinking of the wetland herbaceous taxa, particularly Asteraceae, record high frequencies supporting the existence of grasslands indicative of drier conditions in the area. Notably, there was a substantial presence of microcharcoal (size categories: >10, >50, and

>100µm), pointing to an increased frequency of fires during the later period. Generally, the sediment sequence from Mashishing Fen revealed a predominantly drier climate during the latter half of the early Holocene. It is possible that drier conditions became well established during this time, though it seems to happen much earlier at other sites (e.g., Wonderkrater, Tswaing) in the region (Scott et al., 2012).

This was followed by high open woodland pollen elements such as *Searsia* and Combretaceae, with elements of forest mosaic species such as *Olea* and *Canthium* and increased Cyperaceae and fern spores after ca. 6700 cal. yr BP, indicating an increase in moisture. This accords with phytolith data at Verloren Valei, Versailles and Graskop in Mpumalanga, indicating warmer and wetter conditions between ca. 8000-4000 BP (Breman et al., 2019)**.** Also, this corresponds well to the increased moisture recorded at nearby sites during the middle Holocene, which may attest to the possibility of moisture spreading gradually southwards due to precessional influences (Scott, 1993; Eitel et al., 2001; 2002, 2004; Scott et al., 2012). While the moisture increase was recorded ca. 8-7ka at Tate Vondo and Rietvlei Dam, it was not recorded until ca. 7-6 ka at Wonderkrater, Moreletta stream and Tswaing (Scott, 1982, 1984, 1989; Scott and Vogel, 1983; Scott et al., 2003; Kristen et al., 2010; Metwally et al., 2014). This, however, contrasts with stalagmites isotope data in the Makapansgat valley, indicating cool and dry conditions during the mid-Holocene (Holmgren et al., 2003).

This period of increased moisture coincided with the expansion of Wilton-type industries comprising scrapers and backed tools after ca. 7.5ka (Deacon, 1974; Deacon et al., 1984; Mitchell 2000, 2005). They suggest that the homogenous shifts from large stone tools (Oakhurst) to smaller tools (Wilton-type) possibly reflect changes in behavioural adaptation due to changes in diet, societal structure and population growth brought about by favourable climatic conditions.

It is possible that these conditions favoured the LSA hunter-gatherers to hunt more small game animals (particularly bovids) and heavily rely on plant resources, hence leading to increased population and expansion over the vast parts of South Africa.

After ca. 5900 cal. yr BP, the Mashishing Fen pollen record is dominated by Asteraceae, Apiaceae, and *Anthospermum*, while tree pollen declined, which might indicate more pronounced seasonality and/or open grassy in the area (O'Connor and Bredenkamp, 1997). High abundancy of charred fragments indicating high fire frequency were also recorded around this period. The correlation between elevated microcharcoal levels and arid conditions (reduced moisture) appears to be a recurrent coincidence of high fire activity associated with dry periods in the Mashishing Fen record, similar to records from other sites (e.g., Hahn et al., 2021).

### *4.5. Zone 2 ca. 4000–500 cal. yr BP (224–82 cm)*

A rapid increase in Amaranthaceae (ca.78%) at ca. 4000 cal. yr BP, indicate cool, relatively dry saline, and/or evaporative conditions (Coetzee, 1967; Dyer, 1975; Scott 1982c; Cooremans, 1989; O'Connor and Bredenkamp, 1997; Pooley, 2005; Boon, 2010). The concomitant increase of *Anthospermum* pollen (8.2%) which is common in grasslands (Scott, 1982c) may indicate open grassy vegetation. The associated decline in *Podocarpus, Olea, Searsia* and *Celtis* tree pollen coupled with an abrupt increase of Amaranthaceae ca. 4000 cal. yr BP further indicate diminishing forests during this period and the dominance of more open vegetation (Li et al., 2008; Ryu et al., 2021). This is likely due to climate and/or anthropogenic impact. An apparent forest retreat with increased Cyperaceae and other aquatics may indicate brief moist conditions. The parallel decrease in Asteraceae pollen might also support brief humid conditions (e.g., Metwally et al., 2014; Neumann et al., 2014). Possible deforestation is further supported for this period by the indications of forest clearance by increased fire intensity, particularly <50 and >50

µm charred particles (Fig. 3).

By ca. 1500 cal. yr BP, a notable decrease in tree pollen was observed in the Mashishing Fen record. This decline coincided with the appearance of large Poaceae pollen (>40 µm), which could indicate the cultivation of cereals. However, it is important to note that this pollen may also belong to the wild Poaceae group (Bonnefile and Riollet, 1980). Caution should be taken when interpreting the pollen data as large Poaceae has been observed in pollen records prior to the earliest evidence of farming in southern Africa (e.g., Baxter, 1996). The appearance of >40 µm Poaceae pollen and the general pollen data corresponds with the arrival of Early Farming Communities in the region. Archaeological records from Silver Leaves, Eiland Saltworks and Riverside posited the earliest human occupation by farmers between the 4th and 6th century CE (Evers, 1974; Klapwijk, 1974; Maggs, 1977; Klapwijk and Huffman, 1996; Huffman, 1998; Jordaan, 2017). It appears that the early farmers played a role in burning, tree felling for wood as fuel, and clearing vegetation for farming, settlements, and pastures. This also coincides with an increase in Cyperaceae, *Gunnera* and other aquatics, indicating locally wet conditions for this period (Bergman et al., 1992; Partridge, 1993; Bergman, 2002; Gillson, 2006). *Glomus*, a mycorrhizal fungus often interpreted as an indicator of erosion (Anderson et al., 1984), also increased (Fig. 4) likely due to the opening of the vegetation by intensified human activities in the area. Although this has been questioned as the spores was suggested to have been likely produced by mycorrhizal mycelia of the host plants growing into the sediments above the deposits (Kołaczek et al., 2013), a forest management experiments indicated that the mycorrhizal colonization of roots in forests taxa is higher if a considerable amount of forest is cleared (Zhou et al., 1997; Rull et al., 2011).

The accompanying high frequencies of Amaranthaceae and Asteraceae pollen might further suggest possible human impact on the vegetation during this period, especially considering the simultaneous decline of forest pollen (Baxter and Davies, 1994). Asteraceae is almost everywhere in South Africa and often indicates generally less rain and/or dry, cool summers or might signal anthropogenic impact when found in association with high frequencies of other open-land indicators (e.g., Amaranthaceae) (Coetzee, 1967; Cooremans, 1989; O'Connor and Bredenkamp, 1997; Olatoyan et al., 2022). Possible anthropogenic disturbance is further suggested by high local fire activity from a relatively high number of large (>50 µm) charred particles, which might be linked to a decline of trees and the concurrent increase of open-land indicators for this period. The pollen record is supported by regional data suggesting widespread vegetation changes expected due to anthropogenic impact with the evidence of the decline of tree pollen, increase in open- land indicators (e.g., Amaranthaceae, Asteraceae), increase in spores of coprophilous fungi, indicative of animal herding, charred fragments, and larger Poaceae pollen grains (>40 µm) at ca. 1400-1500 BP in the Marine (Hahn et al., 2021), Grassland (Scott and Vogel, 1983; Rosen et al., 1999), the Indian Ocean Coastal Belt (Turner and Plater, 2004; Finch and Hill, 2008; Neumann et al., 2008) and Savanna (Scott, 1982a, b, 1984a, 1987; Carrión et al., 2000; Scott et al., 2003) Biomes of South Africa (see Olatoyan et al., 2022 for discussion). Pastoralism and farming began in South Africa ca. 2000 years ago with evidence of iron age technology in the region, crop cultivation (e.g., sorghum, millet), cattle and sheep. While these crops often require summer rain and specific sedentary lifestyles, the cattle and sheep thrive better in moister conditions with sufficient grasses (Lander and Russell, 2018; Schoeman, 2020; Smith, 2021). It appears that a warmer and wetter climate facilitated the emergence and expansion of farmers into the area (Vogel and Fuls, 1999). The presence of farmers for this

period is supported by the direct evidence of *Cenchrus americanus* (pearl millet) seed impressions on pottery at Silver Leaves (Klapwijk, 1974; Klapwijk and Huffman, 1996), carbonised seeds at Ficus Cave (Partridge, 1966; Moore, 1981), carbonised sorghum seeds at SK 17 (Meyer, 1986) and pearl millet, finger millet and melon seeds recovered at Magogo (Maggs and Ward, 1984; Voigt, 1984).

### *4.6. Zone 1 ca. 500-0 cal. yr BP (82–0 cm)*

The uppermost zone begins with another spike in Amaranthaceae and Caryophyllaceae, an increase in *Glomus* and a decline of trees, suggesting the diminishing of forests likely due to anthropogenic disturbances ca. 500 cal. yr BP (ca. 1450 CE). This coincides with the increase of Cyperaceae, *Phragmites* and fungal spores, indicating wet conditions and a higher water table (Gajewski et al., 2002). The decreasing of Poaceae and Asteraceae pollen provides further evidence of humid conditions and possible local disturbances of grass cover. The accompanying increase of charred particles further supports possible deforestation due to increased fire.

After ca. 500 cal. yr BP, Amaranthaceae remained dominant coupled with increased Asteraceae, indicating the continued impact of anthropogenic disturbances possibly through overgrazing by Farming Communities occupation (Carrión et al., 2000; Nyakale and Scott, 2002), open and dry grassland environment (Cooremans, 1989) and/or probably strong local evaporative conditions (Dyer, 1975; Pooley, 1998). This period notably correlates with Later Farming Communities, particularly the Bokoni sites known for specialised farming methods around the $15^{th}/16^{th}$ century to the $19^{th}/20^{th}$ century (Widgren et al., 2016; Birin et al., 2021). These Later Farming Communities established settlements that comprised stone-walled terraces, tracks and enclosure units with remains found within the Gustav Klinbiel Nature Reserve and across Mpumalanga, stretching from Ohrigstad in the north through Mashishing and Machadodorp to Carolina in the

south (Delius et al., 2012). The recovery of carbonised seeds of *Sorghum* sp. and *Vignia* sp. at Khutwaneng (formerly Badfontein) around this period provides direct evidence of agriculture within the area (Collett, 1982).

The presence of >40 µm Poaceae pollen (possibly cultivated cereals) and *Pinus* (pine tree) pollen perhaps indicates continuous crop cultivation alongside the presence of pines in the area ca. 280 cal. yr BP (ca. 1670 CE). Although *Pinus* is known to have been introduced to South Africa by European settlers as early as the mid-17$^{th}$ century CE, it only became established in plantations in the 1900s (Richardson et al., 1997; van Wilgen and Richardson, 2012; Bennett and Kruger, 2015). The appearance of *Pinus* pollen in the Mashishing Fen sequence only after ca. 500 cal. yr BP likely suggests the early introduction of pines by Europeans for timber production. It is possible that humans cleared vegetation for the cultivation of crops (e.g., *Sorghum*, *Pennisetum*) and planting of neophytic trees (e.g., *Pinus*). Since major pine plantations have been documented ca. 15km from Mashishing Fen, its pollen supports previous, modern pollen studies showing that *Pinus* has the potential to be overrepresented at great distances from the source owing to its high pollen productivity and dispersal efficiency by wind (Williams, 2008; Quamar, 2019; Chevalier et al., 2020; Olatoyan et al., 2022).

Towards the end of the pollen sequence at Mashishing Fen, the frequency of *Pinus* pollen reached its peak simultaneously with the first appearance of *Platanus* (plane tree), which is, to our knowledge, the first evidence of *Platanus* pollen in a South African palynological record.

*Platanus* was introduced to South Africa during the 19th century (late 1800s) as an ornamental tree, frequently used for shading along roadways (Wilson, 1923; Gwedla and Shackleton, 2017; Newete et al., 2022). Recent aerobiological studies conducted in Secunda, Mpumalanga,

revealed a prevalence of *Platanus* pollen and fungal spores, indicating a period of high humidity (Berman, 2017). The presence of *Platanus* and the peak in *Pinu*s pollen levels suggest that the cultivation of exotic trees in the region became established around the late 1800s to early 1900s (Burgess and Wingfield, 2001; Van Wilgen and Richardson, 2012; Bennett and Kruger, 2015), indicating the anthropogenic impacts coinciding with the arrival of European settlers in the area. This period also corresponds to an increase in the pollen frequencies of *Anthospermum* and Poaceae, indicating the dominance of open vegetation during this time. The presence of Cyperaceae, fern, and fungal spores further supports the indication of locally wet conditions during this period.

## CONCLUSION

The Mashishing Fen contributes a well-dated sequence to local and regional vegetation changes spanning the last 11,700 cal. yr BP from the summer rainfall region in northeastern South Africa. The data provides a continuous and finely-tuned sequence from the Early to Late Holocene period. The pollen and charcoal records show a transition from relatively moist to drier conditions ca. 10,900 cal. yr BP. The early Holocene was generally wetter, supporting the growth of forest vegetation and aquatic taxa, after 10,900 cal. BP, the vegetation changes suggest a return to warm and moister conditions until ca. 8600 cal. yr BP when drier grassy conditions seem to prevail with the dominance of Asteraceae and Poaceae, while Cyperaceae, fern spores and other aquatics decline. By ca. 1500 cal. yr BP marked vegetation changes and erosion increase remarkably at Mashishing. It cannot be excluded that humans cleared vegetation to cultivate cereal crops, settle, and collect wood for fuel. Pre-European farming and pastoral activities triggered soil erosion beginning from ca. 1500 BP, likely due to the area's opening of the vegetation by human activities. Consequently, human impact might or might not overshadow

the effects of climate and other factors as drivers of vegetation changes in the pollen composition. After ca. 500 cal. yr BP, direct pollen indicators of farming activities include the likely cultivation of cereal crops and the planting of exotic trees (e.g., *Pinus, Platanus*) since the late 1800s- early 1900s  within the region. While the Mashishing Fen provides valuable insights into the local and regional environmental changes of the summer rainfall region of northeastern South Africa, multiproxy analysis, including additional sites in the region, is required to reconstruct a robust palaeoenvironmental history for the region.

## REFERENCES


Andersen, S.T., 1979. Identification of wild grass and cereal pollen [fossil pollen, annulus diameter, surface sculpturing]. Danmarks Geologiske Undersøgelse Årbog, 69–92.

Anderson, R.S., Homola, R.L., Davis, R.B., Jacobson Jr, G.L., 1984. Fossil remains of the mycorrhizal fungal *Glomus fasciculatum* complex in postglacial lake sediments from Maine. Canadian Journal of Botany 62, 2325-2328.

Antonites, A., 2013. Archaeological salt production at the Baleni spring, northeastern South Africa. South African Archaeological Bulletin 68(198), 105-118.

Antonites, A., 2016. The organization of salt production in early first millennium CE South Africa. Journal of Anthropological Archaeology 44, 31-42.

Antonites, A., Antonites, A. R., Roodt, F., 2014. Report on excavations at Penge, a first-millennium Doornkop settlement. Southern African Humanities 26(1), 177-192.

Archibald, S., Staver, A.C., Levin, S.A., 2012. Evolution of human-driven fire regimes in Africa. Proceedings of the National Academy of Sciences 109, 847-852.

Backwell, L., Wadley, L., D'errico, F., Banks, W.E., de La Peña, P., Stratford, D., Sievers, C., Laue, G., Vilane, B., Clark, J., Tribolo, C., 2022. Border Cave: a 227,000-year-old archive from the southern African interior. Quaternary Science Reviews 291, 107597.

Badenhorst, S., 2018. Exploitation of sheep (*Ovis aries*) and goats (*Capra hircus*) by Iron Age farmers in southern Africa. Quaternary International 495, 79-86.

Bader, G.D., Linstädter, J., Schoeman, M.H., 2020. Uncovering the Late Pleistocene LSA of Mpumalanga Province, South Africa: early results from Iron Pig Rock Shelter. Journal of African Archaeology 18, 19-37.

Baxter, A.J., 1996. Late Quaternary palaeoenvironments of the Sandveld, Western Cape Province, South Africa. PhD Thesis. University of Cape Town, Cape Town.

Baxter, A.J., Davies, B.R., 1994. Palaeoecological insights for the conservation of aquatic ecosystems in dryland environments: a case study of the Verlorenvlei system, South Africa. Aquatic Conservation: marine and freshwater ecosystems 4(3), 255-271.

Bennett, B., Kruger, F., 2015. Forestry + Water Conservation in South Africa: history, science + policy. Canberra: ANU Press.

Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. Pollen analysis and pollen diagrams. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons, Chichester, pp. 455-484.

Bergman, B., 2002. The *Nostoc-Gunnera* Symbiosis. In: Rai, A.N., Bergman, B., Rasmussen, U. (Eds.), Cyanobacteria in Symbiosis. Springer Netherlands, Dordrecht, pp. 207-232.

Bergman, B., Johansson, C., Soderback, E., 1992. The *Nostoc Gunnera* symbiosis. New Phytologist 122(3): 379-400.

Birin, R-A., Schoeman, M.H., Evans, M., 2021. The construction and habitation of one of the earliest homesteads at Komati Gorge Village 1, Bokoni, South Africa. Journal of Archaeological Science Reports 38, 103020.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian analysis 6, 457-474.

Bond, W.J., Midgley, G.F., Woodward, F.I., 2003a. What controls South African vegetation - climate or fire? South African Journal of Botany 69, 79-91.

Bond, W.J., Midgley, G.F., Woodward, F.I., 2003b. The importance of low atmospheric $CO_2$ and fire in promoting the spread of grasslands and savannas. Global Change Biology 9: 973-982.

Bonnefile, R., Riollet, G., 1980. Pollens Des Savanes d'Afrique Orientale. Paris: Éditions du Centre National de la Recherche Scientifique (CNRS).

Boon, R., 2010. Pooley’s Trees of eastern South Africa: a complete guide. Flora and Fauna Publications Trust, Durban.Bousman, C. B., Brink, J. S., 2018. The emergence, spread, and termination of the Early Later Stone Age event in South Africa and southern Namibia. Quaternary International 495, 116-135.

Breman, E., Ekblom, A., Gillson, L., Norström, E., 2019. Phytolith-based environmental reconstruction from an altitudinal gradient in Mpumalanga, South Africa, 10,600 BP- present. Review of Palaeobotany and Palynology 263, 104-116.

Breman, E., Gillson, L., Willis, K., 2011. How fire and climate shaped grass-dominated vegetation and forest mosaics in northern South Africa during past millennia. The Holocene 22, 1427-1439.

Bronk Ramsey, C., 2023. OxCal Program, Version 4.4 Oxford Radiocarbon Accelerator Unit. University of Oxford, Oxford.

Carbutt, C., Edwards, T.J., 2004. The flora of the Drakensberg Alpine Centre. Edinburgh Journal of Botany 60(3), 581–607.

Cardoso, A.W., Archibald, S., Bond, W.J., Coetsee, C., Forrest, M., Govender, N., Lehmann, D., Makaga, L., Mpanza, N., Ndong, J.E., 2022. Quantifying the environmental limits to fire spread in grassy ecosystems. Proceedings of the National Academy of Sciences 119(26), e2110364119.

Carrión, J.S., Scott, L., Huffman, T., Dreyer, C., 2000. Pollen analysis of Iron Age cow dung in southern Africa. Vegetation History and Archaeobotany 9, 239-249.

Chase, B. M., Lim, S., Chevalier, M., Boom, A., Carr, A. S., Meadows, M. E., Reimer, P. J., 2015. Influence of tropical easterlies in southern Africa's winter rainfall zone during the Holocene. Quaternary Science Reviews 107, 138-148.

Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter rainfall zone. Earth-Science Reviews 84, 103-138.

Chase, B. M., Quick, L.J., 2018. Influence of Agulhas forcing of Holocene climate change in South Africa’s southern Cape. Quaternary Research 90(2), 303-309.

Chevalier, M., Chase, B.M., 2015. Southeast African records reveal a coherent shift from high- to low-latitude forcing mechanisms along the east African margin across last glacial-interglacial transition. Quaternary Science Reviews 125, 117–130.

Chevalier, M., Chase, B., Quick, L., Scott, L., 2021. An atlas of southern African pollen types and their climatic affinities. Palaeoecology of Africa 35, 239-258.

Chevalier, M., Cheddadi, R., Chase, B.M., 2014. CREST (Climate REconstruction SofTware): a probability density function (PDF)-based quantitative climate reconstruction method. Climate of the Past 10(6), 2081-2098.

Chevalier, M., Davis, B.A.S., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., Kühl, N., Yoshi Maezumi, S., Tipton, J.R., Carter, V.A., Brussel, T., Phelps, L.N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., de Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P.S., Chaput, M. & Kupriyanov, D., 2020. Pollen-based climate reconstruction techniques for late Quaternary studies. Earth-Science Reviews 210, 103384.

Coetzee, J.A., 1967. Pollen analytical studies in East and Southern Africa. Palaeoecology of Africa 3, 1-146.

Coetzee, J.A., Praglowski, J., 1984. Pollen evidence for the occurrence of Casuarina and Myrica in the Tertiary of South Africa. Grana 23, 23-41.

Coetzee, J.A., van Zinderen Bakker, E.M., 1952. The pollen spectrum of the southern middle-veld of the Orange Free State. South African Journal of Science 48, 275-281.

Collett, D.P., 1979. The archaeology of the stone-walled settlements in the eastern Transvaal, South Africa. Master's thesis. University of the Witwatersrand, Johannesburg.

Collett, D., 1982. Excavations of stone-walled ruin types in the Badfontein Valley, eastern Transvaal, South Africa. The South African Archaeological Bulletin 37(135), 34-43.

