



The Reconstruction of the Late Pleistocene and Holocene Vegetation Dynamics in Lake Eyasi Basin, Northern Tanzania

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Abstract

Lake Eyasi Basin of northern Tanzania plays a pivotal role in the study of human-environment interactions and in understanding human flexibility and adaptability through technological innovations over time and space. In this study, phytoliths from ancient soils and fossil pollen proxies from radiocarbon-dated sequences from Kisimangeda on the north-eastern edge of the Lake Eyasi Basin, are used to interpret trends in climatic changes recorded since the Last Glacial Maximum (LGM) to the present. We used pollen and phytolith abundances from a core that was recovered on the northern margin of saline Lake Eyasi at the depth of five metres. The application of principal component and cluster analysis, together with linear regression provides insight into dataset structure and grouping with reference to the modern comparative datasets that in turn allow us to classify the various palaeoenvironments and paleohabitats occupied by the late Later Stone Age, Pastoral Neolithic, and Iron Age inhabitants of Kisimangeda. The chronological order, pollen and phytolith records in the studied part of the basin signify palaeoenvironments analogous to the Somalia-Maasai bushland and grassland ecosystems of today.

Keywords: Palaeoenvironments, Late Pleistocene, Holocene, pollen, phytoliths, human adaptation.

Introduction

Pleistocene and Holocene represent epochs in the geologic time that witnessed global climatic shifts associated with the last glacial age. In the Holocene, the Earth system was already trying to stabilize following the last glaciation and the terminal Pleistocene melting of northern hemisphere ice sheets (Ashley et al. 2011). Unlike the northern hemisphere which experienced temperature change, in Africa, the climatic change

scenario was more a matter of fluctuating water budgets and irregularities in the distribution of moisture contents as well as vegetation distribution on the landscape, than of temperature changes (Kropelin et al. 2008, Ashley et al. 2011). The assumption is often made that climate and cultural changes are somehow linked (Ashley et al. 2011). However considerable data is needed to validate the presumed reciprocal influence between environmental change and the

evolution of human behaviour (Owen et al. 2018). It should be noted that climatic and environmental changes are not synonymous. Environment might have not responded linearly to climatic changes in Africa. Changes in climate and water budgets had great impacts to the reliability of food and water resources for human and animal populations, hence may have in turn affected the choice of subsistence strategy to be adopted (Kusimba 1999, Ashley et al. 2011).

Evidence from the Mumba rock-shelter (Mehlman 1989, Prendergast et al. 2007) suggests that in northern Tanzania, by the mid-Holocene, hunting and gathering communities adapted the use of ceramics (Kansyore ware) together with microlithic stone tools (5,000–4,000 BP). Communities here relied on diversified wild food resources such as plants, fauna, mollusks, and aquatic foodstuff (Mwitondi et al. 2021). It is widely agreed that climatic and demographic pressure after 6,000 BP, pushed Neolithic pastoralists living in the Nile River Basin southwards to Eastern Africa savannah habitats in the Rift Valley System (Prendergast et al. 2014, Marchant et al. 2018, Mwitondi et al. 2021). These migrants were attracted to East African ecosystems and considered the area a place to engage in herding. They eventually inhabited the Lake Eyasi Basin and other parts of northern Tanzania around 4,000 years ago (Mwitondi et al. 2021). Therefore, the northeastern part of Lake Eyasi Basin (Figure 1) is a very crucial area to examine the spatial extent of herders and sustainable environmental conditions.

Neolithic adaptations in East Africa were not merely the initial adoption of animal keeping, because the livestock keeping required biological adaptability of livestock being introduced to this new, and potentially challenging, environment. Ever since, East Africa witnessed the initial spread of food production that marked the beginning of the Pastoral Neolithic (PN) between 5000 and 1200 BP (Marshall 1990, Gifford-Gonzalez 2000). Unlike other areas across the globe, mobile livestock herding of cattle (*Bos taurus*), sheep (*Ovis aries*) and goat (*Capra*

hircus) supported by donkeys (*Equus asinus*) preceded sedentary farming in much of prehistoric Africa (Marshall et al. 2011). Increasing aridity in the Sahara during the mid-Holocene may have been the driving force leading to the southward movement of pastoralists into East Africa (Marshall et al. 2011). The East African Rift Valley (EARV) is one of the possible corridors through which pastoralism spread into East Africa (Prendergast et al. 2014). The spread of herders may relate to multiple environmental and social factors. These include drought, bimodal rainfall together with possible expansion of grasslands (Marshall 1990), the ability of herders to manage zoonotic diseases (Gifford-Gonzalez 2000), social response to increased aridity and rainfall unpredictability (Chritz et al. 2018), as well as new mobility patterns and social networks (Marshall et al. 2011). The Lake Eyasi Basin on the eastern edge of EARS is therefore a crucial location to examine the spatial usage of herders and the environmental conditions of northern Tanzania during the early phases of Neolithic adaptation. At the same time, environmental proxy records from the Basin are of special interest in answering the question of the possible links between climatic and cultural changes.

Lake Eyasi (Figure 1) is a shallow endorheic saline lake on the floor of the EARV, south of the Serengeti Plains and southwest of the Ngorongoro crater highlands of northern Tanzania. The principal inflow to the lake is the Sibiti River which enters the lake at the southwestern end, Barai River is the secondary inflow on the northeastern side of the lake (Bushozi et al. 2020), while seasonal water fluctuations in the lake are dramatic. For example, during heavy rain seasons like the era of El Niño, the lake floods its banks but during the dry seasons, the lake may completely dry out (Mehlman 1989). The preserved Holocene sediments related to lacustrine deposits in the area are rich in fossil records and archaeological artefacts as an indicator of human presence within the landscape (Domínguez-Rodrigo et al. 2007, Prendergast et al. 2007, Gliganic et al. 2012, Bushozi et al. 2017, 2020). Thus,

past generations of East Africans left highly visible traces across the landscape in form of abundant stone tools, animal bones, ceramics and other micro and macro-implements. For example, traces of fossil records and archaeological artefacts of the herding community are very rich in Holocene sediments ranging from 4,000 years to the historic period (Mehlman 1989, Mwitondi et

al. 2021). Neolithic archaeological assemblage has been accumulated in rock-shelters such as Mumba and Sonai (Mehlman 1989, Prendergast et al. 2007) and along the alluvial and aeolian deposits widely displayed on the lakeshore at Jangwani and Laghangerer-Ishimijega localities (Mwitondi et al. 2021).

