Vegetation dynamics of Kisima Ngeda freshwater spring reflect hydrological changes in northern Tanzania over the past 1200 years: Implications for paleoenvironmental reconstructions at paleoanthropological sites

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ABSTRACT

Kisima Ngeda (KN), a spring on the northern margin of saline Lake Eyasi, Tanzania, sustains an *Acacia-Hyphaene* palm woodland and *Typha* swamps, while the surrounding vegetation is semi-desert. To study the vegetation changes associated with this spring, which represents a plausible modern analog for the fossil springs documented in the nearby paleoanthropological and archaeological sites of Olduvai Gorge, we analyzed the pollen content of a 43 cm-long sediment core that documents vegetation changes since the last ~1200 years (from cal yrs. C.E. 841 to 2011). Our results show that (1) *Hyphaene* palms, which require meso-halophytic soil conditions were most abundant in the area of the coring site until cal yrs. C.E. ~1150 when the groundwater supplying the KN spring was likely lower than at present, allowing intrusions of saline lake waters. (2) From cal yrs. C.E. ~1200, a peat began to develop, the palm woodland was replaced by a Mimosaceae woodland, and the increased presence of *Typha* pollen indicates the presence of more wetlands. (3) From cal yrs. C.E. 1600, the groundwater level of the KN spring increased and reached its highest level in the last 1200 years. (4) Peaks of wetland expansion, which reflect increased groundwater flow and level in response to amplified rainfall in the recharge area (Mt Oldeani, Ngorongoro Highlands), occurred at cal yrs. C.E. ~1200–1400 and ~1650–2011. These outflows of groundwater at Kisima Ngeda were linked to the intensity and frequency of positive Indian Ocean Dipole (IOD) events, which trigger heavy rains in eastern Africa. We conclude that the Kisima Ngeda hydrological system, which has been active for more than 1200 years, responds rapidly to regional climate change driven by changes in the sea surface temperatures (SSTs) of the Indian Ocean. Yet, it is also capable of remaining active during dry intervals as inferred from the Kisima Ngeda record prior to cal yrs. C.E. 1200. Our results support the hypothesis that this type of system helped to maintain Plio-Pleistocene hominin populations and activities in the arid lowlands of the rift on a multi-decennial scale.

1. Introduction

The eastern branch of the East African Rift System (EARS) is characterized by lowlands formed by a succession of arid grabens where evapotranspiration largely exceeds precipitations and many lakes are saline or alkaline (Frostick, 1997). In these arid environments, vegetation structure and composition greatly varies according to soil water availability (Caylor and Shugart, 2006). Micro-habitats with denser woody cover and higher plant diversity than the surrounding xerophytic vegetation are observed near rivers, shallow aquifers, and groundwater sources (springs) (Friis et al., 2010; Greenway and Vesey-Fitzgeral, 1969). In an arid landscape, riparian environments increase habitat diversity, spatial heterogeneity and species diversity (Reynolds et al., 2016).

In the geological record, tufas (fossil springs) are often associated with abundant faunal remains including hominins and artefacts (Ashley

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et al., 2009), which suggests that springs and their associated micro-habitats may have offered valuable ressources to early humans (see review in Barboni et al., 2019). Ashley et al. (2009) showed an active hominin exploitation of spring resources at Olduvai in the early Pleistocene (~1.79–1.74 million years ago, Ma) with the presence of specific stone tools at the paleo-spring level. Magill et al., 2013a showed that freshwater springs were important for *Homo* and *Paranthropus* hominin species subsistence at Olduvai particularly during periods of low precipitation between 2.0 and 1.8 Ma, suggesting that places of foci like springs may have enhanced competition among species during dry periods (Barboni, 2014). Springs and their associated palm woodlands may also have played an important role in the ecology and locomotion of early hominins (Barboni et al., 2019). Springs may have served as hydro-refugia during arid climate periods (Cuthbert and Ashley, 2014), and facilitated geographical dispersion of hominins (Cuthbert et al., 2017). The Plio-Pleistocene record of springs, however, is discontinuous and lacks sufficient temporal resolution in any given area to study their dynamics and their impact on the ecosystems. How stable are the micro-habitats associated with the springs on the pluri-decennial to pluri-centennial time-scale? How does the groundwater discharge evolve on human (ca. 100 year) timescales? Is it continuous and stable, continuous and variable, or temporary?

Modelling studies have partially answered these questions (Cuthbert et al., 2019, 2017). They showed that in the EARS groundwater discharge dynamics dependent on climate, topography, and the geological structure of the basement (Cuthbert et al., 2019), making reconstructions of groundwater discharge dynamics complex. Except for the eastern part of the Afar Triangle and the northern part of Lake Turkana, Cuthbert et al. (2019)'s model indicates that in the EARS the time required for a groundwater system to re-equilibrate itself after a climate change, which depends on the distance between recharge area and local aquifers, is about 10–1000 years, ca. 500 years on average. In fact, the grabens of the eastern branch of the EARS include finely intertwined zones of short and long groundwater response time of 10–100 yr or 100–1000 yr (Cuthbert et al., 2019). If a given spring responds to climate change with a delay of 100–1000 yr or more, than such spring may indeed have played a critical role in mitigating climate impact on hominin dispersion and ecology. On the contrary, if the delay is in the range 10–100 yr, then it is unlikely that the spring was responsible for the development or maintenance of hominin activities in lowlands of the rift during dry periods. In this later case, the co-occurrence of hominin remains and springs at a given archaeological site would have to be treated with caution as it may be potentially biased by taphonomic processes and/or fossil collection strategies (Behrensmeyer and Reed, 2013). Real-world data offering adequate temporal resolution are therefore needed.

Olduvai Gorge is a world-famous site located in the Crater Highlands at the southern edge of the Serengeti Plains (Leakey, 1971, Leakey, 1966). The abundance of tufa mounds in paleosurfaces associated with anthropological and archaeological sites has been recognized at several Olduvai sites including FLK N (1.79 Ma) and FLK Zinj (1.89 Ma) (Ashley et al., 2010a, 2010b). Oxygen isotopic analyses of the tufas indicates groundwater was fresh (Ashley et al., 2010a), while paleolake Olduvai was saline/alkaline (Hay and Kyser, 2001). Phytolith and pollen data from FLK Zinj and FLK N paleosurfaces show that localized palm woodlands within an otherwise grass-dominated landscape were present near the springs (Arráiz et al., 2017; Ashley et al., 2010a; Barboni et al., 2010; Bonnefille, 1984). These paleo-springs have enabled the development of dense wooded vegetation despite the semi-arid paleoclimate (paleoprecipitations of 250 to 700 mm/yr, Magill et al., 2013a) and saline/alkaline waters of paleolake. The presence of paleo-springs is also suspected in the nearby paleontological sites of Laetoli and Peninj (Barboni, 2014), and many springs are still active today in this region of northern Tanzania, such as at Esere near Laetoli (Barboni et al., 2019), and at the northern edges of Lake Manyara (Greenway and Vesey-Fitzgeral, 1969) and Lake Eyasi (Albert et al., 2015). Springs are

therefore persistent hydrogeological features in the Crater Highlands region of north Tanzania, which modern representative may serve as analogs.

We focused our research on the spring of Kisima Ngeda locality at the northern edge of Lake Eyasi because this spring is associated to a palm woodland and is located at the edge of a saline/alkaline lake. Kisima Ngeda spring offers the opportunity to study the dynamics of an hydrosystem analog to the fossil springs of Olduvai Plio-Pleistocene hominins sites. Kisima Ngeda spring recharge occurs in the Ngorongoro Volcanic Highlands (Deocampo, 2002), like for Olduvai paleo-springs located about 50 km north of Lake Eyasi (Ashley et al., 2009). Rainwater infiltrates and is transported to the dry lowlands by moving groundwater. Groundwater flows down-slope in the sub-surface within pyroclastic beds (tuffs) between relatively impermeable basaltic beds (Norton, 2019). Under pressure, groundwater discharges within alluvium at the surface or near the surface in the lowlands at the foothills of Ngorongoro Volcanic Highlands (Norton, 2019; Shilling, 2013), but it is not clear yet if groundwater discharges through faults, fractures, or dikes as suggested elsewhere in the Ngorongoro area (Deocampo, 2002), or where the aquifer intersects the surface due to the slope topography (Norton, 2019). Faults were not directly observed in the area of Kisima Ngeda (Pickering, 1964), but the continued hydrological activity may have altered fault contacts and fractures and made them hard to see on the surface (Deocampo, 2002). At the foothills of Oldeani volcano, water table is high, and a dense wooded vegetation belt with tall *Acacia xantophloea* and *Hyphaene petersiana* palm trees develops despite the semi-arid climate (Fick and Hijmans, 2017) (Figs. 1, 2). Recently, nomenclature of *Acacia* has been revised; the botanical genus is now separated into *Vachellia* and *Senegalia* for Africa. For consistency with the names of vegetation and pollen types, *Acacia* will still be used here.

In order to study the influence of Kisima Ngeda spring on the vegetation, how this micro-habitat in the northeastern margin of Lake Eyasi possibly responded to past climatic changes, and its resilience, we analyzed the pollen content of a sediment core that was collected in one of the spring-fed swamps of this area (Fig. 1).