Collins, N.B., 2011. Phytosociology and ecology of selected depression (pan) and valley-bottom wetlands of the Free State Province. PhD thesis. University of the Free State, Bloemfontein.

Cooremans, B., 1989. Pollen production in central southern Africa. Pollen et spores 31, 61-78.

Crawford, A.J., Belcher, C.M., 2014. Charcoal morphometry for paleoecological analysis: the effects of fuel type and transportation on morphological parameters. Applications in Plant Sciences 2(8), 1400004.

Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. Vegetation History and Archaeobotany 19, 391-408.

da Cruz, P., 2015. Lydenburg – Merensky 132kV Power lines Project – Surface Water Impact Assessment Study – Revision 3. Royal Haskoning DHV.

Daniau, A.L., Loutre, M.F., Swingedouw, D., Laepple, T., Bassinot, F., Malaizé, B., Kageyama, M., Charlier, K., Carfantan, H., 2023. Precession and obliquity forcing of the South African monsoon revealed by sub-tropical fires. Quaternary Science Reviews 310, 108128.

Deacon, J., 1974. Patterning in the radiocarbon dates for the Wilton/Smithfield complex in southern Africa. The South African Archaeological Bulletin 29(113/114), 3-18.

Deacon, J. 1984. The Later Stone Age of Southernmost Africa. British Archaeological Reports, Oxford.

Deacon, H. J., Deacon, J., 1999. Human beginnings in South Africa: uncovering the secrets of the Stone Age. David Philip, Cape Town.

Deacon, J., Lancaster, N., Scott, L. ,1984. Evidence for Late Quaternary climatic change in southern Africa. In: Vogel, J.C. (Ed.), Late Cainozoic palaeoclimates of the southern hemisphere. Balkema, Rotterdam, pp. 399-404.

De Swardt, D., 1990. Birds of the Gustav Klingbiel Nature Reserve & Sterkspruit Area, Lydenburg. Witwatersrand Bird Club.

De Swardt, D.H., 2014. Bird distribution changes in the Lydenburg area, Mpumalanga (2530AB Lydenburg and 2530BA Long Tom Pass) using SABAP data to compare with historical data: a period since the 1980s. Biodiversity Observations, 431-449.

Delius, P., Maggs, T., Schoeman, M., 2012. Bokoni: old structures, new paradigms? Rethinking pre-colonial society from the perspective of the stone-walled sites in Mpumalanga. Journal of Southern African Studies 38, 399-414.

Dyer, R.A., 1975. The Genera of Southern African Flowering Plants. Department of Agricultural Technical Service, Botanical Research Institute, Pretoria.

Eitel B., Blümel W.D., Hüser K., Mauz B., 2001. Dust and loessic alluvial deposits in northwestern Namibia (Damaraland, Kaokoveld): sedimentological and palaeoclimatic evidence based on luminescence data. Quaternary International 76, 57–65.

Eitel, B., Blümel, W.D., Hüser, K., 2002. Environmental transitions between 22 ka and 8 ka in monsoonally influenced Namibia - A preliminary chronology. Zeitschrift für Geomorphologie (Supplement-Band) 126, 31-57.

Eitel, B., Blümel, W.D., Hüser, K., 2004. Palaeoenvironmental transitions between 22 ka and 8 ka in monsoonally influenced Namibia. In: Smykatz-Kloss, W., Felix-Henningsen, P. (Eds.), Palaeoecology of Quaternary Drylands. Springer-Verlag, Berlin, Heidelberg, pp. 167-194.

Eriksson, P.G., Altermann, W., 1998. An overview of the geology of the Transvaal Supergroup dolomites (South Africa). Environmental Geology 36 (1-2), 179-188.

Evers, T.M., 1974. Three Iron Age industrial sites in the eastern Transvaal Lowveld. Master's Thesis. University of the Witwatersrand, Johannesburg.

Evers, T., 1975. Recent Iron Age research in the eastern Transvaal, South Africa. The South African Archaeological Bulletin 30(119/120), 71-83.

Evers, T., 1977. Recent progress in studies of the Early Iron Age in the eastern Transvaal, South Africa. South African Journal of Science 73, 78-81.

Evers, T., 1980. Klingbeil Early Iron Age sites, Lydenburg, Eastern Transvaal, South Africa. The South African Archaeological Bulletin 35(131), 46-57.

Evers, T.M., 1982. Excavations at the Lydenburg Heads Site, eastern Transvaal, South Africa. The South African Archaeological Bulletin 37(135), 16-33.

Evers, T.M., Vogel, J.C., 1980. Radiocarbon dates for Iron Age sites at Lydenburg and White River, eastern Transvaal. South African Journal of Science 76, 230-231.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. John Wiley & Sons, Chichester.

Ferrar, A.A., Lötter, M.C., 2007. Mpumalanga biodiversity conservation plan handbook. Mpumalanga Tourism & Parks Agency, Nelspruit.

Finch, J.M., Hill, T.R., 2008. A late Quaternary pollen sequence from Mfabeni Peatland, South Africa: Reconstructing forest history in Maputaland. Quaternary Research 70, 442-450.

Finné, M., Norström, E., Risberg, J., Scott, L., 2010. Siliceous microfossils as late-Quaternary paleo-environmental indicators at Braamhoek wetland, South Africa. The Holocene 20(5), 747-760.

Fitchett, J.M., Bamford, M.K., 2017. The validity of the Asteraceae: Poaceae fossil pollen ratio in discrimination of the southern African summer-and winter-rainfall zones. Quaternary Science Reviews 160, 85-95.

Gajewski, K., Lézine, A.-M., Vincens, A., Delestan, A., Sawada, M., 2002. Modern climate–vegetation–pollen relations in Africa and adjacent areas. Quaternary Science Reviews 21, 1611-1631.

Geldenhuys, C.J., von dem Bussche, G.B., 1997. Performance of *Podocarpus falcatus* provenances in South Africa. Southern African Forestry Journal 178, 15-24.

Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C., Verschuren, D., 2011. Modern non-pollen palynomorphs from East African lake sediments. Review of Palaeobotany and Palynology 164, 143-173.

Giddey, B.L., Baard, J.A., Kraaij, T., 2022. Fire severity and tree size affect post-fire survival of Afrotemperate forest trees. Fire ecology 18, 5.

Gillson, L., 2006. A ‘large infrequent disturbance’ in an East African savanna. African Journal of Ecology 44, 458-467.

Gosling, W.D., Miller, C.S., Livingstone, D.A., 2013. Atlas of the tropical West African pollen flora. Review of Palaeobotany and Palynology 199, 1-135.

Granger, R., Meadows, M. E., Hahn, A., Zabel, M., Stuut, J. B. W., Herrmann, N., Schefuß, E., 2018. Late-Holocene dynamics of sea-surface temperature and terrestrial hydrology in southwestern Africa. The Holocene 28(5), 695-705.

Grimm, E.C., 2011. Tilia 2.1.1 Software. Illinois State Museum, Springfield.

Hahn, A., Compton, J.S., Meyer-Jacob, C., Kirsten, K.L., Lucasssen, F., Mayo, M.P., Schefuß, E., Zabel, M., 2016. Holocene paleo-climatic record from the South African Namaqualand mudbelt: A source to sink approach. Quaternary International 404, 121-135.

Hahn, A., Neumann, F.H., Miller, C., Finch, J., Frankland, T., Cawthra, H.C., Schefuß, E., Zabel, M., 2021. Mid-to Late Holocene climatic and anthropogenic influences in Mpondoland, South Africa. Quaternary Science Reviews 261, 106938.

Haliuc, A., Daniau, A.L., Mouillot, F., Chen, W., Leys, B., David, V., Hanquiez, V., Dennielou, B., Schefuß, E., Bayon, G., Crosta, X., 2023. Microscopic charcoals in ocean sediments off Africa track past fire intensity from the continent. Communications Earth & Environment 4(133), 1-11.

Hall, M., 1990. “Hidden history”: Iron Age archaeology in southern Africa. In: Robertshaw, P., (Ed.), A History of African Archaeology. James Currey, London, pp. 59–77.

Hantson, S., Padilla, M., Corti, D., Chuvieco, E., 2013. Strengths and weaknesses of MODIS hotspots to characterize global fire occurrence. Remote sensing of Environment 131, 152-159.

Haour, A., 2005. African Archaeology: An Introductory but critical synthesis. In: Stahl, A.B. (Ed.), African archaeology: A critical introduction. Blackwell, Oxford, pp. 392-419.

Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Ramsey, C.B., Pearson, C., 2020. SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. Radiocarbon 62(4), 759-778.

Holmgren, K., Karlén, W., Lauritzen, S.E., Lee-Thorp, J.A., Partridge, T.C., Piketh, S., Repinski, P., Stevenson, C., Svanered, O., Tyson, P.D., 1999. A 3000-year high-resolution stalagmite based record of palaeoclimate for northeastern South Africa. The Holocene 9(3), 295-309.

Holmgren, K., Lee-Thorp, J.A., Cooper, G.R., Lundblad, K., Partridge, T.C., Scott, L., Sithaldeen, R., Talma, A.S., Tyson, P.D., 2003. Persistent millennial-scale climatic variability over the past 25,000 years in Southern Africa. Quaternary Science Reviews 22, 2311-2326.

Huffman, T. N., 1996. Archaeological evidence for climatic change during the last 2000 years in southern Africa. Quaternary International 33, 55-60.

Huffman, T.N., 1998. Presidential address: the antiquity of lobola. The South African Archaeological Bulletin 53, 57-62.

Huntley, B., Midgley, G.F., Barnard, P., Valdes, P.J., 2014. Suborbital climatic variability and centres of biological diversity in the Cape region of southern Africa. Journal of Biogeography 41(7), 1338-1351.

Klapwijk, M., 1974. A preliminary report on pottery from the north-eastern Transvaal, South Africa. The South African Archaeological Bulletin 29(113/114), 19-23.

Klapwijk, M., Huffman, T., 1996. Excavations at Silver Leaves: a final report. The South African Archaeological Bulletin 51(164), 84-93.

Klein, R. G., 1984. Later Stone Age faunal samples from Heuningneskrans Shelter (Transvaal) and Leopard's Hill Cave (Zambia). The South African Archaeological Bulletin 39(140), 109-116.

Kołaczek, P., Zubek, S., Błaszokowski, A., Mleczko, P., Margielewski, W., 2013. Erosion of plant succession—how to interpret the presence of arbuscular mycorrhizal fungi (Glomeromycota) spores in pollen profiles collected from mires. Review of Palaeobotany and Palynology 189, 29–37.

Korsman, S., Plug, I., 1994. Two Later Stone Age sites on the farm Honingklip in the eastern Transvaal. The South African Archaeological Bulletin 49(159), 24-32.

Kristen, I., Fuhrmann, A., Thorpe, J., Rohl, U., Wilkes, H., Oberhansli, H., 2007. Hydrological changes in southern Africa over the last 200 Ka as recorded in lake sediments from the Tswaing Impact Crater. South African Journal of Geology 110, 311-326.

Kristen, I., Wilkes, H., Vieth, A., Zink, K.-G., Plessen, B., Thorpe, J., Partridge, T., Oberhänsli, H., 2010. Biomarker and stable carbon isotope analyses of sedimentary organic matter from Lake Tswaing: evidence for deglacial wetness and early Holocene drought from South Africa. Journal of Paleolimnology 44, 143-160.

Kusimba, C. M., Kusimba, S. B., 2005. Mosaics and interactions: East Africa, 2000 BP to the present. In: Stahl, A.B. (Ed.), African archaeology: A critical introduction. Blackwell, Oxford, pp. 392-419.

Lander, F., Russell, T., 2018. The archaeological evidence for the appearance of pastoralism and farming in southern Africa. PLoS ONE 13(6), e0198941.

Lander, F., Russell, T., 2020. A southern African archaeological database of organic containers and materials, 800 cal BC to cal AD 1500: Possible implications for the transition from foraging to livestock-keeping. PLoS ONE 15, e0235226.

Lenhardt, N., Eriksson, P.G., Catuneanu, O., Bumby, A.J., 2012. Nature of and controls on volcanism in the ca. 2.32–2.06 Ga Pretoria Group, Transvaal Supergroup, Kaapvaal Craton, South Africa. Precambrian Research 214, 106-123.

Li, Y., Zhou, L., Cui, H., 2008. Pollen indicators of human activity. Chinese Science Bulletin 53, 1281-1293.

Lombard, M., 2003. The lithic rings of Honingklip, Goergap, Olieboomspoort and Windsorton: a functional interpretation based on microscopy. The South African Archaeological Bulletin 58(177), 6-13.

Lombard, M., Bradfield, J., Caruana, M. V., Makhubela, T. V., Dusseldorp, G. L., Kramers, J. D., Wurz, S., 2022. The southern African Stone Age Sequence updated (II). South African Archaeological Bulletin 77(217), 172-212.

Lombard, M., Wadley, L. Y. N., Deacon, J., Wurz, S., Parsons, I., Mohapi, M., Swart, J., Mitchell, P., 2012. South African and Lesotho Stone Age sequence updated (I). South African Archaeological Bulletin 67(195), 123-144.

Lorente, M. S.-E., González-Ruibal, A., Pardo, J. F. J., Suárez, C. M., 2016. The Iron Age in West Central Africa: radiocarbon dates from Corisco Island (Equatorial Guinea). The Journal of African History 57, 345-365.

Maggs, T., 1977. Some recent radiocarbon dates from eastern and southern Africa. The Journal of African History 18, 161-191.

Maggs, T., Ward, V., 1984. Early Iron Age sites in the Muden area of Natal. Annals of the Natal Museum 26(1), 105-140.

Maggs, T., Whitelaw, G., 1991. A review of recent archaeological research on food-producing communities in southern Africa. The Journal of African History 32, 3-24.

Maggs, T., Widgren, M., 2023. Moxomatsi: the organisation of space in a major Bokoni settlement. Southern African Humanities 36(1), 61-88.

Marker, M. E., Evers, T. M., 1976. Iron Age settlement and soil erosion in the Eastern Transvaal, South Africa. The South African Archaeological Bulletin 31(123/124), 153-165.

Marlon, J.R., Bartlein, P.J., Daniau, A.L., Harrison, S.P., Maezumi, S.Y., Power, M.J., Tinner, W., Vanniére, B., 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. Quaternary Science Reviews 65, 5-25.

Masolo, A., 2020. The Archaeology of Moxomatsi, A 17th Century Bokoni Capital, Mpumalanga, South Africa. Master's Thesis. University of the Witwatersrand, Johannesburg.

Matthys, C., Jubase, N., Visser, V. & Geerts, S., 2022. Distribution of *Melaleuca rugulosa* (Schlechtendal ex Link) Craven (Myrtaceae) in South Africa: Assessment of invasiveness and feasibility of eradication. South African Journal of Botany 148, 228-237.

Metwally, A.A., Scott, L., Neumann, F., Bamford, M., Oberhänsli, H., 2014. Holocene palynology and palaeoenvironments in the Savanna Biome at Tswaing Crater, central South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 402, 125-135.

Meyer, A., 1984. A profile of the Iron Age in the Kruger National Park. In: Hall, M., Avery, G., Avery, D.M., Wilson, M.L., Humphreys, A.J.B. (Eds.), Frontiers, African Archaeology Today. British Archaeological Reports, Oxford, pp. 215–227.

Meyer, A., 1986. 'n Kultuurhistoriese interpretasie van die ystertydperk in die Nasionale Krugerwildtuin. PhD Thesis. University of Pretoria, Pretoria.

Meyer, A., 1998. The archaeological sites of Greefswald: stratigraphy and chronology of the sites and a history of investigations. University of Pretoria, Pretoria.

Mitchell, P., 2002. The Archaeology of Southern Africa. Cambridge University Press, Cambridge.

Mitchell, P., 2005. Why hunter-gatherer archaeology matters: a personal perspective on renaissance and renewal in southern African Later Stone Age research. The South African Archaeological Bulletin 60(182): 64-71.

Mitchell, P., Parkington, J., Wadley, L., 1998. A tale from three regions: The archaeology of the Pleistocene/Holocene transition in the Western Cape, the Caledon Valley and the Lesotho Highlands, Southern Africa. Quaternary International 49, 105-115.

Mitchell, P., Whitelaw, G., 2005. The archaeology of southernmost Africa from c. 2000 BP to the early 1800s: a review of recent research. Journal of African History 46(2), 209-241.

Mooney, S., Radford, K., 2001. A simple and fast method for the quantification of macroscopic charcoal from sediments. Quaternary Australasia 19, 43-46.

Mooney, S.D., Tinner, W., 2011. The analysis of charcoal in peat and organic sediments. Mires and Peat 7, 1-18.

Mucina, L., Hoare, D.B., Lotter, M.C., du Preez, P.J., Rutherford, M.C., Scott-Shaw, C.R., Bredenkamp, G.J., Powrie, L.W., Scott, L., Cilliers, S.S., Bezuidenhout, H., Mostert, T.H., Camp, K.G.T., Siebert, S.J., Winter, P.J.D., Burrows, J.E., Dobson, L., Ward, R.A., Stalmans, M., Oliver, E.G.H., Siebert, F., Kobisi, K., Kose, L., 2006. Grassland Biome. In: Mucina, L., Rutherford, M. (Eds.), Vegetation of South Africa, Lesotho & Swaziland. Strelitzia, pp. 349-437.

Mucina, L., Rutherford, M. C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Mucina, L., Rutherford, M.C., 2010. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Mustart, P.J., Cowling, R.M., 1993. The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. Ecology 7,4 1490-1499.

Nakagawa, T., Brugiapaglia, E., Digerfeldt, G., Reille, M., Beaulieu, J-L.D., Yasuda, Y., 1998. Dense-media separation as a more efficient pollen extraction method for use with organic sediment/deposit samples: comparison with the conventional method. Boreas 27, 15-24.

Nash, D.J., Meadows, M.E., Gulliver, V.L., 2006. Holocene environmental change in the Okavango Panhandle, northwest Botswana. Quaternary Science Reviews 25, 1302-1322.

Neumann, F.H., Botha, G.A., Scott, L., 2014. 18,000 years of grassland evolution in the summer rainfall region of South Africa: evidence from Mahwaqa Mountain, KwaZulu-Natal. Vegetation History and Archaeobotany 23, 665-681.

Neumann, K., Fahmy, A., Lespez, L., Ballouche, A., Huysecom, E. 2009. The Early Holocene palaeoenvironment of Ounjougou (Mali): phytoliths in a multiproxy context. Palaeogeography, Palaeoclimatology, Palaeoecology 276, 87-106.

Neumann, K., Kahlheber, S., Uebel, D., 1998. Remains of woody plants from Saouga, a medieval west African village. Vegetation History and Archaeobotany 7, 57-77.

Neumann, F.H., Scott, L., 2018. EM van Zinderen Bakker (1907–2002) and the study of African Quaternary palaeoenvironments. Quaternary International 495, 153-168.

Neumann, F., Scott, L., Bamford, M., 2011. Climate change and human disturbance of fynbos vegetation during the late Holocene at Princess Vlei, Western Cape, South Africa. The Holocene 21, 1137-1149.

Neumann, F.H., Scott, L., Bousman, C., Van As, L., 2010. A Holocene sequence of vegetation change at Lake Eteza, coastal KwaZulu-Natal, South Africa. Review of Palaeobotany and Palynology 162, 39-53.

Neumann, F.H., Stager, J.C., Scott, L., Venter, H.J., Weyhenmeyer, C., 2008. Holocene vegetation and climate records from Lake Sibaya, KwaZulu-Natal (South Africa). Review of Palaeobotany and Palynology 152, 113-128.

Norman, N., Whitfield, G., 2006. A Traveller's Guide to South Africa's Rocks and Landforms: Geological Journeys. Struik Nature, Cape Town, South Africa, p. 232.

Norström, E., Scott, L., Partridge, T., Risberg, J., Holmgren, K., 2009. Reconstruction of environmental and climate changes at Braamhoek wetland, eastern escarpment South Africa, during the last 16,000 years with emphasis on the Pleistocene–Holocene transition. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 240-258.

Nyakale, M., Scott, L., 2002. Interpretation of late Holocene pollen in channel fills in the Eastern Free State, South Africa, in terms of local conditions and sediment reworking. South African Journal of Botany 68, 464-468.

O’Connor, T.G., Bredenkamp, G.J., 1997. Grassland. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp. 215-257. Olatoyan, J.O., Neumann, F.H., Orijemie, E.A., Sievers, C., Evans, M., Mvelase, S., Hattingh, T., Schoeman, M.H., 2022. Archaeobotanical evidence for the emergence of pastoralism and farming in southern Africa. Acta Palaeobotanica 62, 50-75.

Partridge, T.C., 1993. Warming phases in Southern Africa during the last 150,000 years: An overview. Palaeogeography, Palaeoclimatology, Palaeoecology 101, 237-244.

Partridge, T.C., 1966. Ficus Cave: an Iron Age living site in the central Transvaal. The South African Archaeological Bulletin 21(83), 125-132.

Plug, I., 1981. Some research results on the late Pleistocene and early Holocene deposits of Bushman Rock Shelter, eastern Transvaal. The South African Archaeological Bulletin 36(133), 14-21.

Pooley, E., 1998. A Field Guide to Wildflowers KwaZulu-Natal and the eastern region. Natal Flora Publications Trust, Durban.

Pooley, E., 2003. The Complete Field Guide to Trees of Natal, Zululand and Transkei. Natal Flora Publications Trust, Durban.

Pooley, E., 2005. Mountain flowers, a Field Guide to the flora of the Drakensberg and Lesotho. Natal Flora Publications Trust, Durban.