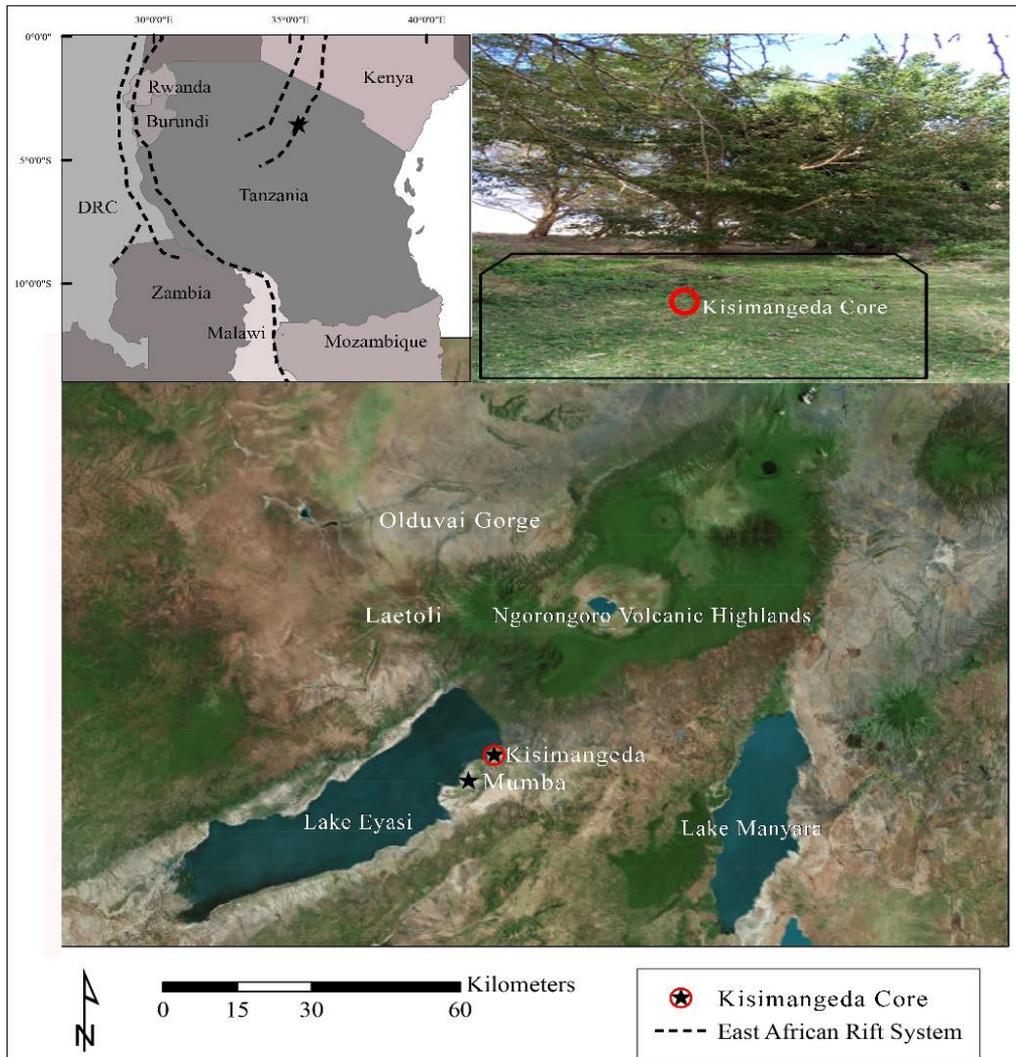


Figure 1: Top left: map of Tanzania showing the East African Rift Valley System, top right: location of the core drill at Kisimangeda, centre: part of northern Tanzania showing prominent archaeological sites at Lake Eyasi Basin (Bushozi et al. 2020).

A current interdisciplinary research effort focused on the northeastern side of Lake Eyasi, provides an opportunity to evaluate the

possible connection between climatic changes and subsistence strategies practised by people living in the basin during the

Holocene. This study's attention were on a core drilled at Kisimangeda on the northeastern edge of the lakeshore (Figure 1) to; (i) provide the chronological framework and environmental setting of the region since the Late Pleistocene, (ii) compare the paleoclimate contexts from analysis of pollen and phytoliths hosted in the Late Pleistocene and Holocene deposits preserved in the area, (iii) comment on the environmental drivers that may have influenced the cultural evolution of ancient communities in the region, (iv) correlate the proxies from this site with those from other well-known sites for inference related to local and regional environmental changes.

Holocene and present-day environmental conditions in the Lake Eyasi Basin

In tropical Africa, the beginning of the Holocene (~12 kya) was marked by wet-dry cycles. However, the influence that contributed to the environmental oscillations is highly debated. The dry circles are conceptually associated with astronomically controlled (Milankovitch) precession cycles between 19 and 23 kya (Ashley et al. 2011); the effect of paleo El Niño Southern Oscillation (ENSO) on the African environment (Kaboth-Bahr et al. 2021); the resistance of African tropical forests to rapid environmental change in glacial and interglacial circles (Bennett et al. 2021); or the Indian Ocean and biannual north-south migration of intertropical convergence zone (ITCZ) that govern the distribution of moisture and rainfall in the region (Tierney et al. 2011). According to Ashley et al. (2011), solar input to the Earth's surface (watts/m^2) varies seasonally and with latitude in response to the precession cycle. Increased isolation in the Northern Hemisphere during the Holocene is reported to have caused an increase in summer monsoon intensity, which led to higher annual rainfall (Ashley et al. 2011). Alternatively, it was conceptually influenced by the resistance of African tropical forests to rapid environmental changes or the effect of Paleo-ENSO (Kaboth-Bahr et al. 2021). Thus, the ITCZ and Paleo-ENSO seemed to have increased

the size of ecotone regions and were manifested in the increase in water on the surface (rivers and lakes) and subsurface ground rivers during the Late Pleistocene and Holocene periods (Prendergast 2008, Kaboth-Bahr et al. 2021, Bennett et al. 2021). Generally, the complexity of the atmosphere was among the major causes of local vegetation dynamic that characterized the region from the late Pleistocene to the present.

At Lake Eyasi, the climate became warmer ca 11,000-6,000 BP possibly due to increased solar radiation, during this time the rise of lake levels reached to its highest point (Prendergast 2008). Research indicates that the lake levels dropped dramatically in the Mid Holocene at 5000–3000 BP and it has continuously stayed at low levels until the present (Prendergast 2008). The causal mechanisms for the fluctuations in lake levels during this time scale are unknown changes in the orbit axis of the Earth (Prendergast 2008) or minor changes in solar radiation are possible (Ashley et al. 2011). On the decadal scale, rainfall may vary with a complex series of climatic changes affecting the equatorial regions (like El Niño) (Kaboth-Bahr et al. 2021). The current precipitation is commonly monomial, ranging from November to April with an average of 800–1000 mm (Bushozi et al. 2017).

Recently, the Lake Eyasi Basin is an arid environment comprising open grasslands and shrubs classified as Somali-Maasai phytoregion (Domínguez-Rodrigo et al. 2007). However, the vegetation cover tends to change depending on the nature of the soil, water availability, basement rocks, and altitude (Bushozi et al. 2020). The lowland plain in the eastern and southeast aspects of the region is characterized by open grassland with scattered shrubs in the river valleys. The northeast highlands and northwest escarpment are covered by montane forests. The areas have a broad exposure of podocarps, *Juniperus procera*, and *Olea capensis* and parallel biota characterize the Pleistocene pollen spectral in the lakeshore (Domínguez-Rodrigo et al. 2007). Analyses of both present and past biota from pollen

and phytoliths, combined with alluvial grain sand and mudflats from an old fan delta, demonstrate considerable variations in the regional environment at different phases (Middle Pleistocene, Upper Pleistocene, early Holocene and the present) (Bushozi et al. 2017, Mercader et al. 2021). This trend shows that microhabitat variability and ecological diversity were very important in human evolution (Mercader et al. 2021). Even though the Eyasi basin is dry and open, some microhabitats would have provided assorted foodstuffs.