2. Study area

The eastern branch of the EARS, or Gregory Rift, contains a series of connected faults and grabens (Dawson, 2008). The Eyasi Basin located in the southern extremity of Gregory Rift between the Ngorongoro Volcanic Highlands and the Iramba Plateau is 160 km long and 30 km wide. It is composed of the East Eyasi Basin with Lake Eyasi (100 km long) and the West Eyasi Basin with Lake Kitingiri (60 km long) (Ebinger et al., 1997). The East Eyasi Basin is very flat and lies at 1030 m above sea level. It is bordered by the Eyasi Fault and the Nuguruman escarpment to the west, the Ngorongoro Volcanic Highlands to the north, and minor faulting of a basement warp to the east (Fig. 1) (Foster et al., 1997). East Eyasi Basin has an half-graben morphology; its modern position and morphology was likely acquired about 1 Myr ago (Foster et al., 1997). The northeast margin of the lake is bordered by the Neogene trachy-andesitic Oldeani volcano, which lies at 2800 m.

In the region encompassing East Eyasi Basin, Ngorongoro Volcanic Highlands, Salei Plains, and southern Serengeti Plains, the climate is very contracted due to significant relief variations. It is principally subtropical semi-arid in the lowlands, and warm temperate semi-arid in the highlands (Holdridge, 1967) with mean annual temperatures (TANN) of 15°–24 °C and mean annual precipitations (PANN) of 500–900 mm/yr (Fick and Hijmans, 2017). At the level of the East Eyasi Basin, the climate is sub-tropical arid with TANN of 22–24 °C and PANN of 550–650 mm/yr. The Ngorongoro Volcanic Highlands allow the local development of a colder and wetter climate, with TANN between 12 °C and 17 °C and PANN between 1100 mm/yr and 1200 mm/yr. Moderate to low rainfall and intense evaporation of about 2500 mm/yr in the lowlands has allowed the development of the alkaline saline lakes in the region (Deocampo, 2005).
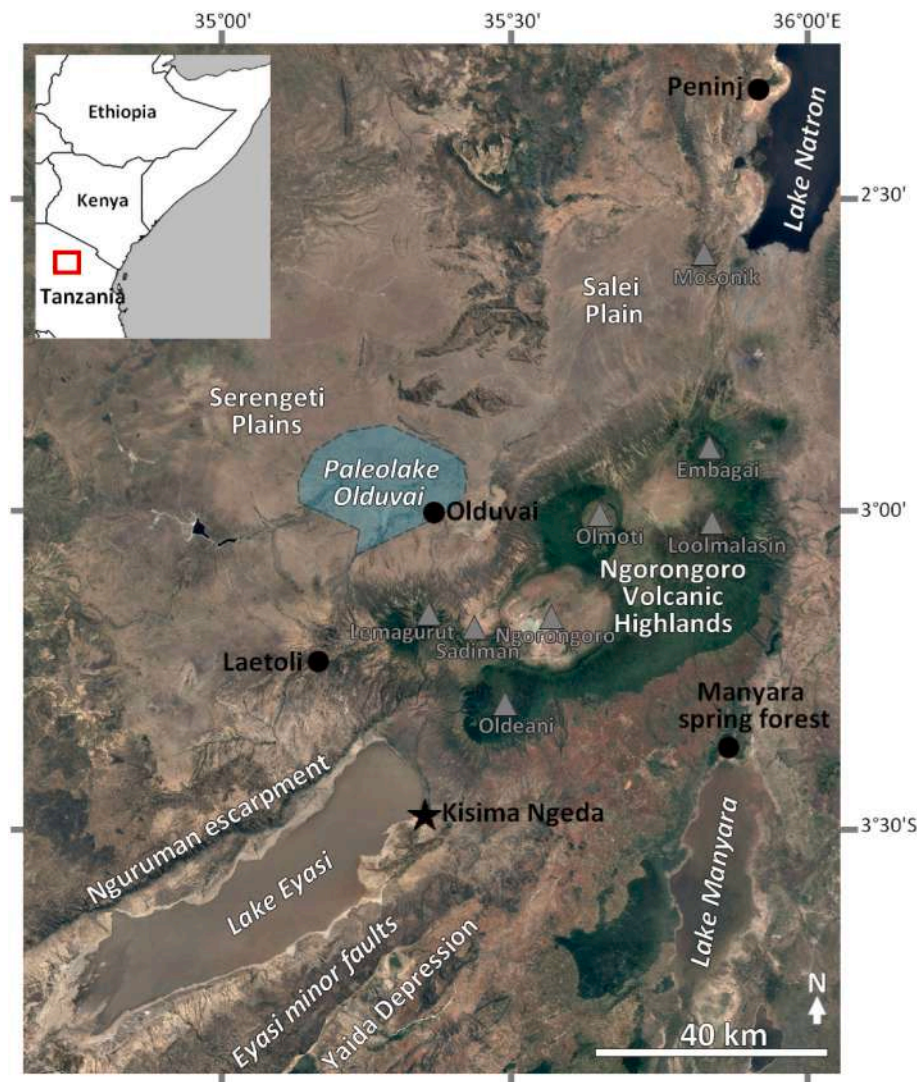
Fig. 1. Satellite image (Google Earth) of sector around the Ngorongoro Volcanic Highlands. Grey triangles are volcanoes, black circles are hominin paleontological sites (Ashley et al., 2009; Barboni, 2014) and Manyara spring forest, and black star is our study site. The approximate contour of paleolake Olduvai is for 1.75 Ma age. Lake Emakat is the crater lake at Embagai.

In the northeastern edge of Lake Eyasi, six vegetation zones can be defined based on the literature and our personal observations. (1) The Afromontane zone occurs above ca. 1600 m and 2450 m on the eastern and western wall of Mount Oldeani, respectively. It is constituted of Afromontane forest with trees of *Albizia gummifera*, several *Olea* species, and *Hagenia abyssinica* (Herlocker and Dirschl, 1972). The lower part of the Afromontane forest is delimited by an *Acacia lahai* high woodland belt. (2) The xerophytic zone covers most of the landscape below the Afromontane zone, and is constituted of *Acacia-Commiphora* bushlands. On the slopes of Mount Oldeani above ca. 1250 m, the *Acacia-Commiphora* bushlands include trees of *Commiphora madagascariensis*, *Acacia tortilis*, *A. mellifera*, and *A. senegal* and grasses are common (Herlocker and Dirschl, 1972). Below ca. 1250 m, bushes become more abundant than trees with decreasing elevation, and include *Acacia oerfota*, *Maerua trichophylla*, *Cordia rothii*, and *Commiphora* species. Grasses are scarce and plants more adapted to arid conditions are present such as *Adansonia digitata* (baobabs) and *Euphorbia candelabrum* (cactoid trees) (Herlocker and Dirschl, 1972). (3) The halo-xerophytic zone occurs on Lake Eyasi margins where salt mudflats bare of vegetation are numerous. Vegetation on the lakeshore is scarce and exclusively constituted of salt loving species such as *Suaeda monoica*, *Volkensinia prostrata*, *Neuracanthus scaber*, and *Senecio mesogrammoides* (Rea, 1935).

At the foothills of Mount Oldeani, between the *Acacia-Commiphora* bushlands and Lake Eyasi margin, a discontinuous vegetation belt can be identified on satellite images by its green color contrasting with the generally pale-yellow color of the surrounding xerophytic bushlands. This localized vegetation belt is formed by what we call a mesophytic zone, a halo-mesophytic zone, and an hydrophytic zone. (4) The mesophytic zone is a 0.5 km wide and ca. 7 km long discontinuous strip of groundwater-fed tall *Acacia xanthophloea* and *Hyphaene petersiana* palm woodland stretching along the north-eastern side of Lake Eyasi. In this part of the landscape, groundwater does not emerge but is close enough (ca. 1 m) to the surface to maintain dense woodlands with dense grass cover (in situ observation). (5) The halo-mesophytic zone is characterized by high concentration of *Hyphaene petersiana* palm trees (with more or less bare soil); *Hyphaene* favoring more salty/alkaline water than the *Acacia xantophloea* trees, the halo-mesophytic zone occupies the edge of the spring woodland facing the lake margin (in situ observations) (Fig. 3). (6) The hydrophytic zone corresponds to a complex of water ponds and swamps which develop where groundwater emerges at ground level. It is located between the halophytic and mesophytic zones. Cattail *Typha* sp. and sedges such as *Cyperus laevigatus* are present in the swamps along with the small water-loving tree *Sesbania sesban* (Fig. 2). Short herbaceous swamps with sedges (probably

Fig. 2. Satellite images (Google Earth) of the localized vegetation belt on the northeastern margin of Lake Eyasi with a zoom on the Kisima Ngeda area (Tanzania). Sw: swamp, Wg: wet grassland. The letters A and B are respectively the positions of the photo in Fig. 3.A and the photo in Fig. 3.B.