Porraz, G., Val, A., 2019. Heuningneskrans and the Stone Age sequence of the Ohrigstad River catchment on the eastern border of the great escarpment, Limpopo Province, South Africa. The South African Archaeological Bulletin 74(209), 46-55.

Porraz, G., Val, A., Dayet, L., De La Pena, P., Douze, K., Miller, C. E., Murungi, M. L., Tribolo, C., Schmid, V. C., Sievers, C., 2015. Bushman Rock Shelter (Limpopo, South Africa): a perspective from the edge of the Highveld. The South African Archaeological Bulletin 70(202), 166-179.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H., Carcaillet, C., Cordova, C., Mooney, S., 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. Climate dynamics 30(7-8), 887-907.

Prior, J., Williams, D. P., 1985. An investigation of climatic change in the Holocene Epoch using Archaeological charcoal from Swaziland, southern Africa. Journal of Archaeological Science 12, 457-475.

Quamar, M.F., 2019. Palynological study of surface soil samples from the Kartala Forest Range of the Korba District, Chhattisgarh, central India: Modern pollen-rain/vegetation relationship. Geophytology 49, 37-48.

Reason, C. J. C., Engelbrecht, F., Landman, W. A., Lutjeharms, J. R. E., Piketh, S., Rautenbach, C. D. W., Hewitson, B. C., 2006. A review of South African research in atmospheric science and physical oceanography during 2000-2005. South African Journal of Science 102(1), 35-45.

Rhodes, A.N., 1998. A method for the preparation and quantification of microscopic charcoal from terrestrial and lacustrine sediment cores. The Holocene 8, 113-117.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien Plant Invasions. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp. 535-570.

Rius, D., Vannière, B., Galop, D., Richard, H., 2011. Holocene fire regime changes from multiple-site sedimentary charcoal analyses in the Lourdes basin (Pyrenees, France). Quaternary Science Reviews 30(13-14), 1696-1709.

Rosen, D.Z., Lewis, C.A., Illgner, P.M., 1999. Palaeoclimatic and archaeological implications of organic-rich sediments at tifftidell ski resort, near Rhodes, Eastern Cape province, South Africa. Transactions of the Royal Society of South Africa 54, 311-321.

Rull, V., González-Sampériz, P., Corella, J.P., Morellón, M., Giralt, S., 2011. Vegetation changes in the southern Pyrenean flank during the last millennium in relation to climate and human activities: the Montcortès lacustrine record. Journal of Paleolimnology 46, 387-404.

Ryu, J., Liu, K.B., Bianchette, T.A., 2021. Holocene environmental history of a freshwater wetland in southern Louisiana: a sedimentary record of delta development, coastal evolution and human activity. Journal of Quaternary Science 36, 980-990.

Sadr, K., 2002. Encapsulated Bushmen in the archaeology of Thamaga. In: Kent, S. (Ed.), Ethnicity, Hunter-gatherers, and the 'other': Association or Assimilation in Africa. Smithsonian Institution Press, Washington, pp. 28–47.

Sadr, K., 2008. An ageless view of first millennium AD southern African ceramics. Journal of African Archaeology 6(1),103-129.

Sadr, K., 2014. Radiocarbon dates, stone tools and the origin of herding on the west coast of South Africa. In Reports in African Archaeology, 6. Africa Magna Verlag, Frankfurt am Main.

Sadr, K., 2015. Livestock first reached southern Africa in two separate events. PLoS ONE 10(8), e0134215.

Sadr, K., 2019. Atop Kasteelberg: social complexity in the Later Stone Age of South Africa. African Archaeological Review 36(1), pp.89-103.

Sadr, K., Sampson, C.G., 2006. Through thick and thin: early pottery in southern Africa. Journal of African Archaeology 4(2), 235-252.

Sampson, C. G., 1974. The Stone Age Archaeology of Southern Africa. Academic Press, New York.

Schoeman, M.H., 1997. The Ndzundza archaeology of the Steelpoort River Valley. Master's thesis. University of the Witwatersrand, Johannesburg.

Schoeman, M.H., 1998a. Excavating Ndzundza Ndebele identity at KwaMaza. Southern African Field Archaeology 7, 42-52.

Schoeman, M.H., 1998b. Material culture 'under the animal skin': excavations at Esikhunjini, a Mfecane Period Ndzundza Ndebele site. Southern African Field Archaeology 7, 72-81.

Schoeman, M.H., 2020. Archaeology of Farming Communities in Mpumalanga Province and the adjacent lowveld in Northeastern South Africa. Oxford Research Encyclopedia of African History. https://doi.org/10.1093/acrefore/9780190277734.013.767.

Schoonraad, M., Beaumont, P., 1971. The Welgelegen Shelter, Eastern Transvaal. In: Schoonraad, M. (Ed.), Rock Paintings of Southern Africa. Supplement to the South African Journal of Science, Special Publication 2, 62-69.

Scott, L., 1982a. A Late Quaternary pollen record from the Transvaal bushveld, South Africa. Quaternary Research 17, 339-370.

Scott, L., 1982b. A 5000-year old pollen record from spring deposits in the bushveld at the north of the Soutpansberg, South Africa. Palaeoecology of Africa 14, 45-55.

Scott, L., 1982c. Late Quaternary fossil pollen grains from the Transvaal, South Africa. Review of Palaeobotany and Palynology 36, 241-278.

Scott, L., 1984a. Reconstruction of Late Quaternary palaeoenvironments in the Transvaal region, South Africa, on the basis of palynological evidence. In: Vogel, J.C. (Ed.), Late Cainozoic Palaeoclimates of the Southern Hemisphere. Balkema, Rotterdam, pp. 317-327.

Scott, L., 1984b. Palynological evidence for Quaternary paleoenvironments in southern Africa. In: Klein, R.G. (Ed.), Southern African Prehistory and Palaeoenvironments. Balkema, Rotterdam, pp. 65–80.

Scott, L., 1987. Late Quaternary forest history in Venda, southern Africa. Review of Palaeobotany and Palynology 53, 1-10.

Scott, L., 2016. Fluctuations of vegetation and climate over the last 75 000 years in the Savanna Biome, South Africa: Tswaing Crater and Wonderkrater pollen sequences reviewed. Quaternary Science Reviews 145, 117-133.

Scott, L., Holmgren, K., Partridge, T.C., 2008. Reconciliation of vegetation and climatic interpretations of pollen profiles and other regional records from the last 60 thousand years in the Savanna Biome of Southern Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 257, 198-206.

Scott, L., Holmgren, K., Talma, A.S., Woodborne, S., Vogel, J.C., 2003. Age interpretation of the Wonderkrater spring sediments and vegetation change in the Savanna Biome, Limpopo province, South Africa. South African Journal of Science 99, 484-488.

Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E., Metwally, A., 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. Quaternary Science Reviews 32, 100-118.

Scott, L., Nyakale, M., 2002. Pollen indications of Holocene palaeoenvironments at Florisbad spring in the central Free State, South Africa. The Holocene 12, 497-503.

Scott, L., Thackeray, J.F., 1987. Multivariate analysis of Late Pleistocene and Holocene pollen spectra from Wonderkrater, Transvaal, South Africa. South African Journal of Science 83, 93-98.

Scott, L., Vogel, J.C., 1983. Late Quaternary pollen profile from the Transvaal highveld, South Africa. South African Journal of Science 79, 266-272.

Siebert, S.J., Van Wyk, A.E., Bredenkamp, G.J., 2002. The physical environment and major vegetation types of Sekhukhuneland, South Africa. South African Journal of Botany 68, 127-142.

Sjöström, J., Norström, E., Risberg, J., Schoeman, M.H., 2017. Late Holocene palaeoenvironmental reconstruction from Mpumalanga Province (South Africa) inferred from geochemical and biogenic proxies. Review of Palaeobotany and Palynology 246, 264-277.

Smith, J.M., 2005. Climate change and agropastoral sustainability in the Shashe/Limpopo River Basin from AD 900. PhD thesis. University of the Witwatersrand, Johannesburg.

Smith, A.B., 2016. Why would southern African hunters be reluctant food producers? Hunter Gatherer Research 2(4), 415-435.

Smith, A.B., 2021. Pastoralism in Africa. Oxford Research Encyclopaedia of African History. https://doi.org/10.1093/acrefore/9780190277734.013.1066.

Smith, J., Lee-Thorp, J., Hall, S., 2007. Climate change and agropastoralist settlement in the Shashe-Limpopo River Basin, southern Africa: AD 880 to 1700. The South African Archaeological Bulletin 62, 115-125.

Stager, J.C., Ryves, D.B., King, C., Madson, J., Hazzard, M., Neumann, F.H., Maud, R., 2013. Late Holocene precipitation variability in the summer rainfall region of South Africa. Quaternary Science Reviews 67, 105-120.

Stockmarr, J., 1971. Tables with spores used in absolute pollen analysis. Pollen et Spores 13, 615-621.

Summers, R., 1950. Iron Age cultures in southern Rhodesia. South African Journal of Science 47, 95-108.

Tomlinson, R.W., 1973. The Inyanga area: an essay in regional biogeography. University of Rhodesia Occasional Paper 1, 1–67.

Truc, L., Chevalier, M., Favier, C., Cheddadi, R., Meadows, M.E., Scott, L., Carr, A.S., Smith, G.F., Chase, B.M., 2013. Quantification of climate change for the last 20,000 years from Wonderkrater, South Africa: implications for the long-term dynamics of the Intertropical Convergence Zone. Palaeogeography, Palaeoclimatology, Palaeoecology 386, 575-587.

Turner, S., Plater, A., 2004. Palynological evidence for the origin and development of late Holocene wetland sediments: Mdlanzi Swamp, KwaZulu-Natal, South Africa. South African Journal of Science 100, 220-229.

Tyson, P. D., Lee-Thorp, J., Holmgren, K., Thackeray, J. F., 2002. Changing gradients of climate change in southern Africa during the past millennium: implications for population movements. Climatic Change 52, 129-135.

Tyson, P.D., Preston-Whyte, R.A., 2000. Weather and Climate of Southern Africa. Oxford University Press, Cape Town.

Umbanhowar, C.E., McGrath, M.J., 1998. Experimental production and analysis of microscopic charcoal from wood, leaves and grasses. The Holocene 8, 341-346.

Van Geel, B., 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro-and microscopic remains of fungi, algae, cormophytes and animals. Review of Palaeobotany and Palynology 25, 1-120.

Van Leeuwen, T.T., van der Werf, G.R., Hoffmann, A.A., Detmers, R.G., Rücker, G., French, N.H., Archibald, S., Carvalho Jr, J.A., Cook, G.D., de Groot, W.J., Hély, C., 2014. Biomass burning fuel consumption rates: a field measurement database. Biogeosciences 11(24), 7305-7329.

Vannière, B., Blarquez, O., Rius, D., Doyen, E., Brücher, T., Colombaroli, D., Connor, S., Feurdean, A., Hickler, T., Kaltenrieder, P., Lemmen, C., 2016. 7000-year human legacy of elevation-dependent European fire regimes. Quaternary Science Reviews 132, 206-212.

Van Wilgen, B.W., 2009. The evolution of fire management practices in savanna protected areas in South Africa. South African Journal of Science 105,343-349.

Van Wilgen, B.W., Richardson, D.M., 2012. Three centuries of managing introduced conifers in South Africa: benefits, impacts, changing perceptions and conflict resolution. Journal of Environmental Management 106, 56-68.

Vogel, J.C., Fuls, A., 1999. Spatial distribution of radiocarbon dates for the Iron Age in southern Africa. The South African Archaeological Bulletin 54(170), 97–101.

Voigt, E.A., 1984. The faunal remains from Magogo and Mhlopeni: Small stock herding in the Early Iron Age of Natal. Annals of the Natal Museum 26, 141–163.

Von Bezing, K.L., Inskeep, R.R., 1966. Modelled terracotta heads from Lydenburg, South Africa. Man 1, 102-104.

Wadley, L.,1989. Legacies from the Later Stone Age. Goodwin Series 6, 42-53.

Wadley, L., 1993. The Pleistocene Later Stone Age south of the Limpopo River. Journal of World Prehistory 7, 243-296.

Walker, N.D., 1990. Links between South African summer rainfall and temperature variability of the Agulhas and Benguela Current systems. Journal of Geophysical Research: Oceans 95(C3), 3297-3319.

Whitelaw, G., 1996. Lydenburg revisited: another look at the Mpumalanga Early Iron Age sequence. The South African Archaeological Bulletin 51(164), 75-83.

Widgren, M., Maggs, T., Plikk, A., Risberg, J., Schoeman, M.H., Westerberg, L-O., 2016. Precolonial agricultural terracing in Bokoni, South Africa: typology and an exploratory excavation. Journal of African Archaeology 14, 33-53.

Williams, C.G., 2008. Aerobiology of *Pinus taeda* pollen clouds. Canadian Journal of Forest Research 38(8), 2177-2188.

Wilson, E.H., 1923. Northern trees in southern lands. Journal of the Arnold Arboretum 4(2), 61-90.

Woodborne, S., Gandiwa, P., Hall, G., Patrut, A., Finch, J., 2016. A regional stable carbon isotope dendro-climatology from the South African summer rainfall area. PLoS ONE 11 (7), e0159361.

Woodborne, S., Hall, G., Robertson, I., Patrut, A., Rouault, M., Loader, N.J., Hofmeyr, M., 2015. A 1000-year carbon isotope rainfall proxy record from South African baobab trees (*Adansonia digitata* L.). PLoS ONE 10, e0124202.

Zhou, M., Sharik, T.L., Jurgensen, M.F., Richter, D.L., 1997. Ectomycorrhizal colonization of Quercus rubra seedlings in response to vegetation removals in oak and pine stands. Forest Ecology and Management 93, 91–99.

# CHAPTER 6: SYNTHESIS

## 6.1. INTRODUCTION

Generally, vegetation, climate, and anthropogenic activities are intimately interwoven, making the recovery of pollen, spores and charcoal invaluable in understanding present/past vegetation and environmental changes. While pollen and spores represent the relative distribution of plant communities, the frequency of microcharcoal indicates fire history (Bamford *et al.* 2016). In southern Africa, pollen and spores preserve well in i) natural archives ranging from lacustrine environments (Scott *et al.* 2008; Neumann *et al.* 2010), wetlands (e.g., fens, swamps) (Norström *et al.* 2009; Neumann *et al.* 2014; Breman *et al.* 2019); springs (Mao *et al.* 2006); speleothems (Burney *et al.* 1994; Brook *et al.* 1997, 2010; Caseldine *et al.* 2008; Festi *et al.* 2016) to ii) dung/hyrax deposits (Carrión *et al.* 2000; Scott *et al.* 2004; Kuzmicheva *et al.* 2013).

The potential of using pollen in palaeoenvironmental studies lies in the pollen outer wall (exine) containing a highly resistant material called sporopollenin, which is often preserved for thousands/millions of years when transported and/or deposited in favourable preservation conditions (Bryant & Holloway 1983). However, differential pollen preservation, production, dispersal, and depositional environments hinder or facilitate their recovery and interpretation (Bryant & Holloway 1983; Bell & Fletcher 2016; Morales-Molino *et al.* 2020). For instance, while acidic soils favour pollen preservation, highly alkaline soils (pH >8.5) often lead to the deterioration of fossil pollen (Dimbleby 1957; Havinga 1967; Bryant & Holloway 1983). Also, an aerobic environment causes oxidation of the sporopollenin, thereby aggravating the vulnerability to microbial decomposition (Havinga 1967; Xu *et al.* 2016). Furthermore, water-constrained landscapes (e.g., pans) exhibit a considerable degree of vegetation stability over

time. As a result, when the drivers of vegetation shifts, such as fire and grazing change, they may not be represented in the palaeo-records despite being readily present on the broader landscape (Ekblom *et al.* 2017).

Another factor that may limit the potential of pollen is the over-representation of certain pollen types in assemblages. For example, wind-pollinated species, e.g., conifers like pines (*Pinus*) or yellow woods (*Podocarpus*, *Afrocarpus*), produce abundant pollen grains with aerodynamic properties like air bladders and are frequently over-represented in pollen spectra, whereas insect-pollinated species produce fewer, heavy, ornamented pollen grains and are generally under-represented or absent in pollen spectra, even when observed in current vegetation (Faegri & Iversen 1989; Nohro *et al.* 2019; Quamar 2019). Hence, the differential pollen preservation, production and dispersal, limit or enhance recovery and their interpretation (Bryant & Holloway 1983). This calls for studies that investigate the relationship between modern pollen assemblages and contemporary source vegetation of a region before palaeoenvironmental studies.

Certain pollen grains are unidentifiable beyond the family level (e.g., Poaceae >25 μm, Asteraceae undifferentiated), and the morphology of some pollen grains is often undifferentiated when only using light microscopy (e.g., *Stoebe/Elytropappus*, Combretaceae/Melastomataceae) (Scott 1982b; Bryant & Holloway 1983; Erdtman 1986). Nevertheless, most plant species produce distinct pollen grains and spores, and their recovery and precise identification to genus/species levels aids palaeoenvironmental interpretations. It is, however, advantageous to combine pollen with other proxies (e.g., phytoliths, which are useful for identifying Poaceae subfamilies) (Alexandré *et al.* 1997; Parker *et al.* 2011; Breman *et al.* 2019; Cordova *et al.* 2019) to provide a more robust understanding of the palaeoenvironment.

Archaeobotanical research in southern Africa, particularly pollen and spore studies, focuses mostly on reconstructing past climatic changes rather than the possible role that anthropogenic activities relating to farming and pastoralism might have exerted on the vegetation, especially during the last 2000 years. This is partly due to the dominance of climate as a major driver of vegetation change for most periods, as well as research bias in interpreting climatic influences (Fitchett *et al*. 2017b).

This bias, coupled with sparse direct archaeobotanical evidence (e.g., fruits/seeds, faunal), has hindered the comprehensive understanding of the beginnings and spread of farming and pastoralism in the region. Generally, the continued efforts to reconstruct the available evidence in the past decades have suggested that the emergence of farming and pastoralism in Sub-Saharan Africa varied significantly owing to several factors relating to migration, predictability of resources, diffusion, scheduled consumption, vegetation, climate, and sedentism (Wetterstrom 1993; Marshall & Hildebrand 2002; Mitchell 2005). This calls for a synthesis of reliable, independent proxies (e.g.,palynology, phytolith analyses, anthracology) to ascertain a narrative of pastoralism and farming that is consistent with existing archaeobotanical and archaeological data and to provide new insights for identifying anthropogenic impacts and cultivars in the palaeo-records.

Several archaeological sites provide evidence of apparent shifts in technology, human occupation and subsistence. However, sparse palaeo-records are available, particularly during the Holocene, to compare these shifts and explore the relationship between humans, climate and vegetation. This is often due to the scarcity of pollen-bearing archives close to archaeological sites, scanty continuous terrestrial records as well as spatial disparities between palaeo-records as a result of diverse climatic conditions in various regions (Klein 1984; Prior & Williams 1985; Korsman &

Plug 1994; Porraz *et al.* 2015; Bousman & Brink 2018). Hence, the relationships between subsistence patterns, technology and environmental changes are often assumed. Similarly, broader-scale changes such as the African Humid Period, Younger Dryas, Medieval Warm Period, and Little Ice Age which have been confirmed for the Northern Hemisphere but not verified for the Southern Hemisphere are used to interpret technological and subsistence changes during the Holocene without considering regional or local variations (Deacon 1984; Huffman 1996; Mitchell *et al*. 1998; Vogel & Fuls 1999; Badenhorst 2018). There is a need to explore local palaeoenvironmental records, particularly for the last 2000 years BP, where several sites in South Africa provide significant archaeological evidence of pastoralism and farming as well as diverse temporal oscillations in moisture levels, potentially indicating the presence of pastoralists and farmers within the local landscape (Scott *et al.* 2012; Lander & Russell 2018).

This thesis demonstrates the need for multiproxy studies in present and past environmental contexts to address palaeoenvironmental issues. Analysing pollen, spores, and microcharcoal in modern and sedimentary records demonstrates the potential of a multiproxy approach to reconstruct and highlight possible differences between anthropogenic and climate impacts on landscapes during the Holocene.

## 6.2. HUMAN & CLIMATE-VEGETATION RELATIONSHIPS

This thesis explored the potential of pollen, spores and charcoal in reconstructing the impact of anthropogenic activities and climate change on vegetation, particularly during the last 11,700 years. The assessment of the relationship between climate, human activities and vegetation in southern Africa during the first millennium CE, through in-depth study of existing literature, shows similar patterns of vegetation changes across the biomes, indicating possible

anthropogenic impact (Olatoyan *et al.* 2022/Paper 1 for discussion). The study of the relationship between modern pollen assemblages and contemporary vegetation in and around a wetland, Mashishing Fen, Mpumalanga province, northeastern South Africa, showed that modern pollen assemblages are invaluable for identifying different vegetation, especially when combined with other proxies (e.g., phytoliths), thus facilitating palaeoenvironmental reconstruction (Olatoyan *et al.* 2023/Paper 2). Also, the analysis of the core sediment samples from the Mashishing Fen provided a chronological sequence for the past 11,700 years, showing the influence of climate and anthropogenic activities on the vegetation from the Early to Late Holocene for the region. Here, the data from the studies are synthesised to evaluate the patterns of vegetation changes caused by climate and/or human activities and compare them with similar studies (Olatoyan *et al.* in prep./Paper3).