Geographical location and description of the Kisimangeda site

The swamp site of the Kisimangeda (03°47'41" S; 35°35'50" E), also spelt Kishimangeda (Mehlman 1989), is situated in the eastern corner of Lake Eyasi (Figure 1), on the southern slopes of the Oldeani Mountain range. To the east and west are the Mango'la village and Kisimangeda Camping Site, respectively. Lake Eyasi is situated to the southwest, while Kisimangeda village is to the north. The vegetation types on the swamp floors are dominated by *Cyperus alopecuroides*, *Typha latifolia*, Poaceae including *Andropogon* sp. and *Digitaria diagonalis*, and ferns such as *Asplenium* sp. and *Thelypteris palustris* (Domínguez-Rodrigo et al. 2007).

The transitional zone located between the swamps and forest area is characterized by shrubs, herbs, and climbers. The vegetation cover includes *Crotalaria agatiflora* subsp. *imperialis*, *Indigofera arrecta*, *Justicia insularis*, *Justicia matammensis*, *Nymphaea* sp., *Rubus rigidus*, and lianas; along with Asteraceae such as *Coryza gangreneux* and *Eryngium tirucalli*. Trees include *Ficus sur* and *Rauvolfia caffra*. Cultivated plants (farmlands) include *Allium cepa*, *Commelina benghalensis*, *Ipomoea batatas*, *Ludwigia leptocarpa*, *Lycopersicon esculentum*, *Mussa capensis*, *Abelmoschus esculentus*, and *Solanum tuberosum*. Forest area vegetation includes *Vachelia xanthophloea*, *V. polyacantha*, *V. mellifera*, *Salvadora persica*, *Commiphora Africana*, and *Commiphora tanganyikensis* (Bourel et al. 2021).

Materials and Methods

Lithology and stratigraphic sequences

Five meters (5 m) core was drilled at the centre of the swamp using a hand pushed Russian D-shaped corer in 50 cm segments with >10 cm overlap for each drive to minimise contamination (Jowsey 1965). Samples were transferred to PVC guttering, wrapped in aluminium foil and polythene sheeting at the site, and transported to the University of Dar es Salaam laboratory for cold storage at 4 °C. Cores were described stratigraphically, subsampled, and analysed. The sub-samples were later transported to the Palaeobotany and Palynology Laboratory, National Museum of Kenya (NMK) in Nairobi for processing and laboratory analysis of pollen and phytolith samples. The stratigraphy of the cored interval is given in Table 1. Eleven bulk samples were selected for accelerator mass spectrometry (AMS) radiocarbon dating (Table 1). The sample material was alkali-acid-alkali pre-treated; ¹⁴C measurements were corrected for isotopic fractionation with δ¹³C values measured on the prepared graphite using the AMS spectrometer by Direct AMS (11822 North Creek Parkway N, Suite #107, Bothell, WA 98011 Tel (425) 481-8122- www.DirectAMS.com, WA, USA). Radiocarbon ages (¹⁴C year BP) were calibrated using the Southern Hemisphere calibration curve (Hogg et al. 2013).

Calibrated and un-calibrated age-depth models were developed using linear interpolation of calibrated 2σ age ranges and un-calibrated age ranges, respectively. The upper part of the sediment deposit from the core provided sufficient organic compounds for radiocarbon dating (Table 1). The rest provided minimum ages (possibly due to small sample sizes or potential absence of organic materials and humates) (Table 1) and did not follow a monotonic sequence. However, Radiocarbon dates on five levels with less organic and humate samples carried were problematic because of insufficient humates or plant fragments for carbon analysis, however, they were treated using protocols for AMS Radiocarbon Dating by Direct AMS (D-AMS) procedures.

Table 1: Stratigraphic sequences of the Kisimangeda core, indicating uncalibrated ages (Source: Field data 2019)

Direct AMS code	Depth (cm)	Fraction of modern pMC $\pm 1\sigma$ error	Radiocarbon age		Lithological changes
			BP	1 σ error	
D-AMS 034829	0-50	99.851 \pm 0.35	Modern	0	Decomposed black peat, rich organic matter/fibrous material
D-AMS 034830	50-100	97.21 \pm 0.29	227	24	Decomposed black peat, less fibrous material
D-AMS 034831	100-135	76.59 \pm 0.24	2142	25	Grey, sandy-clay, less fibrous material
D-AMS 034832	135-165	72.50 \pm 0.26	2583	29	Light grey, sandy-clay, less organic matter
D-AMS 034833	165-175	47.77 \pm 0.17	5935	29	Reddish brown, sandy-clay, less organic matter
D-AMS 034834	175-195	26.77 \pm 0.14	10587	42	Light grey, sandy-clay, less organic matter
D-AMS 034835	195-200	78.03 \pm 0.27	1993	28	Yellowish red, sandy-clay, less organic matter
D-AMS 034836	200-300	78.68 \pm 0.30	1926	31	Yellow, sandy-clay
D-AMS 034837	300-350	69.40 \pm 0.29	2934	34	Dark grey, sandy-clay
D-AMS 034838	350-400	Insufficient carbon for analysis			Pale yellowish, sandy-clay
D-AMS 034839	400-500	Insufficient carbon for analysis			Dark grey, sand

Preparation and analysis of fossil pollen

The preparation of sediments for pollen studies was based on revised standard procedures published in Faegri and Iversen (1989) and Moore et al. (1991). 51 samples were taken every 10 cm from the core and analysed for pollen content. Dissolution of the carbonates and silicate was achieved with diluted HCl (10%) and cold HF (48%), respectively, whereas removal of colloidal silica was accomplished with warm diluted HCl, and destruction of humic acids was done by dilution in KOH (10%) solution. The obtained residue was diluted in glycerol. For each sample, at least 300 pollen grains were counted. Then, identification was confirmed by comparison with a reference collection of over 6,000 slides of modern East African pollen held at the Department of Earth Sciences (Palynology and Paleobotany Section) at the NMK. The identifications also made use of a range of publications (Bonnefille and Rioulet 1988) and digital photographs of pollen types obtained from the African pollen database (<http://www.geo.arizona.edu/palynology/apd.html>). Pollen identification was made to the lowest taxonomic level, although some pollen

types could only be identified at the family level, with the nomenclature following that of Benninghoff and Kapp (1962). The confidence in the identification of the microfossils is indicated by suffixes to known types: when the fossil pollen is comparable to known types. This is meanwhile a degree of uncertainty, and when the identification of the genus is certain. The total count per sample generally ranged between 250 and 500 grains, except for a few samples where preservation was poor.