Cyperus laevigatus) and grasses (e.g. *Sporobolus spicatus, Diplachne fusca*) and *S. sesban* trees are also present (Hughes, 1992), as well as tussocks of the tall grass *Sporobolus consimilis* mixed with low sedges (probably *Cyperus laevigatus*) (Fig. 3).

3. Materials and methods

During the summer of 2011, we collected a 43 cm-long core with a Livingston-Bolivia drive rod piston corer in a *Typha* wetland of the hydrophytic zone near the groundwater-fed locality of Kisima Ngeda at 3°29′8.5″S and 35°20′53.5″E (elevation: 1030 m a.sl.) (Fig. 2). Core KN1A was described as black peat with plant debris in the upper interval from 0 to 31 cm, and light grey silty clay without any visible plant debris in the lower interval from 32 cm to 43 cm (Fig. 4). The contact of the upper and lower intervals is not horizontal, and may be the result of coring. Samples of 1 cm-thickness taken every 2 cm from the level 0-1 cm to 42-43 cm were used for pollen analyses. Level 30–31 cm was taken from the upper interval of the core.

Pollen grains were concentrated by acid digestion using HCl (33%, 4 h) to dissolve carbonates, HF (48%, 12 h) and HCl to remove fluosilicates, and KOH (20%, 10′) to remove humic acids. Sieving was done at 150 μm. Pollen were stained using safranin. Identifications are based on the pollen reference collection available at CEREGE (Aix-en-Provence, France) and pollen atlases (e.g. Bonnefille and Riollet, 1980). Pollen types are based on Vincens et al. (2007). Pollen percentages were calculated excluding undeterminable pollen grains and spores. In the lower part of the core, all samples have low (<150) counts due to poor preservation (Table S1). These samples were not excluded from the analysis given their importance in documenting paleovegetation before the peat inception. However, we calculated confidence intervals associated with percentages of *Typha* in Fig. 7 to consider the potential bias linked to such low pollen counts. Calculation of confidence intervals follows Suchéras-Marx et al. (2019).

Pollen concentrations were not measured and results presented here are uniquely based on pollen taxa relative abundances. Pollen grains for ^{14}C dating were obtained by the same chemical treatment, without using ethanol and safranin to avoid carbon contamination. We chose to date pollen concentrates rather than bulk organic matter to minimize the reservoir effect (Li et al., 2012). The radiocarbon age of material was determined by Beta Analytic (Miami, Florida) and ARTEMIS instrument (Saclay, France) (Table S2), at depths 22–23 cm and 30–31 cm in the upper part of the core, and at 37.5–38 cm and 42–43 cm in the lower part of the core (Fig. 4). Calibration of the radiocarbon ages (Table S2) and age model (Table S3) were carried out with the R package CLAM (Classical Age-Depth Modelling of Cores from Deposits) (Blaauw, 2010), using the IntCal20 calibration (Reimer et al., 2020), a linear interpolation between dated levels and 95% confidence ranges, and the option to have the results in cal yrs. C.E. A hiatus was inferred at 31 cm, and the date of cal yrs. C.E. 2011 ± 1 (year of core sampling) at 0 cm. Based on the sedimentary facies, the lower interval of the core is probably playa lake margin sediments. We added a hiatus because it is possible that there are erosion surfaces and gaps in this part. Hence, it is necessary to remain cautious with the age model of this lower core interval.

Pollen counts are given along with ecological and physiological information about the plant taxa they represent (Table S1). Information about plant habitus, plant preferred ecological zone, salt tolerance, life cycle (for herbaceous taxa), and leaf phenology (for arboreal taxa) were obtained from the literature ("African Plant Database", 2019; Agnew
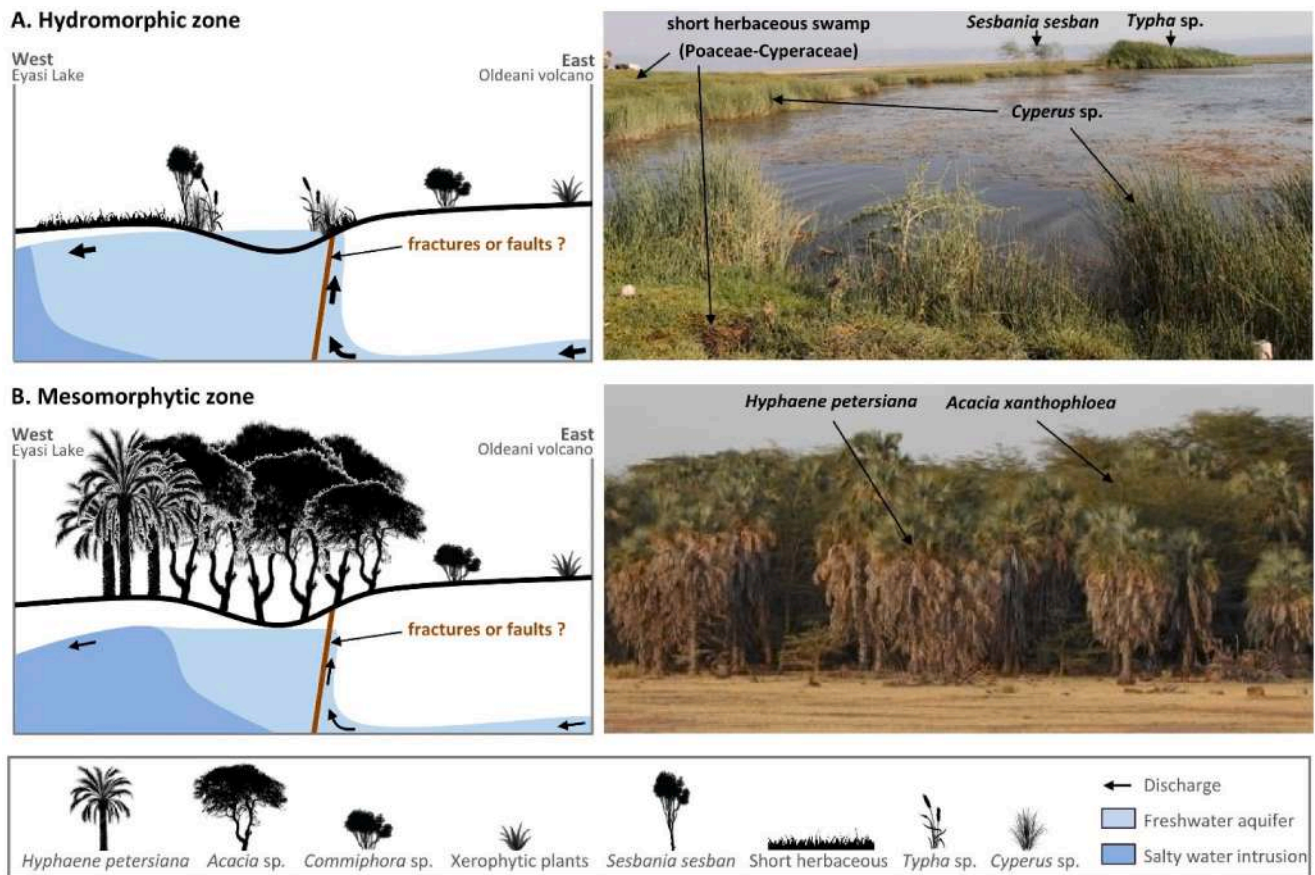
Fig. 3. Theoretical drawing showing vegetation according to the groundwater level which controls the spatial extent of the hydrophytic (A) and mesophytic (B) zones. Photographs show how the two zones may look like in the area of Kisima Ngeda (photographs taken by D. Barboni and G.M. Ashley in 2011).

and Agnew, 1994; Dale and Greenway, 1961; Greenway and Vesey-Fitzgeral, 1969; Loth and Prins, 1986). The ecological and physiological traits indicated for the pollen taxa of KN1A core correspond to plant species potentially present in the study area. For example, *Albizia* pollen likely represent the deciduous *Albizia anthelmintica,* that is currently present in the spring woodland at the northern edge of Lake Manyara (Greenway and Vesey-Fitzgeral, 1969). Pollen percentages by ecological zones (cf. Study area) and by plant habitus were calculated excluding pollen types with undifferentiated ecological zones and plant habitus (Table S1). Cyperaceae, which occur in both the hydrophytic and mesophytic zones (without being able to distinguish the different species by their pollen morphology) were excluded from synthetic diagrams in Fig. 6. Palaeoenvironmental interpretations inferred by percentage variations of dominant pollen types are based on the ecology of the different plants and floristic associations presented in the study area. All taxa were considered for our interpretations (Fig. 5).

4. Results

4.1. Pollen preservation, representation and age model

Core KN1A produced an abundant pollen record with well-preserved pollen grains particularly in the upper part of the core (above 30–31 cm). In total, 50 different pollen types were identified (Table S1). The age model indicates that the core records about 1200 years, and that a gap of about 330 years is possible between the upper (peat) and lower (silty) parts of the core (Fig. 4).