## 6.3. TREE AND SHRUB POLLEN

The modern pollen assemblage around the Mashishing Fen is best associated with the presence of *Euclea, Diospyros* and *Podocarpus* pollen, representing the forest vegetation in the study area (Olatoyan *et al.* 2023/Paper 2). Also, the pollen of Combretaceae, Myrtaceae, and Rubiaceae was represented, comprising the typical pollen assemblage of the fen and forest margin. Forest elements in the pollen assemblages usually indicate high rainfall in the area (Gillson & Ekblom 2009; Truc *et al.* 2013; Zhao *et al.* 2016). Although the tree pollen proportion corresponds to the recorded vegetation, pollen of some species from Combretaceae, Myrtaceae, and Euphorbiaceae families documented in the modern pollen assemblage were not recorded in the botanical survey (Olatoyan *et al.* 2023/Paper 2). This lack of correlation between pollen and vegetation might be due to the identification of some pollen only to the family level, and some of these pollen may originate from plant species found in different vegetation types. It may also be due to limited

sample plots for the botanical survey. Additionally, many tree pollen are transported by wind and can be widely dispersed and abundant, even in areas where they are not growing locally. Therefore, it is important to exercise caution when interpreting forested regions precisely based solely on the ratio of Non-Arboreal Pollen to Arboreal Pollen. Also, subsequent studies on modern studies would investigate more sediment samples and sample plots.

Generally, studies focusing on modern pollen-vegetation relationships are relatively sparse for South Africa. This limited a comprehensive comparison of the results from Mashishing Fen. Similar modern pollen studies from sites (e.g., Scot Farm, Wonderkrater) in the Savanna Biome have also shown that the distinction of modern pollen spectra can be utilised to identify the diverse vegetation types within the region. For instance, significant pollen taxa, e.g., *Podocarpus*, Combretaceae and *Euclea*, pointed to defined veld types after Acocks (1975) (e.g., dry Kalahari Thornveld marked by the occurrence of Tarchonanthaceae, and Capparaceae, [Scott 1982a, 1984]). A more recent study in the montane belt of the KwaZulu-Natal Drakensberg recorded a high degree of heterogeneity within the Afrotemperate forest vegetation, showing the dominance of *Podocarpus* and *Celtis* (Hill & Finch 2021). This reflects the long distant transport of wind pollinated pollen especially in high mountainous areas. Like the modern pollen records from the Mashishing Fen, the modern pollen assemblages also indicated an area dominated by trees with relatively few representations of the pollen of Asteraceae and Poaceae, which are commonly recorded in other sites (Hill & Finch 2021).

Similar to the modern pollen records at Mashishing, the presence/increase of pollen of trees like *Podocarpus*, and Myrtaceae, which typically associates with forests, also occur in the Mashishing Fen palaeo-records, likely indicating moist conditions (Scott 1982a; Mustart & Cowling 1993; Geldenhuys & von dem Bussche 1997; Matthys *et al*. 2022). While the pollen of *Searsia* was

regularly detected in the modern and palaeo-records at Mashishing Fen, the pollen of *Olea* and *Canthium*, commonly associated with forest margins and streams (Campbell & Moll 1977; McKenzie *et al.* 1977; Scott 1982b; Hlwatika & Bhat 2002), were seldom recorded in the modern pollen records but were prominent in the palaeo-records. The reason for this disparity remains unclear. The relatively high frequencies of *Canthium* in the pollen palaeo-record possibly suggest that the trees grow locally in the past in the area because the pollen grains are usually not well dispersed (Scott 1982b).

A decline in the pollen frequencies of trees (forest) observed during vegetation reconstruction can be driven by climate (e.g., Scott *et al.* 2003; Chevalier & Chase 2016), human activities (e.g., Shi *et al.* 1998; Li *et al.* 2008), or a combination of both drivers (Finch & Hill 2008; Neumann *et al.* 2008). During the early Holocene (ca. 10,900 cal. yr BP), the decline of tree pollen (e.g., *Olea*, *Canthium*, Myrtaceae) documented in the pollen record at Mashishing Fen (Olatoyan *et al.* in prep./Paper3) likely suggests the prevalence of dry conditions (Cowling 1999; Levis *et al.* 1999; Monnin *et al.* 2001). The local conditions likely became drier and cooler to favour the growth of grasses over trees and aquatics. This phenomenon was also recorded at different times (e.g., ca. 10,900, 8600, 5900 cal. yr. BP) in the pollen records at Mashishing Fen, where the main forest tree pollen taxa decreased. This is usually accompanied by a decrease in Cyperaceae, *Phragmites* and other aquatics (Olatoyan *et al.* in prep./Paper 3), further suggesting a local decrease in available moisture for these periods (Burgoyne *et al.* 2000; Mabhungu *et al.* 2019). Also, pollen taxa (e.g., *Stoebe*, *Artemisia,* Asteraceae), which could indicate cool and/or relatively dry conditions increased during these periods (Coetzee 1967; Morrison 1968; Scott 1984) or the dominance of local overgrazing in grassland communities (Carrión *et al.* 2000; Nyakale & Scott 2002). The former is more likely, as there is no evidence of intensified grazing in the area during

the early and middle Holocene periods. A general decrease in the pollen percentages of trees could be indicative of a reduction in forest cover due to a combination of factors, such as cool and dry conditions or frequent fires, as well as human activities like anthropogenic fires or land use changes (Ekblom 2008; Finch & Hill 2008; Neumann *et al.* 2008, 2010; Walther & Neumann 2011). The cool and dry conditions may be less favourable for tree growth and survival, which could result in a decline in forest cover over time. Similarly, frequent natural fires or human-set fires could also contribute to forest loss by vegetation clearance and preventing their regeneration (e.g., Breman *et al.* 2011). The coincidence of high frequencies of microcharcoal, especially the peak of >100 µm size class (possibly of local origin), with the decline of tree pollen suggests the occurrence of veld fires. It is plausible that this phenomenon is indicative of natural veld fires, which are frequent occurrences in the Grassland Biome (Bond *et al.* 2003a, 2003b). The previous pollen zones, which had more moisture, likely allowed forest growth, resulting in increased biomass as fuel. Subsequently, the dry conditions in the current zone might have contributed to the increased susceptibility to combustion.

The assessment of the relationship between humans, climate, and vegetation from published archaeobotanical data revealed a decline in trees such as *Podocarpus* (and sometimes *Olea*) in various locations across South Africa, Zambia, and Mozambique, at the Savanna, Grassland, IOCB, and Fynbos Biomes (See Table 1; Olatoyan *et al.* 2022/Paper 1). This decline could be attributed to various factors, including the selective exploitation of trees for their wood, unfavourable climatic conditions that impede forest growth, or a combination of both human and climate-related impacts.

An anthropogenic impact was more likely during the first millennium AD because the tree decline was commonly synchronous with the increase of other possible anthropogenic indicators

(e.g., spores of coprophilous fungi, open-land taxa, large Poaceae [Cerealia-type] pollen [>40 µm], charred plant fragments) in the palaeo-records. This is supported by several archaeobotanical data showing similar vegetation changes during the first millennium CE (Olatoyan *et al.* 2022/Paper 1) and other archaeological evidence in the region (Lander & Russell 2018). Given the diversity of southern African climates, as well as the significant temporal and spatial variability across the subcontinent, it is unlikely that the various biomes experienced the same climatic fluctuations during the first millennium AD (Tyson & Preston-Whyte 2000; Chevalier & Chase 2016). Thus, similar vegetation changes observed in pollen assemblages were more likely caused by human activities rather than climate variations.

## 6.4. OPEN LAND INDICATORS

Poaceae and Asteraceae grow in a broad range of ecological and climatic conditions (Carbutt & Edwards 2004; Chevalier *et al.* 2021), and pollen from these families is widespread. Poaceae is present almost everywhere in South Africa and is generally associated with high rainfall during summer in the grasslands. In contrast, Asteraceae, which is also ubiquitous in the region, often signals generally less rain and/or dry, cool summers or might signal anthropogenic impact when found in association with high frequencies of other open-land indicators (e.g., Amaranthaceae) (Coetzee 1967; Cooremans 1989; O'Connor & Bredenkamp 1997).

The modern pollen assemblage for the grass patches within thickets near Mashishing Fen showed the dominance of Poaceae and Asteraceae with a mixture of *Burkea* and *Spirostachys* (tree) pollen (Olatoyan *et al*. 2023/Paper 2). Similarly, in the southern Middleveld in the southern Free State province, high Poaceae and Asteraceae with low *Searsia* (tree) pollen was recorded (Coetzee & van Zinderen Bakker 1952; Hill 1995). A slight contrast was observed in

the modern spectra from Ladybrand in the eastern Free State region, where a mixture of high tree pollen comprising *Celtis, Searsia, Clutia,* and non-tree pollen of Poaceae, Asteraceae, and *Cliffortia* were recorded (Scott 1982a).

Also, at Deelpan in the western Free State region, the modern spectra revealed considerable heterogeneity between the modern pollen assemblages of various sampling sites, suggesting that fossil pollen often correlates with local vegetation changes rather than climate change (Scott 1988). In addition, the modern spectra from the Blue Mountain Pass in the Lesotho highlands yielded pollen of Ericaceae, indicative of high altitudes, Poaceae, Cyperaceae, Asteraceae, *Passerina, Anthospermum,* and Aizoaceae, which are present in the existing open-land vegetation within the study area (Scott 1984). The modern pollen assemblages from these regions indicate similarities to the contemporary vegetation, representing an open grassy landscape with the presence of open savanna/woodland (Lötter *et al.* 2014; O'Donoghue *et al.* 2020; Hahn *et al.* 2021). Recent studies in the Kruger National Park, northeastern South Africa, showed the dominance of Poaceae/Cyperaceae except for two sampling sites where *Spirostachys africana* and Combretaceae pollen were present at considerably higher frequencies. Low *Acacia*-type (inclusive of all *Senegalia* and *Vachellia* spp., *Albizia* spp.) pollen occurrence was also recorded despite being highly represented in the contemporary source vegetation, possibly due to insect-pollinated plants producing a comparatively low number of large polyads (Duffin & Bunting 2008). Also, Poaceae and Asteraceae are among the most prominent grassland taxa in the region (Hill 1995).

The pollen of Poaceae and Asteraceae regularly occurred at the beginning of the early Holocene in the Mashishing Fen pollen record (Olatoyan *et al*. in prep./Paper 3), which is consistent with regional records (Scott & Vogel 1983; Norström *et al.* 2009; Scott *et al.* 2012; Neumann *et al.*

2014). The increase in the pollen of Poaceae and Asteraceae suggests the dominance of open grassy vegetation due to prevailing less moist conditions for this period, especially when accompanied by the decline of tree pollen and aquatics with no recorded evidence of human occupation within the area or climate-induced fires. It is also likely that the decline of Cyperaceae and *Phragmites* commonly associated with wetlands indicates the shrinking of the wetland, further suggesting the dominance of dry local conditions for this period. The Mashishing Fen pollen records also indicate the decline of trees, while Apiaceae, *Anthospermum,* and Asteraceae pollen increased after ca. 5900 cal. yr BP might suggest less pronounced seasonality and/or dominance of open grassy vegetation in the area (O'Connor & Bredenkamp 1997). The coincidence of increased microcharcoal suggests frequent fires caused by natural or human activities or a combination of both. This phenomenon was regularly observed in the Mashishing Fen records and other sites (e.g., Hahn *et al.* 2021). Similar pollen assemblages comprising the high frequencies of open-land indicators (e.g., Amaranthaceae, Asteraceae) were recorded across the different biomes in the reviewed archaeobotanical data (Table 1; Olatoyan *et al.* 2022). This might be related to the impact of anthropogenic activities, particularly farming (Baxter & Davies 1994; Neumann *et al.* 2011; Hahn *et al.* 2021), but could also indicate regional aridity (Scott *et al.* 2003; Chevalier & Chase 2015, 2016). These open-land indicators more likely point to anthropogenic impact during the first millennium CE based on their regular association with large Poaceae pollen (>40 µm). The large Poaceae pollen are tentatively interpreted as cultivated cereals (e.g., sorghum, pearl millet), and their presence coincides with the beginnings of farming in South Africa from sites such as Mpondoland and Mdlanzi (Turner & Plater 2004; Hahn *et al.* 2021). Thus, the available evidence suggests a strong link between anthropogenic activities and vegetation changes.

This phenomenon was also documented in the Mashishing Fen records during the first millennium CE. By ca. 1500 cal. yr BP (ca. 434–649 CE), a notable decline in tree pollen is synchronous with the first appearance of large Poaceae pollen (>40µm) in the Mashishing Fen record, which could potentially indicate the cultivation of cereals. However, the pollen could also belong to the wild Poaceae group (Bonnefile & Riollet 1980). Caution should be exercised when interpreting the pollen because large Poaceae pollen has been documented in pollen records prior to the arrival of farming in southern Africa (e.g., Baxter 1996). The accompanying high frequencies of Amaranthaceae and Asteraceae might further suggest an anthropogenic impact on the vegetation during this period, especially with the co-occurrence of the decline of forest pollen (Baxter & Davies 1994). The high frequency of microcharcoal with the concurrent increase of open-land indicators and decreased tree pollen in the Mashishing Fen record for this period suggests local burning driven by farmers within the area. The pollen data for this period corresponds with the arrival of Early Farming Communities in the area (e.g., Klapwijk & Huffman 1996; Klapwijk 1974; Whitelaw 1996; Jordaan 2017). It seems that early farmers were responsible for the felling of trees for wood and vegetation clearance for farming, settlements and pastures.

Around 500 cal. yr BP (ca. 1450 CE), a sudden surge in the pollen of Amaranthaceae and Caryophyllaceae alongside the reduction in tree pollen observed in the Mashishing Fen pollen sequence suggests that the forest was receding, which could be attributed to anthropogenic disturbances or aridity (Baxter 1996; Finch & Hill 2008; Hahn *et al.* 2021). The accompanying increase of the pollen percentage of Cyperaceae, *Phragmites* and fungal spores, indicating locally moist conditions and a higher water table, suggests that anthropogenic impact is more likely. The accompanying decrease of Poaceae and Asteraceae might further suggest more humid

conditions and possible local disturbances of grass cover for this period or could indicate the spread of other taxa. This period corresponds fairly with the presence of Later Farming Communities (e.g., at Bokoni sites) who used specialised farming (stone walling) systems around the 15th/16th– 19th/20th century (Widgren *et al.* 2016; Birin *et al.* 2021). Later Farming Community sites, often including the stone-walled terraces, tracks, and enclosure units, have been identified In the Gustav Klingbiel Nature Reserve (study site) and across Mpumalanga, stretching from Ohrigstad in the north, via Lydenburg and Machadodorp, to Carolina in the south (Delius *et al.* 2012). The recovery of carbonised seeds of *Sorghum* sp. (sorghum) and *Vignia* sp. (cowpea) at Khutwaneng (formerly Badfontein) during this period further provides direct evidence of agriculture.

## 6.5. WETLANDS / AQUATIC TAXA

In the Wetlands, the modern pollen assemblage indicates that the fen vegetation is best associated with the presence of *Typha*, Sparganiaceae and *Phragmites* and fern spores (Olatoyan *et al.* 2023/Paper 2). These pollen assemblages are common components of wetlands globally and are regularly found in South African wetlands vegetation (Burgoyne *et al.* 2000; Myburgh & Bredenkamp 2004; Sieben 2011, 2014; Mabhungu *et al.* 2019), hence, indicate (locally) moist conditions. While there are no comparable modern pollen studies from similar vegetation communities in South Africa, studies from other regions recorded the dominance of *Typha* and *Phragmites* in wetland communities (Finkelstein & Davis 2005; Yang *et al.* 2016; Zhao *et al.* 2016; Muller *et al.* 2022). The fen vegetation is also associated with shrublets and herbs (e.g., Amaranthaceae, *Crassula*) which are usually interpreted as indicators of drier and strong evaporative (summer) conditions in South African palaeoecological studies (Scott & Nyakale 2002; Scott *et al.* 2003; Neumann *et al.* 2011; Marais *et al.* 2015; Chevalier & Chase 2015, 2016;

Quick *et al.* 2018, 2022). However, their associative presence with the fen vegetation suggests they are not exclusively indicative of drier environments. Often, these taxa (e.g., Amaranthaceae) might serve as obligate indicators of wet environments and/or signify anthropogenic disturbances (Sieben *et al.* 2017; Van Ginkel & Cilliers 2020; Olatoyan *et al.* 2022/Paper 1). While *Crassula* is a known succulent indicating drier environments (Scott & Cooremans 1992; Cook 2004; Manning & Goldblatt 2007), it could occur in varying ecological conditions (Scott 1982a) and may also indicate anthropogenic disturbances, especially in recent times (Norström *et al.* 2009). This corresponds to the contemporary wetland vegetation components comprising shrubs, succulents and herbs recorded at the eastern Lesotho highlands (Fitchett *et al.* 2017b).

Similar pollen assemblages recorded in the Mashishing Fen record indicate the dominance of (locally) moist conditions. During the early Holocene, the high frequencies of the pollen of aquatics and swamp elements, e.g., Cyperaceae and *Gunnera,* might suggest local moist conditions (Olatoyan *et al.* 2023/Paper 2). While *Gunnera* grows naturally in highly humid areas and around waterbodies (Bergman *et al.* 1992; Bergman 2002), Cyperaceae usually grow in wetlands, though a few species have also been recorded in the grasslands and savannas. The increase in Cyperaceae could be associated with wetter conditions, which provide an expanded habitat for its growth (Partridge 1993; Gillson 2006; Breman *et al.* 2011). The dominance of the strong fluctuations of Poaceae, though on a smaller scale with high frequency of Cyperaceae in the Mashishing Fen sequence during the early Holocene, likely indicates open grassland surrounding the site. The accompanying presence of the pollen of trees such as *Podocarpus,* Proteaceae and Myrtaceae, typically associated with montane forests, further signal moist conditions for this period (Scott 1982a; Mustart & Cowling 1993; Geldenhuys & von dem Bussche 1997; Matthys *et al.* 2022).

On the other hand, the decline of the pollen of wetland elements is usually synchronous with the increase of open-land indicators and the decline of tree pollen except during periods of known anthropogenic impact in the record. For instance, the surrounding grasslands indicated by the high frequencies of the pollen of Poaceae and Asteraceae prevailed until ca. 10,900 cal. yr BP. During this period, the pollen record also showed a decline in tree pollen (e.g., *Olea, Canthium,* Myrtaceae), Cyperaceae and other aquatics, which might suggest the prevalence of dry conditions (Scott 1982b). The sparseness of *Phragmites* pollen, a typical wetland element, might indicate decreased wetland size, further suggesting local dryness for this period (Burgoyne *et al.* 2000; Mabhungu *et al.* 2019). After ca. 10,900 cal. yr BP, the relatively high frequencies of *Canthium, Podocarpus,* Proteaceae and *Olea* pollen might suggest a return to warm and moist conditions. The forests likely recovered after the relatively drier period due to favourable warm and moist conditions. The accompanying peak of Cyperaceae alongside the high frequencies of fern spores further suggests possible local conditions. At ca. 10,000 cal. yr BP, the increase of the pollen frequencies of typical forest trees (e.g., *Canthium, Olea,* Proteaceae) and Combretaceae at Mashishing Fen, which might indicate the prevalence of warm subhumid conditions, suggest that the forest was prominent in the entire zone. The increase of wetland pollen taxa (e.g., Cyperaceae, *Typha*) and fern spores coupled with the relative decrease of the pollen frequencies of *Artemisia* and *Stoebe* further suggests that local moist conditions generally occurred during this zone. Microcharcoal, particularly smaller and larger classes, remain low at this time, suggesting minimal burning likely due to moist conditions. At ca. 8600 cal. yr BP, the pollen of Cyperaceae, *Typha, Phragmites* and fern spores continued to decline. In contrast, Poaceae pollen became dominant, indicating the dominance of open grassy vegetation likely due to prevailing less moist conditions. The increase in the pollen of herbs, especially Asteraceae,

might suggest the dominance of grassy vegetation due to dry local conditions for this period. It is also likely that the decline of aquatics associated with wetlands (e.g., Cyperaceae, *Phragmites*) suggests the shrinking of the wetland.

After ca. 6700 cal. yr BP, the high frequencies of the pollen of open woodland taxa (e.g., *Searsia*, Combretaceae) and forests (e.g., *Olea, Canthium*) were recorded, likely indicating increased moist conditions in the area. The accompanying increase of Cyperaceae pollen and fern spores further suggests local moist conditions for this period.

However, the decline of the wetland elements was no longer synchronous with the decline of trees, possibly resulting from anthropogenic activities in the area even during favourable environmental conditions. At ca. 1500 BP, the decrease in forest (tree) pollen was recorded alongside the high frequencies of Amaranthaceae and Asteraceae pollen, which might suggest an anthropogenic impact on the vegetation during this period. The simultaneous decrease in forest pollen and increase in open land indicators, such as Amaranthaceae and Asteraceae, observed within an archaeological context, is more indicative of anthropogenic impact (Baxter & Davies 1994). The accompanying increase of the pollen frequencies of Cyperaceae, *Gunnera* and other aquatics further suggest locally wet conditions for this period (Olatoyan *et al.* 2023/Paper 2). At ca. 500 cal. yr BP (ca. 1450 CE), the pollen zone begins with a sudden increase in Amaranthaceae and Caryophyllaceae coupled with the decline of trees, suggesting the diminishing of forests likely due to anthropogenic disturbances or aridity (compare Baxter 1996; Finch & Hill 2008; Hahn *et al.* 2021). Possible anthropogenic disturbance is supported by the increase in the pollen frequencies of Cyperaceae, *Phragmites* and fungal spores, indicating locally moist conditions and higher water table during the period.