Preparation and analysis of fossil phytoliths

The phytolith morphological classifications and identifications were based on various sources including the International Code of Phytolith Nomenclature 2.0 (ICPT 2019, Piperno 2006, Twiss 1992, Rossouw 2009). Samples were analysed and compared to the pollen collection housed at the Palynology and Palaeobotany Departments in the National Museums of Kenya, in Nairobi. Pollen types that did not exceed 2% were excluded from the pollen diagram. CONISS was applied to the data using a numerical clustering package within the TILIA

programme, with the results identifying six stratigraphic clusters of samples with similar floristic composition. The study found a noted trend of diversity in the total abundance, morphotype richness, and phytolith assemblage index from the layers dated to the Last Glacial Maximum at 24,400 BP through the Holocene period (Figure 2).

Approximately 10 g of sediment were used for each phytolith analysis. The phytoliths were extracted by the dissolution of carbonates using acetic acid buffered at pH of 3, oxidation of the organic matter using 30% hydrogen peroxide at the temperature of 90 °C until the reaction subsided, and then mechanical removal of clays. Densitometric separation of phytoliths from sediment was achieved by separation in a zinc bromide solution with a density of 2.3 g/cm³ (ICPT 2019). This light fraction, including opal phytoliths, was mounted on microscope slides using glycerin as a mounting medium. Microscopic observations were done at 40 x 100 magnification with a minimum count of 350 phytoliths. The phytolith tallies per type were transformed into percentages, as the count for our comparative baseline was originally distributed across the multiple contemporaneous samples versus the stratigraphic sequences (Table 1). Stratigraphic sequences were presented in units of per cent modern carbon (pMC) and uncalibrated age before present (BP). Phytolith samples were analysed using morphological descriptions (Mauquoy et. al. 2010).

The data were plotted using TILIA Program 1.7.16 (Grimm 1987). CONISS (Grimm 1987) was used to define the pollen assemblages (zones) and the location of the boundary using a clustering algorithm. To verify the effectiveness of the results from the constrained zonation method (Grimm 1987), and to establish any relationships between non-contiguous samples and zones, the technique was checked by a stratigraphically unconstrained clustering technique by CONISS.

Results

Stratigraphy and chronology

The Kisimangeda core is dominated by black peat, rich organic matter, and fibrous material from 0–50 cm (227 cal. yr. BP to present). From 50–165 cm (2583–227 cal. yr. BP), the sediments vary between light grey (10 R 7/1) to reddish grey colour (10R 6/1) with sandy-clay texture and less organic matter. An anomaly exists at 165–175 cm depth (5935–2583 BP), where sediments were characteristically reddish brown (2.5 YR 5/2) and coinciding with documented lake level fluctuations (Bushozi et al. 2017). Changes in lake levels recorded at the Mumba rock-shelter were associated with abrupt geomorphological changes and edaphic features including the presence of stromatolites, aquatic remains, and coated calcium carbonate of algae origins (Mehlman 1989). These cycles are revealed in the sedimentary deposits that resulted from southern oscillations (El Niño), leading to over flooding and raised shorelines, sometimes reaching the hill slope of Laghangerer-Ishimijega in the eastern ends (Mehlman 1989). Although Holocene sediments of Mumba have been accidentally destroyed through increased human activities (burial practices) and other geomorphologic processes (Bushozi et al. 2020), the reddish-brown (2.5 YR 5/2) sediments from Kisimangeda core dates of similar age and complement analogous features. From 175–195 cm depth (10,875 BP), there existed light yellowish brown (10 YR 6/4) sandy-clay sediments with less organic matter. Sediments from 195–500 cm mark the prolonged period of Upper Pleistocene deposits ranging from 24,400 to 10,875 BP (Figures 2 and 3). This is supported by ¹⁴C measurements corrected for isotopic fractionation with $\delta^{13}\text{C}$ values using the AMS spectrometer by Direct-AMS, which indicates that sediments have insufficient or no organic carbon at all. The plausible explanation is that there is probably a hiatus introduced by removal of original sediments due to high mineralogical mixing which resulted from dry conditions that preceded the Last Glacial

Maximum (LGM) in most parts of Africa
(Mumbi et al. 2008).

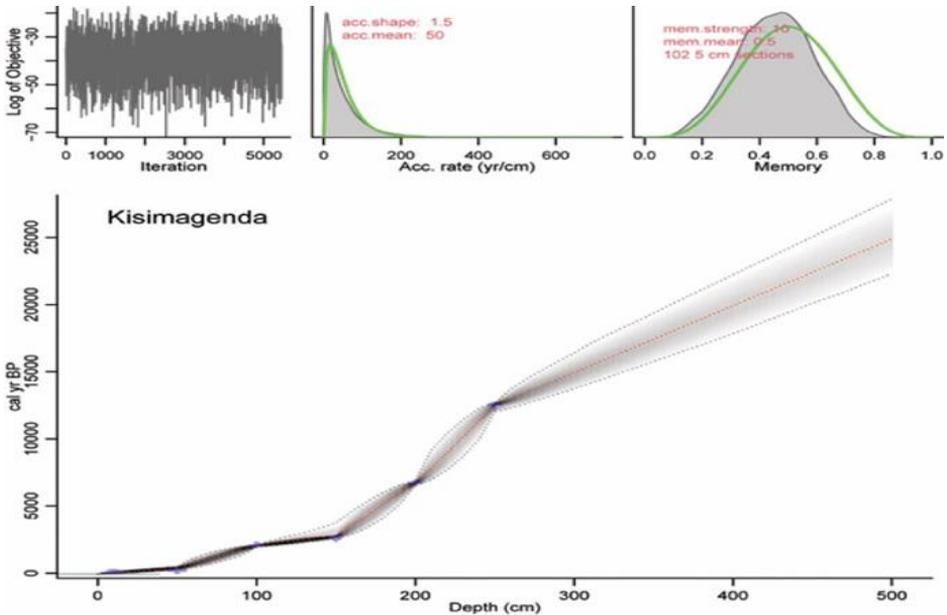


Figure 2: Calibrated age-depth model for the Kisimangeda core (Source: Field data 2019 www.DirectAMS.com, WA, USA).

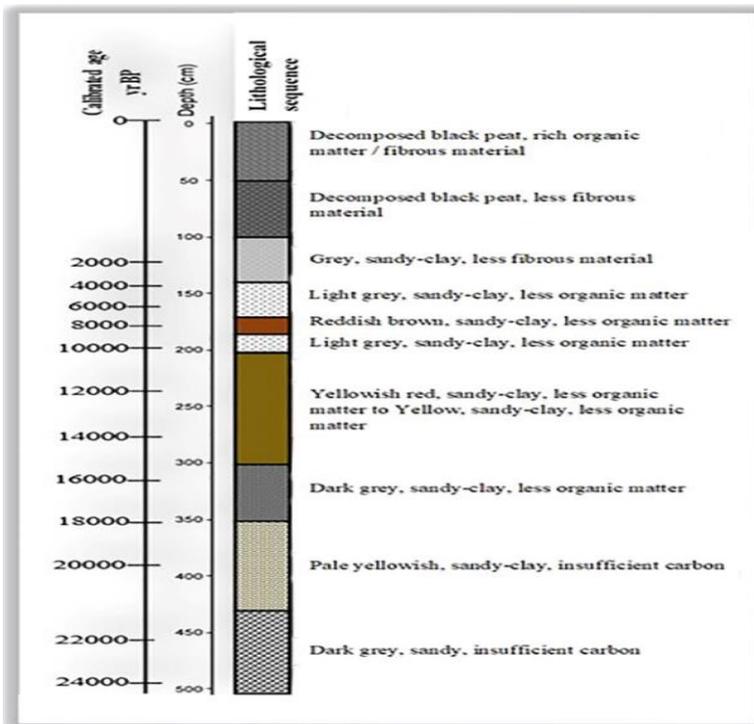


Figure 3: The chronological and lithological sequence of Kisimangeda core site (Source: Field data 2019).