Pollen assemblage of the top core (0-1 cm) is consistent with the vegetation surrounding the coring site in 2011. Pollen of *Typha* (54%) and Cyperaceae (34%) are abundant, typical of *Typha* sp. and *Cyperus* sp.

swamps, but pollen of *Hyphaene* are not recorded (Fig. 6), despite the presence of some palm trees about 50 m from the site (Fig. 2). The small hydrophytic tree *S. sesban* present at the site accounts for 0.1% of the total pollen sum. Thus, *Hyphaene* and *S. sesban* are likely underrepresented in the pollen assemblages. Poaceae in the surrounding short herbaceous swamp near the site only account for 8% of the total pollen sum. The pollen signal of allochthonous plants include *Suaeda monoica*-type (1%) from the salty lake margins, *Acacia* (2%) from the nearby (ca. 1 km away) tall *Acacia xanthophloea* woodland, and *Maerua*-type *crassifolia* (0.1%) from the surrounding xerophytic bushland.

4.2. Pollen zones and paleoenvironments

4.2.1. Pollen zone A: below 31 cm (cal yrs. C.E. 841 to cal yrs. C.E. 1282)

This zone is characterized by relatively high percentages of *Hyphaene* (>12%), low percentages of Poaceae (<12%), low taxonomical diversity (6 to 9 taxa at the most) and a silty clay lithology (Fig. 5). Pollen from the halo-mesophytic zone represent 17% to 61% (Fig. 6). Given the very low capacity of palm pollen to travel, finding high percentages of *Hyphaene* implies palms were growing close to the coring site at that time. The site was likely a *Hyphaene* palm woodland within a halo-mesophytic zone, where vegetation has access to fresh groundwater while still being very much influenced by the salty water of Lake Eyasi. (Fig. 3). The presence of this palm woodland also suggests a low water table. Pollen zone A can be divided into three subsets.

(1) Sub-zone A1, from the base of the core to 38–39 cm (cal yrs. C.E. 841 to cal yrs. C.E. 966), has highest percentages of *Hyphaene* (>37%), which is incompatible with a wetland setting (Fig. 5). Instead, it suggests a dense *Hyphaene* palm woodland almost
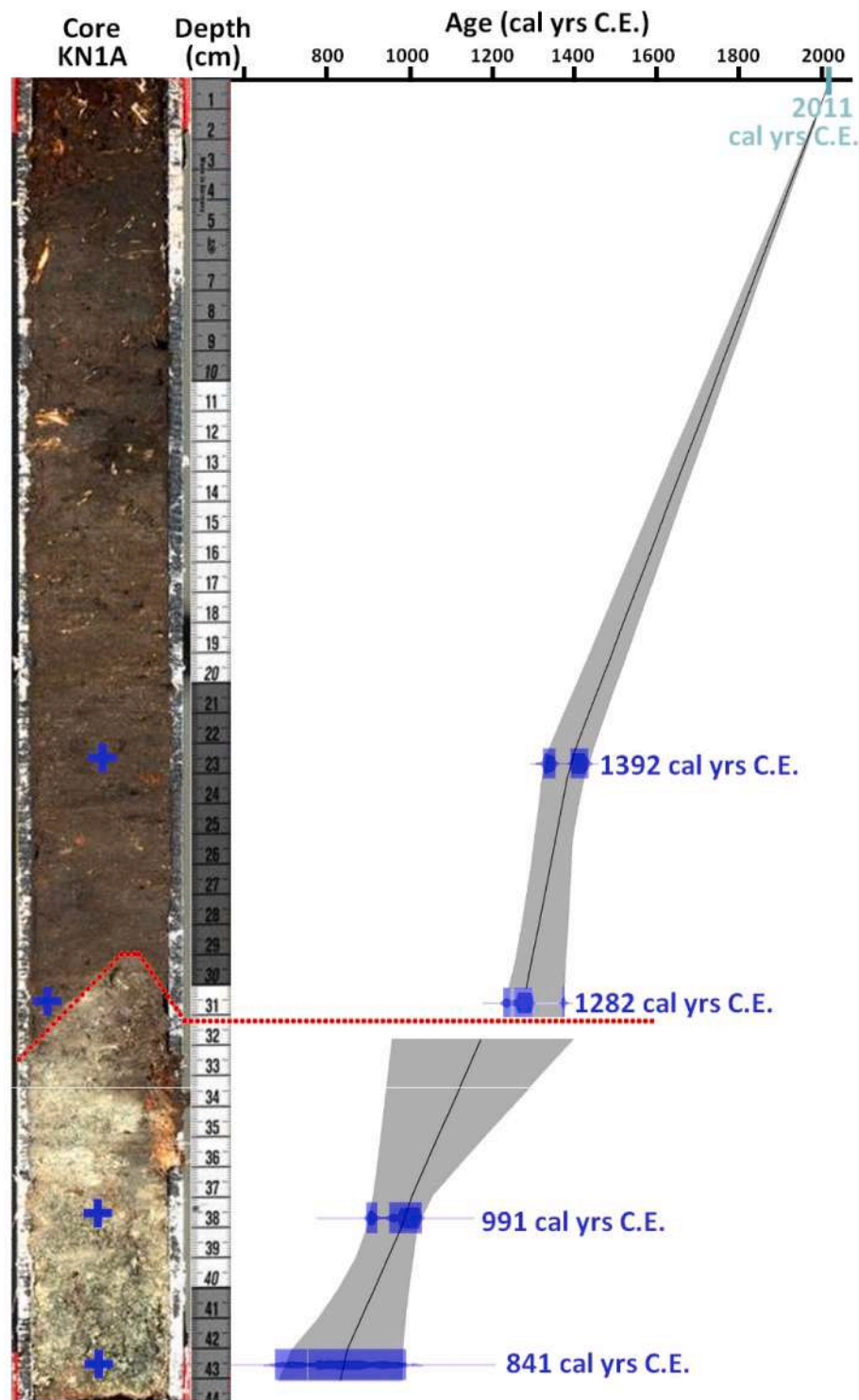
Fig. 4. Photograph of core KN1A cut in half with age models in cal yr C.E. based on ^{14}C dating of concentrated pollen grains. Calibration of the radiocarbon ages and age model were carried out with the R package CLAM (c.f. Materials and methods). Blue crosses indicate position of samples for ^{14}C dating. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

devoid of grasses within a persistent halo-mesophytic zone. *Typha* indicates the presence of fresh water, but its low percentage (<20%), the high abundance of *Hyphaene* (>37%) that cannot live in hydrophytic zone, and the silty clay lithology imply that fresh-water swamps were present not directly at the site. The groundwater discharge activity at the coring site was likely low at that time.