## 6.6. CHARRED PLANTS FRAGMENTS

Charred plant fragments being a product of partial combustion, serve as a proxy indicator of fire, providing a record of fire occurrences and history when recovered in soils, peat, and lake sediments (Komarek *et al.* 1973; Umbanhowar & McGrath 1998; Nichols *et al.* 2000; Rose 2004). In the veld, fires are mostly from grass fuels, and the amount/composition of grasses on the landscape is a good indicator of the frequency of fire (Patterson *et al.* 1987; Scott 2002; Van Wilgen 2009; Archibald *et al.* 2012; Nyamadzawo *et al.* 2013, Cardoso *et al.* 2022). During fire occurrences, charred grasses are transported by wind and/or water and usually deposited as microcharcoal (Patterson *et al.* 1987; S. Woodborne pers. comm. 2019)

One of the possible indicators of human presence and activity are microcharcoal, though it remains challenging to differentiate from natural fires. Nonetheless, previous studies have suggested a likely connection between increased charred fragments and human impact (Archibald *et al.* 2012; Nyamadzawo *et al.* 2013; Bond & Zaloumis 2016; Dubois *et al.* 2018; Cardoso *et al.* 2022; Razanatsoa *et al.* 2022). Pastoralists and farmers routinely used fire to clear vegetation to prepare land for fields and settlements and to stimulate grass growth (Nkala *et al.* 2011; Neary & Leonard 2020). Human-caused fires are frequently distinguished from naturally induced fires when microcharcoal is recovered with other likely anthropogenic indicators such as weeds, large Poaceae pollen (>40 m), and open-land indicators, which are often associated with evidence of human occupation and impact (Li *et al.* 2008; Archibald *et al.* 2012; Razanatsoa *et al.* 2022) but coincidences cannot be ruled out. In southern Africa, the decline of trees and co-occurrence of open-land indicators suggest the impact of anthropogenic burning, especially when archaeological evidence supports the presence of human occupation (Scott 1982b; Roos *et al.* 2016; Scott *et al.* 2022). This phenomenon was documented at several sites across all the biomes

of southern Africa (e.g., Versailles, PrincessVlei, GeoB 1023, Mahwaqa Mountain, and Mdlanzi Swamp) (Olatoyan *et al.* 2022). Nevertheless, some sites with evidence of possible anthropogenic impact did not show a peak in microcharcoal along with other indicators (e.g., Broederstroom, Mdlanzi, Mpondoland) (Olatoyan *et al.* 2022). The absence of evidence for microcharcoal could be attributed to effective fire management (Scott 2002) or a limited population of farmers who moved into a landscape managed by hunter-gatherers (Wadley 1987, 1996).

The Mashishing Fen pollen sequence showed a general decrease in the pollen percentages of trees at ca. 10,000 cal. yr BP, likely suggesting that the forest diminished due to the predominant cool and dry conditions and/or frequent natural fire or with the combination of anthropogenic fire. The additional evidence of high frequencies of microcharcoal in the record, particularly the peak of >100 µm size class (likely large charcoal of local origin), might have resulted from natural veld fires. This is supported by the idea that naturally ignited veld fires are common in the Grassland Biome (Bond *et al.* 2003a, 2003b). It seems likely that the prevailing moist conditions in the previous zone, which favoured forest trees, led to increased forest biomass as fuel. The dry conditions recorded in the current zone might have favoured burning as frequent fires occur in dry periods more than wetter periods (van Wilgen 2009; Archibald *et al.* 2012; Cardoso *et al.* 2022). Generally drier conditions during the mid-Holocene with a significantly charred particles >10, >50 and >100µm were recorded in the Mashishing Fen sediment sequence, indicating high fire frequency during the later period. The pollen records further indicate the decline of trees while Apiaceae, *Anthospermum,* and Asteraceae pollen increased after ca. 5900 cal. yr BP, which might suggest less pronounced seasonality conditions and/or dominance of open grassy vegetation in the area (O'Connor & Bredenkamp 1997). This was

accompanied by high abundancy of microcharcoal, indicating high fire frequency due to natural or anthropogenic activities or a combination of both. It seems that the coincidence of high microcharcoal with dry conditions (less moisture) regularly occurred in the Mashishing Fen record as in other sites (e.g., Hahn *et al.* 2021). Also, the forest decline, which is likely due to unfavourable dry conditions, is further supported by high microcharcoal particularly <50 and >50µm, indicating increased fire intensity due to dry conditions after ca. 4000 cal. yr BP. Nevertheless, the concomitant decrease in forest pollen and rise in open land indicators such as Amaranthaceae and Asteraceae, observed within an archaeological context, more plausibly point towards anthropogenic influence (Baxter & Davies 1994). The high microcharcoal with the concurrent increase of open-land indicators and decreased tree pollen recorded around ca. 1500 BP likely suggest local burning driven by farmers within the area.

## 6.7. LARGE POACEAE (>40 µm)

The occurrence of large Poaceae pollen grains (>40 µm) in various locations within the Grassland Biome, as well as marine and IOCB sites from reviewed archaeobotanical data (Olatoyan *et al.* 2022/Paper 1), may potentially suggest the presence of crop cultivation. In the southern African region, these pollen grains were frequently observed alongside open-land indicators, the decline in tree pollen as well as increased microcharcoal (Table 1&2; Olatoyan *et al.* 2022), which suggests the possibility of farming practices having been adopted in the area. While it is feasible to draw a connection between the large Poaceae pollen grains and early cultivated cereals (such as *Pennisetum glaucum* – syn. for *Cenchrus americanus* and *Sorghum)*, as has been demonstrated in other contexts (e.g., Turner & Plater 2004; Hahn *et al.* 2021), the aforementioned size overlap with wild grass species (Bonnefile & Riollet 1980) in the summer rainfall areas of South Africa, where the first farmers settled, must be taken into account.

Additionally, the presence of large Poaceae pollen grains (>40 µm) may not necessarily indicate the cultivation of grasses in the fynbos since they are commonly detected in pollen records predating the first millennium AD when farming was known to have commenced in southern Africa (e.g., Baxter 1996). Therefore, interpreting them as cultivated cereals in the fynbos requires caution.

Similar to the pollen assemblages from the reviewed sites (Table 1, Olatoyan *et al.* 2022), the decrease in forest tree pollen coincides with the first occurrence of large Poaceae pollen (>40µm) at Mashishing Fen by ca. 1500 cal. yr BP (c. 434–649 CE), which could be interpreted tentatively as cultivated cereals, although the pollen of wild Poaceae (grasses) cannot be excluded (Bonnefile & Riollet 1980). However, this should be taken with caution as larger Poaceae pollen have been recorded in pollen records before farming in southern Africa (e.g., Baxter 1996; Olatoyan *et al.* 2022/Paper 1 for discussion). The accompanying high frequencies of Amaranthaceae and Asteraceae might further suggest an anthropogenic impact on the vegetation during this period. The decline of forest pollen coupled with the increase of open land indicators (e.g., Amaranthaceae, Asteraceae) within an archaeological context more likely indicates anthropogenic impact (Baxter & Davies 1994). The pollen frequencies of Amaranthaceae and Asteraceae prevailed after ca. 500 cal. yr BP, which might be interpreted as the continued impact of anthropogenic disturbances, possibly through farming/overgrazing (Carrión *et al.* 2000; Nyakale & Scott 2002), or local solid evaporative conditions (Dyer 1975; Pooley 1998) or possibly the dominance of open and dry grassland environment (Cooremans 1989). Likely anthropogenic impact is supported by the presence of larger Poaceae >40µm (perhaps cultivated cereals) in the pollen record at Mashishing Fen. This could be related to the expansion of Later Farming Communities into new areas while they reconstruct their specialised

farming systems to facilitate crop production despite localised challenging environmental conditions.

## 6.7. EXOTIC TAXA

Generally, wind-pollinated exotic species, e.g., conifers like pines (*Pinus*), produce abundant pollen grains with aerodynamic properties like air bladders and are frequently over-represented in pollen spectra. Their high pollen productivity and dispersal rate means that *Pinus* is often dominant in pollen assemblages even when pines are not recorded in the local source vegetation (Scott 1984; Williams 2008; Klemm *et al.* 2016; Quamar 2019; Chevalier *et al.* 2020). In the modern pollen records from the study site, a general over-representation of *Pinus* pollen was recorded (except in the forested area), even though *Pinus* was not documented in the contemporary vegetation surrounding the fen (Olatoyan *et al.* 2023/Paper 2). Significant pine plantations are recorded ca. 15 km away from the Mashishing Fen, suggesting that the pollen could have been transported by the prevailing easterly winds (Burgess & Wingfield 2001; van Wilgen & Richardson 2012; Bennett & Kruger 2015). While this substantiates *Pinus*'s high pollen production capacity and efficient wind dispersal abilities (Scott 1984; Quamar 2019), it also confirms that open landscapes allow upward transport, thereby facilitating the pine pollen dispersal to higher elevations (Markgraf 1980). In addition, previous research has demonstrated that *Pinus* pollen can be transported over long distances of 30-1000 km from its nearest source (Williams 2008; Klemm *et al.* 2016). In contrast to the results from the study site, *Pinus* pollen was not often recorded in the available surface samples from the grasslands in the region. The location of the study area in the high altitudes likely contributed to the over-representation due to the strong activities of wind transport. However, the over-representation of *Pinus* pollen in modern pollen assemblages has been recorded in other regions outside South Africa due to long-

distance transport by wind (Court- Picon *et al.* 2006; Ma *et al.* 2008; Chen *et al.* 2017; Quamar & Kar 2020).

*Pinus* was introduced as early as the mid-17th century AD to South Africa by European settlers, and in the 1900s, *Pinus* became established in plantations (Richardson *et al.* 1997; van Wilgen & Richardson 2012; Bennett & Kruger 2015). *Pinus* pollen appeared in the Mashishing Fen sequence only after ca. 500 BP, probably indicating Europeans' early introduction of pines for timber production. It seems that people cleared the vegetation for crop cultivation and planting of exotics (e.g., *Pinus*). Unlike other studies (e.g., Breman *et al.* 2011), where the dominance of *Pinus* plantation forestry was recorded around the site, this scenario was not documented in the vicinity of Mashishing Fen. The pollen frequency of *Pinus* reached a maximum alongside the first appearance of *Platanus* (plane tree) pollen towards the end of the pollen sequence at Mashishing Fen. *Platanus* was introduced in South Africa around the 19th century as an ornamental tree and for shade, often lining roadways (Wilson 1923; Newete *et al.* 2022; Gwedla & Shackleton 2017). Recent aerobiological studies at Secunda, Mpumalanga, recorded the dominance of *Platanus* pollen and fungal spores, indicating high humidity conditions (Berman 2017). The appearance of *Platanus* and the peak of *Pinus* pollen implies that the planting of exotics in the region became established during the 19th century (Burgess & Wingfield 2001; Van Wilgen & Richardson 2012; Bennett & Kruger 2015), and signal the anthropogenic impacts that accompanied the arrival of the European settlers in the region. This coincides with the increase in the pollen frequencies of *Anthospermum* and Poaceae, suggesting the dominance of open vegetation for this period. Also, Cyperaceae, fern and fungal spores support locally wet conditions at this time.

## 6.9. CRYPTOGAM AND FUNGAL SPORES

The sediment pollen archives in the Savanna, Grasslands and IOCB Biomes have yielded a plethora of fungal spores such as *Sordaria, Sporormiella,* and *Gelasinospora*, which are commonly associated with dung, and *Glomus,* often associated with increased erosion (Olatoyan *et al.* 2022/Paper 1, for discussion). These records suggest the presence of anthropogenic impact (e.g., pastoralism) across South Africa, Botswana, and Mozambique, dating as far back as 2000–1500 BP (e.g., Neumann *et al.* 2014; Ekblom *et al.* 2014; Cordova *et al.* 2017; Hahn *et al.* 2021).

Previous research on dung fungal spores has shown a link to herbivore dung, though some fungal taxa, such as *Gelasinospora,* have been found growing on other substrates (Cheruiyot *et al.* 2020; van Asperen *et al.* 2020). A significant increase in dung fungal spores could indicate grazing during the periods of pastoralism documented in the archaeological record, particularly when coprophilous fungi spores are synchronous with crops and weed pollen. However, the absence of coprophilous fungi spores in other southern African biomes, such as fynbos, or other palaeoenvironmental contexts does not necessarily imply a lack of pastoralism, as the presence of these spores is more noticeable than their absence (Cheruiyot *et al.* 2020).

In the modern pollen record at Mashishing Fen, although spores associated with dung are absent, the regular presence of *Glomus* spores (Olatoyan *et al.* 2023/Paper 2), a mycorrhizal fungus with high dispersal efficiency, was documented, and this might suggest erosional disturbances possibly due to anthropogenic activities (Anderson *et al.* 1984; Neumann *et al.* 2014). As expected, ferns such as monolete spores (e.g., *Thelypteris*) and trilete spores are commonly associated with the fen vegetation in the modern pollen record, representing local components Olatoyan *et al.* 2023/Paper 2) which are likely of local origin, indicating high rainfall

experienced in the highveld area (Burgoyne *et al.* 2000).

Similarly, in the Mashishing Fen sediment records, high frequencies of fern spores were recorded alongside the peak of Cyperaceae, suggesting possible local moist conditions. This was synchronous with the relatively high frequencies of *Canthium, Podocarpus*, and Proteaceae pollen and the peak of *Olea* after ca. 10,900 cal. yr BP (Olatoyan *et al.* 2023 /Paper 2). Similar pollen records comprising the increase of wetland pollen taxa (e.g., Cyperaceae, *Typha*) and fern spores coupled with the relative decrease of the pollen frequencies of *Artemisia* and *Stoebe* also suggesting local moist conditions have been recorded at other periods (e.g., ca. 10,000, 6700 BP) in the sequence.

Also, *Glomus*, fungal spores often interpreted as an indicator of erosion (Anderson *et al.* 1984), increased likely due to the opening of the vegetation by anthropogenic activities in the area ca. 1500 BP. Recent anthropogenic disturbance is supported by the coincidence of the increase of *Glomus* spores alongside the increase in the pollen frequencies of Cyperaceae and *Phragmites*, indicating locally moist conditions and a higher water table during the period at ca. 500 BP**.**

# CHAPTER 7: CONCLUSION AND FUTURE RESEARCH

## 7.1. SUMMARY OF ACHIEVEMENTS

My research question was whether pollen, spores and charcoal could be used to reconstruct and distinguish between anthropogenic and climatic impacts on the landscapes of Mpumalanga, northeastern South Africa, during the last 11,700 years. I answered this question by achieving my thesis objectives, which were:

1. Assessment of the relationship between vegetation, climate and human activities in southern Africa within the first millennium AD, using published archaeobotanical and archaeological evidence.

The results of the reviewed archaeobotanical data from southern Africa within the first millennium AD were presented in chapter 3 as a published paper (Olatoyan *et al.* 2022). This study comprised a review of archaeobotanical and archaeological data. Common macro botanical evidence indicating human subsistence and occupation include fruits and/or seeds, e.g., *Cenchrus americanus* (pearl millet), *Sorghum, Eleusine coracana* (finger millet), *Citrullus* (melon), and *Vigna unguiculata* (cowpea). Possible anthropogenic indicators associated with microfossil assemblages include a decline in the tree (forest) pollen (e.g., *Podocarpus, Olea*), increase in open land/disturbance indicators (e.g., Asteraceae, Amaranthaceae)/ light adapted trees (e.g., *Macaranga, Trema)*, increase in microcharcoal, increase in spores of coprophilous fungi (e.g., *Sordaria, Sporormiella, Gelasinospora*), and increase in ruderal species (e.g., *Tribulus*).

Similar patterns of vegetation change were observed across the biomes of southern Africa from the archaeobotanical data during the first millennium CE. Given the diversity of southern African

climates and the region's high degree of temporal and spatial variability, it is unlikely that climate in different biomes fluctuated similarly during the first millennium AD. Consequently, we suggested that climate fluctuations alone cannot fully explain vegetation changes, particularly as they relate to the gradual decline of forest tree pollen alongside the increase of light-adapted trees/open land/disturbance indicators.

2. Examination of the correlation between modern pollen and phytoliths and the contemporary source vegetation around the Mashishing Fen, northeastern South Africa and documentation of pollen microphotographs for Gustav Klingbiel Nature Reserve, Mpumalanga, to extend reference collections in northeastern South Africa.

The results of the modern-pollen-phytolith vegetation relationship around the Mashishing Fen were presented in chapter 4 as a published paper (Olatoyan *et al.* 2023). The results showed a strong correlation of the pollen and phytolith records with the contemporary vegetation affirms that these proxies complement each other and can be used to reconstruct past vegetation patterns. The study showed that modern pollen assemblages are a reliable indicator of forest and wetland vegetation, while modern phytolith assemblages are a better representation of grassland vegetation. Forest vegetation is often depicted through the presence of *Euclea*, *Diospyros, and Podocarpus* pollen, while wetland elements can be identified through the significant presence of *Phragmites,* Sparganiaceae and *Typha* pollen, and fern spores. On the other hand, grassland communities can be identified through Panicoideae and Chloridoideae phytoliths. Thus, combining both pollen and phytolith analyses can provide a more precise basis for interpreting fossil spectra in palaeoenvironmental reconstructions. The multivariate CA illustrates that pollen

and phytoliths do not track each other, thus indicating differing preferences for primary vegetation and environmental signals. Another contribution of this research was the production of photomicrographs of palynomorphs from Gustav Klingbiel Nature Reserve. The documentation was achieved using a Color View Soft Imaging System, an AxioCam ICc 1 camera, and Analysis™ software. This contributed to the regional pollen flora reference collection for an area in South Africa where no pollen atlas exists.

3. Reconstruction of the vegetation history and chronology of the Mashishing Fen region using pollen, spores and microcharcoal records from core sediment records for the last 11,700 years BP.

The Holocene palaeoenvironmental reconstruction of landscapes from Mashishing Fen is presented in Chapter 5 as a paper in preparation. A total of 18 AMS radiocarbon dates were obtained from the Mashishing Fen core, dating to the last 11,7000 years, spanning the whole Holocene. Generally, the pollen and charcoal records indicated relatively warm and moist conditions during the beginning of the early Holocene, though with fluctuations (alternating dry and wet conditions).

The pollen sequence showed generally drier conditions during the mid-Holocene with a significantly high presence of microcharcoal (size categories: >10, >50 and >100µm), indicating high fire frequency during the later period. The Later Holocene sequence showed the dominance of open-land indicators (e.g., Amaranthaceae, Asteraceae) and the decline of trees throughout the sequence, which could result from climate (drier conditions) and/or anthropogenic disturbances. However, the decline of trees and increased open vegetation ca. 1500 BP might be due to

anthropogenic disturbances rather than climate change. The sudden spike in Amaranthaceae and Caryophyllaceae at this time, accompanied by a decline in trees, indicates possible deforestation, which is further supported by high fire activity and the appearance of large Poaceae pollen grains (>40 µm), tentatively interpreted as cultivated cereals. Overall, the pollen record is consistent with other regional data, suggesting widespread vegetation changes during different periods are likely due to anthropogenic impact.

## 7.2. LIMITATIONS

This research explored the potential of using pollen, spores, and charcoal to reconstruct vegetation changes and environmental conditions. Limitations encountered during the study included the challenge of distinguishing the pollen of wild forms of exploited plants from the domesticates, which is especially difficult for Poaceae (Bonnefile & Riollet 1980). This limits the definitive identification of cereal pollen grains, as it is currently based on measurements of the diameter of Poaceae pollen grains and variable surface sculpture (Scott 1982a; Neumann *et al.* 2008, 2014). Consequently, it is difficult to differentiate the pollen of African cereals *Pennisetum glaucum* (pearl millet), *Sorghum bicolor* (sorghum/great millet), and *Eleusine coracana* (finger millet) from wild grasses because of overlaps in size and an overall similar pollen morphology (Tomlinson 1973; Andersen 1979; Bonnefile & Riollet 1980). It is therefore imperative to study the modern pollen of crops and weeds to ascertain their status.

Despite Mpumalanga's rich archaeological sequence, the scarcity of well-dated palaeoenvironmental records in Mpumalanga limits detailed comparisons with nearby sites to improve the overall model of vegetation change and environmental conditions for the region.

The inherent differential pollen production, preservation, and dispersal affected the recovery of some pollen grains. For instance, tree taxa (e.g., *Myrica* sp., *Myrsine* sp., *Olea* sp.) are less commonly recorded, and some taxa (e.g., Cucurbitaceae) are absent in the modern pollen assemblage even though they constituted the contemporary source vegetation in the area.

Certain pollen grains are unidentifiable beyond the family level (e.g., Poaceae >25 μm, Asteraceae undifferentiated), and the morphology of some pollen grains is often undifferentiated when only using light microscopy. Considering the great ecological variations within families, this prevents a more detailed reconstruction of their plants' ecology.

A few sample depths from the core sequence had extremely low pollen counts, where up to ten pollen slides were mounted for some sample depths, thereby impacting the accuracy of the reconstruction of vegetation changes.

Also, it is challenging to differentiate between natural and human-induced fires, thus often difficult to ascertain whether changes in the charcoal record are the result of natural, climatic fluctuations or anthropogenic activities such as burning for farming or vegetation clearance (Scott 2002; Kuenzer & Stracher 2012; Finch *et al.* 2022).