Pollen and phytolith analyses on the 51 samples document variations in the terrestrial vegetation from the regional catchment and among the local palaeolake/wetland aquatic macrophytes. 58 pollen taxa, belonging to trees, shrubs, lianas, grasses, and herbs were documented from the studied core sample. Two sets of fossil pollen sums were calculated; the first consists of the total sum of Poaceae and wetland/local taxa (Cyperaceae, *Nymphaea*, and *Typha*). Poaceae is considered local taxa because of the dominance it shows (local over-representation) among the fossil pollen flora assemblage and the inference made from numerous grasses growing in the Lake Eyasi catchment area in the present-day settings.

The second fossil pollen sum includes regional taxa or land pollen with unknown and undifferentiated pollen grains included. The trees were grouped as montane taxa, with shrubs and lianas forming a woodland taxa group, while all the herbs were collected together as herbaceous taxa. The three terrestrial groups (land pollen) were regarded as regional, although some of the herbs are likely to be derived from both local and regional parent taxa (Figure 4). In this case, they are all included in the pollen sum of the regional taxa.

Pollen and phytolith stratigraphies

Pollen and phytolith zone-1 (500–405 cm; ~24,400–22,900 cal. yr. BP)

This zone rests at the base of the 5 m core, and is distinguished by relatively high percentages of Cyperaceae and Poaceae, but a low percentage of *Typha*. Montane taxa (only *Juniperus*) are reduced in this zone. Woodland taxa, such as *Acacia* and *Acalypha*, are prevalent, while *Boscia*, *Commiphora*, *Cordia*, *Combretum*, and *Hyphaena* sporadically appear in low abundances. Herbaceous taxa such as *Aloe*, Amaranthaceae/Chenopodiaceae, Asteraceae, *Cleome*, *Ludwigia*, and *Urtica* also sporadically appear in low abundances. On the other hand, phytoliths are dominated by high percentages of spheroid scabrate followed by other moderate contributors such as spheroid verrucate and spheroid globular

originating from woody morphotypes. Poaceae morphotypes (Panicoidae and Chloridoideae) show relatively high percentages in this zone. Herbaceous morphotype of spheroid psillate and Cyperaceae morphotype of achene show a relatively high percentage. Total phytolith assemblage shows a relatively high percentage in this zone.

Pollen and phytolith zone-II (405–320 cm; ~22,400–15,929 cal. yr. BP)

This pollen zone is characterized by high percentages of Poaceae, Cyperaceae and *Typha*, indicating an increasing influence from the previous zone. Within the montane taxa component, *Juniperus* and Rubiaceae are common. *Juniperus* and Rubiaceae show higher levels here than in any other zone. Woody taxa are characterised by high levels of *Cordia*, *Grewia*, *Hyphaena*, and *Solanum*, with *Acacia* and *Acalypha* emerging as important contributors, supported by *Commiphora* and *Euphorbia*, while *Salvadora* sporadically appears in this zone. Herbaceous taxa, which are common, include Amaranthaceae/Chenopodiaceae, Asteraceae, *Justicia*, *Indigofera*, *Justicia*, *Hibiscus*, *Stemodia* and *Urtica*. This zone is distinguishable in that it contains very low total pollen grains, but they increase in abundance in the upper part of the zone (Table 2). However, phytoliths are mainly dominated by high percentages of spheroid scabrate followed by other moderate contributors such as spheroid verrucate and spheroid globular originating from woody morphotypes. Poaceae morphotypes (Panicoidae and Chloridoideae) continue to show relatively high percentages in this zone. Herbaceous morphotypes of paralleliped psillate, paralleliped scabrate, spheroid psillate, cylindroid psillate and cylindroid crenate are also moderate distributors (Figure 5). Cyperaceae morphotype of achene show a relatively high percentage. Total phytolith assemblage shows a relatively high percentage in this zone.

Pollen zone-III (320–220 cm; ~15,929–7800 cal. yr. BP)

This zone is characterised by a wide distribution and high percentages of Poaceae, Cyperaceae and *Juniperus*. Woody taxa are represented by abundant *Acacia* and contributions from *Acalypha*, *Hyphaena*, *Lannea* and *Solanum*. Herbaceous taxa, which make important contributions, include Amaranthaceae/Chenopodiaceae, Asteraceae, *Indigofera*, *Justicia*, *Stemodia*, and *Tapura*. *Urtica* and Umbelliferae had very low pollen counts. This zone had a very low pollen count relative to other zones, but was nevertheless characterised by abundant Poaceae and Cyperaceae. The phytolith is characterised by the evidence that majority of taxa contribute

either high, moderate, or low percentages of poaceae, woody, herbaceous or Cyperaceae morphotypes. Woody morphotypes are dominant in this zone with spheroid scabrate showing highest percentages both longitudinally and latitudinally. Poaceae morphotype (Chloridoideae), herbaceous morphotype (spheroid psillate, paralleliped psillate, paralleliped scabrate) show relatively high percentages; with achene (Cyperaceae) also an important contributor albeit lowly represented as compared to the above morphotypic taxa. Honeycomb polyhedral and epidermal cells emerge for the first time in this record. Total phytolith assemblages continue to show relatively high percentages in this zone (Table 2).