(2) Sub-zone A2, from 36 to 37 cm to 34–35 cm (cal yrs. C.E. 1024 to cal yrs. C.E. 1091) shows a decrease of *Hyphaene* pollen (<21%, but still >10%) correlated with a significant increase of *Typha* pollen (35%), while lithology remains silty clay (Fig. 5). This reflects the development of a short-lived wetland at the detriment of a part of the *Hyphaene* palm woodland. We prefer to talk here about "short-lived wetland" and not "wetland" or "swamps"
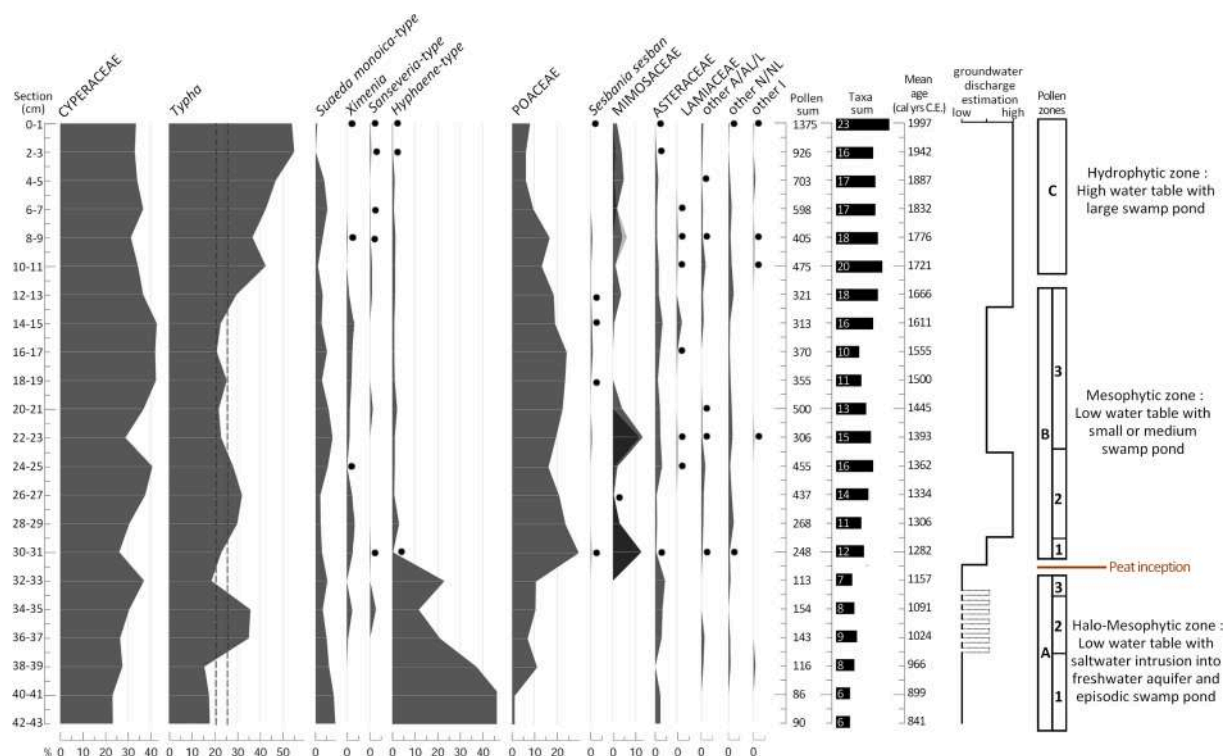
Fig. 5. Pollen diagram with major pollen types, pollen zones, and interpretation of the pollen signal. Mimosaceae include *Albizia*-type in black, *Acacia* in grey and *Calpocalyx*-type *letestui* in light grey. Black dots indicate pollen percentages <0.5%. Groundwater discharge estimation is based on percentage of pollen.
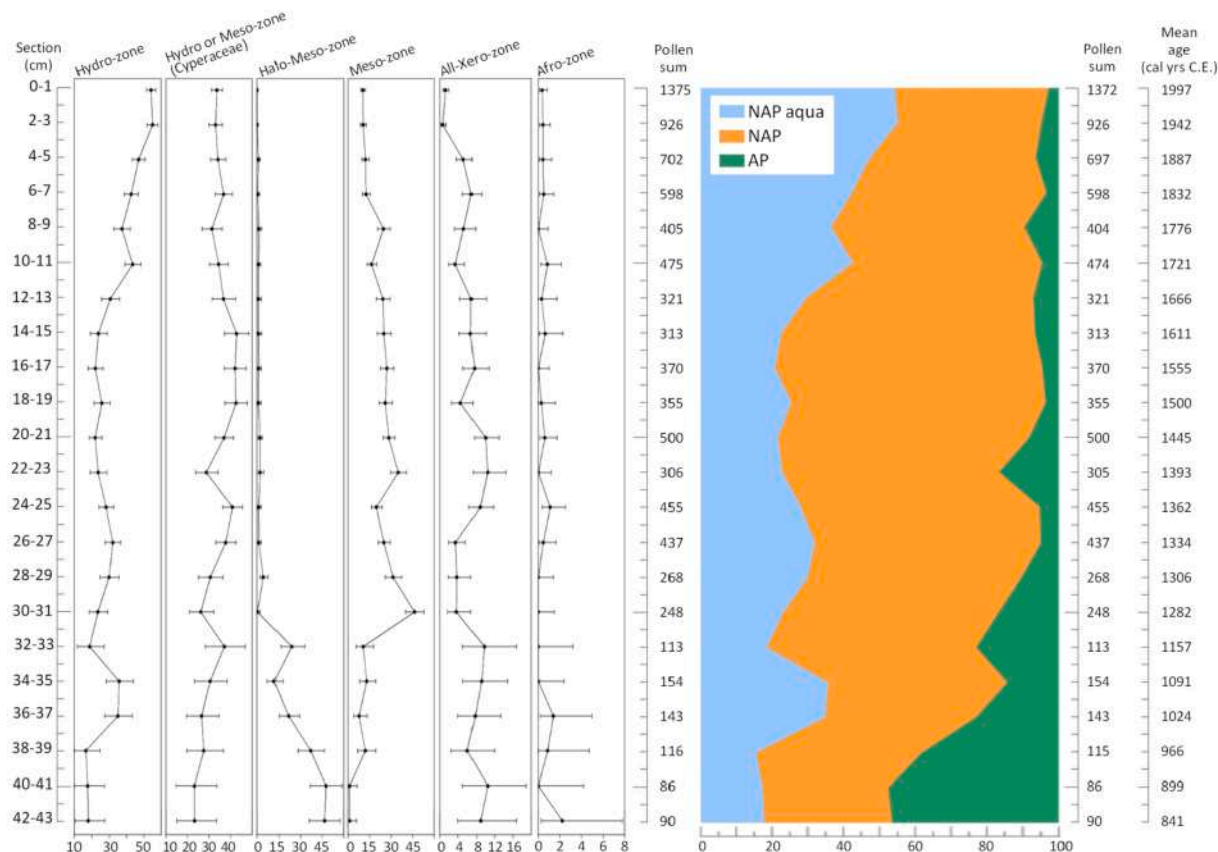

Fig. 6. Synthetic pollen diagrams by ecological zones (Ubiquist excluded, cf. Table S1) and by pollen habitus (undifferentiated excluded, cf. Table S1). AP: arboreal plants; Halo: halophyte; Hydro: hydrophyte; Meso: mesophyte; NAP: non-arboreal plants; NAP aqua: non-arboreal aquatic plants; Xero: xerophyte. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

because *Hyphaene* pollen is still represented by >10% which implies a maintenance of the halo-mesophytic zone. This indicates moderate and intermittent groundwater discharge activity at the coring site.

(3) Sub-zone A3, at 32–33 cm (cal yrs. C.E. 1157) shows 23% of *Hyphaene* but reduced relative abundance of *Typha* (<20%), and an important proportion of pollen from the halo-mesophytic zone (40%) as observed earlier (sub-zone A1) The site reverts to a dense *Hyphaene* palm woodland almost devoid of grasses within a persistent halo-mesophytic zone with fresh-water swamps present not directly at on the site. it is likely that the groundwater discharge activity at the coring site became low again.

4.2.2. Pollen zone B: 30–31 cm to 14–15 cm (cal yrs. C.E. 1282 to cal yrs. C.E. 1911)

This pollen zone corresponds to a major change in lithology. Between 32 and 33 cm and 30-31 cm (dated cal yrs. C.E. 1157–1282) an organic-rich peat starts developing and pollen composition changes drastically. Pollen zone B is characterized by very low percentages of *Hyphaene* (<3%), Poaceae between 16% and 30%, and *Typha* between 21% and 32% (Fig. 6). Compared to pollen zone A, the proportions of pollen representing the mesophytic zone (24% to 46%) and the hydrophytic zone (22% to 32%) are higher, at the expense of thoe of the halo-mesophytic zone, which decrease sharply (<5%). This shows that the coring site, which was previously covered with palm trees within a halo-mesophytic zone (before cal yrs. C.E. 1282, 30–31 cm), became rapidly transformed into a grassy, species-rich woodland with trees, shrubs, and lianas afterwards. After cal yrs. C.E. 1282, various species of *Acacia, Albizia, Celtis, Combretum, Erythrococca, Macaranga,* and *Ximenia* are recorded. They could thrive likely because more fresh water became more accessible to the vegetation (Fig. 5 and Table S1). This could be due to a higher lake level or to a higher flow and discharge of fresh groundwater after cal yrs. C.E. 1282. We can rule out the hypothesis of a higher lake level because, if Lake Eyasi were higher, then it is unlikely that pollen grains of *Hyphaene* palms would have been preserved in greater abundance than pollen of the salt-loving species such as the Amaranthaceae *Suaeda monoica* and *Volkensinia prostrata,* which thrive today on the salty lake margins. The hypothesis of a higher flow and discharge of fresh groundwater above 30–31 cm (cal yrs. C.E. 1282) should be favored because when pressure of fresh water on the salt water aquifer of the lake is high, salty water cannot penetrate inland (e.g., Fan et al., 1997), leading to less saline soil conditions and, therefore, to the reduction of the meso-halophytic palm zone. All this implies at least a moderate activity of the flow and discharge of fresh groundwater above 30–31 cm (cal yrs. C.E. 1282). The proportions of pollen from the hydrophytic zone are low (<32%) compared to the present (>54%) and the proportions of pollen from the mesophytic zone are high (>24%) compared to the present (<10%) (Fig. 6). The freshwater swamp was therefore likely smaller than at present. It is possible to divide this pollen zone B into 5 subsets.

(1) Sub-zone B1, at 30–31 cm (cal yrs. C.E. 1282), is characterized by high percentages of *Albizia* (>10%), a species with low pollen dispersing capacity. A grassy *Albizia* woodland with a low arboreal cover (arboreal pollen ca. 15%). This type of vegetation and the high proportion of pollen from mesophytic zone (>45%) (Fig. 5) imply moderate activity of the flow and discharge of fresh groundwater.

(2) Sub-zone B2, from 28 to 29 cm to 24–25 cm (cal yrs. C.E. 1306 to cal yrs. C.E. 1362), shows a significant decrease in the percentage of *Albizia* (<3%) and an increase in percentage of *Typha* (>28%) compared to B1. This indicates a development of the hydrophytic zone at the detriment of the mesophytic zone linked to an increase in the activity of groundwater discharge: moderate at 28–29 cm (*Typha* < 25%) and high from 26 to 27 cm to 24–25 cm (*Typha* > 25%). With arboreal pollen <15%, the grassy *Albizia*

woodland becomes a grassland with few trees still present (Fig. 6).