## 7.3. FUTURE RESEARCH POTENTIAL

The review of archaeobotanical data shed light on the presence of farmers and pastoralists across southern Africa. There is, however, a need to obtain more dated, direct evidence and sequences focused on the last 2000 years to obtain a comprehensive picture of the spread of farming and pastoralism in the region. This includes sampling for high-resolution micro-botanical data (pollen

and phytoliths) from a range of sites associated with farming in this period to provide detailed information on the vegetation changes and likely crops cultivated. More work is required combining pollen and phytoliths as these proxies often complement each other and can give a more complete depiction of palaeoenvironments and evidence of anthropogenic impact (e.g., Scott *et al.* 2012, 2020; Fitchett *et al.* 2017b; Sjöström *et al.* 2017; Esteban *et al.* 2018; Breman *et al.* 2019; Hahn *et al.* 2021).

Also, high-resolution sampling should be supplemented with regional palynological data. While high-resolution sampling is likely to prevent the obscuring of events associated with human activities, pollen sampling from sites covering a wider area helps to inform the complexities of the vegetation changes in the region. Thus far, many of the cores for palynological studies have not been close to archaeological sites, thereby limiting the extrapolation of the information captured in the cores. We suggest a methodological shift that combines onsite (archaeological site) and nearby off-site (wetlands, lakes, etc.) coring, which is more likely to enable comparisons to ascertain the farming signatures. Hence, this calls for synergy among palynologists and archaeologists.

The identification of cereal pollen in the palaeo-records is tentative based on their larger sizes (>40-50µm) relative to other Poaceae pollen. There is a need to explore further the possibilities of providing a more accurate and reliable method for identifying cultivated cereals in the pollen record. Applying the phase contrast technique and scanning electron microscopy on the Poaceae pollen grains has the potential of recognising surface features such as sculpture and ornamentation in high resolution that would allow possible distinction between cultivated cereals and wild grasses (Andersen & Bertelsen 1972; Andersen 1979). Also, there is a need to conduct pollen-morphological studies on grasses.

The study of the relationships between modern assemblages from surface sediments and contemporary vegetation showed positive and negative correlations across different vegetation communities. Considering the vegetation diversity of the Mpumalanga region, the small number of samples analysed may not accurately represent the modern pollen-vegetation relationship for the region. More work is required comprising a larger number of samples over an extended area within the region to facilitate the interpretation of palaeoenvironmental reconstruction.

Analysis of more proxies bearing archives in the region is required to explore the role of soil moisture levels, altitude, open landscape (grassy) versus forested areas, and wetlands versus drier areas, fire, and humans to facilitate comparison of data between regions and obtain a more robust history of vegetation changes and environmental conditions for the region across different spatial and time scales.

Further studies are required integrating pollen, spores, and charcoal with other proxies (e.g., isotopes, diatoms). Since $C_3$ (e.g., trees, herbs, shrubs, grasses, sedges) and $C_4$ (e.g., grasses, sedges) plants have different photosynthetic pathways that result in distinct isotopic ratios (δ13C) within their tissues, stable carbon isotope composition (δ13C) in a soil sample provides invaluable information about the distribution of $C_3$ and $C_4$ plants that contributed to the organic matrix in fossil sediments when combined with other proxies (Van der Merwe 1982; Wiesenberg & Schwark 2006; Esteban *et al.* 2020; Diefendorf & Freimuth 2017; Sjöström *et al.* 2017).

As indicated above, there is much potential for future research to elaborate on the work undertaken for this thesis and to add further detail to the palaeoreconstruction of the last 2000 years of farming landscapes in Mpumalanga, northeastern South Africa.

# REFERENCES


Acocks, J.P.H. 1975. Veld types of South Africa. *Memoir of the Botanical Survey of South Africa* 40: 1-128.

Alexandré, A., Meunier, J.D., Lézine, A.M., Vincens A. & Schwartz, D. 1997. Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 136: 213-229.

Andersen, S.T. 1979. Identification of wild grass and cereal pollen [fossil pollen, annulus diameter, surface sculpturing]. *Danmarks Geologiske Undersøgelse Årbog*: 69-92.

Andersen, T.S. & Bertelsen, F. 1972. Scanning electron microscope studies of pollen of cereals and other grasses. *Grana* 12: 79-8.

Anderson, R.S., Homola, R.L., Davis, R.B. & Jacobson, G.L. 1984. Fossil remains of the mycorrhizal fungal *Glomus fasciculatum* complex in postglacial lake sediments from Maine. *Canadian Journal of Botany* 62: 2325-2328.

Antonites, A. & Antonites, A.R. 2014. The archaeobotany of Farming Communities in South Africa. In: Stevens, C.J., Nixon, S., Murray, M.A. & Fuller, D.Q. (eds) *The Archaeology of African Plant Use*: 225–232. New York: Routledge.

Antonites, A., Antonites, A.R. & Roodt, F. 2014. Report on excavations at Penge, a first-millennium Doornkop settlement. *Southern African Humanities* 26: 177-192.

Archibald, S., Staver, A.C. & Levin, S.A. 2012. Evolution of human-driven fire regimes in Africa. *Proceedings of the National Academy of Sciences* 109: 847-852.

Backwell, L., Wadley, L., D'errico, F., Banks, W.E., de La Peña, P., Stratford, D., Sievers, C., Laue, G., Vilane, B., Clark, J. & Tribolo, C. 2022. Border Cave: a 227,000-year-old archive from the southern African interior. *Quaternary Science Reviews* 291: 107597.

Badenhorst, S. 2018. Exploitation of sheep (*Ovis aries*) and goats (*Capra hircus*) by Iron Age farmers in southern Africa. *Quaternary International* 495: 79-86.

Bader, G.D., Linstädter, J. & Schoeman, M.H. 2020. Uncovering the Late Pleistocene LSA of Mpumalanga Province, South Africa: early results from Iron Pig Rock Shelter. *Journal of African Archaeology* 18: 19-37

Baker, A., Pedentchouk, N., Routh, J. & Roychoudhury, A.N. 2017. Climatic variability in Mfabeni peatlands (South Africa) since the late Pleistocene. *Quaternary Science Reviews* 160: 57-66.

Baker, A., Routh, J., Blaauw, M. & Roychoudhury, A.N. 2014. Geochemical records of palaeoenvironmental controls on peat forming processes in the Mfabeni peatland, Kwazulu Natal, South Africa since the Late Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 395: 95-106.

Bamford, M., Neumann, F. & Scott, L. 2016. Pollen, charcoal and plant macrofossil evidence of Neogene and Quaternary environments in southern Africa. In: Knight, J. & Grab, S. (eds) *Quaternary Environmental Change in Southern Africa: physical and human dimensions*: 306-323. Cambridge: Cambridge University Press.

Barham, L. & Jarman, C.L. 2005. New radiocarbon dates for the Early Iron Age in the Luangwa Valley, eastern Zambia. *Azania* 40: 114-121.

Baxter, A.J. 1996. Late Quaternary palaeoenvironments of the Sandveld, Western Cape Province, South Africa. Unpublished PhD Dissertation. Cape Town: University of Cape Town.

Baxter, A.J. & Davies, B.R. 1994. Palaeoecological insights for the conservation of aquatic ecosystems in dryland environments: a case study of the Verlorenvlei system, South Africa. *Aquatic Conservation: marine and freshwater ecosystems* 4(3): 255-271.

Bell, B.A. & Fletcher, W.J. 2016 Modern surface pollen assemblages from the Middle and High Atlas, Morocco: insights into pollen representation and transport. *Grana* 55: 286-301.

Bennett, B. & Kruger, F. 2015. *Forestry + Water Conservation in South Africa: history, science + policy*. Canberra: ANU Press.

Berglund, B.E. & Ralska-Jasiewiczowa, M. 1986. Pollen analysis and pollen diagrams. In: Berglund, M.E. (ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*: 455-484. Chichester: John Wiley & Sons.

Bergman, B. 2002. The *Nostoc-Gunnera* Symbiosis. In: Rai, A.N., Bergman, B. & Rasmussen, U. (eds) *Cyanobacteria in Symbiosis*: 207-232. Dordrecht: Springer Netherlands.

Bergman, B., Johansson, C. & Soderback, E. 1992. The *Nostoc Gunnera* symbiosis. *New Phytologist* 122(3): 379-400.

Berman, D. 2017. Regional-specific pollen and fungal spore allergens in South Africa. *Current Allergy & Clinical Immunology* 30: 245-250.

Birin, R-A, Schoeman, M.H. & Evans, M. 2021. The construction and habitation of one of the earliest homesteads at Komati Gorge Village 1, Bokoni, South Africa. *Journal of Archaeological Science: reports* 38: 103020.

Birks, H.J.B. & Gordon, A.D. 1984. *Numerical Methods in Quaternary Pollen Analysis.* Orlando: Academic Press.

Blaauw, M. & Christen, J.A. 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6: 457-474.

Bond, W.J., Midgley, G.F. & Woodward, F.I. 2003a. The importance of low atmospheric $CO_2$ and fire in promoting the spread of grasslands and savannas. *Global Change Biology* 9: 973-982.

Bond, W.J., Midgley, G.F. & Woodward, F.I. 2003b. What controls South African vegetation—climate or fire? *South African Journal of Botany* 69: 79-91.

Bond, W. & Zaloumis, N.P. 2016. The deforestation story: testing for anthropogenic origins of Africa's flammable grassy biomes. *Philosophical Transactions of the Royal Society B: biological sciences* 371: 20150170.

Bonnefile, R. & Riollet, G. 1980. *Pollens Des Savanes d'Afrique Orientale*. Paris: Éditions du Centre National de la Recherche Scientifique (CNRS).

Bousman, C.B. & Brink, J.S. 2018. The emergence, spread, and termination of the Early Later Stone Age event in South Africa and southern Namibia. *Quaternary International* 495: 116-135.

Bradley, R.S. 1999. *Paleoclimatology: reconstructing climates of the Quaternary.* San Diego: Elsevier Academic Press.

Breman, E., Ekblom, A., Gillson, L. & Norström, E.J. 2019. Phytolith-based environmental reconstruction from an altitudinal gradient in Mpumalanga, South Africa, 10,600 BP-present. *Review of Palaeobotany and Palynology* 263: 104-116.

Breman, E., Gillson. L. & Willis, K. 2011. How fire and climate shaped grass-dominated vegetation and forest mosaics in northern South Africa during past millennia. *The Holocene* 22: 1427-1439.

Bronk Ramsey, C. 2023. *OxCal Program, Version 4.4 Oxford Radiocarbon Accelerator Unit.* Oxford: University of Oxford.

Brook, G.A., Cowart, J.B., Brandt, S.A. & Scott, L. 1997. Quaternary climatic change in southern and eastern Africa during the last 300 ka: the evidence from caves in Somalia and the Transvaal region of South Africa. *Zeitschriftfr Geomorphologie NF Supplement Band* 108: 15-48.

Brook, G.A., Railsback, L.B., Scott, L., Voarintsoa, N.R.G. & Liang, F. 2015. Late Holocene stalagmite and tufa climate records for Wonderwerk Cave: relationships between archaeology and climate in Southern Africa. *African Archaeological Review* 32: 669-700.

Brook, G.A., Scott, L., Railsback, L.B. & Goddard, E.A. 2010. A 35 ka pollen and isotope record of environmental change along the southern margin of the Kalahari from a stalagmite and animal dung deposits in Wonderwerk Cave, South Africa. *Journal of Arid Environments* 74: 870-884.

Bryant, Jr, V.M. & Holloway, R.G. 1983. The role of palynology in archaeology. *Advances in Archaeological Method and Theory* 6: 191-224.

Burgess, T. & Wingfield, M.J. 2001. Exotic pine forestry in the Southern Hemisphere: a brief history of establishment and quarantine practices. *Southern African Forestry Journal* 192: 79-84.

Burney, D.A., Brook, G.A. & Cowart, J.B. 1994. A Holocene pollen record for the Kalahari Desert of Botswana from a U-series dated speleothem. *The Holocene* 4 (3): 225-232.

Burgoyne, B.M., Bredenkamp, G.J. & Van Rooyen, N. 2000. Wetland vegetation in the north-eastern Sandy Highveld, Mpumalanga, South Africa. *Bothalia* 30: 187-200.

Campbell, B.M. & Moll, E.J. 1977. The forest communities of Table Mountain, South Africa *Vegetatio* 34: 105-115.

Carbutt, C. & Edwards, T.J. 2004. The flora of the Drakensberg Alpine Centre. *Edinburgh Journal of Botany* 60(3): 581-607.

Cardoso, A.W., Archibald, S., Bond, W.J., Coetsee, C., Forrest, M., Govender, N., Lehmann, D., Makaga, L., Mpanza, N. & Ndong, J.E. 2022. Quantifying the environmental limits to fire spread in grassy ecosystems. *Proceedings of the National Academy of Sciences* 119(26): e2110364119.

Carrión, J.S., Scott, L., Huffman, T. & Dreyer, C. 2000. Pollen analysis of Iron Age cow dung in

southern Africa. *Vegetation History and Archaeobotany* 9: 239-249.

Caseldine, C.J., McGarry, S.F., Baker, A., Hawkesworth, C.A. & Smart, P.L. 2008. Late Quaternary speleothem pollen in the British Isles. *Journal of Quaternary Science* 23: 193-200.

Chase, B.M., Faith, J.T., Mackay, A., Chevalier, M., Carr, A.S., Boom, A., Lim, S. & Reimer, P.J. 2018. Climatic controls on Later Stone Age human adaptation in Africa's southern Cape. *Journal of Human Evolution* 114: 35-44.

Chase, B.M., Meadows, M.E., Carr, A.S. & Reimer, P.J. 2010. Evidence for progressive Holocene aridification in southern Africa recorded in Namibian hyrax middens: implications for African monsoon dynamics and the 'African Humid Period'. *Quaternary Research* 30: 67-80.

Chen, X., Huang, X., Wu, D., Zhang, X., Dodson, J., Zhou, A. & Chen, F. 2017. Modern pollen assemblages in topsoil and surface sediments of the Xingyun Lake catchment, central Yunnan Plateau, China, and their implications for interpretation of the fossil pollen record. *Review of Palaeobotany and Palynology* 241: 1-12.

Cheruiyot, V.C., Gebregiorgis, D., Opiyo, B. & Kiage, L.M. 2020. Revisiting the palaeoenvironmental and climatic history of the Cherangani Hills using fungal spores. *Journal of Quaternary Science* 35: 737-742.

Chevalier, M. & Chase, B.M. 2015. Southeast African records reveal a coherent shift from high to low-latitude forcing mechanisms along the east African margin across last glacial–interglacial transition. *Quaternary Science Reviews* 125: 117-130.

Chevalier, M. & Chase, B.M. 2016. Determining the drivers of long-term aridity variability: a southern African case study. *Journal of Quaternary Science* 31: 143-151.

Chevalier, M., Chase, B., Quick, L. & Scott, L. 2021. An atlas of southern African pollen types and their climatic affinities. *Palaeoecology of Africa* 35: 239-258.

Chevalier M., Davis, B.A.S., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., Kühl, N., Yoshi Maezumi, S., Tipton, J.R., Carter, V.A., Brussel, T., Phelps, L.N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., de Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P.S., Chaput, M. & Kupriyanov, D. 2020. Pollen-based climate reconstruction techniques for late Quaternary studies. *Earth-Science Reviews* 210: 103384.

Coetzee, H.B. 2005. Interpreting distribution patterns of Iron Age sites using landscape archaeology and GIS. Unpublished Honours project. Pretoria: University of Pretoria.
Coetzee, J.A. 1967. Pollen analytical studies in East and Southern Africa. *Palaeoecology of Africa* 3: 1-146.

Coetzee, J.A. & van Zinderen Bakker, E.M. 1952. The pollen spectrum of the southern middle-veld of the Orange Free State. *South African Journal of Science* 48: 275-281.

Collett, D.P. 1979. The archaeology of the stone-walled settlements in the eastern Transvaal, South Africa. Unpublished MSc thesis. Johannesburg: University of the Witwatersrand.

Collett, D. 1982. Excavations of stone-walled ruin types in the Badfontein Valley, Eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 37(135): 34-43.

Cook, C.D.K. 2004. *Aquatic and Wetland Plants of Southern Africa*. Leyden: Backhuys Publishers.

Cooremans, B. 1989. Pollen production in central southern Africa. *Pollen et Spores* 31: 61-78.

Cordova, C.E., Kirsten, K.L., Scott, L., Meadows, M. & Luecke, A. 2019. Multi-proxy evidence of late-Holocene paleoenvironmental change at Princessvlei, South Africa: the effects of fire, herbivores, and humans. *Quaternary Science Reviews* 221: 105896.

Cordova, C.E., Scott, L., Chase, B.M. & Chevalier, M. 2017. Late Pleistocene-Holocene vegetation and climate change in the Middle Kalahari, Lake Ngami, Botswana. *Quaternary Science Reviews* 171: 199-215.

Court-Picon, M., Buttler, A. & de Beaulieu, J.-L. 2005. Modern pollen vegetation relationships in the Champsaur Valley (French Alps) and their potential in the interpretation of fossil pollen records of past cultural landscapes. *Review of Palaeobotany and Palynology* 135: 13-39.

Court-Picon, M., Buttler, A. & de Beaulieu, J-L. 2006. Modern pollen/vegetation/land-use relationships in mountain environments: an example from the Champsaur Valley (French Alps). *Vegetation History and Archaeobotany* 15: 151-168.

Cowling, S.A. 1999. Simulated effects of low atmospheric $CO_2$ on structure and composition of North American vegetation at the Last Glacial Maximum. *Global Ecology and Biogeography Letters* 8: 81-93.

Crowther, A., Prendergast, M.E., Fuller, D.Q. & Boivin, N. 2018. Subsistence mosaics, forager-farmer interactions, and the transition to food production in eastern Africa. *Quaternary International* 489: 101-120.

Cugny, C., Mazier, F. & Galop, D. 2010. Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. *Vegetation History and Archaeobotany* 19: 391-408.

Deacon, J. 1984. *The Later Stone Age of Southernmost Africa*. Oxford: British Archaeological Reports.

Deacon, H.J. & Deacon, J. 1999. *Human beginnings in South Africa: uncovering the Secrets of the Stone Age*. Cape Town: David Philip.

Delius, P., Maggs, T. & Schoeman, M. 2012. Bokoni: old structures, new paradigms? Rethinking pre-colonial society from the perspective of the stone-walled sites in Mpumalanga. *Journal of Southern African Studies* 38: 399-414.

Delius, P. & Schoeman, M.H. 2008. Revisiting Bokoni: populating the stone ruins of the Mpumalanga Escarpment. In: Swanepoel, N., Bonner, P. & Esterhuysen, A. (eds) *Five Hundred Years Rediscovered: southern African precedents and prospects*: 135-168. Johannesburg: Wits University Press.

Denbow, J.R. & Wilmsen, E.N. 1986. Advent and course of pastoralism in the Kalahari. *Science* 234: 1509-1515.

Diefendorf, A.F. & Freimuth, E.J. 2017. Extracting the most from terrestrial plant-derived n-alkyl lipids and their carbon isotopes from the sedimentary record: a review. *Organic Geochemistry* 103: 1-21.

Dimbleby, G.W. 1957. Pollen analysis of terrestrial soils. *New Phytologist* 56: 12-28.

Dubois, N., Saulnier-Talbot, É., Mills, K., Gell, P., Battarbee, R., Bennion, H., Chawchai, S., Dong, X., Francus, P., Flower, R., Gomes, D. F., Gregory-Eaves, I., Humane, S., Kattel, G., Jenny, J., Langdon, P., Massaferro, J., McGowan, S., Mikomägi, A. & Valero-Garcés, B. 2018. First human impacts and responses of aquatic systems: a review of palaeolimnological records from around the world. *The Anthropocene Review* 5(1): 28-68.

Duffin, K.I. & Bunting, M.J. 2008. Relative pollen productivity and fall speed estimates for southern African savanna taxa. *Vegetation History and Archaeobotany* 17: 507-525.

Dyer, R.A. 1975. *The Genera of Southern African Flowering Plants*. Pretoria: Department of Agriculture Technical Service, Botanical Research Institute.

Ekblom, A. 2008. Forest–savanna dynamics in the coastal lowland of southern Mozambique since c. AD 1400. *The Holocene* 18(8): 1247-1257.

Ekblom, A., Gillson, L. & Notelid, M. 2011. A historical ecology of the Limpopo and Kruger National Parks and lower Limpopo Valley. *Journal of Archaeology and Ancient History* 1(1): 1-29.

Ekblom, A., Gillson, L. & Notelid, M. 2017. Water flow, ecological dynamics, and management in the lower Limpopo Valley: a long-term view. *Wiley Interdisciplinary Reviews, Water* 4(5): e1228.

Ekblom, A., Risberg, J. & Holmgren, K. 2014. Coastal forest and Miombo woodland history of the Vilankulo region, Mozambique. *The Holocene* 24: 284-294.

Ellery, W.N., Grenfell, S.E., Grenfell, M.C., Powell, R., Kotze, D.C., Marren, P.M. & Knight, J. 2016. Wetlands in southern Africa: a geomorphic threshold perspective. *Quaternary Environmental Change in Southern Africa*: *physical and human dimensions*: 188-202. Cambridge: Cambridge University Press.

Erdtman, G. 1986. *Pollen Morphology and Plant Taxonomy-Angiosperms*. Stockholm: Almqvist & Wiksell.