Table 2: Fossil pollen and present-day plant taxa at Kisimangeda site (Source: Field data 2019)

Family	Plant Taxon	Synonym	P & A	Fern	CP	SHL	WP	MF
Acanthaceae	<i>Justicia insularis</i>					V		
	<i>Justicia matammensis</i>					V		
	<i>Peristriophe bicalyculata</i>				v			
Amaranthaceae	<i>Amaranthus hybridus</i>				V			
Amaryllidaceae	<i>Allium cepa</i>				v			
Anacardiaceae	<i>Lannea acida</i>						V	
	<i>Rhus natalensis</i>						V	
Apocynaceae	<i>Plumeria rubra</i>				v			
Arecaceae	<i>Hyphaena petersiana</i>	Palmae					V	
Asparagaceae	<i>Asparagus racemosus</i>	<i>Longicladodius</i>			v			
Aspleniaceae	<i>Asplenium arcumontanum</i>			v				
Asteraceae	<i>Coryza gangreneux</i>				v	V		
	<i>Eryngium tirucalli</i>					V		
	<i>Rumex crispus</i> (invasive)					v		
Burseraceae	<i>Boswellia sacra</i>						V	
	<i>Commiphora Africana</i>					V		
	<i>Commiphora tanganyikensis</i>					V		
Boraginaceae	<i>Cordia africana</i>						V	
Capparaceae	<i>Cadaba farinose</i>					V		
	<i>Capparis fascicularis</i>					V		
	<i>Cleome gynandra</i>				v			
Calyophylliaceae	<i>Dianthus caryophyllus</i>				v			
Chenopodiaceae	<i>Chenopodium fasciculosum</i>					V		
Combretaceae	<i>Combretum molle</i>						V	
	<i>Terminalia brownii</i>						v	

Family	Plant Taxon	Synonym	P & A	Fern	CP	SHL	WP	MF
Commelinaceae	<i>Commelina benghalensis</i>		v		v			
Convolvulaceae	<i>Ipomoea batatas</i>		v		v			
Cucurbitaceae	<i>Cucurbita maxima</i>		v		v			
	<i>Kedrostis foetidissima</i>		v		v			
Cupressaceae	<i>Juniperus procera</i>							V
Cyperaceae	<i>Cyperus alopecuroides</i>		V					
Dichapetalaceae	<i>Tapura Africana</i>						v	
Euphorbiaceae	<i>Acalypha fruticosa</i>						V	
	<i>Euphorbia eyassiana</i>						v	
Fabaceae	<i>Boscia coriacea</i>					v		
	<i>Crotalaria agatiflora</i>					V		
	<i>Indigofera arrecta</i>					v		
Labiatae	<i>Leonitis grandiosa</i>	Lamiaceae				v		
Lilliaceae	<i>Aloe babatiensis</i>				v	v		
Malvaceae	<i>Abelmoschus esculentus</i>				v			
	<i>Grewia bicolor</i>						v	
	<i>Hibiscus cannanibus</i>				v			
Malphiaceae	<i>Morella salicifolia</i>							V
Mimosaceae	<i>Valchelia mellifera</i>	<i>Acacia</i>					V	
	<i>Valchelia xanthophloea</i>	<i>Acacia</i>					V	
Moraceae	<i>Ficus sur</i>						V	
Musaceae	<i>Musa capensis</i>				v			
Nyctaginaceae	<i>Commicarpus sp.</i>				v			
Nymphaceae	<i>Nymphaea stuhlmannii</i>		v		v			
Oleaceae	<i>Olea Africana</i>							V
Onagraceae	<i>Ludwigia leptocarpa</i>				v			
Plantaginaceae	<i>Stemodia sp.</i>						v	
Podocarpaceae	<i>Podocarpus latifolius</i>							V
Poaceae	<i>Andropogon greenwayi</i>		V					
	<i>Digitaria diagonalis</i>		V					
	<i>Zea mays</i>		V					
Rubiaceae	<i>Rubus rigidus</i>							V
Salvadoraceae	<i>Dobera glabra</i>						v	
	<i>Salvadora persica</i>						v	
Typhaceae	<i>Typha latifolia</i>		V					
Thelypteridaceae	<i>Thelypteris palustris</i>			V				
Ulmaceae	<i>Celtis Africana</i>					v		
Urticaceae	<i>Urtica dioica</i>						v	V

The nomenclature is after the African Pollen Database (APD 2010). Plant taxonomic groupings are listed as used in this study. P & A = Poaceae and Aquatics; Fern = Ferns; CP = Cultivated Plants; SHL = Shrubs, herbs and lianas; WP = Woody Plants; MF = Montane Forest; V = predominantly occurs; v = present. Taxa in bold **V** are highly represented in the pollen diagram and present-day vegetation.

Pollen zone-IV (220–135 cm; ~7800–2500 cal. yr. BP)

This record registers an abundant and wide distribution of Cyperaceae, Poaceae, and *Typha* across the entire zone. Compared to the previous zones, this precinct is

characterised by an increase in *Juniperus* at the base of the zone and termination of the same at the middle and upper sections of the zone. Woodland taxa are sparsely distributed within the entire zone, with contributions from *Acacia*, *Acalypha*, *Combretum*,

Commiphora, *Cordia*, *Dobera*, *Rhus*, *Salvadora*, *Solanum*, and *Terminalia*. Herbaceous taxa are largely represented by *Urtica* with very low pollen representation from Asteraceae, *Stemodia* and Amaranthaceae. Chenopodiaceae pollen is missing in this zone. Regarding phytolith classification, the zone is characterised by the abundant representation of Poaceae morphotype (Chloridoideae and Panicoideae) over other morphotypes. Woody plant morphotypes show a wide distribution by all taxa with spheroid scabrate showing high percentages. Herbaceous morphotype (spheroid psillate) shows a wide distribution along the zone. Parallelipiped psillate, parallelipiped scabrate, cylindroid psilate, and cylindroid scabrate show relative sparse distribution with increasing percentages along the zone. Cyperaceae morphotype (globar achinete) shows increasing percentages in the upper part of the zone. Total phytolith assemblages show decreasing percentages in this zone compared to previous and subsequent zones.

Pollen zone-V (135–65 cm; ~2500–700 cal. yr. BP)

The zone is distinguished by low pollen grain counts as depicted in KIS-II and KIS-III zones. Surprisingly, Cyperaceae is almost missing, and Poaceae is very low except for the upper section of the zone. Montane and woodland taxa are missing, and there is abundant Urticaceae, low percentages of Poaceae and *Typha*, a single count of Cyperaceae, and generally low percentages of most taxa. A total pollen count is very low in this zone. In this zone, the majority of morphotypic taxa are characterised by a slight increase in Poaceae (Chloridoideae and Panicoideae). Woody morphotypes (spheroid scabrate, spheroid verrucate, tracheids and irregular forms) show increasing trends at the base, while the case is opposite in the upper sections of the zone. Herbaceous morphotype (spheroid psillate) show a wide distribution along the zone. Parallelipiped psillate, parallelipiped scabrate, cylindroid crenate, cylindroid psilate, and cylindroid scabrate show increased percentages in the middle

part of the zone. Cyperaceae morphotype (achene) shows the highest percentages in this zone than any other zone. Total phytolith assemblages show the highest percentages compared to the previous zones and subsequent zone.

Pollen zone-VI (65–0 cm; ~700–0 cal. yr. BP)

This zone is recent to present one and is characterised by the representation of higher diversity of species compared to the previous zones. Cyperaceae and Poaceae remained dominant with less *Typha*, while *Vachelia*, *Salvadora*, and *Hyphaena* were abundant in the woodland category. Amaranthaceae/Chenopodiaceae and Asteraceae are highly registered at this zone. The total pollen count is high in this zone and so do the phytoliths (Figure 5). High abundance of Poaceae morphotype (Chloridoideae) and wide distribution of Panicoideae morphotype are witnessed in this zone. Woody plant morphotypes show a wide distribution of spheroid scabrate along the zone, while spheroid verrucate, spheroid globular, spheroid echinate (Palmae), tracheids, Polyhedrals, and irregular forms show increasing percentages towards the upper part of the zone. Herbaceous morphotype (spheroid psillate) shows a wide distribution and abundance along the entire zone, while parallelipiped psillate, cylindroid psillate, cylindroid sinuate, cylindroid scabrate, honeycomb polyhedral, and epidermal cells show relative increasing percentages at the upper part of the sub-zone. Cyperaceae morphotype (achene) shows increasing percentages from the previous sub-zone. Total phytolith assemblages show increasing percentages compared to the previous sub-zone (Figure 5).