(3) Sub-zone B4, from 22 to 23 cm to 12–13 cm (cal yrs. C.E. 1445 to cal yrs. C.E. 1611), the percentage of *Typha* is <25% except at 12–13 cm (30%), which we interpret as a return to moderate groundwater discharge activity with an increase in the activity of groundwater discharge at 12–13 cm (Fig. 5). The grassland is still present (arboreal pollen <15%) (Fig. 6). Finally, between the beginning and the end of B4, there is a replacement of *Albizia* pollen by *Acacia* pollen.

4.2.3. Pollen zone C: 10–11 cm to 0–1 cm (cal yrs. C.E. 1721 to cal yrs. C.E. 1997)

This pollen zone is in line with the observations made in pollen zone B: organic-rich peat and *Hyphaene* < 3% (Fig. 5). Consequently, as for pollen zone B, the fresh groundwater had greater influence on vegetation than the salty water from Lake Eyasi. The pollen zone C differs to zone B by the percentages of Poaceae and by percentages of *Typha* > 37%. The percentage of *Typha* increases from 30% at the end of pollen zone B to 43% at the beginning of pollen zone C. The percentage of *Typha* tends to increase with time with values around 55% at the core top. There is a significant increase of pollen from the hydrophytic zone at the detriment of pollen from the mesophytic zone (Fig. 6). All this shows that groundwater discharge flow and, consequently, the size of the wetland (the hydrophytic zone) thus appear to have increased from cal yrs. C.E. 1721 to the present, where they are at their maximum. This marks phases where the activity of groundwater discharge becomes high. In the mesophytic zone, there is always a grassland with some trees.

4.3. Pollen signal of regional vegetation

The pollen of Afromontane taxa represent <3% in all levels and confidence intervals associated to the percentages are too high to allow interpreting differences between levels (Fig. 6). The pollen signal of all xerophytic zones, reflecting the regional aridity in the lowlands, shows high values (>6%) in pollen zone A, then globally low values in B1 and B2 (<3%). Finally, at the base of B3, values are at 10.5% and then tend to decrease progressively to the top of C (~1%).

5. Discussion

5.1. Comparison with other regional records

An increase of fresh groundwater flow and discharge is expected after increased rainfall in the highlands (Cuthbert and Ashley, 2014). It is therefore possible to compare KN pollen record with other regional records of past hydroclimate.

Before cal yrs. C.E. 1200, a generally dry interval of ~400 years is recorded at Lake Emakat (partially) (Ryner et al., 2008), Lake Naivasha (Verschuren, 2001), Lake Edward (Russell and Johnson, 2005), and is also observed in the spring activity of Kisima Ngeda (as inferred from the percentage of *Typha* pollen in KN1A core). Indeed, this period is characterized at Kisima Negeda by the presence of *Hyphaene* palm woodland, a low water table and a flow of fresh groundwater too low to stop the advance of saltwater intrusion from the lake into the land. We note, however, that this dry period seems to be interrupted by intermittent decadal wet episodes between cal yrs. C.E. 1000 and cal yrs. C.E. 1100 at Kisima Ngeda, with a temporary reduction of the salty influence and the establishment of short-lived wetlands. Such wet episodes can also be observed at L. Edward and L. Naivasha but rather between cal yrs. C.E. 900 and cal yrs. C.E. 1000. (Russell and Johnson, 2007; Verschuren et al., 2009) (Fig. 7). This age shift probably indicates that the age model for the lower part of the core (below 31 cm) (Fig. 4) slightly overestimates the true ages. This would not be surprising because the age model of the lower part is less well constrained than that of the upper
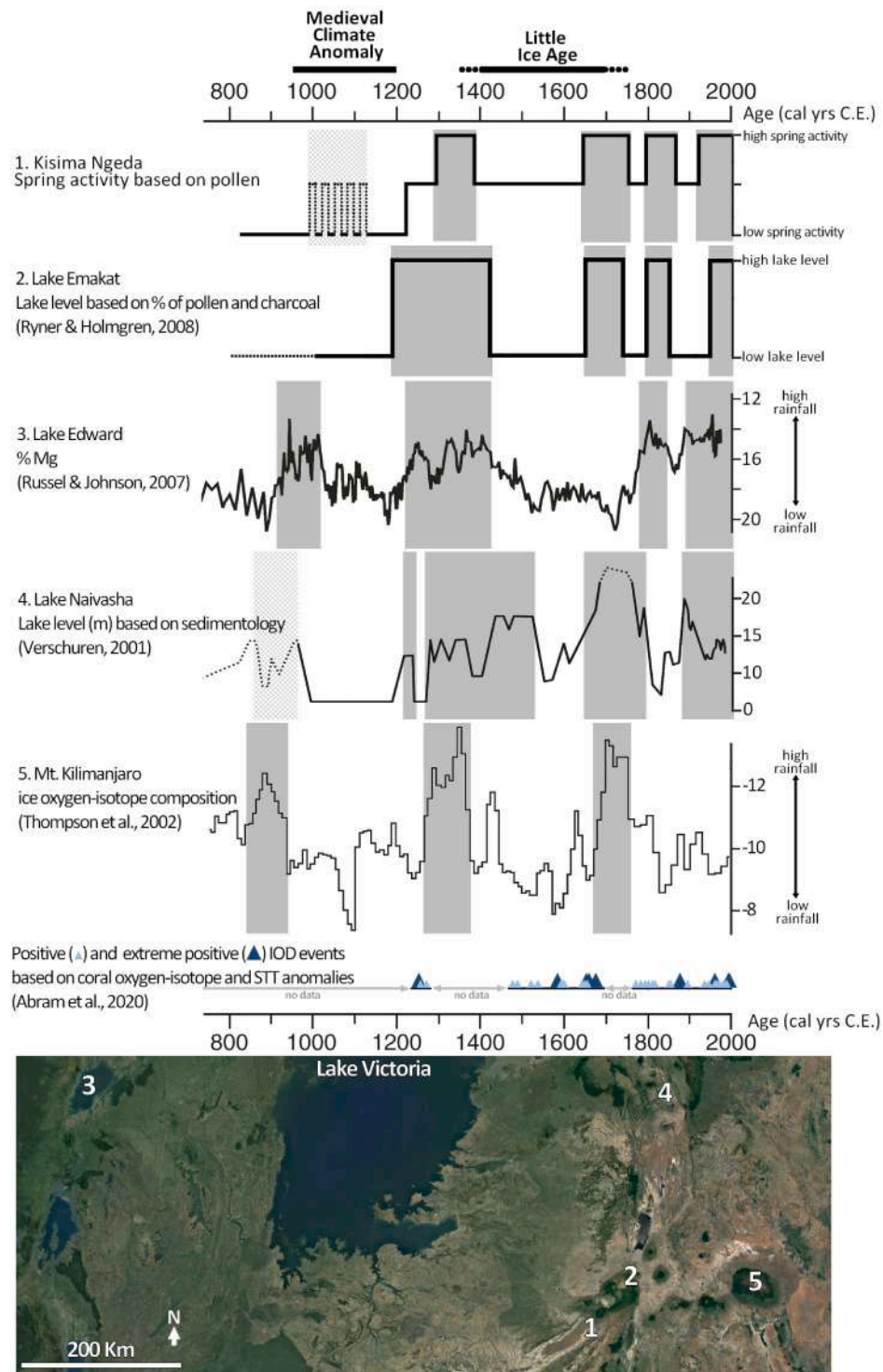
Fig. 7. Spring activity of Kisima Ngeda based on pollen percentages over the past 1200 years compared with other regional proxy records reflecting moisture variations and Indian Ocean Dipole (IOD) events. Light grey stripes indicate the "wet" phases.

part. Altogether this seems to mark a generally dry period well recognized in the northern hemisphere as the (warmer than normal) Medieval Climate Anomaly (MCA). In Africa, the MCA (~cal yrs. C.E. 950–1200) is characterized by important changes in the hydroclimate, with strong regional differences. The latest data compilation shows that Eastern Africa was drier south of the equator and west of a SSW-NNE line separating the drier inland sites (L. Edward, L. Victoria, L. Masoko, L. Tanganika, Kismia Ngeda included) from the wetter coastal eastern African sites during the MCA (L. Challa, L. Malawi) (Lüning et al., 2018).

The peat inception at Kisima Ngeda at cal yrs. C.E. ~1200 (between cal yrs. C.E. 1157 and cal yrs. C.E. 1282) is concomitant with the beginning of a wet (pluvial) episode at L. Emakat, L. Edward, L. Challa, and L. Naivasha around cal yrs. C.E. 1200 (Russell and Johnson, 2007; Ryner et al., 2008; Tierney et al., 2013; Verschuren et al., 2009), and with peat inceptions at other groundwater-fed localities in Kenya such as the Solai (Goman et al., 2017) and Loboi swamps (Ashley et al., 2004; Driese et al., 2004). This marks the end of the MCA.