Esteban, I., Bamford, M.K., House, A., Miller, C.S., Neumann, F.H., Schefuß, E., Pargeter, J., Cawthra, H.C. & Fisher, E.C. 2020. Coastal palaeoenvironments and hunter-gatherer plant-use at Waterfall Bluff rock shelter in Mpondoland (South Africa) from MIS 3 to the Early Holocene. *Quaternary Science Reviews* 250: 106664.

Esteban, I., Marean, C.W., Fisher, E.C., Karkanas, P., Cabanes, D. & Albert, R.M. 2018. Phytoliths as an indicator of early modern humans plant gathering strategies, fire fuel and site occupation intensity during the Middle Stone Age at Pinnacle Point 5-6 (south coast, South Africa). *PLoS* One 13(6): e0198558.

Evers, T.M. 1974a. Iron Age Trade in the Eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 29(113/114): 33-37.

Evers, T.M. 1974b. Three Iron Age industrial sites in the eastern Transvaal Lowveld. Unpublished MSc dissertation. Johannesburg: University of the Witwatersrand.

Evers, T. 1975. Recent Iron Age research in the eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 30(119/120): 71-83.

Evers, T. 1977a. Plaston Early Iron Age site, White River District, Eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 32(126): 170-178.

Evers, T. 1977b. Recent progress in studies of the Early Iron Age in the eastern Transvaal, South Africa. *South African Journal of Science* 73(3): 78.

Evers, T. 1980. Klingbeil Early Iron Age sites, Lydenburg, Eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 35(131): 46-57.

Evers, T.M. 1982. Excavations at the Lydenburg Heads Site, eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 37(135): 16-33.

Faegri, K. & Iversen, J. 1989. *Textbook of Pollen Analysis*. Chichester: John Wiley & Sons.

Festi, D., Hoffmann, D.L. & Luetscher, M. 2016. Pollen from accurately dated speleothems supports alpine glacier low-stands during the Early Holocene. *Quaternary Research* 86(1): 45-53.

Fietz, S., Baker, A., Miller, C.S., Naafs, B.D.A., Peterse, F., Finch, J., Humphries, M., Schefuß, E., Roychoudhury, A.N. & Routh, J. 2023. Terrestrial temperature evolution of southern Africa during the late Pleistocene and Holocene: evidence from the Mfabeni Peatland. *Quaternary Science Reviews* 299: 107870.

Finch, J.M. & Hill, T.R. 2008. A late Quaternary pollen sequence from Mfabeni Peatland, South Africa: reconstructing forest history in Maputaland. *Quaternary Research* 70: 442-450.

Finch, J.M., Hill, T.R., Meadows, M.E., Lodder, J. & Bodmann, L. 2022. Fire and montane vegetation dynamics through successive phases of human occupation in the northern Drakensberg, South Africa. *Quaternary International* 611: 66-76.

Finkelstein, S.A. & Davis, A.M. 2005. Modern pollen rain and diatom assemblages in a Lake Erie coastal marsh. *Wetlands* 25: 551-563.

Finné, M., Norström, E., Risberg, J. & Scott, L. 2010. Siliceous microfossils as late-Quaternary paleo-environmental indicators at Braamhoek wetland, South Africa. *The Holocene* 20(5): 747-760.

Fish, L. 1999. *Preparing Herbarium Specimens.* Pretoria: National Botanical Institute.

Fitchett, J.M., Grab, S.W., Bamford, M.K. & Mackay, A.W. 2017b. Late Quaternary research in southern Africa: progress, challenges and future trajectories. *Transactions of the Royal Society of South Africa* 72: 280-293.

Fitchett, J.M., Mackay, A.W., Grab, S.W. & Bamford, M.K. 2017a. Holocene climatic variability indicated by a multi-proxy record from southern Africa's highest wetland. *The Holocene* 27: 638650.

Geldenhuys, C.J. & von dem Bussche, G.B. 1997. Performance of *Podocarpus falcatus* provenances in South Africa. *Southern African Forestry Journal* 178: 15-24.

Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C. & Verschuren, D. 2011. Modern non-pollen palynomorphs from East African lake sediments. *Review of Palaeobotany and Palynology* 164: 143-173.

Gillson, L. 2006. A 'large infrequent disturbance' in an East African savanna. *African Journal of Ecology* 44: 458-467.

Gillson, L. & Ekblom, A. 2009. Untangling anthropogenic and climatic influence on riverine forest in the Kruger National Park, South Africa. *Vegetation History and Archaeobotany* 18: 171-185.

Gosling, W.D., Miller, C.S. & Livingstone, D.A. 2013. Atlas of the tropical West African pollen flora. *Review of Palaeobotany and Palynology* 199: 1-135.

Grimm, E.C. 2011. *Tilia 2.1.1 Software.* Springfield: Illinois State Museum.

Gwedla, N. & Shackleton, C.M. 2017 Population size and development history determine street tree distribution and composition within and between Eastern Cape towns, South Africa. *Urban Forestry & Urban Greening* 25: 11-18.

Hahn, A., Neumann, F.H., Miller, C., Finch, J., Frankland, T., Cawthra, H.C., Schefuß, E. & Zabel, M. 2021. Mid- to Late Holocene climatic and anthropogenic influences in Mpondoland, South Africa. *Quaternary Science Reviews* 261: 106938.

Hattingh, T. 2014. A Phytolith analysis of Bokoni Soils. Unpublished MSc dissertation. Johannesburg: University of the Witwatersrand.

Havinga, A.J. 1967. Palynology and pollen preservation. *Review of Palaeobotany and Palynology* 2: 81-98.

Hill, T.R. 1995. Analysis of contemporary pollen rain in South Africa - a review. *Transactions of the Royal Society of South Africa* 50: 27-39.

Hill, T.R. & Finch, J.M. 2021. Modern pollen-vegetation relationships in the Drakensberg Mountains, South Africa. In: Gosling, W.D., Lezine, A.M. & Scott, L. (eds) *Quaternary Vegetation Dynamics: the African pollen database*: 275-292. Leiden: CRC Press.

Hlwatika, C.N.M. & Bhat, R.B. 2002. An ecological interpretation of the difference in leaf anatomy and its plasticity in contrasting tree species in Orange Kloof, Table Mountain, South Africa. *Annals of Botany* 89: 109-114.

Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Ramsey, C.B. & Pearson, C. 2020. SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. *Radiocarbon* 62(4): 759-778.

Holmgren, K., Karlén, W., Lauritzen, S.E., Lee-Thorp, J.A., Partridge, T.C., Piketh, S., Repinski, P., Stevenson, C., Svanered, O. & Tyson, P.D. 1999. A 3000-year high-resolution stalagmite based record of palaeoclimate for northeastern South Africa. *The Holocene* 9(3): 295-309.

Holmgren, K., Lee-Thorp, J.A., Cooper, G.R., Lundblad, K., Partridge, T.C., Scott, L., Sithaldeen, R., Talma, A.S. & Tyson, P.D. 2003. Persistent millennial-scale climatic variability over the past 25,000 years in Southern Africa. *Quaternary Science Reviews* 22(21-22): 2311-2326.

Hopper, C., Sealy, J.C. & Dewar, G. 2018. Little Ice Age drought event reconstructed from isotopic analysis of archaeological springbok (*Antidorcas marsupialis*) teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 495: 105-112.

Huang, X., Chen, X. & Du, X. 2018. Modern pollen assemblages from human-influenced vegetation in northwestern China and their relationship with vegetation and climate. *Vegetation History and Archaeobotan*y 27: 767-780.

Huffman, T.N. 1989. Ceramics, settlements and late Iron Age migrations. *African Archaeological Review* 7: 155-182.

Huffman, T.N. 1996. Archaeological evidence for climatic change during the last 2000 years in southern Africa. *Quaternary International* 33: 55-60.

Huffman, T.N. 2004. The archaeology of the Nguni past. *Southern African Humanities* 16: 79-111.

Inskeep, R.R. & Maggs, T.M.O'C. 1975. Unique art objects in the Iron Age of the Transvaal, South Africa. *The South African Archaeological Bulletin* 30(119/120): 114-138.

Jordaan, G. 2017. An archaeological study of two Early Farming sites in the southern Kruger National Park, South Africa. Unpublished MSc dissertation. Pretoria: University of Pretoria.

Julier, A.C., Jardine, P.E., Adu-Bredu, S., Coe, A.L., Duah-Gyamfi, A., Fraser, W.T., Lomax, B.H., Malhi, Y., Moore, S., Owusu-Afriyie, K. & Gosling, W.D. 2018. The modern pollen–vegetation relationships of a tropical forest–savannah mosaic landscape, Ghana, West Africa. *Palynology* 42(3): 324-338.

Klapwijk, M. 1974. A preliminary report on pottery from the north-eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 29(113-114): 19-23.

Klapwijk, M. & Huffman, T. 1996. Excavations at Silver Leaves: a final report. *The South African Archaeological Bulletin* 51(164): 84-93.

Klein, R.G. 1984. Later Stone Age faunal samples from Heuningneskrans Shelter (Transvaal) and Leopard's Hill Cave (Zambia). *The South African Archaeological Bulletin* 39(140): 109-116.

Klemm, J., Herzschuh, U. & Pestryakova, L.A. 2016. Vegetation, climate and lake changes over the last 7000 years at the boreal treeline in north-central Siberia. *Quaternary Science Reviews* 147: 422-434.

Komarek, E.V., Carlysle, T.C. & Komarek, B.B. 1973. *The Ecology of Smoke Particulates and Charcoal Residues from Forest and Grassland Fires: a preliminary atlas*. Tallahassee: Tall Timbers Research Station.

Korsman, S. & Plug, I. 1994. Two Later Stone Age sites on the farm Honingklip in the Eastern Transvaal. *The South African Archaeological Bulletin* 49(159): 24-32.

Kristen, I., Fuhrmann, A., Thorpe, J., Rohl, U., Wilkes, H. & Oberhansli, H. 2007. Hydrological changes in southern Africa over the last 200 ka as recorded in lake sediments from the Tswaing Impact Crater. *South African Journal of Geology* 110(2-3): 311-326.

Kristen, I., Wilkes, H., Vieth, A., Zink, K.-G., Plessen, B., Thorpe, J., Partridge, T. & Oberhänsli, H. 2010. Biomarker and stable carbon isotope analyses of sedimentary organic matter from Lake Tswaing: evidence for deglacial wetness and early Holocene drought from South Africa. *Journal of Paleolimnology* 44: 143-160.

Kuenzer, C. & Stracher, G.B. 2012. Geomorphology of coal seam fires. *Geomorphology* 138: 209-222.

Kuzmicheva, E.A., Debella, H., Khasanov, B., Krylovich, O., Babenko, A., Savinetsky, A., Severova, E. & Yirga, S. 2013. Holocene hyrax dung deposits in the Afroalpine belt of the Bale Mountains (Ethiopia) and their palaeoclimatic implication. *Environmental Archaeology* 18(1): 72-81.

Lander, F. & Russell, T. 2018. The archaeological evidence for the appearance of pastoralism and farming in southern Africa. *PLoS ONE* 13(6): e0198941.

Levis, S., Foley, J. & Pollard, D. 1999. $CO_2$, climate, and vegetation feedbacks at the Last Glacial Maximum. *Journal of Geophysical Research* 104: 31191-31198.

Li, Y., Zhou, L. & Cui, H. 2008. Pollen indicators of human activity. *Chinese Science Bulletin* 53: 1281-1293.

Lombard, M., Bradfield, J., Caruana, M.V., Makhubela, T.V., Dusseldorp, G.L., Kramers, J. D. & Wurz, S. 2022. The southern African Stone Age sequence updated (II). *South African Archaeological Bulletin* 77(217): 172-212.

Lombard, M., Wadley, L., Deacon, J., Wurz, S., Parsons, I., Mohapi, M., Swart, J. & Mitchell, P. 2012. South African and Lesotho Stone Age sequence updated (I). *South African Archaeological Bulletin* 67(195): 123-144.

Lötter, M.C., Mucina, L. & Witkowski, E.T.F. 2014. Classification of the indigenous forests of Mpumalanga Province, South Africa. *South African Journal of Botany* 90: 37-51.

Ma, Y., Liu, K., Feng, Z., Sang, Y., Wang, W. & Sun A. 2008. A survey of modern pollen and vegetation along a south–north transect in Mongolia. *Journal of Biogeography* 35: 1512-1532.

Mabhungu, L., Adam, E. & Newete, S.W. 2019. Monitoring of phytoremediating wetland macrophytes using Remote Sensing: the case of common reed (*Phragmites australis* (cav.) Trin. Ex steud.) and the giant reed (*Arundo donax* L.): a review. *Applied Ecology and Environmental Research* 17: 7957-7972.

Maggs, T. 1995. Neglected rock art: the rock engravings of agriculturist communities in South Africa. *The South African Archaeological Bulletin* 50(162): 132-142.

Maggs, T. 2008. The Mpumalanga Escarpment settlements: some answers, many questions. In: Swanepoel, N., Esterhuysen, A.B. & Bonner, P. (eds) *Five Hundred Years Rediscovered: southern African precedents and prospects*: 169-181. Johannesburg: Wits University Press.

Maggs, T. & Ward, V. 1984. Early Iron Age sites in the Muden area of Natal. *Annals of the Natal Museum* 26(1): 105-140.

Maggs, T. & Whitelaw, G. 1991. A review of recent archaeological research on food-producing communities in southern Africa. *The Journal of African History* 32: 3-24.

Manning, J. & Goldblatt, P. 2007. *West Coast: South African wild flower guide* 7. Cape Town: Botanical Society of South Africa.

Mao, L., Zhang, L. & Bi, H. 2006. Modern pollen deposits in coastal mangrove swamps from northern Hainan Island, China. *Journal of Coastal Research* 22(6): 1423-1436.

Marais, E., Scott, L., Gil-Romera, G. & Carrión, J.S. 2015. The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia. *Transactions of the Royal Society of South Africa* 70: 109-115.

Marker, M.E. & Evers, T.M. 1976. Iron Age settlement and soil erosion in the Eastern Transvaal, South Africa. *The South African Archaeological Bulletin* 31(123/124): 153-165.

Markgraf, V. 1980. Pollen dispersal in a mountain area. *Grana* 19: 127-146.

Marshall, F. & Hildebrand, E. 2002. Cattle before crops: the beginnings of food production in Africa. *Journal of World prehistory* 16: 99-143.

Matthys, C., Jubase, N., Visser, V. & Geerts, S. 2022. Distribution of *Melaleuca rugulosa* (*Schlechtendal* ex Link) Craven (*Myrtaceae*) in South Africa: Assessment of invasiveness and feasibility of eradication. *South African Journal of Botany* 148: 228-237.

McCarthy, T.S. & Hancox, P.J. 2000. Wetlands. In: Partridge, P.C. & Maud, R.R. (eds) *The Cenozoic of Southern Africa*: 218-235. Oxford: Oxford University Press.

McCarthy, T.S., Tooth, S., Kotze, D.C., Collins, N.B., Wandrag, G. & Pike, T. 2010. The role of geomorphology in evaluating remediation options for floodplain wetlands: the case of Ramsar-listed Seekoeivlei, eastern South Africa. *Wetlands Ecology and Management* 18: 119-134.

McKenzie, B., Moll, E.J. & Campbell, B.M. 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. *Vegetatio* 34: 41-53.

Metwally, A.A., Scott, L., Neumann, F., Bamford, M. & Oberhänsli, H. 2014. Holocene palynology and palaeoenvironments in the Savanna biome at Tswaing Crater, central South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 402: 125-135.

Meyer, A. 1986. 'n Kultuurhistoriese interpretasie van die ystertydperk in die Nasionale Krugerwildtuin. Unpublished PhD dissertation. Pretoria: University of Pretoria.

Miller, C., Finch, J., Hill, T., Peterse, F., Humphries, M., Zabel, M. & Schefuß, E. 2019. Late Quaternary climate variability at Mfabeni peatland, eastern South Africa. *Climate of the Past* 15(3): 1153-1170.

Mitchell, P.J. 1993. Archaeological investigations at two Lesotho Rock-shelters: terminal Pleistocene/Early Holocene assemblages from Ha Makotoko and Ntloana Tsoana. *Proceedings of the Prehistoric Society* 59(1): 39-60.

Mitchell, P.J. 1996. Filling a gap: the early and middle Holocene assemblages from new excavations at Sehonghong Rock Shelter, Lesotho. *Southern African Field Archaeology* 5: 17-27.

Mitchell, P. 2002. *The Archaeology of Southern Africa*. Cambridge: Cambridge University Press.

Mitchell, P. 2005. Why hunter-gatherer archaeology matters: a personal perspective on renaissance and renewal in southern African Later Stone Age research. *The South African Archaeological Bulletin* 60(182): 64-71.

Mitchell, P. & Arthur, C. 2014. Ha Makotoko: Later Stone Age occupation across the Pleistocene/Holocene transition in western Lesotho. *Journal of African Archaeology* 12(2): 205-232.

Mitchell, P., Parkington, J. & Wadley, L. 1998. A tale from three regions: the archaeology of the Pleistocene/Holocene transition in the Western Cape, the Caledon Valley and the Lesotho Highlands, Southern Africa. *Quaternary International* 49: 105-115.

Mitchell, P. & Whitelaw, G. 2005. The archaeology of southernmost Africa from c. 2000 BP to the early 1800s: a review of recent research. *Journal of African History* 46(2): 209-241.

Mohale, N.E., Codron, D. & Horwitz, L.K. 2022. Stable isotope evidence for mid-Pleistocene paleoenvironmental conditions at the site of Kathu Pan 1 (central interior, South Africa). *Quaternary International* 614: 37-49.

Monnin, E., Indermühle, A., Dällenbach, A., Flückiger, J., Stauffer, B., Stocker, T.F., Raynaud, D. & Barnola, J-M. 2001. Atmospheric $CO_2$ concentrations over the Last Glacial Termination. *Science* 291: 112-114.

Morales-Molino, C., Devaux, L., Georget, M., Hanquiez, V. & Goñi, M.F.S. 2020. Modern pollen representation of the vegetation of the Tagus Basin (central Iberian Peninsula). *Review of Palaeobotany and Palynology* 276: 104193.

Morrison, M.E.S. 1968. Vegetation and climate in the uplands of south-western Uganda during the later Pleistocene period: I. Muchoya Swamp, Kigezi District. *The Journal of Ecology* 56: 363-384.

Mucina, L. & Rutherford, M.C. 2006. *The Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: South African National Biodiversity Institute.

Muller, S.D., Daoud-Bouattour, A., Fauquette, S., Bottollier-Curtet, M., Rifai, N., Robles, M., Saber, E-R., El Madihi, M., Moukrim, S. & Rhazi, L. 2022. Holocene history of peatland communities of central Rif (Northern Morocco). *Geobios* 70: 35-53.

Mustart, P.J. & Cowling, R.M. 1993. The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. *Ecology* 74: 1490-1499.

Myburgh, W.J. & Bredenkamp, G.J. 2004. Macro-channel riparian vegetation of the Olifants River System in the Grassland Biome. Mpumalanga. *Koedoe* 47: 41-54.

Nakagawa, T., Brugiapaglia, E., Digerfeldt, G., Reille, M., Beaulieu, J.L.D.E. & Yasuda, Y. 1998. Dense-media separation as a more efficient pollen extraction method for use with organic sediment/deposit samples: comparison with the conventional method. *Boreas* 27: 15-24.

Neary, D.G. & Leonard, J.M. 2020. Effects of fire on grassland soils and water: a review. In: Kindomihou, V.M. (ed.) *Grasses and Grassland Aspects*: 57-78. Rijeka: IntechOpen.

Neumann, F.H., Botha, G.A. & Scott, L. 2014. 18,000 years of grassland evolution in the summer rainfall region of South Africa: evidence from Mahwaqa Mountain, KwaZulu-Natal. *Vegetation History and Archaeobotany* 23: 665-681.

Neumann, F.H., Scott, L. & Bamford, M. 2011. Climate change and human disturbance of fynbos vegetation during the late Holocene at Princess Vlei, Western Cape, South Africa. *The Holocene* 21: 1137-1149.

Neumann, F.H., Scott, L., Bousman, C. & Van As, L. 2010. A Holocene sequence of vegetation change at Lake Eteza, coastal KwaZulu-Natal, South Africa. *Review of Palaeobotany and Palynology* 162: 39-53.

Neumann, F.H., Stager, J.C., Scott, L., Venter, H.J. & Weyhenmeyer, C. 2008. Holocene vegetation and climate records from Lake Sibaya, KwaZulu-Natal (South Africa). *Review of Palaeobotany and Palynology* 152: 113-128.

Newete, S.W., Abutaleb. K. & Byrne, M.J. 2022. Mapping the distribution and tree canopy cover of *Jacaranda mimosifolia* and *Platanus* × *acerifolia* in Johannesburg's urban forest. *Scientific Reports* 12: 5998.

Nichols, G.J., Cripps, J.A., Collinson, M.E. & Scott, A.C. 2000. Experiments in waterlogging and sedimentology of charcoal: results and implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 164: 43-56.

Nkala, P., Mango, N.A.R., Corbeels, M., Veldwisch, G.J.A. & Huising, E.J. 2011. The conundrum of conservation agriculture and livelihoods in southern Africa. *African Journal of Agricultural Research* 6(24): 5520-5528.

Nohro, S., Bera, S.K. & Jayakumar, S. 2019. Modern pollen representation from the marshy area of the Pala Wetland Reserve Forest, Mizoram, India. *Research Journal of Life Sciences, Bioinformatics, Pharmaceuticals and Chemical Sciences* 5(1): 12-20.