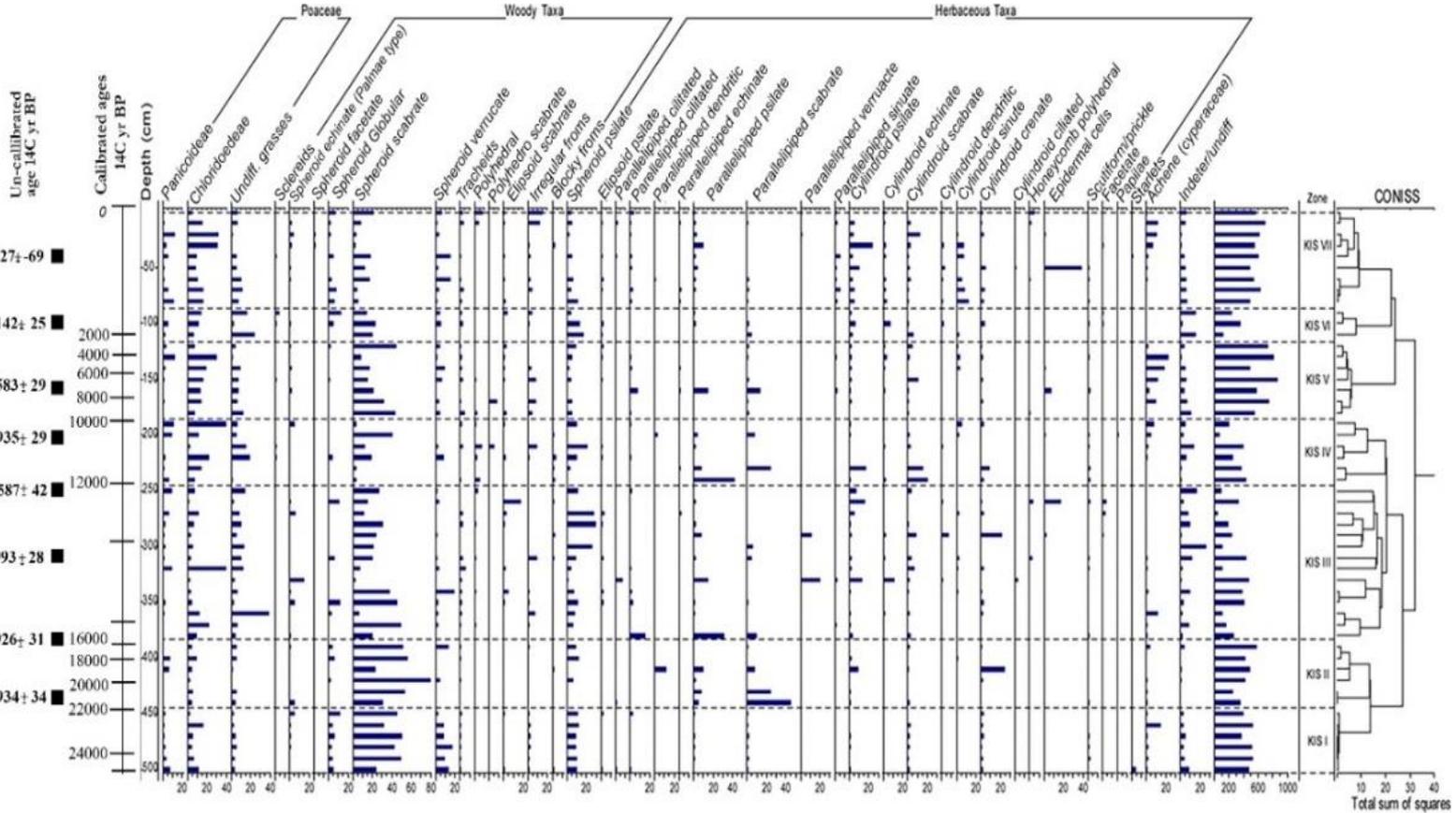


Figure 5: Phytolith percentage diagram of Kisimangeda core. Taxa are grouped according to their ecological preferences reflecting Poaceae, woody forest, and herbaceous plants that make the phytolith sum. Radiocarbon ages (un-calibrated and calibrated), depth scale, pollen zones, and CONISS cluster dendrogram are shown (Source: Field data 2019).

Discussion

Pollen analysis indicates significant variations in regional terrestrial vegetation composition in the catchment. Phytolith analysis shows that grasses and woody plants are both an abundant component of the vegetation in Lake Eyasi Basin, at least since the Late Pleistocene. The period between 24,383–22,895 cal. yr. BP is distinguished by high percentages of Cyperaceae and relatively high Poaceae, with sporadic increases of herbaceous taxa such as Amaranthaceae. This suggests a series of dry episodes within and around the basin (Mercader et al. 2021). The pollen data (Figure 4) suggests a series of relatively dry with limited humid periods manifested through the presence of drought-related herbaceous taxa (Amaranthaceae and *Aloe*) and woodland taxa (*Acalypha*, *Cordia*, *Commiphora*, and *Vachelia*). Amaranthaceae, as a family, are adapted to a wide range of climatic factors and soil conditions. They grow best in the sun or the light shade up to 1400 m altitude (Maundu and Tengnas 2005). *Sericocomopsis*, for example, which could have contributed to this pollen, thrives in a habitat rich in nitrogen and prefers soils that are rich in nutrients, although they can also grow on sandy and saline soils. They are drought-resistant and can even grow under very arid conditions (Maundu and Tengnas 2005). They are commonly used as good indicators of arid conditions in pollen palaeoenvironmental studies (Rucina et al. 2010, Muiruri et al. 2021). However, there are a series of very short phases of wet conditions as indicated by the presence of minor aquatic *Typha* and Asteraceae.

The presence of Poaceae, and in particular, common Cyperaceae, probably reflects the presence of a shallow lake. The Cyperaceae are a large pollen family of mostly herbaceous plants that are mainly associated with moist temperate to wet tropical regions with > 40 genera in Africa (Tieszen et al. 1979). They include sedges, which are mostly perennial or sometimes annual herbs. In East Africa, sedges are often found in wetlands (some are entirely aquatic) and along watercourses. There are also

terrestrial taxa associated with moist grasslands and forest margins. Most of the African species are also well distributed in moist to wet habitats such as fresh and salt marshes, ponds and lakeshores, meadows, bogs, fens, and savannahs. They often form an important component in the pollen record but are regarded as local taxa as most are restricted to aquatic ecosystems. Phytolith results demonstrate the presence of Chloridoideae type, which is adapted to warm and dry climatic or edaphic conditions (Tieszen et al. 1979, Twiss 1992). Such a scenario indicates the trend for climate variability over time between a diverse landscape that includes wetland and dryland grasses in agreement with pollen data. The spheroid phytoliths have also been described in the intercostal zones of the epidermis of Chloridoideae and Panicoideae, though they appear in small amounts (Twiss 1992). Undifferentiated grass morphotypes are well represented in the entire core, although they are prominent in the woody cover morphotype.