From ~cal yrs. C.E. 1200 to ~cal yrs. C.E. 1400–1450, the

development of a peat and a wooded grassland at Kisima Ngeda occurs while all neighboring lakes record high levels (Russell and Johnson, 2007; Ryner et al., 2008; Verschuren, 2004, 2001) and high δ^{18}O is measured at Kilimanjaro (Thompson et al., 2002), which the authors interpreted as increased rainfall (rather than cooling) (Barker et al., 2001; Rozanski et al., 1993). Between ~cal yrs. C.E. 1400–1600, the groundwater discharge at Kisima Ngeda is moderate but sufficient to preserve the wetland bordered by grassland. This interval corresponds to low lake level at L. Emakat and drought inferred at L. Edward (Russell and Johnson, 2007) and at other small lakes in western Uganda (Russell et al., 2007) and Malawi (Brown and Johnson, 2005; Johnson et al., 2001; Johnson and McCave, 2008), but to high lake level at L. Victoria (Stager et al., 2005) and L. Naivasha (Verschuren et al., 2000; Verschuren, 2001). Lake Challa, L. Masoko and L. Tanganika, do not match any of the pattern cited before, and show contrasting and varying patterns over this ~cal yrs. C.E. 1400–1650 time period (Tierney et al., 2013). Hence, at the scale of Eastern Africa the Little Ice Age (LIA), which seems to be recorded from as early as cal yrs. C.E. 1350 to as late as cal yrs. C.E. 1750 with a core period between cal yrs. C.E. 1400 and cal yrs. C.E. 1700 (Table S4), shows very contrasting patterns. At Kisima Ngeda, the LIA is marked between 1400 and 1600 by a period of moderate spring activity between two periods of high spring activity. Later on, between cal yrs. C.E. 1650 and cal yrs. C.E. 1750, while drought is recorded in the western rift zone at L. Malawi, L. Masoko, L. Tanganika, and L. Edward, a pluvial interval is recorded in the eastern rift zone at L. Naivasha, L. Emakat, and in the ice of Kilimanjaro, which marks the end of LIA in this part of the rift. This interval corresponds at Kisima Negeda to a period of high spring activity that marks the beginning of the swamp expansion. After cal yrs. C.E. 1750, the activity of the spring remains high, which correlates with L. Emakat and L. Edward (Russell and Johnson, 2007; Ryner et al., 2008) but is not correlated with L. Naivasha level and Kilimanjaro δ^{18}O record. From cal yrs. C.E. ~1750, spring activity has been increasing at Kisima Ngeda and has not weakened since (Fig. 7), despite marked droughts recorded throughout the African continent in the 1820s and 1830s and since 1990 (Lyon and DeWitt, 2012).

As shown by the regional comparison attempted here and more thoroughly elsewhere, trends between different site archives are rarely shared over the last 1200 years (i.e., over the entire period) in Eastern Africa (Nash et al., 2016; Tierney et al., 2013). The Kisima Ngeda record of spring activity over this period is sometimes consistent with sites in the south and west (e.g., Masoko, Tanganika, Edward) and sometimes with the more coastal sites (e.g., Challa and Naivasha) depending on the time interval considered, but it also shows no signs of any early-19th century drought, and no signs either for other severe drought events in the final decades of the 19th century like in the Kenya Rift Valley (Nicholson et al., 2012; Lyon and DeWitt, 2012), or in Ethiopia or elsewhere in northern Tanzania where as much as 40–75% of pastoralist Maasai may have succumbed (Iliffe, 1987). The climate mitigating effect of the Kisima Ngeda spring needs to be examined in more details. Nevertheless, the spring activity of Kisima Ngeda is well correlated with the level of L. Emakat (Fig. 1). This relatively small 3 km-wide lake enclosed in a 6 km-wide crater on the Ngorongoro Volcanic Highland is hydrological closed and fed directly by rainfall. The inter-annual level variations of Lake Emakat are directly related to rainfall variability on Ngorongoro Volcanic Highlands (Frame et al., 1975; Ryner et al., 2008) that feed wetlands of northeastern margin of Lake Eyasi (Ryner et al., 2008; Thompson et al., 2002; Verschuren, 2001; Verschuren et al., 2000). The good temporal correlation between the activity reconstruction of KN1A spring and the paleo-levels of Lake Emakat shows that the response of the KN1A spring (discharge peaks) to regional rainfall variations in the highlands is very fast (decadal scale). Finally, although spring activity shows general trends that are inverse to regional lowland aridity (e.g. part 4.3), but the detail of the spring activity cannot be explained by regional variations of aridity in lowland.

5.2. Spring vegetation response to IOD positive events

It is now established that precipitation in Eastern Africa is strongly correlated with sea surface temperatures (SSTs) of the Indian Ocean (Latif et al., 1999; Tierney et al., 2013), and that the Indian Ocean Dipole (IOD) is responsible for extreme precipitations in Eastern Africa and coeval extreme droughts in Indonesia (Saji et al., 1999). IOD is an air-sea interaction process independent of El Niño/Southern Oscillation which is characterized by an anomalous west to east gradient of decreasing (instead of increasing) SSTs as well as anomalous winds and sea heights in the tropical Indian ocean (Saji et al., 1999; Webster et al., 1999). According to the δ^{18}O record in the corals from the southern Mentawai Island chain, offshore of Sumatra, several positive and extreme positive IOD events occurred during the last millennium (Abram et al., 2020). Fig. 8 shows that peaks of *Typha* pollen, which we interpreted as wetland expansion following increased groundwater flow and discharge, systematically occurred several years after extreme-positive and positive IOD events. The increased frequency of IOD events since cal yrs. C.E. 1500 may be responsible for the wetland expansion at Kisima Ngeda. Positive IOD events may also be observed on the Kilimanjaro δ^{18}O ice record (Thompson et al., 2002), if accepting some uncertainty associated with the age model (Fig. 7). The correspondence between spring activity as recorded by the pollen record and IOD events frequency and intensity could be used in modelling future spring activity and response to climate warming (e.g. Cuthbert et al., 2019).
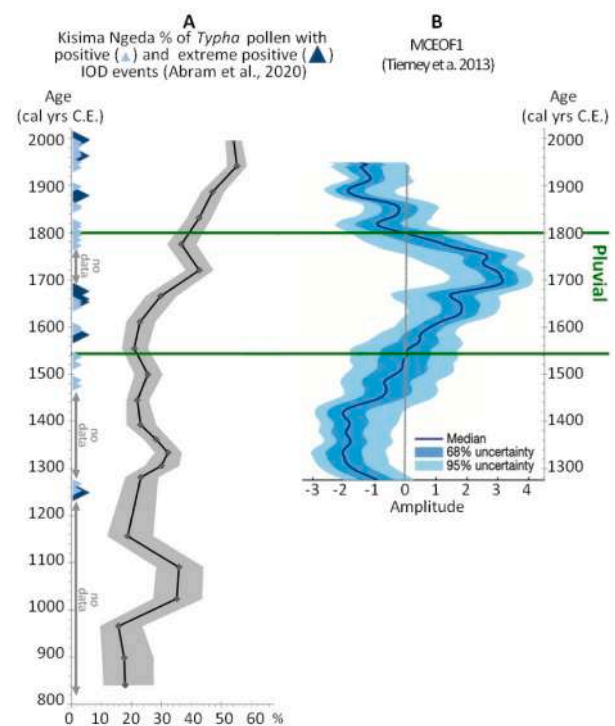

Fig. 8. Kisima Ngeda spring response (wetland expansions) to mega-regional and regional events. (a) Relative abundance of *Typha* pollen with 95% confidence interval (dark grey envelope) in KN1A core at Kisima Ngeda, Lake Eyasi, N Tanzania with positive and extreme positive Indian Ocean Dipole (IOD) events according to the coral δ^{18}O record of the southern Mentawai Islands, offshore of Sumatra (Abram et al., 2020). Note that, to date, there is no isotopic record of IOD events older than cal yrs. C.E. 1240. (b) Amplitude of the first Monte Carlo empirical orthogonal factor (MCEOF) showing a coherent statistical signal of rainfall (as inferred by various proxies) in Eastern Africa over the cal yrs. C.E. 1300–2000 time period.