Norström, E., Neumann, F.H., Scott, L., Smittenberg, R.H., Holmstrand, H., Lundqvist, S., Snowball, I., Sundqvist, H.S., Risberg, J. & Bamford, M. 2014. Late Quaternary vegetation dynamics and hydro-climate in the Drakensberg, South Africa. *Quaternary Science Reviews* 105: 48-65.

Norström, E., Scott L., Partridge, T., Risberg, J. & Holmgren, K. 2009. Reconstruction of environmental and climate changes at Braamhoek wetland, eastern escarpment South Africa, during the last 16,000 years with emphasis on the Pleistocene–Holocene transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271: 240-258.

Nyakale, M. & Scott, L. 2002. Interpretation of late Holocene pollen in channel fills in the Eastern Free State, South Africa, in terms of local conditions and sediment reworking. *South African Journal of Botany* 68: 464-468.

Nyamadzawo, G., Gwenzi, W., Kanda, A., Kundhlande, A. & Masona, C. 2013. Understanding the causes, socio-economic and environmental impacts, and management of veld fires in tropical Zimbabwe. *Fire Science Reviews* 2(2): 1-13.

O'Connor, T.G. & Bredenkamp, G.J. 1997. Grassland. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds) *Vegetation of Southern Africa*: 215-257. Cambridge: Cambridge University.

O'Donoghue, T.L., Slater, K. & Brown, L.R. 2020. Seasonal habitat utilisation and morphological characteristics of *Chamaeleo dilepis* on Telperion Nature Reserve, Mpumalanga, South Africa. *African Journal of Herpetology* 69(2): 82-199.

Olatoyan, J.O., Neumann, F.H., Orijemie, E.A., Sievers, C., Evans, M., Mvelase, S., Hattingh, T. & Schoeman, M.H. 2022. Archaeobotanical evidence for the emergence of pastoralism and farming in southern Africa. *Acta Palaeobotanica* 62(1): 50-75.

Olatoyan, J.O., Neumann, F.N., Orijemie, E.A., Sievers, C., Evans, M., Hattingh, T. & Schoeman, M.H. 2023. Modern pollen-and phytolith-vegetation relationships at a wetland in northeastern South Africa. *South African Journal of Botany* 161: 780-796.

Parker, A.G., Lee-Thorp, J. & Mitchell, P.J. 2011. Late Holocene Neoglacial conditions from the Lesotho highlands, southern Africa: phytolith and stable carbon isotope evidence from the archaeological site of Likoaeng. *Proceedings of the Geologists' Association* 122: 201-211.

Partridge, T.C. 1993. Warming phases in Southern Africa during the last 150,000 years: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101: 237-244.

Patterson, W.A., Edwards, K.J. & Maguire, D.J. 1987. Microscopic charcoal as a fossil indicator of Fire. *Quaternary Science Reviews* 6: 3-23.

Piperno, D.R. 2006. *Phytoliths: a comprehensive guide for archaeologists and paleoecologists*. Oxford: Altamira Press.

Plug, I. 1988. Hunter and herders: an archaeozoological study of some prehistoric communities in the Kruger National Park. Unpublished PhD Dissertation. Pretoria: University of Pretoria.

Pooley, E. 1998. *A Field Guide to Wildflowers: KwaZulu-Natal and the eastern region*. Durban: Natal Flora Publication Trust, Natal Herbarium.

Porraz, G. & Val, A. 2019. Heuningneskrans and the Stone Age sequence of the Ohrigstad River catchment on the eastern border of the great escarpment, Limpopo Province, South Africa. *The South African Archaeological Bulletin* 74(209): 46-55.

Porraz, G., Val, A., Dayet, L., De La Pena, P., Douze, K., Miller, C.E., Murungi, M.L., Tribolo, C., Schmid, V.C. & Sievers, C. 2015. Bushman Rock Shelter (Limpopo, South Africa): a perspective from the edge of the Highveld. *The South African Archaeological Bulletin* 70(202): 166-179.

Prior, J. & Williams, D.P. 1985. An investigation of climatic change in the Holocene Epoch using Archaeological charcoal from Swaziland, southern Africa. *Journal of Archaeological Science* 12: 457-475.

Quamar, M.F. 2019. Palynological study of surface soil samples from the Kartala Forest Range of the Korba District, Chhattisgarh, central India: Modern pollen-rain/vegetation relationship. *Geophytology* 49(1&2): 37-48.

Quamar, M.F. & Kar, R. 2020. Modern pollen dispersal studies in India: a detailed synthesis and review. *Palynology* 44: 217-236.

Quick, L., Chase, B., Carr, A., Chevalier, M., Grobler, B. & Meadows, M. 2022. A 25,000 year record of climate and vegetation change from the southwestern Cape coast, South Africa. *Quaternary Research* 105: 82-99.

Quick, L.J., Chase, B.M., Wündsch, M., Kristen, K.L., Chevalier, M., Mäusbacher, R., Meadows, M.E. & Haberzetti, T. 2018. A high-resolution record of Holocene climate and vegetation dynamics from the southern Cape coast of South Africa: pollen and microcharcoal evidence from Eilandvlei. *Journal of Quaternary Science* 33: 487-500.

Razanatsoa, E., Gillson, L., Virah-Sawmy, M. & Woodborne, S. 2022. Synergy between climate and human land-use maintained open vegetation in southwest Madagascar over the last millennium. *The Holocene* 32: 57-69.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H. & Henderson, L. 1997. *Alien Plant Invasions*. In: Cowling, R.M., Richardson, D.M. and Pierce, S.M. (eds) *Vegetation of Southern Africa:* 535-570. Cambridge: Cambridge University Press.

Roos, C.I., Field, J.S. & Dudgeon, J.V. 2016. Anthropogenic burning, agricultural intensification, and landscape transformation in Post-Lapita Fiji. *Journal of Ethnobiology* 36: 535-553.

Rose, R.A. 2004. Holocene fire regimes reconstructed from peat core charcoal analysis, in the South Island, New Zealand. Unpublished MSc dissertation. New Zealand: University of Canterbury.

Rutherford, M.C. & Westfall, R.H. 1994. Biomes of Southern Africa: an objective categorization. *Memoirs of the Botanical Survey of South Africa* 63: 1-94.

Sampson, C.G. 1974. *The Stone Age Archaeology of Southern Africa*. New York: Academic Press.

Schmidt, F., Oberhänsli, H. & Wilkes, H. 2014. Biocoenosis response to hydrological variability in Southern Africa during the last 84 ka BP: A study of lipid biomarkers and compound-specific stable carbon and hydrogen isotopes from the hypersaline Lake Tswaing. *Global and Planetary Change* 112: 92-104.

Schoeman, M.H. 1997. The Ndzundza archaeology of the Steelpoort River Valley. Unpublished MA dissertation. Johannesburg: University of the Witwatersrand.

Schoeman, M.H. 1998a. Excavating Ndzundza Ndebele identity at KwaMaza. *Southern African Field Archaeology* 7: 42-52.

Schoeman, M.H. 1998b. Material culture ‘under the animal skin’: excavations at Esikhunjini, a *Mfecane* Period Ndzundza Ndebele site. *Southern African Field Archaeology* 7: 72-81.

Schoeman, M.H. 2020. *Archaeology of Farming Communities in Mpumalanga Province and the adjacent lowveld in Northeastern South Africa*. Oxford Research Encyclopaedia of African History. https://doi.org/10.1093/acrefore/9780190277734.013.767.

Schoeman, M.H., Aub, B., Burrows, J., Hall, G. & Woodborne, S. 2019. Past climatic conditions for Bokoni at Buffelskloof, Mpumalanga using δ13C analysis of Prunus Africana and *Pittosporum viridiflorum* tree-rings. *Journal of African Archaeology* 7: 150-160.

Schoonraad, M. & Beaumont, P. 1971. The Welgelegen Shelter, Eastern Transvaal. In: Schoonraad, M. (ed.) *Rock Paintings of Southern Africa*. *Supplement to the South African Journal of Science, Special Publication* 2: 62-69.

Scott, L. 1982a. A Late Quaternary pollen record from the Transvaal bushveld, South Africa. *Quaternary Research* 17: 339-370.

Scott, L. 1982b. Late Quaternary fossil pollen grains from the Transvaal, South Africa. *Review* of *Palaeobotany and Palynology* 36: 241-278.

Scott, L. 1984. Palynological evidence for Quaternary palaeoenvironments in southern Africa. In: Klein, R.G. (ed.) *Southern African Prehistory and Palaeoenvironments*: 65-80. Rotterdam: Balkema.

Scott, L. 1987. Late Quaternary forest history in Venda, southern Africa. *Review of Palaeobotany and Palynology* 53: 1-10.

Scott, L. 1988. Holocene environmental change at western Orange Free State pans, South Africa, inferred from pollen analysis. *Collection Palaeoecology of Africa and the Surrounding Islands* (19): 109-118.

Scott, L. 1989. Late Quaternary vegetation history and climatic change in the eastern Orange Free State, South Africa. *South African Journal of Botany* 55: 107-116.

Scott, L. 1999. Vegetation history and climate in the Savanna biome South Africa since 190,000 ka: a comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan) and Wonderkrater. *Quaternary International* 57: 215-223.

Scott, L. 2002. Microscopic charcoal in sediments: Quaternary fire history of the grassland and savanna regions in South Africa. *Journal of Quaternary Science* 17: 77-86.

Scott, L. 2016. Fluctuations of vegetation and climate over the last 75 000 years in the Savanna Biome, South Africa: Tswaing Crater and Wonderkrater pollen sequences reviewed. *Quaternary Science Review* 145: 117-133.

Scott, L. & Cooremans, B. 1992. Pollen in recent *Procavia* (hyrax), *Petromus* (dassie rat) and bird dung in South Africa. *Journal of Biogeography* 19(2): 205-215.

Scott, L., Holmgren, K. & Partridge, P.C. 2008. Reconciliation of vegetation and climatic interpretations of pollen profiles and other regional records from the last 60 thousand years in the Savanna Biome of Southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257: 198-206.

Scott, L., Holmgren, K., Talma, A.S., Woodborne, S. & Vogel, J.C. 2003. Age interpretation of the Wonderkrater spring sediments and vegetation change in the Savanna Biome, Limpopo province, South Africa. *South African Journal of Science* 99: 484-488.

Scott, L., Marais, E. & Brook, G.A. 2004. Fossil Hyrax dung and evidence of Late Pleistocene and Holocene vegetation types in the Namib Desert. *Journal of Quaternary Science* 19(8): 829-832.

Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E. & Metwally, A. 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. *Quaternary Science Review*s 32: 100-118.

Scott, L., Neumann, F.H., van Aardt, A.C. & Botha, G.A. 2023. Palaeoenvironmental sequences surrounding Border Cave, South Africa, and review of conditions during Middle and Later Stone Age occupation. *Quaternary Science Reviews* 300: 107894.

Scott, L. & Nyakale, M. 2002. Pollen indications of Holocene palaeoenvironments at Florisbad spring in the central Free State, South Africa. *The Holocene* 12: 497-503.

Scott, L., Sobol, M., Neumann, F.H., Romera, G.G., Fernández-Jalvo, Y., Bousman, C.B., Horwitz, L.K. & Van Aardt, A.C. 2022. Late Quaternary palaeoenvironments in the central semi-arid region of South Africa from pollen in cave, pan, spring, stream and dung deposits. *Quaternary International* 614: 84-97.

Scott, L. & Thackeray, J.F. 1987. Multivariate analysis of Late Pleistocene and Holocene pollen spectra from Wonderkrater, Transvaal. South Africa. *South African Journal of Science* 83: 93-98.

Scott, L. & Vogel, J.C. 1983. Late Quaternary pollen profile from the Transvaal highveld, South Africa. *South African Journal of Science* 79: 266-272.

Shi, N., Dupont, L.M., Beug, H-J. & Schneider, R. 1998. Vegetation and climate changes during the last 21 000 years in SW Africa based on a marine pollen record. *Vegetation History and Archaeobotany* 7: 127-140.

Sieben, E.J.J. 2011. *Compiling Vegetation Data in Wetlands in KwaZulu-Natal, Free State and Mpumalanga, Providing Minimum Data Requirements and a Sampling Protocol*. Pretoria: Water Research Commission.

Sieben, E.J.J., Glen, R.P. & Muasya, A.M. 2017. The wetland flora of South Africa: occurrence patterns, frequency and dominance across a diverse landscape. *Aquatic Botany* 142: 112-118.

Sieben, E.J.J., Mtshali, H. & Janks, M. 2014. *National Wetland Vegetation Database: classification and analysis of wetland vegetation types for conservation planning and monitoring*. Pretoria: Water Research Commission.

Sjöström, J., Norström, E., Risberg, J. & Schoeman, M.H. 2017. Late Holocene palaeoenvironmental reconstruction from Mpumalanga Province (South Africa) inferred from geochemical and biogenic proxies. *Review of Palaeobotany and Palynology* 246: 264-277.

Smith, A.B. 1992. *Pastoralism in Africa: origins and development ecology.* London/Athens/ Johannesburg: Hurst & Company. Ohio University Press/Witwatersrand University Press.

Smith, J.M. 2005. Climate change and agropastoral sustainability in the Shashe/Limpopo River Basin from AD 900. Unpublished PhD thesis. Johannesburg: University of the Witwatersrand

Smith, J., Lee-Thorp, J. & Hall, S. 2007. Climate change and agropastoralist settlement in the Shashe-Limpopo River Basin, southern Africa: AD 880 to 1700. *The South African Archaeological Bulletin* 62(186): 115-125.

Stager, J.C., Ryves, D.B., King, C., Madson, J., Hazzard, M., Neumann, F.H. & Maud, R. 2013. Late Holocene precipitation variability in the summer rainfall region of South Africa. *Quaternary Science Reviews* 67: 105-120.

Stynder, D.D. 2009. Craniometric evidence for South African Later Stone Age herders and hunter–gatherers being a single biological population. *Journal of Archaeological Science* 36(3): 798-806.

Stynder, D.D., Ackermann, R.R. & Sealy, J.C. 2007. Craniofacial variation and population continuity during the South African Holocene. *American Journal of Physical Anthropology* 134(4): 489-500.

Tomlinson, R.W. 1973. The Inyanga area: an essay in regional biogeography. *University of Rhodesia Occasional Paper* 1: 1-67.

Truc, L., Chevalier, M., Favier, C., Cheddadi, R., Meadows, M.E., Scott, L., Carr, A.S., Smith, G.F. & Chase, B.M. 2013. Quantification of climate change for the last 20,000 years from Wonderkrater, South Africa: Implications for the long-term dynamics of the Intertropical Convergence Zone. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386: 575-587.

Turner, S. & Plater, A. 2004. Palynological evidence for the origin and development of late Holocene wetland sediments: Mdlanzi Swamp, KwaZulu-Natal, South Africa. *South African Journal of Science* 100: 220-229.

Tyson, P.D., Karlen, W., Holmgren, K. & Heiss, G.A. 2000. The Little Ice Age and Medieval warming in South Africa. *South African Journal of Science* 96(3): 121-126.

Tyson, P.D. & Lindesay, J.A. 1992. The climate of the last 2000 years in southern Africa. *The Holocene* 2: 271-278.

Tyson, P.D. & Preston-Whyte, R.A. 2000. *Weather and Climate of Southern Africa.* Oxford: Oxford University Press.

Umbanhowar, C.E. & McGrath, M.J. 1998. Experimental production and analysis of microscopic charcoal from wood, leaves and grasses. *The Holocene* 8: 341-346.

Van Asperen, E.N., Kirby, J.R. & Shaw, H.E. 2020. Relating dung fungal spore influx rates to animal density in a temperate environment: implications for palaeoecological studies. *The Holocene* 30: 218-232.

Van Der Merwe, N.J. 1982. Carbon isotopes, photosynthesis, and archaeology: Different pathways of photosynthesis cause characteristic changes in carbon isotope ratios that make possible the study of prehistoric human diets. *American Scientist* 70: 596-606.

Van Doornum, B. 2007. Tshisiku Shelter and the Shashe-Limpopo confluence area hunter-gatherer sequence. *Southern African Humanities* 19(1): 17-67.

Van Geel, B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro-and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology* 25: 1-120.

Van Ginkel, C.E. & Cilliers, C.J. 2020. *Aquatic and Wetland Plants of Southern Africa*. Pretoria: Briza Publications.

Van Hoepen, E.C.N. 1939. A pre-European Bantu culture in the Lydenburg District. *Archaeological Research of the National Museum, Bloemfontein* 2(5): 47-74.

Van Wilgen, B.W. 2009. The evolution of fire management practices in savanna protected areas in South Africa. *South African Journal of Science* 105: 343-349.

Van Wilgen, B.W. & Richardson, D.M. 2012. Three centuries of managing introduced conifers in South Africa: benefits, impacts, changing perceptions and conflict resolution. *Journal of Environmental Management* 106: 56-68.

Villa, P., Soriano, S., Tsanova, T., Degano, I., Higham, T.F., d'Errico, F., Backwell, L., Lucejko, J.J., Colombini, M.P. & Beaumont, P.B. 2012. Border cave and the beginning of the Later Stone Age in South Africa. *Proceedings of the National Academy of Sciences* 109(33): 13208-13213.

Vogel, J.C. & Fuls, A. 1999. Spatial distribution of radiocarbon dates for the Iron Age in southern Africa. *The South African Archaeological Bulletin* 54(170): 97–101.

Wadley, L. 1987. *Later Stone Age Hunters and Gatherers of the Southern Transvaal: social and ecological interpretation*. Cambridge Monographs in African Archaeology 25. British Archaeological Reports International Series 380. Oxford: BAR Publishing.

Wadley, L. 1993. The Pleistocene Later Stone Age south of the Limpopo River. *Journal of World Prehistory* 7: 243-296.

Wadley, L. 1996. Changes in the social relations of precolonial hunter–gatherers after agropastoralist contact: an example from the Magaliesberg. *South Africa Journal of Anthropological Archaeology* 15: 205-217.

Walker, M.J., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisher, D.A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O. & Weiss, H. 2012. Formal subdivision of the Holocene Series/Epoch: a discussion paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). *Journal of Quaternary Science* 27(7): 649-659.

Walther, S.C. & Neumann, F.H. 2011. Sedimentology, isotopes and palynology of late Holocene cores from Lake Sibaya and the Kosi Bay system (KwaZulu-Natal, South Africa). *South African Geographical Journal* 93(2): 133-153.

Weldeab, S., Stuut, J.B., Schneider, R.R. & Siebel, W. 2013. Holocene climate variability in the winter rainfall zone of South Africa. *Climate of the Past* 9(5): 2347-2364.

Wetterstrom, W. 1993. Foraging and farming in Egypt: the transition from hunting and gathering to horticulture in the Nile Valley. In: Shaw, T., Sinclair, P., Bassey, A. & Okpoko, A. (eds) *The Archaeology of Africa: food, metals and towns*: 165-226. London: Routledge.

Whitelaw, G. 1991. Precolonial iron production around Durban and in southern Natal. *Southern African Humanities* 3: 29-39.

Whitelaw, G. 1996. Lydenburg revisited: another look at the Mpumalanga Early Iron Age sequence. *The South African Archaeological Bulletin* 51(164): 75-83.

Widgren, M., Maggs, T., Plikk, A., Risberg, J., Schoeman, M.H. & Westerberg, L-O. 2016. Precolonial agricultural terracing in Bokoni, South Africa: typology and an exploratory excavation. *Journal of African Archaeology* 14: 33-53.

Williams, C.G. 2008. Aerobiology of *Pinus taeda* pollen clouds. *Canadian Journal of Forest Research* 38: 2177-2188.

Wilson, E.H. 1923. Northern trees in southern lands. *Journal of the Arnold Arboretum* 4:61-90.

Wiesenberg, G. L. B. & Schwark, L. 2006. Carboxylic acid distribution patterns of temperate $C_3$ and $C_4$ crops. *Organic Geochemistry* 37: 1973-1982.

Woodborne, S., Gandiwa, P., Hall, G., Patrut, A. & Finch, J. 2016. A regional stable carbon isotope dendro-climatology from the south African summer rainfall area. *PLoS ONE* 11(7): e0159361.

Woodborne, S., Hall, G., Robertson, I., Patrut, A., Rouault, M., Loader, N.J. & Hofmeyr, M. 2015. A 1000-year carbon isotope rainfall proxy record from South African baobab trees (*Adansonia digitata* L.). *PLoS ONE* 10(5): e0124202.

Xu, Q., Zhang, S., Gaillard, M.-J., Li, M., Cao, X., Tian, F. & Li, F. 2016. Studies of modern pollen assemblages for pollen dispersal- deposition- preservation process understanding and for pollen-based reconstructions of past vegetation, climate, and human impact: a review based on case studies in China. *Quaternary Science Reviews* 149: 151-166.

Yang, S.X., Liu, K.B., Yi, S., Ye, S.Y., Li, J., Yuan, H.M., Zhao, G.M., Shao, F.P. & He, L. 2016. Distribution and provenance of modern pollen and spores in the surface sediments of Liaodong Bay. *China Marine Geology* 376: 1-14.

Zinke, J., Loveday, B.R., Reason, C.J.C., Dullo, W.C. & Kroon, D. 2014. Madagascar corals track sea surface temperature variability in the Agulhas Current core region over the past 334 years. *Scientific Reports* 4(1): 4393.

Zhao, X., Dupont, L., Meadows, M.E. & Wefer, G. 2016. Pollen distribution in the marine surface sediments of the mudbelt along the west coast of South Africa. *Quaternary International* 404: 44-56.