Subsequently, the period between 22,395–8,951 cal. yr. BP is distinguished by a significant expansion of grassy woodland types of vegetation with above-average percentages of grasses (mean value > 60 %) and sedges (mean ~40 %) (Figures 4 and 5). The woodland and herbaceous layer expanded within this part of the zone including concurrent wet (*Urticaceae*, *Asteraceae*, and *Justicia*) and dry taxa (*Aloe*, *Commiphora*, *Cordia*, *Grewia*, and *Vachelia*, etc). This suggests that the climate varied between wet and dry cycles, perhaps with long-lived droughts that might account for several horizons that lack pollen. The same is supported by the lack of *Urticaceae*, which occurs on forest edges and along the shores of rivers or lakes. The vegetation cover probably ranged from relatively closed settings (though with fewer tree densities) to open habitats with more dispersed trees. Dry cycles are also witnessed in this period by the presence of common to dominant drought-related montane forest taxa (*Juniperus*) and bushland taxa (*Commiphora* and *Vachelia* with a few *Cordia* and *Grewia*), along with

prominent *Amaranthaceae* at multiple levels. The possible source of *Juniperus* pollen in the Lake Eyasi Basin could be *Juniperus procera*, which is the only common species reported in East Africa today. Bussmann (1994) notes that *Juniperus procera* is included in a variety of different forests with a wide range of ecological conditions that range from very dry to fairly wet over a broad range of about 800 m. Other studies (Maundu and Tengnas 2005, Mumbi et al. 2008) describe *Juniperus* as a dry Afromontane forest tree that can also be found in transitional settings that range into semi-evergreen bushland and thicket and could have been the case in and around the Lake Eyasi Basin during the Last Glacial Maximum.

Between 8,951 cal. yr. BP to present, pollen and phytolith data are characterized by an increased diversity of floral species and high pollen count, which is greater than any other zone in the entire record. The Kisimangeda records show that the percentage of grassland pollen accounted for about 20–60 % (Figures 4 and 5), broadly supporting previously inferred changes from warmer, wetter conditions to drier environments during the Late Pleistocene to Holocene (Kariuki Githumbi et al. 2018, Muiruri et al. 2021).

Protracted dry periods can be inferred for this zone. They include drought-related taxa such as *Commiphora*, *Cordia*, *Cleome*, *Terminalia*, *Vachelia*, and termination of prominent *Juniperus* in the entire record, supported by herbaceous taxa such as *Amaranthaceae*, which appear, together with *Aloe*, *Crotolaria*, *Salvadora*, and *Stemodia*, sporadically and which vary from level to level. The grassland/woodland vegetation is supported by the woody cover morphotype. The wet related taxa include *Ficus*, *Asteraceae*, and conspicuously *Urticaceae*. Individual *Commiphora* species tend to prefer sandy, loamy-clayey and gravel soil types and grow well in open canopy settings and can also do well with low rainfall. *Capparis* sp., *Cassia* sp., *Commiphora*, and *Euphorbia nivulia* are variously associated with *Vachelia nilotica*, *Vachelia senegal*, and *Zizyphus* sp.

(Maundu and Tengnas 2005). In East Africa, most *Vachelia* is found in open or bushy grassland and woodland, especially on foothills and plains, where they are often the most dominant trees (Mercader et al. 2021), as in the Lake Eyasi Basin case today. *Hyphaene* (Palmae) pollen is variable in different levels in the upper part of the record. It was reported as comprising robust perennial taxa that can grow up to 20–30 m tall in a wide range of conditions, ranging from fertile to semi-arid. Their survival mostly depends on the presence of a high-water table. In East Africa, the Palmae is found from sea level to 1000 m altitude and are present in both low and high rainfall areas. An indication of variable wet and dry cycles within this period is demonstrated by the fluctuations of *Typha latifolia*, *Urticaceae*, and *Ficus*, most of which are indicators of wet conditions. *Typha latifolia* is a rhizomatous aquatic herb that grows in shallow (fresh) waters of lakes, swamps, dams and rivers (Ashley et al. 2011), and also indicates precipitation. This plant's extensive root system makes it very good for stabilising wet soil with taxa such as *Typha domingensis*, often forming a fringe around wetter papyrus swamps (Ashley et al. 2011). Sometimes it is overrepresented in the pollen record and is generally regarded as local aquatic taxa.

Though the climate was not the primary contributory factor to cultural change, there is a little doubt that it has played significant roles in the history of human evolution, particularly, in the early stages when human fortune depended on locally found ecological resources (Cohen et al. 2007, Bushozi et al. 2017). Changes in climate prompted the spatial distribution of ecological resources and it also discerned patterns in cultural response. However, the linking of climatic change with specific cultural transformations at the Lake Eyasi Basin has been challenging for many reasons. The reasons include severe climatic variability since the last interglacial maximum (Cohen et al. 2007), the synchronous nature of environment changes (Mumbi et al. 2008), and the existence of

uneven regional habitats (Mercader et al. 2021). The influence of environmental changes on humans and innovations lack high-resolution environmental proxies from archaeological contexts across East Africa. Likely, people inhabited the region from the Late Pleistocene through the Holocene, and they adapted to diverse and changing environmental conditions comprising steppe, woodlands and grasslands. However, intensive studies about ecological niches from the Last Glacial Maximum (MIS-2) to Holocene about human habitation are encouraged to make meaningful conclusions (Muiruri et al. 2021).

Conclusions

The Kisimangeda core provides a roughly ~24,500-year sedimentary record of vegetation change and archaeological histories in the Lake Eyasi Basin and the surrounding landscape. This is based on pollen, and phytolith records supported by radiocarbon chronology. These pollen and phytolith records from the Lake Eyasi Basin provide the foundation for environmental variability and pave the way for further studies. This is without belittling palaeoecological results from the nearby Mumba rock-shelter where phytoliths and pollen proxies have been recently retrieved and discussed (Mercader et al. 2021). That said, we appreciate building on the previous studies at Mumba by combining newly collated and analysed palynological and phytolith datasets generated to provide insights into the drivers of temporal heterogeneity in this semi-arid wooded grassland ecosystem and its temporal variability over the last 25 thousand years. However, analysed phytolith and pollen proxies do not demonstrate a relationship between plant habitats and the transition to the herding economy during the Mid-Holocene. Pollen-based and phytolith-based reveal complex relations between Pleistocene and Holocene vegetation, and they are not analogous to the gradual technological and behavioural changes revealed at Mumba and surrounding regions. A multi-proxy approach which combines several proxies, is highly

suggested for improving our interpretation and understanding of climatic changes, vegetation changes, and human adaptation strategies over time and space.

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