5.3. Acacia-Hyphaene palm woodland versus spring forest

At present and over the 1200 year-long period represented by KN1A record there is no evidence for a well-developed spring forest like in the northern edge of saline/alkaline Lake Manyara (Fig. 1) (Greenway and Vesey-Fitzgeral, 1969; Loth and Prins, 1986). In Manyara spring forest, arboreal pollen taxa diversity in surface samples is up to 27 taxa/sample, and mirrors the tree and shrub diversity of the spring forest (Barboni et al., 2019). At Kisima Ngeda, arboreal pollen taxa diversity never exceeds 17 taxa/sample in surface soil samples (Barboni et al., 2019) and 23 taxa/sample in the fossil (core) samples (this study) (Fig. 5). Low taxa diversity in KN1A core is not related to preservation (except in the bottom part of the core) since it's also observed in the modern soil samples (Barboni et al., 2019). Forests with stratified canopy develop when hydrological conditions are favorable for the growth of highly-demanding large-leaved evergreen tree species, in particular when amount of water is not limiting and access to water is stable for several decades or even centuries. The KN1A core shows that although groundwater input has been stable, even increasing in the last 1250 years, a multi-story evergreen spring forest never developed at Kisima Ngeda. This can be explained by several factors. (1) The groundwater flux at Kisima Ngeda (south-eastern foothills) is likely lower than that at Manyara (south-western foothills), because the south-western slopes of Ngorongoro Volcanic Highlands receive less rainfall than the south-eastern slopes (Herlocker and Dirschl, 1972). Difference in rainfall between the two areas is so great that the lower edge of the Afromontane forest is at ca. 1600 m on the south-western slope (Lake Manyara Basin) and as high as 2450 m on the south-eastern slope (Lake Eyasi Basin) (Herlocker and Dirschl, 1972; Norton, 2019). (2) The vegetation in these spring systems also depends on the geomorphology of the drainage basins, which influences water flows and drainage. At Gorofani, located a few kilometers east of Kisima Ngeda, tall and large trees of *Ficus* sp., *Tamarindus indica* and *Cordia* sp. are still present despite heavy grazing and human presence. This suggests that the local setting might have been more favorable than in KN for the development of a multi-story groundwater forest like at Manyara (D. Barboni, personal observation). (3) The groundwater pH and conductivity are very different between Kisima Ngeda and Manyara spring wetlands. The pH is more acidic at Manyara (pH 5.7) than Kisima (pH 7.4–7.6), and conductivity (dissolved elements) is low and consistent at Manyara (354–384 µS), but high and highly variable at Kisima (640–5600 µS). Water temperature is similar at both sites (about 21 °C) (Ashley, unpublished data).

5.4. Kisima Ngeda, a dual and therefore sustainable groundwater system?

The KN1A pollen record shows that during low spring activity the groundwater table at Kisima Ngeda is still high enough to sustain a palm woodland (e.g. before cal yrs. C.E. 1200 when there is a salty influence) or a grassy Mimosaceae woodland. The hydrological system that feeds this densely wooded localized vegetation belt in the northeastern margin of Lake Eyasi remains active even during arid periods of ~300 years during the Medieval Climate Anomaly, and doesn't seem to be influenced by dry climatic phases. Yet, the pollen record also shows that, at the same time, the groundwater flow at Kisima Ngeda responds very quickly (on a decadal scale) to wet climatic events via discharge peaks. A groundwater system cannot be at the same time non-sensitive and very sensitive to climatic variations. Consequently, the springs around Kisima Ngeda are probably fed by two independent groundwater systems: a groundwater with temporally sensitive short groundwater response time (GSS) and a groundwater with temporally insensitive long groundwater response time (GTI) (Cuthbert et al., 2019). The GSSs are close to the surface with short (decennial) response time, while the GTIs are deeper with large response time, making altogether a dual, sustainable system (Cuthbert et al., 2019).

Additional geological and hydrological data will further enhance our understanding of the Ngorongoro area groundwater GSS and GTI systems (Norton and Ashley, unpublished data). Yet, what we show here is that in this region, some spring systems such as Kisima Ngeda are sustainable over more than a millennium due to stable groundwater discharge, but do also respond to punctual discharge linked to decennial or centennial climatic variations. Such system, therefore, could have sustained early hominin activity such as the active exploitation of spring as observed at Olduvai (Ashley et al., 2009), which could not have developed if springs were ephemeral. Given the reconstructed low precipitation amounts during the Pleistocene in Olduvai area (250–700 mm/yr), it is likely that surface water (permanent rivers) was limited, making early hominins highly dependent on stable freshwater sources (Magill et al., 2013a). In agreement with Magill et al. (2016), our study confirms the stability of these systems on a time scale compatible with human activities and reinforces current paradigms. Our study also supports the idea that this type of groundwater system is consistent with the development of stable woodlands that may have facilitated the movement of the early hominins in the Eastern African rift during arid climate phases (Cuthbert et al., 2017).

5.5. Impact of springs on the geological and paleobotanical records at hominin sites

As mentioned, the hydrological system of Kisima Ngeda seemed to be a potential analog to some Olduvai sites because of the presence of a (paleo) lake nearby that is saline/alkaline, of palms, and of (paleo) springs with fresh groundwater whose recharge occurs in the Ngorongoro Highlands. The Olduvai pollen record (Bonnefille, 1984), however, differs from the KN1A pollen record by the abundance of Poaceae (35–75%), rare *Typha* (0–10%), the absence of *Hyphaene* or other palm taxa, and the abundance of pollen markers of the *Acacia-Commiphora* bushland. Olduvai pollen data alone suggest open semi-desert environment comparable to the present-day vegetation with the presence of very reduced or distant fresh-water swamp, but no spring forest or woodland. Yet, other vegetation proxies (δ^{13}C on pedogenic carbonates, phytoliths, macro-remains) indicate highly heterogeneous woody cover, abundant palms, and *Typha* wetlands (Arráiz et al., 2017; Ashley et al., 2010a; Bamford, 2012; Barboni, 2014; Barboni et al., 2010; Cerling and Hay, 1986; Magill et al., 2013b; Sikes and Ashley, 2007), while tufa mounds are geological evidences attesting for the presence of groundwater discharge areas (springs) at Olduvai (Ashley et al., 2010a). The absence of "spring indicators" in the Olduvai pollen record despite evidences in the geology, geochemistry and phytoliths and macro-remains may be explained by the low pollen production (e.g. *Sesbania sesban*) or low dispersion capacity (e.g. *Hyphaene* or *Acacia*) of spring plant taxa, which makes them less easily recordable than e.g. grasses. Pollen grains of *Hyphaene*, however, were recorded in the Pliocene of Laetoli (Bonnefille and Riollet, 1987). Hence, the depositional context is another factor that could explain the absence of spring pollen markers at Olduvai. As shown in this study, groundwater discharge areas trigger and maintain a landscape heterogeneity, not only in terms of vegetation by allowing the development of dense and tall woodlands and wetlands within an otherwise desert-like vegetation, but also in terms of depositional environments. Indeed, following the groundwater discharge and level, a given area may alternatively accumulate organic-rich peatland material (which favor pollen preservation) or become a sandy clay-rich soil (less likely to preserve pollen). The water table level and spatial position of the discharge areas (spring outlets) likely change over millennia, and swamps, woodlands, and palm groves (the spring-associated vegetation zones) are then displaced laterally by few kilometers. Yet, if these local movements have potentially little impact on the wildlife, they may considerably disturb the geological and paleobotanical records.

Groundwater forests and woodlands have a very distinct but also very local pollen signal, which can go unnoticed (Barboni et al., 2019). Depending on the location of the sampling site, the period studied and the resolution of the record, this type of spring system can give a very

heterogeneous vegetation signal, often interpreted as mosaic environment with swamps, groundwater woodlands, palm groves, bushland/wooded bushland, etc. Hence, to characterize hominin habitats in the East African Rift where springs are common, it is necessary to consider spatial and/or temporal resolution of paleoenvironmental reconstructions (Behrensmeyer and Reed (2013), and to search for evidences of paleo-springs in both the geological and the biological records (Barboni et al., 2019) to avoid interpretation biases.

6. Conclusions

The pollen analysis of the 43 cm-long core KN1A at Kisima Ngeda locality in the north-eastern shore of Lake Eyasi provided interesting insights into a dynamic groundwater system in the EARS during the last 1200 years. It shows that KN spring has been active at least since the last 1200 years, that the water table was low before cal yrs. C.E. 1200 (with discontinuous and sparse discharge at the ground level). It abruptly increased, shortly after cal yrs. C.E. 1200, i.e. shortly after the dry Medieval Climate Anomaly period, and shows a steady increase since cal yrs. C.E. 1650. The groundwater table at Kisima Ngeda varied at the pace of regional precipitation changes that affected a large area encompassing Mt. Kilimanjaro, L. Naivasha, L. Emakat, and as far east as L. Edward, and may have been particularly responsive to extreme rainfall events triggered by extreme positive events of the Indian Ocean Dipole (IOD). The lag of 25–50 years observed between the positive IOD events and peaks of *Typha* pollen shows that Kisima Ngeda spring system mitigates climate change. KN responds to decadal hydroclimatic changes but is also able to persist over several centuries-long dry periods (e.g. the Medieval Climate Anomaly). Kisima Ngeda spring, therefore, is likely controlled by a dual groundwater system which allows maintaining wooded habitats even during dry phases, and which favors the development of wetlands following discharge peaks during wet phases. Such spring-fed wetlands can record relative changes in paleo-precipitation in the highlands. In contrast, Kisima Ngeda spring is not very sensitive to climatic variations in the lowlands where it is located. Yet, because changes in the groundwater discharge modify the spatial extent (but not the presence) of different ecological zones in the spring area, the geological and paleobotanical record (from sedimentary cores) may have hiatuses or be discontinued. The KN1A pollen record did not match the Olduvai fossil pollen record, despite obvious analogy in the geological, geomorphological and geochemical contexts, likely because spring plant taxa such as *Sesbania* and *Hyphaene* are poor pollen producers and dispersers. Although tufas are solid evidences of paleo-springs, they are not sufficient to infer the type of habitat and vegetation associated to it, because the density, development and diversity of the spring vegetation likely depend on the orientation and geomorphology of the drainage basins, and groundwater quality.

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.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110607.

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